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ON THE COVER: *CHIASMOCLEIS BASSLERI* FROM PARQUE NACIONAL DA SERRA DO DIVISOR, ACRE, BRAZIL. PHOTOGRAPHED BY PEDRO L.V. PELOSO.

PELOSO ET AL.: SYSTEMATICS OF *CHIASMOCLEIS* AND *SYNCOPE*

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PHYLOGENY, TAXONOMIC REVISION, AND CHARACTER EVOLUTION OF THE GENERA *CHIASMOCLEIS* AND *SYNCOPE* (ANURA, MICROHYLIDAE) IN AMAZONIA, WITH DESCRIPTIONS OF THREE NEW SPECIES

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## CONTENTS

Abstract . . . . .	4
Introduction . . . . .	4
Geographic Delimitation of the Study . . . . .	5
Taxonomic History of <i>Chiasmocleis</i> and <i>Syncope</i> . . . . .	6
Diversity of <i>Chiasmocleis</i> in the Amazon and the Guiana Shield . . . . .	6
A Brief Taxonomic History of <i>Syncope</i> . . . . .	6
Phylogenetic Relationships and the Current Status of <i>Chiasmocleis</i> and <i>Syncope</i> . . . . .	6
Research Objectives and Rationale for Species Delimitation . . . . .	9
Abbreviations for Collections and Field Series Numbers . . . . .	9
Material and Methods	
Morphology . . . . .	11
Advertisement Calls . . . . .	13
Phylogenetic Analyses . . . . .	13
Character Evolution . . . . .	15
Presentation of Data . . . . .	15
Results	
The Phylogeny of <i>Chiasmocleis</i> . . . . .	17
The <i>Chiasmocleis bassleri</i> Cade . . . . .	20
The <i>Chiasmocleis hudsoni</i> Clade . . . . .	20
The <i>Chiasmocleis shudikarensis</i> Clade . . . . .	20
The <i>Chiasmocleis ventrimaculata</i> Clade . . . . .	21
The <i>Chiasmocleis albopunctata</i> Clade . . . . .	21
Phenotypic Variation . . . . .	21
Species Accounts . . . . .	26
<i>Chiasmocleis albopunctata</i> (Boettger, 1885) . . . . .	26
<i>Chiasmocleis anatypes</i> Walker and Duellman, 1974 . . . . .	30
<i>Chiasmocleis antenori</i> (Walker, 1973) . . . . .	33
<i>Chiasmocleis avilapiresae</i> Peloso and Sturaro, 2008 . . . . .	34
<i>Chiasmocleis bassleri</i> Dunn, 1949 . . . . .	37
<i>Chiasmocleis carvalhoi</i> (Nelson, 1975) . . . . .	42
<i>Chiasmocleis devriesi</i> Funk and Cannatella, 2009 . . . . .	44
<i>Chiasmocleis hudsoni</i> Parker, 1940 . . . . .	46
<i>Chiasmocleis magnova</i> Moravec and Köhler, 2007 . . . . .	51
<i>Chiasmocleis shudikarensis</i> Dunn, 1949 . . . . .	52
<i>Chiasmocleis superciliarba</i> Morales and McDiarmid, 2009 . . . . .	55
<i>Chiasmocleis tridactyla</i> (Duellman and Mendelson, 1995) . . . . .	57
<i>Chiasmocleis ventrimaculata</i> (Andersson, 1945) . . . . .	59
Descriptions of New Species . . . . .	63
<i>Chiasmocleis haddadi</i> , new species . . . . .	63
<i>Chiasmocleis papachibe</i> , new species . . . . .	67
<i>Chiasmocleis royi</i> , new species . . . . .	69
Discussion	
Systematics . . . . .	74
The <i>Chiasmocleis bassleri</i> Clade: a Complex of Species? . . . . .	74
The <i>Chiasmocleis hudsoni</i> Clade: Taxonomy and Evolution . . . . .	76
Phenotypic Variation . . . . .	77
Character Evolution . . . . .	78
Notes on Reproductive Ecology . . . . .	79
Conservation . . . . .	82
Future Work . . . . .	82

Acknowledgments . . . . . 82  
References . . . . . 84  
Appendix 1. Specimens Examined . . . . . 90  
Appendix 2. Specimens Included in Phylogenetic Analysis . . . . . 92  
Plates . . . . . *after page* 96

## ABSTRACT

A taxonomic assessment of the microhylid genera *Chiasmocleis* and *Syncope* occurring in the Amazon basin and Guiana Shield is presented. *Syncope* Walker, 1973, is considered a junior synonym of *Chiasmocleis* Méhelý, 1904, based on the monophyly of the group as a unit. To avoid secondary homonymy with *Syncope carvalhoi* Nelson, 1975 (senior homonym), a replacement name, *Chiasmocleis lacrimae*, nom. nov., is given to *Chiasmocleis carvalhoi* Cruz, Caramaschi, and Izecksohn, 1997 (junior homonym). From integrative analyses of morphological, acoustic, and a phylogenetic analysis of three genes (two mitochondrial, 16S: up to 557 bp, COI: up to 658 bp; and one nuclear, tyrosinase: up to 532 bp), we recognize 16 species in the area of study, 13 of which were previously known and three are described as new: *Chiasmocleis albopunctata*; *C. anatipes*; *C. antenori*; *C. avilapiresae*; *C. bassleri*; *C. carvalhoi*; *C. devriesi*; *C. haddadi*, sp. nov.; *C. hudsoni*; *C. magnova*; *C. papachibe*, sp. nov.; *C. royi*, sp. nov.; *C. shudikarensis*; *C. superciliarba*; *C. tridactyla*; *C. ventrimaculata*. *Chiasmocleis jimi* Caramaschi and Cruz, 2001, is considered a junior synonym of *Chiasmocleis hudsoni* Parker, 1940. Species accounts are provided for all 16 species, as is a compilation of available data, including type specimens, type localities, morphological diagnoses, variation, tadpoles (only from literature), advertisement calls (calls of several populations described for the first time), and natural history. Photographs and updated data on geographical distributions, with maps, are also provided. The evolution of some phenotypic traits is studied in light of a phylogeny of the group.

## INTRODUCTION

*Chiasmocleis* Méhelý, 1904, is the most species-rich Neotropical microhylid genus. Together with its sister taxon *Syncope* Walker, 1973, they form a clade including 28 species, distributed in Panama and tropical South America east of the Andes.<sup>1</sup> Several species of *Chiasmocleis* and *Syncope* were only recently described and some authors independently reported considerable amounts of morphological (Peloso and Sturaro, 2008) and acoustic (Morales and McDiarmid, 2009; Santana et al., 2009) variation among species and populations, adding to the suspicion that diversity in the group is underestimated.

The absence of a comprehensive phylogenetic framework for the group caused past systematic discussions to be based on a geographical perspective, rather than on evolutionary relationships. The status of several Atlantic forest populations of *Chiasmocleis* were assessed in a revisionary work by Cruz et al. (1997), who described three new species. The work by Cruz and his

colleagues fueled a growth in taxonomic knowledge regarding populations of *Chiasmocleis* in the Atlantic forest with several new species subsequently discovered and described (Cruz et al., 1999; Caramaschi and Pimenta, 2003; Cruz et al., 2007a; Cruz et al., 2007b). Caramaschi and Cruz (1997) assessed the taxonomic status of populations from the Cerrado (savannahlike, generally open habitats, typical of central Brazil), and described two new species for the region. Despite some development in recent years, the taxonomic status of several Amazonian populations remains obscure and the possibility of species complexes and unnamed species has been mentioned throughout the years (Lescure and Marty, 2000; Oliveira-Filho and Giarretta, 2006; Peloso and Sturaro, 2008). When naming *C. magnova*, Moravec and Köhler (2007) were uncertain about the inclusion of the species in *Syncope*, or *Chiasmocleis*, finally opting for the later, largely based on the conditions of the presacral vertebrae (eight, with first and second not fused).

Modern revisionary work is not available for either genera and, as a consequence, several populations from northern South America remain unassigned to any species and many specimens in herpetological collections are either unidentified or misidentified (often labeled as *Chiasmocleis* sp., or *Syncope* sp., “cf.”). Some specimens are also misidentified to the generic level, most commonly labeled as

<sup>1</sup>Frost (2013) recognizes 25 species in *Chiasmocleis* and three in *Syncope*. The taxonomic arrangement for New World microhylids provided by de Sá et al. (2012) implies the recognition of only 20 species of *Chiasmocleis*, as five were transferred to *Syncope*. The publication by de Sá et al. (2012) appeared after the *Amphibian Species of the World* (version 5.6) catalog was already sent to press (P.L.V.P., personal obs.).

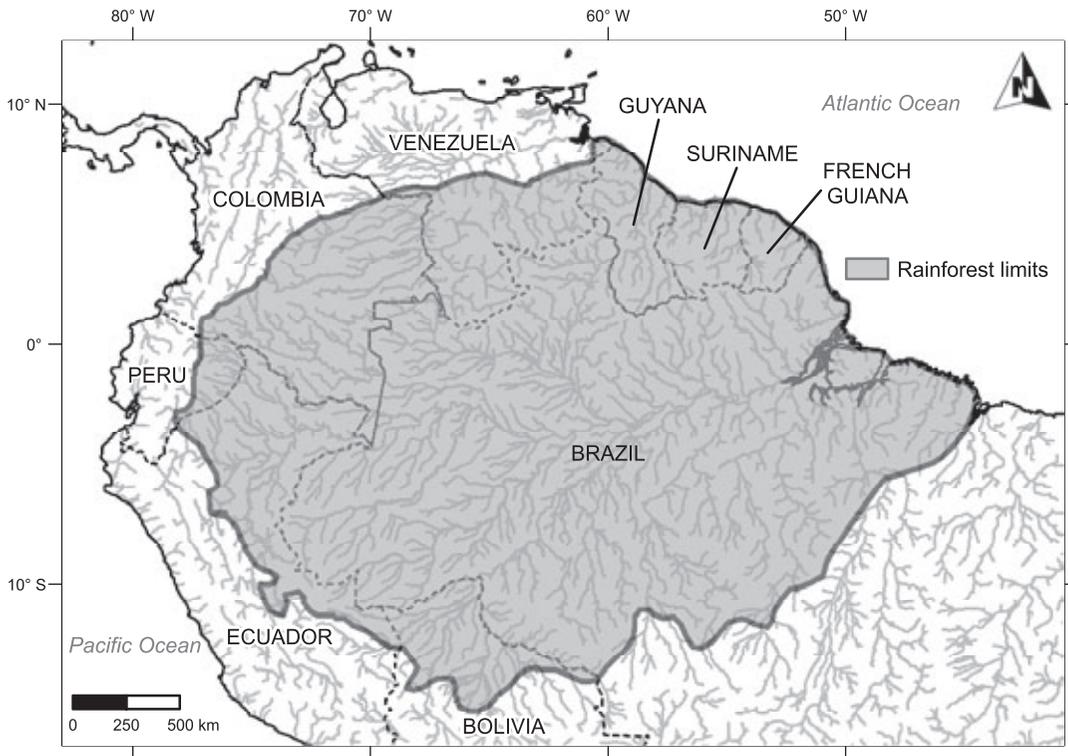


Fig. 1. Geographic limits implemented in this study. The map is adapted from Goulding et al. (2003), and highlights the Amazonian rainforest limits.

*Ctenophryne*, *Elachistocleis*, *Hamptophryne*, or even as Microhylidae sp.

Only recently have more than a couple species of *Chiasmocleis* and *Syncope* been included in a phylogenetic analysis. De Sá et al. (2012), in a broad phylogenetic analysis of microhylids, included 12 species of *Chiasmocleis* and three of *Syncope* (see below), with the two genera recovered as sister taxa. Here, we expand on the dataset of de Sá et al. (2012) to aid our evaluation of species diversity of Amazonian *Chiasmocleis* and *Syncope*.

#### GEOGRAPHIC DELIMITATION OF THE STUDY

We apply an arbitrary geographic delimitation to our study and restrict analysis to species of either *Chiasmocleis* or *Syncope* that occurs within limits of the “Amazonian Rainforest,” as proposed by Goulding et al. (2003; see fig. 1). We are aware that the geographic limits of “Amazonia” are a matter of ongoing controversy and, as a result, multiple alternative limits have been proposed (see Goulding et al.,

2003, and references therein). Goulding et al.’s delimitation of the rainforest includes most of the Amazon River basin, but also a large portion of the Guiana Shield. The actual limits of the Guiana Shield are also a focus of discussion (Berry et al., 1995; Rull, 2005) and no agreement on the matter in the near future seems likely. Technical definitions of what constitutes the Amazon Basin, the Amazonian Rainforest, or the Guiana Shield are beyond the scope of this work, but are nonetheless of little relevance to our ultimate goal.

The geographic limit proposed by Goulding et al. (2003), and adopted here, is a rough definition and includes several areas that are not strictly rainforest (e.g., savannah habitats and tepuis). Nonetheless, the limits used herein are fairly broad and allow for the inclusion of all species from the Amazonian forest and Guiana Shield, but also permits inclusion of *Chiasmocleis albopunctata* (Boettger, 1885), the type species of the genus, although technically not an “Amazonian” species. *Chiasmocleis albopunctata* is present

in open habitats peripheral to the Amazonian rainforest, but widely distributed in the Rio Tocantins (= Tocantins River) basin (Forlani et al., 2011).

We included species when we were able to analyze at least one specimen from within the limits proposed above (with the exception of *Chiasmocleis albopunctata*, for reasons stated earlier; and *C. devriesi* Funk and Cannatella, 2009—from the Iquitos region, Peru—for which we did not examine any specimens but referred to its original description and photos of the holotype whenever necessary). Some specimens from species occurring outside the study area were examined for comparison, or were included in phylogenetic analysis for taxon-sampling completeness, and no species accounts are given for those.

#### TAXONOMIC HISTORY OF *CHIASMOCLEIS* AND *SYNCOPE*

**DIVERSITY OF *CHIASMOCLEIS* IN THE AMAZON AND GUIANA SHIELD:** The type species of the genus is *C. albopunctata* (Boettger, 1885), originally described from Paraguay, but with several records in Brazil (see review in Forlani et al., 2011). The genus was proposed by Méhelý (1904) to accommodate the species *Engystoma albopunctatum*, based on putative morphological differences of the species and the remaining *Engystoma*. *Hamptophryne boliviana* (Parker, 1927) was originally described as *Chiasmocleis* but was later assigned to the monotypic genus *Hamptophryne* (Carvalho, 1954). Several empirical phylogenetic analyses support the distinctiveness of *Hamptophryne* in relation to *Chiasmocleis* (Frost et al., 2006; van der Meijden et al., 2007; Pyron and Wiens, 2011; Trueb et al., 2011) and the species is, therefore, not treated further here. Only a few species of *Chiasmocleis* were described until very recently: *C. hudsoni* Parker, 1940; *C. ventrimaculata* (Andersson, 1945); *C. bassleri* Dunn, 1949; *C. shudikarensis* Dunn, 1949; and *C. anatipes* Walker and Duellman, 1974. No additional species were described for the Amazon basin until early in the 21st century. From 2001 to the present, five new species were named in the region of study: *C. jimii* Caramaschi and Cruz, 2001; *C. magnova* Moravec and Köhler, 2007; *C. avilapiresae*

Peloso and Sturaro, 2008; *C. devriesi* Funk and Cannatella, 2009; and *C. superciliarba* Morales and McDiarmid, 2009. Recently, de Sá et al. (2012) proposed an alternative taxonomy of microhylids, which affected the content of *Chiasmocleis*, and *Syncope*.

**A BRIEF TAXONOMIC HISTORY OF *SYNCOPE*:** *Syncope* was proposed by Walker (1973) to include a diminutive microhylid species with fused presacral vertebrae I and II and reduced digits. On that occasion, the genus was proposed as monotypic, and the sole species *Syncope antenori* was named and described. Soon after that, Nelson (1975) described another species, *Syncope carvalhoi*, from the Loreto region, sharing the fused presacrals I and II and reduced digits. Duellman and Mendelson III (1995) described *Adelophryne tridactyla* from the Loreto region, Peru. Duellman and Mendelson's specimens also had reduced digits, but were assigned to *Adelophryne* without justification for its generic placement. Silva and Meinhardt (1999) noted several shared osteological characters between *Adelophryne tridactyla* and the two known species of *Syncope*, thus transferring *A. tridactyla* to the genus *Syncope*.

**PHYLOGENETIC RELATIONSHIPS AND THE CURRENT STATUS OF *CHIASMOCLEIS* AND *SYNCOPE*:** Most of the characters used for definition of gastrophrynine genera lie on pectoral girdle elements, and this is no different for *Chiasmocleis* and *Syncope*. Some authors have commented on the overall similarity in osteology of the two genera (Walker, 1973; Duellman and Mendelson III, 1995; Moravec and Köhler, 2007) and phylogenetic analyses based on morphology alone had found the two genera to be closely related (Zweifel, 1986; Wild, 1995).

Prior to de Sá et al. (2012), few species of *Chiasmocleis* (and none of *Syncope*) were included in any phylogenetic studies using molecular characters (but see Trueb et al., 2011). The only works to include more than one species were those of van der Meijden et al. (2007), Pyron and Wiens (2011), and Trueb et al. (2011),<sup>2</sup> which included two

<sup>2</sup>The phylogenies by Pyron and Wiens (2011) and Trueb et al. (2011) derive solely from Genbank data, and the sequences for the two species of *Chiasmocleis* included by them investigators derive from van der Meijden et al. (2007).

species of *Chiasmocleis* (*C. hudsoni* and *C. shudikarensis*) in their analysis and found them to form a monophyletic clade, either sister to the remaining Gastrophryninae or sister to all gastrophrynines except *Ctenophryne* and *Nelsonophryne* (currently synonyms, de Sá et al., 2012). De Sá et al. (2012) included a much larger set of *Chiasmocleis* and *Syncope* species, and also included most New World genera of microhylids (missing only *Adelestes*), thus providing rigorous tests of the monophyly of *Chiasmocleis* and *Syncope* and their relationships with other microhylid taxa. *Chiasmocleis* was found to be polyphyletic, and to remedy this situation two changes were made to the classification (de Sá et al., 2012). *Chiasmocleis panamensis* was removed from the genus and transferred to *Elachistocleis*—several phenotypic characters corroborate this arrangement (i.e., osteology, advertisement call, our personal obs.). The second change is larger and more important to this work; de Sá et al. (2012) found *C. magnova*, *C. bassleri*, and *C. hudsoni* to be nested within *Syncope* Walker, 1973 (represented in their analysis by three putative species, one of them labeled as *Syncope*, sp.). They then decided to transfer *C. bassleri*, *C. hudsoni*, *C. jimi*, *C. magnova*, and *C. superciliarba* to *Syncope*, hence maintaining both genera as valid. The authors based their decision on the argument that they “want to recognize the separate evolutionary trajectory of this lineage based on shared morphological and life history traits” (de Sá et al., 2012). Although the taxonomic decision is in accordance with their preferred tree (maximum likelihood; see fig. 2)<sup>3</sup> and with the International Code of Zoological Nomenclature (ICZN, 1999), their arguments are not convincing.

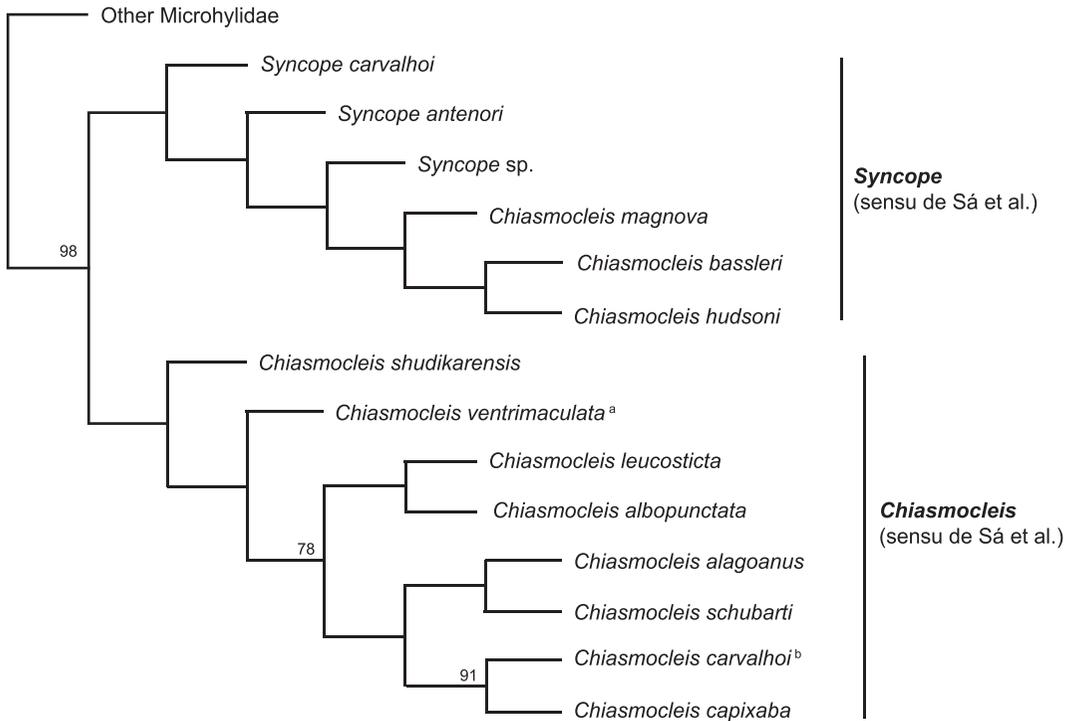
The authors discuss digit and body size reduction and the shape of the clavicles as

morphological support for their arrangement.<sup>4</sup> De Sá et al. (2012) mention “*Syncope* species have lost two vertebrae and have reduced and/or lost fingers I and IV,” and add that “a similar pattern of small adult body size and digit reduction is present in the species of *Chiasmocleis* that we found to share phylogenetic affinities with *Syncope*: *C. bassleri*, *C. hudsoni*, and *C. magnova*.” De Sá et al. (2012) further mention that the new arrangement “is also consistent with morphological variation in the pectoral girdle where there has been a complete loss of the connection between coracoids and epicoracoid in *S. antenori* and *S. magnova* (and a reduced connection in *S. jimi* and *S. hudsoni*) whereas the connection is present in *Chiasmocleis*.” The authors do not mention the state of the clavicles of either *C. bassleri* or *C. superciliarba*, in which a connection of the coracoids with the epicoracoids is present.

De Sá et al. (2012) also suggested that reproductive mode may unite *Syncope* and the few species of *Chiasmocleis* they transferred into *Syncope*. Data on reproduction is scarce for many species of *Chiasmocleis* and *Syncope*, but is sufficiently well known to reject de Sá et al.’s (2012) claim. *Syncope antenori* has free-swimming nonfeeding tadpoles while direct development was suspected to occur in *Syncope carvalhoi* (Krügel and Richter, 1995) and *C. magnova* (Moravec and Köhler, 2007)—this was never proved by empirical evidence, only inferred from the relative large size and pigmentation of the eggs. On the other hand, most members of *Chiasmocleis* lay hundreds of small pigmented eggs and have exotrophic tadpoles (Duellman, 1978; Wogel et al., 2004; Lima et al., 2005; Oliveira-Filho and Giaretta, 2006; Rodrigues et al., 2008; Menin et al., 2011; Santana et al., 2012; P.L.V.P., personal obs.), and species with aquatic free-swimming

<sup>3</sup> Only a maximum likelihood topology is shown in de Sá et al. (2012). Another three optimality criteria were applied to the dataset (Bayesian, evolutionary distance, and parsimony), but topologies derived from other optimality criteria were not given anywhere despite the fact that topological inconsistencies do exist, according to the authors. The sister clade relationships of *Chiasmocleis* and *Syncope* (both sensu de Sá et al., 2012) was apparently not recovered in their parsimony analysis which, most unfortunately, is not shown.

<sup>4</sup> Morphological data for *Chiasmocleis* discussed in de Sá et al. (2009) is largely derived from the 2010 unpublished dissertation by M.C. Forlani. It is noteworthy that de Sá et al.’s (2012) claim that their taxonomic arrangement is supported by morphological data, whereas Forlani (unpublished data) conducted a phylogenetic analysis based exclusively on morphological data and in his analysis all species of *Syncope* (sensu de Sá et al., 2012), albeit forming a monophyletic clade, are deeply nested within the remaining *Chiasmocleis*.



<sup>a</sup> Sequences labeled as *Chiasmocleis ventrimaculata* by de Sá et al. (2012), actually represent *C. royi*, sp. nov., described herein (see text for details).

<sup>b</sup> *Chiasmocleis carvalhoi* Cruz et al., 1997, is renamed in this work (*C. lacrimae*, nom. nov.; see text for details), but kept here to reflect taxonomy used by de Sá et al. (2012).

Fig. 2. Part of the phylogenetic tree of microhylids from de Sá et al. (2012), highlighting the relationship between “*Chiasmocleis*” and “*Syncope*.” Maximum likelihood (ML) tree of molecular data (16S: 673 aligned sites; BDNF: 711 aligned sites; tyrosinase: 551 aligned sites; 28S: 738 aligned sites), using GTR + I + G as the model of nucleotide substitution. Alignments performed using MAFFT (parameters not given, presumably default) and further modified by eye (hypervariable regions excluded). Gaps were presumably treated as missing data. Numbers on nodes refer to ML bootstrap nodal support values. Additional support values (i.e., Bayesian posterior probabilities, minimum evolution “distance” bootstrap) are available in the original. Nodes with no values received less than 70% bootstrap values or were not given in the original.

extrophic larvae include some of those of which de Sá et al. (2012) claim to share reproductive ecology traits with “*Syncope*” (i.e., *C. bassleri*, *C. hudsoni*). The heterogeneity of reproductive modes within “*Syncope*” therefore does not support de Sá et al.’s (2012) hypothesis.

Nonetheless, because de Sá et al. (2012) provide the largest test of phylogenetic relationships within microhylids, we adopt the general microhylid classification proposed by them (but see Results and Discussion sections for a novel classification proposal to

the *Chiasmocleis/Syncope* section of the tree). We took the opportunity provided by de Sá et al. (2012: i.e., the publication of novel DNA sequence data for *Chiasmocleis* and hypothesized evolution of phenotypic characters) to include a phylogenetic framework in our own work. By including a larger taxon sampling and several representatives for each species, we were able to further test the monophyly *Chiasmocleis* and *Syncope* as proposed by de Sá et al. (2012), as well as to infer species limits within both genera.

#### RESEARCH OBJECTIVES AND RATIONALE FOR SPECIES DELIMITATION

The purpose of this work is to reevaluate the current diversity of *Chiasmocleis* and *Syncope* by presenting our findings on the distribution and variation of several characters commonly used in their systematic analysis, and to provide a taxonomic revision of the members of the genera present in the Amazonian rainforest and Guiana Shield. We provide detailed accounts for the species of these genera present in these regions based on analysis of museum specimens, photographs of live and preserved specimens, recordings of advertisement calls, and the literature. Our taxonomic decisions regarding species limits are supported by a phylogenetic analysis, which also calls for further changes in the generic classification proposed by de Sá et al. (2012).

Many species concepts are available but most, if not all, fail to provide objective (i.e., operational) methods for species delimitation (Frost and Kluge, 1994). We therefore do not adopt any formal theoretical concept, but consider a species as a monophyletic lineage composed by populations or metapopulations delimited by a single splitting event (Padial et al., 2010; Padial et al., 2012). As an operational proxy for the above framework, we consider as “putative species” any monophyletic lineage recovered by the phylogenetic analysis that is diagnosable by at least one fixed phenotypic character (i.e., call or morphology), assuming that fixed phenotypic differences are evidence for reduced gene flow among populations (Frost and Hillis, 1990; Frost et al., 1998; Padial et al., 2012). Although provided where pertinent, we do not consider percentage of sequence divergence alone to be a valid measure for species delimitation, as threshold values must be set arbitrarily and there is no basis to ascertain any value in detriment of another (e.g., what percentage of distance should be considered enough for splitting taxa), as nucleotide mutation rates may vary from one branch of the tree to another (see Grant, 2002; Grant et al., 2006). What genetic distances do provide is a hint that some amount of phenetic distance exists between individuals and may be used as a starting point for

investigating species limits using additional inferential methods (Grant et al., 2006).

#### ABBREVIATIONS FOR COLLECTIONS AND FIELD SERIES NUMBERS

**INSTITUTIONAL ABBREVIATIONS:** Effort was made to examine only specimens deposited in scientific collections, but this was not always possible. When no collection number is available, specimens are referred to by their field number.<sup>5</sup> Some specimens illustrated (especially live specimens) do not have any number associated with them and this is noted. A complete list of the material examined is available in appendix 1 (except for type material of newly described species, which are given in the text).

AMNH	American Museum of Natural History, New York
BMNH	Natural History Museum (Formerly the British Museum of Natural History), Department of Zoology, London, United Kingdom
CAS	California Academy of Sciences, San Francisco
CFBH	Coleção de Anfíbios Célio F.B. Haddad, Universidade Estadual Paulista, Rio Claro, São Paulo, Brazil
CHUNB	Coleção Herpetológica da Universidade de Brasília, Brasília, Distrito Federal, Brazil
FNJV	Fonoteca Neotropical Jacques Vielliard, Universidade de Campinas, São Paulo, Brazil
IEPA	Instituto de Pesquisas Científicas e Tecnológicas do Estado do Amapá, Macapá, Amapá, Brazil
INPA	Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil

<sup>5</sup>In cases where field numbers are given, we also provide the collection in which material is reportedly to be deposited. This information is given tentatively as it may change without notice. Some of the paratypes of one of the new taxa described here (*Chiasmocleis haddadi*) are referred to by their field numbers, FL or TQ. These specimens will be deposited in the IEPA collection but were examined before they had been given collection numbers. Until the time of submission, collection numbers could not be obtained, despite several attempts.

KU	University of Kansas Museum of Natural History, Lawrence, Kansas	USNM	Smithsonian Institution, National Museum of Natural History, Washington, D.C.
ICN	Museo de Historia Natural, Universidad Nacional de Colombia, Bogotá, Colombia	ZMB	Universität Humboldt, Zoologisches Museum, Berlin, Germany
LACM	Natural History Museum of Los Angeles County, Section of Herpetology, Los Angeles, California	ZMH	Universität Hamburg Zoologisches Institut und Museum, Hamburg, Germany
MHNSM	Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru		
MNCNADN	Museo Nacional de Ciencias Naturales, Colección de Tejidos y ADN, Madrid, Spain		
MNHNP	Museum National d'Histoire Naturelle, Laboratoire des Amphibiens et Reptiles, Paris, France		
MNRJ	Museu Nacional, Rio de Janeiro, Rio de Janeiro, Brazil	AJC	“Andrew J. Crawford” (not related to a specific locality)
MPEG	Coleção Herpetologica Oswaldo Rodrigues da Cunha, Museu Paraense Emilio Goeldi, Belém, Pará, Brazil	AMNH-FS	“American Museum of Natural History –Field Series” (not related to a specific locality)
MVZ	Museum of Vertebrate Zoology, University of California at Berkeley	CN	“Calha Norte”. Specimens from a series of expeditions to several localities in northern Pará, Brazil. See Ávila-Pires et al. (2010) for details
MZUSP	Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil	FL	“Floresta Nacional”: refers to a specific locality, Igarapé Santo Antônio, Floresta Nacional do Amapá, state of Amapá, Brazil (1°06'04" N / 51°53'36" W), and specimens will be deposited in the IEPA collection (J. Lima, personal commun.).
MZUFV	Museu de Zoologia João Moogen de Oliveira, Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil	JPC	“Janalee P. Caldwell” (not related to a specific locality).
NRM	Naturhistoriska Rijkmuseet, Stockholm, Sweden	JMP	“José Manuel Padiá” (not related to a specific locality).
QCAZ	Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador	MTR	“Miguel T. Rodrigues” (not related to a specific locality), specimens likely to be deposited in MZUSP (M.T. Rodrigues, personal commun.).
OMNH	Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma	TQ	“Tumucumaque”: refers to a specific locality, Parque Nacional Montanhas do Tumucumaque, state of Amapá, Brazil (1°50'41"N / 52°44'28"W), and specimens will be deposited in the IEPA collection (J. Lima, personal commun.).
RMNH	Nationaal Natuurhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands.		
UFACF	Universidade Federal do Acre, <i>campus</i> Floresta, Cruzeiro do Sul, Acre, Brazil		
UFAC-RB	Universidade Federal do Acre, Rio Branco, Acre, Brazil		
UFMT	Universidade Federal de Mato Grosso, Cuiabá, Mato Grosso, Brazil		

FIELD SERIES NUMBERS: Exact meaning of the acronym is given in “quotes” and is followed by additional details on locality (if acronym refers to any specific place and not to a collector’s name).

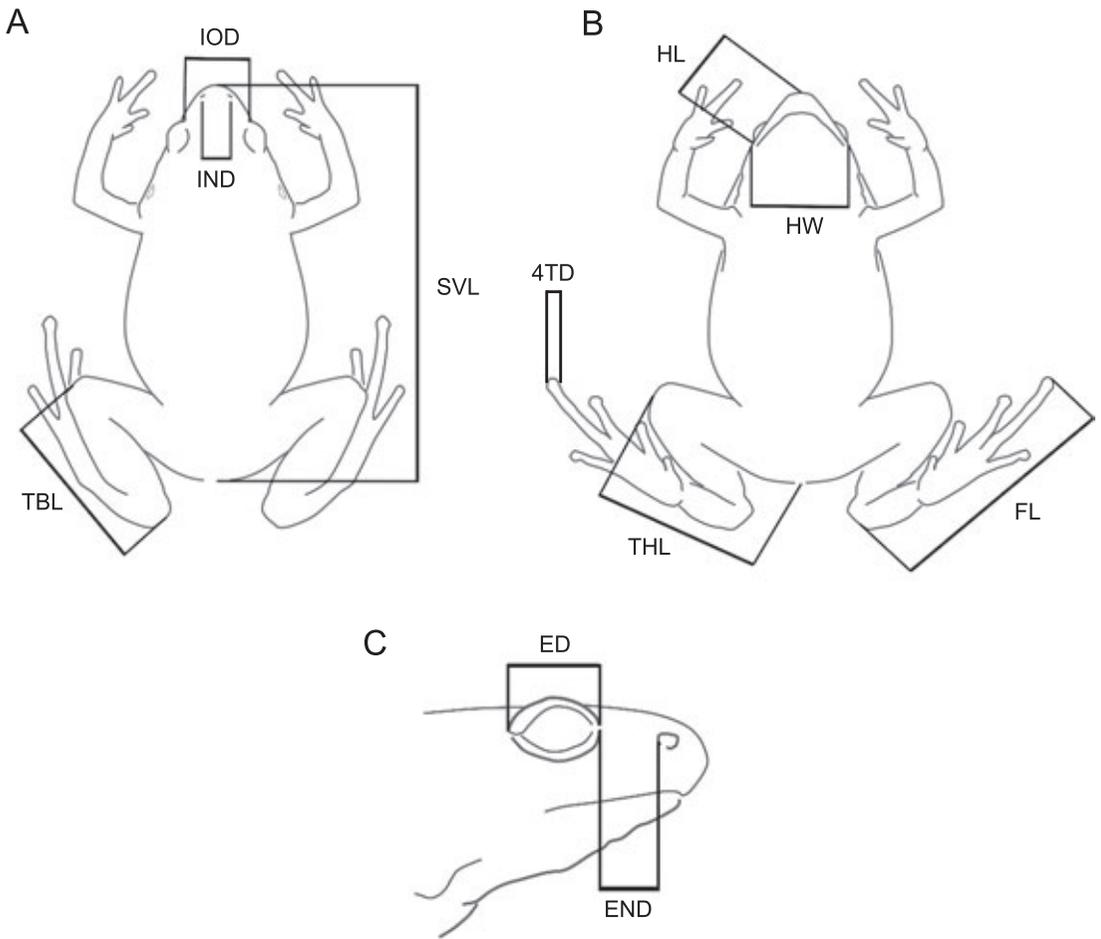


Fig. 3. Outlines of stereotyped gastrophrynine frog in (A) dorsal, (B) ventral, and (C) lateral views, with standardized morphometric variables used in this study: **SVL**, snout-vent length; **HL**, head length; **HW**, head width; **ED**, eye diameter; **IOD**, interorbital distance; **IND**, internarial distance; **END**, eye-nostril distance; **THL**, thigh length; **TBL**, tibia length; **FL**, foot length; **4TD**, diameter of fourth toe disc. Additional measurement details are given in Material and Methods.

#### MATERIAL AND METHODS

**MORPHOLOGY:** The following measurements (adapted from Peloso and Sturaro, 2008) were taken with an electronic caliper under a stereomicroscope (to the nearest 0.1 mm). **SVL** (snout-vent length); **HL** (head length; from snout to angle of the jaw); **HW** (head width; between the angle of jaws); **ED** (eye diameter; between anterior and posterior corner of the eye); **IOD** (interorbital distance; distance between anterior corner of the eyes); **IND** (internarial distance); **END** (eye-nostril distance; from the anterior corner of the eye

to the posterior margin of nostril); **THL** (thigh length; from the middle of the cloacal opening to the outer edge of the flexed knee); **TBL** (tibia length; from the outer edge of the flexed knee to the heel); **FL** (foot length; from tibio-tarsal articulation to tip of fourth toe); **4TD** (diameter of fourth toe disc). Fingers and toes are numbered and abbreviated as follows: Fingers I–IV = FI–IV, Toes I–V = TI–V. Summary of measurements and landmarks are illustrated in figure 3.

Discrete morphological characters were evaluated from direct observation of specimens (see fig. 4 for clarification). Relative

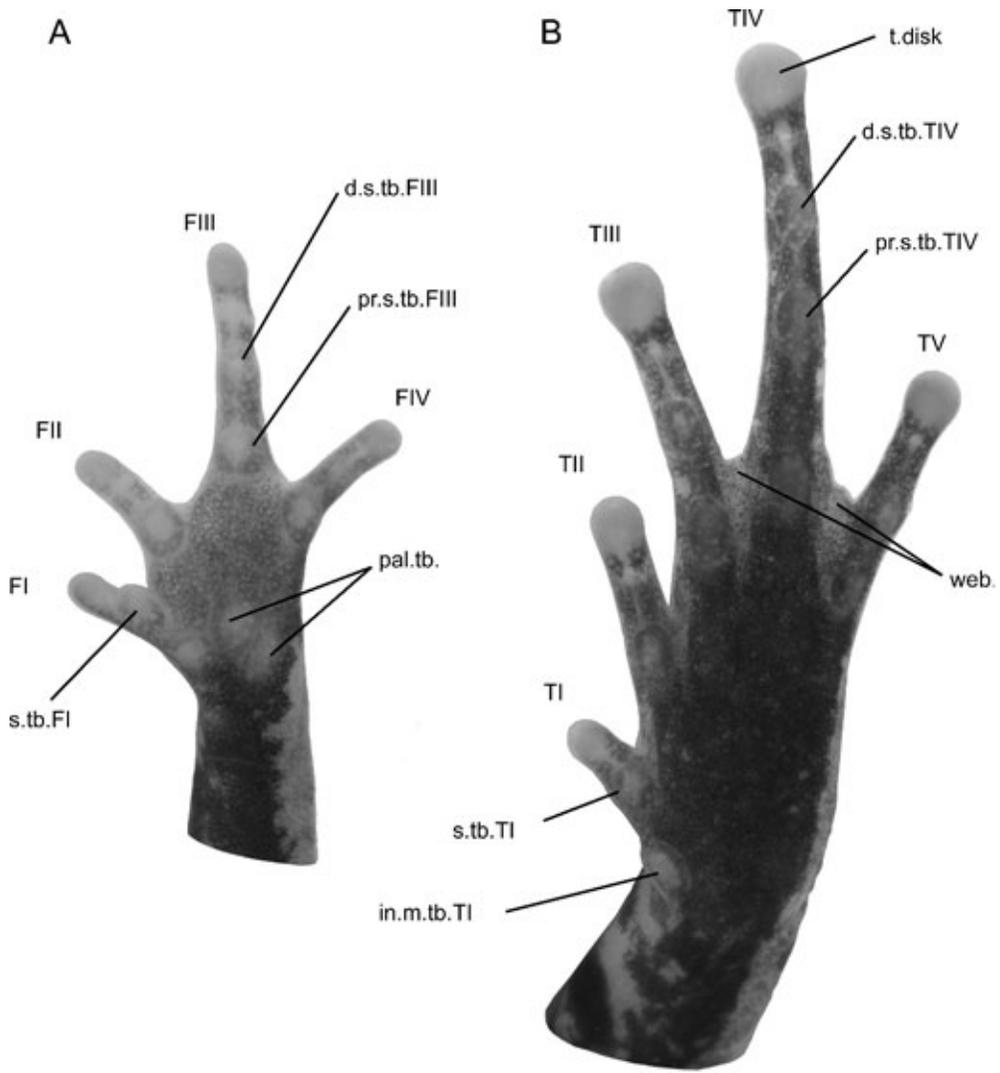


Fig. 4. Ventral views of (A) right hand and (B) right feet of *Chiasmocleis*, evidencing characters frequently mentioned in the diagnosis and comparisons throughout the text. Abbreviations: **F**, finger; **T**, toe; **d.**, distal; **in.**, inner; **m.**, metatarsal; **pal.**, palmar; **pr.**, proximal; **t.**, terminal; **s.**, subarticular; **tb.**, tubercle.

finger and toe lengths were addressed with the following point marks: point where tip of adpressed FI touch subarticular tubercle on FII; point where tip of FIV touch FIII (in relation to the subarticular tubercles on FIII); point where adpressed TI touch TII; point where adpressed TV touch TIV. Presence and distribution of spines: we looked for dermal spines in the chin, cloacal region, dorsum, fingers, and toes. Presence

and development of subarticular tubercles, especially in FI and TI. Presence and development of palmar tubercles. Presence and amount of webbing.

Several color parameters were used to discriminate species. We used mainly ventral color pattern, presence or absence of *inguinal blotches*, and presence or absence of light stripes on the posterior surface of thigh (*femoral lines*). Coloration in life for all

species is based on field notes and photos taken by ourselves and colleagues or are based on descriptions from the literature. Due to time restrictions while visiting some of the collections, and in favor of analyzing a larger volume of material, measurements were not taken for every specimen examined. Sample sizes for each measurement are given.

Some specimens, including type material, were examined solely from photographs (see appendix 1). We used those specimens in the diagnosis of the species only if the images were of high resolution, were taken from different views/angles, and were focused on the diagnostic characters.

**ADVERTISEMENT CALLS:** The advertisement calls of several Amazonian species of *Chiasmocleis* have been described at least once. Santana et al. (2009) presented a discussion of known calls and summarized the main call parameters in a table. Data summarized by Santana et al. (2009) revealed that calls were described idiosyncratically and consequently descriptions are not, in many cases, directly comparable. We attempted to conduct a standardized comparison among available calls of species of *Chiasmocleis* treated here. Availability and quality of recordings was, however, a limiting factor for a thorough review. Advertisement calls were obtained from colleagues or from the acoustic collection of the USNM.

Calls were analyzed using the software Raven, version 3.1 for Mac (Charif et al., 2008), and figures drawn in Praat, version 5.3.23 for Mac (Boersma and Weenick, 2006). For call terminology, we used the following scheme: vocalization is any sound emitted by the vocal apparatus of the animal, while calls and notes are subcategories of vocalizations. Advertisement calls were treated as vocalizations that were discrete temporal units composed of the call emitted by males assumed to be vocalizing to attract females for mating. The calls of all species analyzed here are composed of a series of multipulsed notes. Notes were distinguished from each other when the interval between them was greater than the interval between individual pulses.

Parameters measured were: **CR**, call rate (notes/min); **ND**, note duration (milliseconds, ms; measured from the audiospectrogram,

with doubtful limits checked on the waveform); **IBN**, interval between notes (ms); **DFH**, dominant frequency of first harmonic (Hz); **DFC**, dominant frequency of the call (Hz); **HRN**, number of harmonics by note; **PPN**, number of pulses per note. The dominant frequency (“Max Frequency” in Raven 1.3) as used here is the frequency at which maximum power occurred (Charif et al., 2008).

**PHYLOGENETIC ANALYSES:** To help in the evaluation of species limits in Amazonian species of *Chiasmocleis* we conducted a phylogenetic analysis including up to three genes for 96 specimens of *Chiasmocleis* or *Syncope*. All currently recognized species known to occur within the geographical limits of this study were included with the regrettable exception of *C. superciliarba*. Specimens from the putative new species identified a priori based on the analyses of morphological and acoustic characters were also included. For phylogenetic inference, we used fragments of two mitochondrial (the large ribosomal subunit 16S, up to 557 bp; and cytochrome oxidase I [COI], 658 bp), and one nuclear genes (Tyrosinase, 532 bp).

*Kalophrynus internilineatus* (Kalophryninae) was used to root the tree. In addition to that, another nongastrophrynine microhylid, *Microhyla heymonsi* (Microhylinae), was included as an additional nongastrophrynine outgroup. Seven gastrophrynines were also included as outgroups, including two former members of *Chiasmocleis* (*Hamptophryne boliviana* and *Elachistocleis panamensis*). *Hamptophryne boliviana* was removed from *Chiasmocleis* by Carvalho (1954) on the basis of morphology, whereas *E. panamensis* was moved to *Elachistocleis* by de Sá et al. (2012) based on a phylogenetic analysis of DNA sequences. Additional gastrophrynines included were *Ctenophryne barbatula*, *Ct. geayi*, *Dermatonotus muelleri*, *Gastrophryne carolinensis* and *Elachistocleis helianneae*.

Although inferring relationships outside the *Chiasmocleis/Syncope* clade was not our intention, our outgroup sampling provided the first test of the new positioning of *E. panamensis* proposed by de Sá et al. (2012), and also a further test of the monophyly of the *Chiasmocleis/Syncope* clade.

**Laboratory protocols.** Total genomic DNA was extracted and isolated from frozen and ethanol-preserved tissues using the Qiagen DNeasy kit following the manufacturer's guidelines. Polymerase chain reactions (PCR) for amplification of DNA fragments were carried out in 25  $\mu$ l reactions using either Fisher Taq together with Buffer A (catalog number FB600030) or Illustra PuRe Taq Ready-To-Go PCR Beads (GE Healthcare Life Sciences). Primers used in amplification and sequencing of the 16S and tyrosinase fragments are commonly used in amphibian systematics while a new pair of primers was designed for sequencing the Folmer et al. (1994) fragment of COI. For the 16S fragment, we used 16SAR (forward, 5'-CGCCTGTTTATCAAAAACA T-3') and 16SBR (reverse, 5'-CCGGTCTGA ACTCAGATCACGT-3') (Palumbi et al., 1991). For tyrosinase, we used TyrC (forward, 5'-GGCAGAGGAWCRTGCCAAGATGT-3') and TyrG (reverse, 5'-TGCTGGCRTC-TCCARTCCCA-3') (Bossuyt and Milinkovitch, 2000). A primer pair was designed de novo for targeting a 658 bp fragment of COI; COLPF-A (forward, 5'-TTTCAACHAAYCAYAAAGAYATYGG-3') and COLPR-A (reverse, 5'TANACTTCNGGGTGDCCAAAR-AATCA-3').

PCR setups were those of Faivovich et al. (2005), with standard annealing temperature of 48° C for 16S and COI; 56° C for tyrosinase. PCR products were cleaned and desalted using AMPure (Agencourt Biosciences Corporation) in a Beckman Coulter Biomek 2000 robot ("Becky") or by hand. Cycle sequencing using BigDye Terminators, v. 3.0 (Applied Biosystems), was run in 10  $\mu$ l reactions following the protocol of Platt et al. (2007), and products were cleaned and desalted using cleanSEQ (Agencourt Biosciences Corporation) in "Becky." Sequencing was done with an ABI 3730XL automated sequencer. Samples were sequenced in both directions to check for sequencing errors and ambiguities. Sequence contigs were assembled and edited in Geneious 6.0.3 (Biomatters, www.geneious.com).

**Genbank sequences.** To complement our dataset, several sequences were obtained from previously published works (Genbank; see appendix 2). Only terminals for which at least the 16S was available were included in

the final dataset.<sup>6</sup> One sequence labeled as *C. hudsoni* from Fouquet et al. (2007; accession number, EU201100) was not included. This represents *C. haddadi*, sp. nov. (described below), and derives from the same population (French Guiana, Mont Kotika) for which we sequenced four other individuals.

De Sá et al. (2012) included 23 sequences of *Chiasmocleis* and *Syncope* representing 14 species in their analysis of microhylid relationships. We have included 22 of them in our analyses.<sup>7</sup> Genbank accession numbers for novel and previously published sequences, together with their source, are given in appendix 2.

**Phylogenetic analyses.** Phylogenetic analyses were performed under direct optimization (Wheeler, 1996; Varón and Wheeler, 2012) in POY 5.0 (Varón et al., 2013) using equal weights for all transformations (substitutions and insertion/deletion events) and the parsimony optimality criterion. Justifications for

<sup>6</sup>Two terminals from the de Sá et al. (2012) dataset, *Chiasmocleis bassleri* (voucher number NMPGV 71148) and *Syncope antenori* (QCAZ 23824) do not have Genbank numbers for the 16S fragment given in the manuscript. However, sequences of 16S (*C. bassleri*: 231 bp, and *S. antenori* 256 bp) were apparently included in their final dataset (Nexus file available at TreeBase, www.treebase.org; Study ID 13478). The tyrosinase fragment is available in Genbank for both taxa. Both specimens were included in our analyses, and Genbank accession numbers for the two 16S sequences, generated by de Sá et al. (2012), are given in appendix 2.

<sup>7</sup>During sequence editing, file formatting, and preliminary analysis, we noticed some of the 16S sequences derived from de Sá et al. (2012) had striking—and, considering the close relatedness of the taxa involved in the study, unexpected—differences when compared to the rest of the dataset. Most of these inconsistencies were found at the 5' end and in sequences shorter than average. Given that the same primer pair was employed by de Sá et al. (2012) and us—16SAR/16SBR (Goebel et al., 1999) we assume that some of the sequences by de Sá et al. (2012) likely have sequencing problems. We have trimmed 50–100 bp off the 5' end of these sequences. Few additional bp, from the 5' end, were excluded from these sequences when preparing the dataset for the POY analysis. Total data exclusion is: NMPGV 71148 (KF621255), 29 bp excluded; KC180063, 139 bp; KC180060, 143 bp; KC180062, 125 bp; KC180071, 52 bp; KC180065, 136 bp; KC180074, 27 bp. Preliminary analysis including the sequences as they are in Genbank, trimmed for "bad parts," and completely excluding these sequences were performed. Alignments and results from these analyses are available upon request.

the use of dynamic homologies in parsimony, which we endorse herein, can be found elsewhere (Kluge and Grant, 2006; Wheeler et al., 2006; Grant and Kluge, 2009). Contiguous sequences were preliminarily delimited in fragments of putative homology to allow incorporation of partial sequences and accelerate dynamic homology cost calculations (Wheeler et al., 2006). External gaps due to missing data (and not due to natural length variation) were coded as “N”s.

Analyses were performed using the command “search,” which implements a driven search composed of random addition sequence Wagner builds (RAS), subtree pruning and regrafting (SPR) and tree bisection and reconnection (TBR) branch swapping, parsimony ratcheting (Nixon, 1999), and tree fusing (Goloboff, 1999), storing the shortest trees of each independent run and performing a final round of tree fusing on the pooled trees. When running in parallel, trees are exchanged among processors at the end of each search and the best unique trees are then selected and added to the pool of trees to be fused following the next round of search. Ten consecutive searches runs consisting of 12 hr driven searches were conducted in parallel on 16 Intel Xeon 3.0 GHz processors at the American Museum of Natural History computer cluster. Best trees from each run were saved and pooled together for additional rounds of tree fusing and TBR. For a more thorough search of optimal topologies, trees from the initial searches were submitted to additional rounds of TBR under an iterative pass optimization (Wheeler, 2003).

We report Goodman-Bremer, GB (Goodman et al., 1982; Bremer, 1988; Grant and Kluge, 2008b), for each node on the strict consensus tree of the most parsimonious trees. GB was chosen over other nodal support measurements (e.g., bootstrap, jackknife) because of its objectivity and direct relatedness to optimality criteria (Grant and Kluge, 2008a; Wheeler, 2010). GB was calculated by comparing the strict consensus tree with a pool of suboptimal trees, assembled by saving all trees visited during TBR searches performed on the optimal trees.

Uncorrected pairwise genetic distances for 16S sequences were calculated using MEGA 5.2 (Tamura et al., 2011) based on multiple sequence alignment performed in MUSCLE (Edgar, 2004) using the default parameters.

**CHARACTER EVOLUTION:** During evaluation of phenotypic characters for diagnosis of the species treated here a few were considered consistent enough (fixed within species) to be diagnostic and useful for evaluating their evolution (transformation series). We have selected three morphological characters (femoral line, dermal spines, and amount of webbing in males), and one reproductive character (egg clutch size) for evaluation of their evolution in the study group. Characters were optimized in a summary tree, derived from the strict consensus of the most parsimonious trees, with all terminals representing the same taxon collapsed to a single terminal. Morphological characters were scored as absent or present, while the amount of webbing in males was simplified to constitute only two states, absent (if absent or only basal webbing observed), and present (if extensive webbing observed) (see fig. 5). Because of limited taxon sampling, optimization of characters on the outgroup, which can influence optimization on the ingroup, was a matter of uncertainty. We opted to collapse all outgroup terminals into a single leaf and coded all characters as ambiguous observations (equal probability of the character being present, or absent). Character optimization was accomplished using the parsimony algorithm in Mesquite 2.74 (Maddison and Maddison, 2007).

Coding of phenotypic characters was done from direct observation of specimens (listed in appendix 1) or from the literature. In the later case, the following sources were consulted: Nelson, 1975; Duellman and Menselson III, 1995; Krügel and Richter, 1995; Cruz et al., 1997; Cruz et al., 1999; Nascimento and Skuk, 2006; Moravec and Köhler, 2007; Funk and Cannatella, 2009.

**PRESENTATION OF DATA:** First, we present the results of the phylogenetic analysis. This is followed by a review of relevant characters deemed of importance in *Chiasmocleis* (and *Syncope*) taxonomy. We then present species accounts, with data for all known species and the description of new taxa. For known species, data are presented in the following order: *Holotype* (collection number; whether the specimen was examined; notes on preservation state; photos of most holotypes are included); *Type locality* (usually copied from the original publication; when vague,

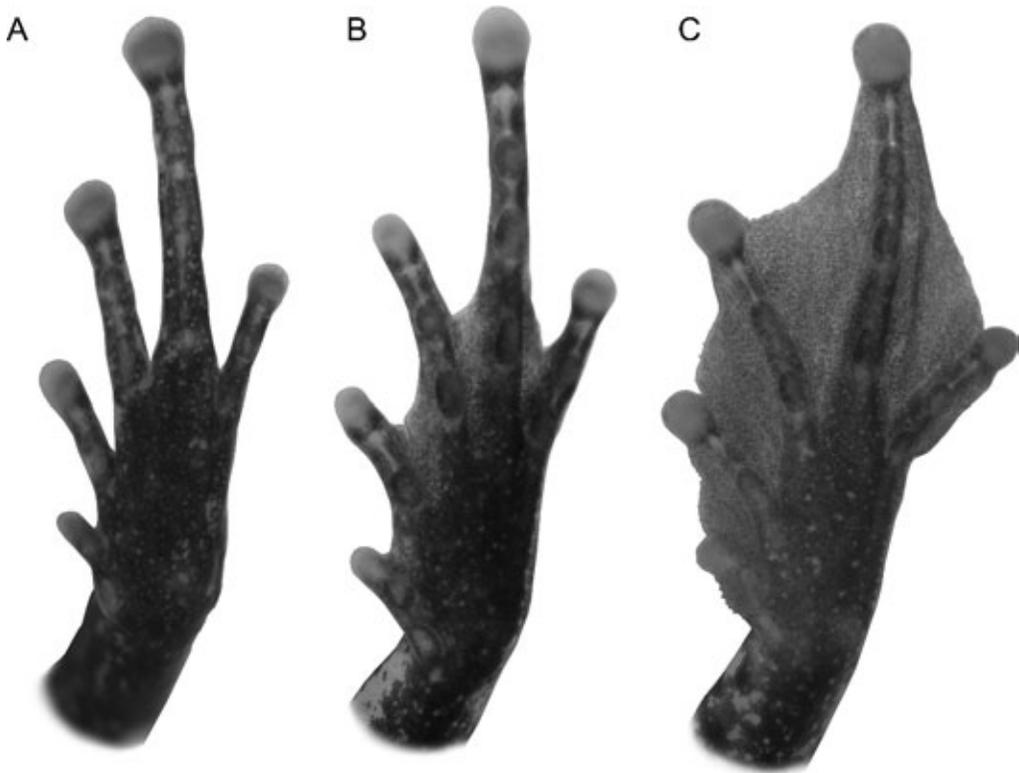


Fig. 5. Variation in amount of toe webbing in *Chiasmocleis*. (A) Webbing absent in a male *C. haddadi*, sp. nov. (FL 454). (B) Basal webbing in a female *C. shudikarensis* (FL 410). (C) Extensive webbing in a male *C. shudikarensis* (FL 487). Note sexual dimorphism in webbing (B–C, syntopic specimens). Not to scale.

additional details are given, if available); *Diagnosis* (based on our observation of specimens; when literature data are used in the diagnosis, that is mentioned); *Variation* (same as for *Diagnosis*); *Calls and Tadpoles* (data on calls are given for newly analyzed calls and reanalyzes of previous descriptions and from the literature); *Remarks* (if needed: any important remarks relevant to the taxonomy or systematics of the taxa are provided); and *Distribution* (a review of available specimen records as well as literature records of populations not examined by us where pertinent; distribution map for the species, except *C. albopunctata*, which was given by Forlani et al., 2011; maps include only records for which we examined at least one specimen, by direct examination or solely from photographs, except for type localities, which are sometimes based solely on the literature, e.g., *C. devriesi*). For new taxa, we provide data as follows: *Holotype*, *Type*

*Locality*, *Paratypes*, *Diagnosis*, *Comparisons* (with all species treated in this work), *Description of the Holotype*, *Measurements of the Holotype*, *Variation*, *Etymology*, *Calls and Tadpoles*, *Remarks* (if needed), and *Distribution*.

A compilation of data on natural history, both from the literature and novel data (based on field notes and photographs), is given at the end of the manuscript, as is a brief comment on conservation. For these final sections, information on all species is compiled together.

## RESULTS

We examined 595 specimens (appendix 1, plus lists of type specimens of new taxa) that we assign to 16 species, three of them named here. The phylogenetic analyses support our conclusions regarding species diversity, but failed to recover reciprocal monophyly of

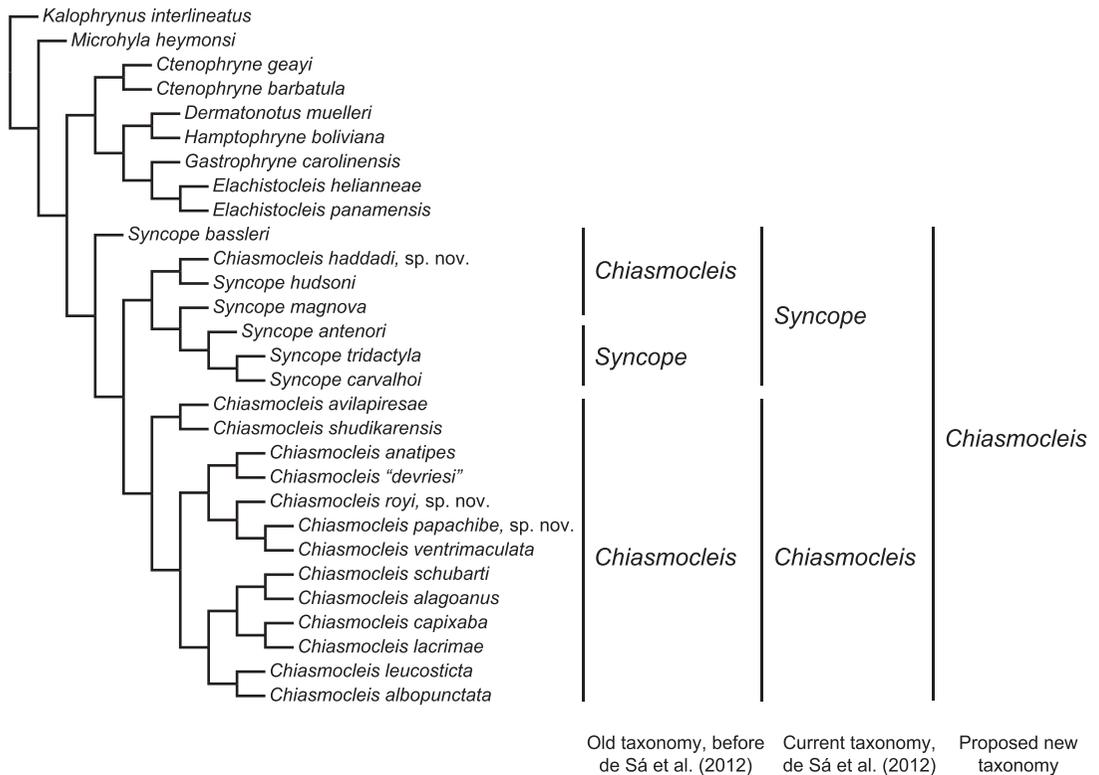


Fig. 6. Summary of the strict consensus of 49 optimal trees with 3290 equally weighted steps, evidencing recent (de Sá et al., 2012), and proposed changes (new classification provided herein) in the taxonomy: *Syncope* is considered a junior synonym of *Chiasmocleis*. *Chiasmocleis jimi* is considered a junior synonym of *C. hudsoni* and is not shown in the tree. *Chiasmocleis devriesi* (with a doubtful status) is nested within *C. anatipes* and is also not shown. See text and figures 7–8 for details and support values for all nodes.

*Chiasmocleis* and *Syncope* as proposed by de Sá et al. (2012).

#### THE PHYLOGENY OF *CHIASMOCLEIS*

Direct optimization parsimony analysis recovered 49 equally parsimonious trees with 3290 steps (figs. 6–8).<sup>8</sup> This tree length was hit multiple times during tree search. The

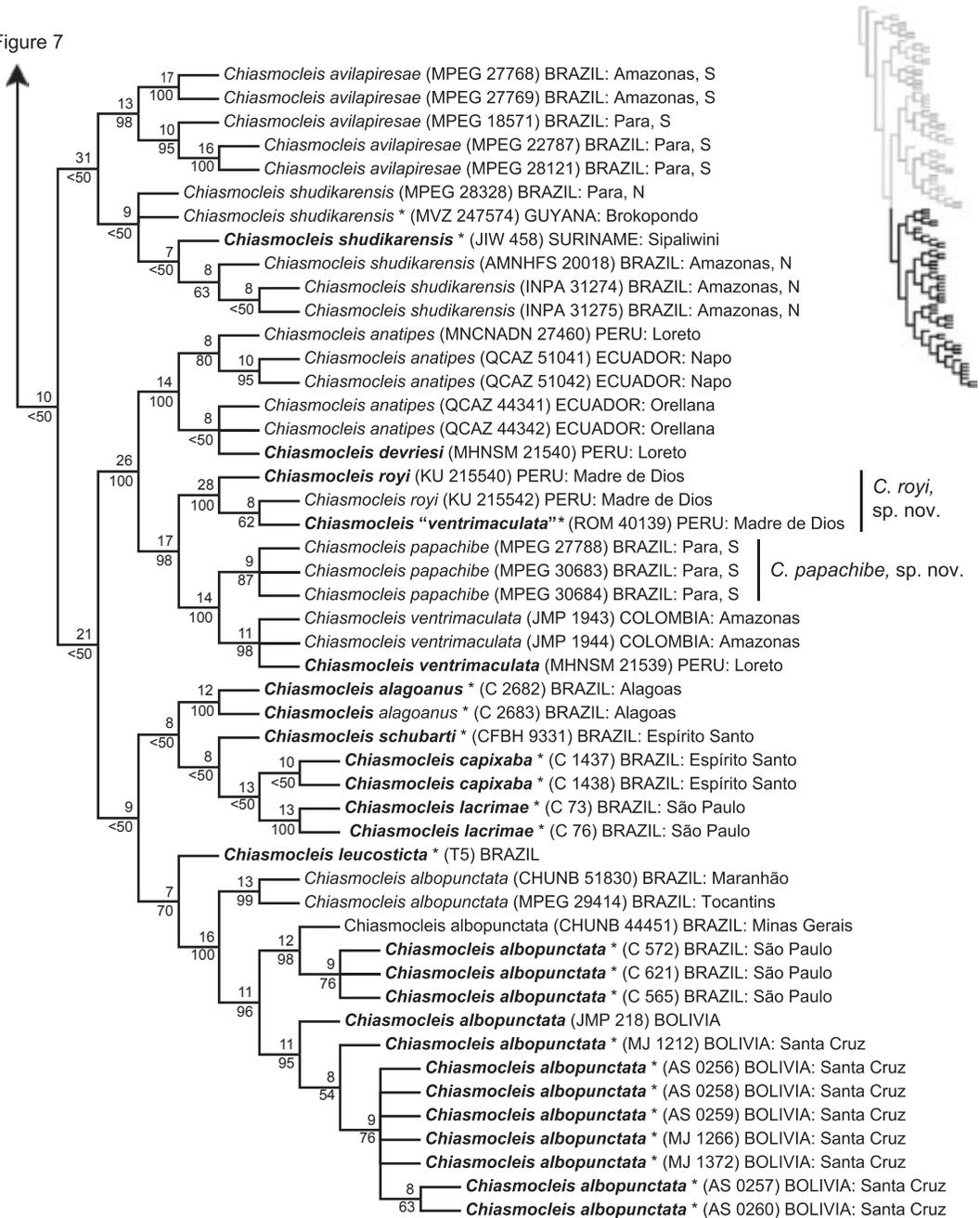
<sup>8</sup>Because our analysis was performed for the purpose of inferring relationships and species limits within *Chiasmocleis*, apart from corroborating the exclusion of *Hamptophryne boliviana* and *Elachistocleis panamensis* from *Chiasmocleis* (see Carvalho, 1954; de Sá et al., 2012), we reserve any further comment on outgroup relationships. The works by Pyron and Wiens (2011) and de Sá et al. (2012) rely on much larger taxon and character sampling, and we regard them as more robust tests of phylogenetic relationships between gastrophryne genera.

majority of taxa were recovered as monophyletic with topological conflicts mostly internal to putative species, except: (1) specimens of *Syncope jimi* and *S. hudsoni* are mixed inside a monophyletic clade; and (2) the sole specimen of *Chiasmocleis devriesi* is nested within individuals of *C. anatipes*.

Our topology differs markedly from that of de Sá et al. (2012) in supporting most species of *Syncope* nested within *Chiasmocleis* while *S. bassleri* is the sister species to all remaining ingroup species. *Syncope bassleri* is the sister taxon to a group containing two major clades, one containing “*Syncope*” sensu de Sá et al. (2012), and another containing the remaining *Chiasmocleis* sensu de Sá et al. (2012). This arrangement renders *Syncope* as paraphyletic with respect to *Chiasmocleis* (fig. 6). We are then faced with two options: (1) propose a new genus for



To Figure 7



Figs. 7 (opposite page) and 8 (above). Strict consensus of 49 optimal trees with 3290 equally weighted steps. Taxa in **bold** are derived from Genbank and were labeled “as is,” except KU 215540, originally labeled as *Chiasmocleis ventrimaculata*—we have examined the specimen and it is one of the paratypes of *C. royi*, sp. nov. Specimens marked with an asterisk (\*) were not examined. Numbers above and below branches are, respectively, Goodman-Bremer and parsimony jackknife values for each node (fig. 8). Generic taxonomy is updated to agree with our proposed classification (see text and fig. 6 for old names).

*Syncope bassleri* (and tentatively include *S. superciliarba*) or (2) consider the two genera as synonyms. We opt for the second alternative, and consider *Syncope* Walker, 1973, a junior synonym of *Chiasmocleis* Méhelÿ, 1904. By adding *Syncope* to the synonymy of *Chiasmocleis*, we maintain a monophyletic taxonomy that is consistent with the phylogeny presented here, and also with the topology presented by de Sá et al. (2012).

This arrangement, however, generates a secondary homonymy between *Syncope carvalhoi* Nelson, 1975 (senior homonym), and *Chiasmocleis carvalhoi* Cruz, Caramaschi, and Izecksohn, 1997 (junior homonym). To remedy this situation, we provide *Chiasmocleis lacrimae*, nomen novum, to the species described by Cruz et al. (1997). The specific epithet *lacrimae* is used as a noun in the genitive case deriving from the Latin word *lacrima*, meaning “tear.” The name is used as an allusion to the teardrop body shape of most gastrophryne microhylids, especially noticeable in many species of *Chiasmocleis*. The diagnosis remains unchanged from the original (Cruz et al., 1997).

We recognize five clades within *Chiasmocleis*: the *Chiasmocleis bassleri* clade (containing *C. bassleri* and *C. superciliarba*, the latter one placed tentatively), the *Chiasmocleis hudsoni* clade (*C. antenori*, *C. carvalhoi*, *Chiasmocleis haddadi*, sp. nov., *C. hudsoni*, *C. magnova*, and *C. tridactyla*), the *Chiasmocleis shudikarensis* clade (*C. avilapiresae* and *C. shudikarensis*), the *Chiasmocleis ventrimaculata* clade (*C. anatipes*, *C. devriesi*, *Chiasmocleis papachibe*, sp. nov., *C. ventrimaculata*, and *Chiasmocleis royi*, sp. nov.), and the *Chiasmocleis albopunctata* clade (*C. alaguanus*, *C. albopunctata*, *C. capixaba*, *C. lacrimae*, *C. leucosticta*, and *C. schubarti*). At this stage, however, we cannot provide any phenotypic synapomorphies for any of the clades.

As mentioned above, *Chiasmocleis bassleri* is at the base of the ingroup and sister to a clade containing all remaining species. Next in branching order is a split between two major lineages, one containing the *C. hudsoni* clade, and another with the remaining three clades. The *C. avilapiresae* clade is sister to the *C. ventrimaculata* + *C. albopunctata* clades. The *C. hudsoni* clade contains all species included

in the genus *Syncope* by de Sá et al. (2012: we did not sample *C. superciliarba*) with the exception of *C. bassleri*. Of the new taxa described here, *C. haddadi*, sp. nov., is included in the *C. hudsoni* clade, while the other two new species, *C. papachibe*, sp. nov., and *C. royi*, sp. nov., are part of the *C. ventrimaculata* clade.

**THE CHIASMOCLEIS BASSLERI CLADE:** This clade contains *C. bassleri* and *C. superciliarba*. Although well supported in our analysis, the position of *C. bassleri* differs markedly from that reported by de Sá et al. (2012), whose sole specimen of *C. bassleri* was found nested within what we recovered as members of the *C. hudsoni* clade. Morales and McDiarmid (2009) suggested that *C. superciliarba* “is related to *C. bassleri* and could be [from] a supra-species group” and proposed the *C. bassleri* species group. We agree that there are striking morphological similarities between the two taxa (e.g., body shape, inguinal spot, digit morphology), and therefore place *C. superciliarba*, although tentatively, as a member of the *C. bassleri* clade. This arrangement is pending further test, preferably in light of a phylogenetic analysis that actually includes specimens of *C. superciliarba*.

**THE CHIASMOCLEIS HUDSONI CLADE:** *Chiasmocleis haddadi*, sp. nov., is sister to a cluster of specimens from several populations identified (original labels) as either *C. hudsoni* and *C. jimi*. Our topology shows that both *C. hudsoni* and *C. jimi* are not monophyletic (*C. jimi* is considered here as a synonym of *C. hudsoni*, see below). *Chiasmocleis magnova* is sister of a clade containing *C. antenori*, *C. tridactyla*, and *C. carvalhoi*. One sequence of *C. carvalhoi* from San Martin, Peru (KU 215720; from de Sá et al., 2012) groups with our sequences of *C. antenori*. Since we have not examined this specimen, we do not take any nomenclatural action regarding *C. antenori* or *C. carvalhoi*. Both sequences of *Syncope* sp. (de Sá et al., 2012) are nested within *S. carvalhoi*, and are tentatively assigned to this taxon, pending examination of the voucher specimens.

**THE CHIASMOCLEIS SHUDIKARENSIS CLADE:** Peloso and Sturaro (2008) described *C. avilapiresae*, differentiating it from *C. shudikarensis* mostly on color pattern, presence/absence

of the inguinal blotch, and development of fringes. Our phylogenetic analysis recovered two well-supported monophyletic lineages, one with all specimens of *C. avilapiresae* and another with all specimens of *C. shudikarensis* (fig. 8). There are considerable differences in the advertisement calls among populations of *C. shudikarensis* as well as a certain degree of morphological variation, which led Peloso and Sturaro (2008) to consider that additional species may be hidden in the name *C. shudikarensis*. Present evidence is insufficient to either support or reject Peloso and Sturaro's (2008) prediction. This is discussed further in the Variation and Remarks section in the *C. shudikarensis* species account.

**THE *CHIASMOCLEIS VENTRIMACULATA* CLADE:** The overall morphological similarity of *C. anatisipes*, *C. devriesi*, *C. papachibe*, sp. nov., *C. royi*, sp. nov., and *C. ventrimaculata* is explained by their close relationship, with the five forming a well supported monophyletic clade. The sole specimen of *C. devriesi* is clustered with some of our samples of *C. anatisipes*, and the two recovered as sister to a clade containing the other three species in the *C. ventrimaculata* clade: *C. royi*, sp. nov., *C. papachibe*, sp. nov., and *C. ventrimaculata*.

The clade as a whole has a curiously disjoint distribution, with most species being found in the western Amazon (Colombia, Ecuador, Peru, Bolivia, and western Brazilian states of Acre and Rondônia), while *C. papachibe* is found in eastern Amazon (vicinities of Belém, Pará). The absence of species of this clade in the majority of the Amazon basin in Brazilian territory (especially in the Tapajós and Xingu river basins) deserves further scrutiny, and the negative effects of inadequate sampling in those areas cannot be disregarded.

**THE *CHIASMOCLEIS ALBOPUNCTATA* CLADE:** A monophyletic "Atlantic Rainforest clade" was not recovered, as *C. albopunctata* is nested within the Atlantic Forest species. *Chiasmocleis leucosticta* is sister to *C. albopunctata*, and the two form a clade that is sister to the Atlantic Forest endemics *C. alagoanus*, *C. capixaba*, *C. lacrimae*, and *C. schubarti*. The arrangement of this clade is similar to that reported by de Sá et al. (2012; most of the sequences used derive from that work), except for the position of *C. schubarti*.

Within samples of *C. albopunctata* we found three well-supported clades, one with specimens from northeastern Brazil (mostly Caa-tinga/Cerrado habitat transition), one with specimens from southeastern Brazil (Cerrado habitats in the states of Minas Gerais and São Paulo), and a third with specimens from Bolivia.

#### PHENOTYPIC VARIATION

**EXTERNAL MORPHOLOGY:** The morphological analyses revealed a great degree of variation in some characters commonly used to diagnose species in the genus *Chiasmocleis* (e.g., inguinal blotches, body stripes, presence and distribution of dermal spines, toe webbing, and ventral color patterns), which we feel deserves further scrutiny.

**MORPHOMETRICS:** Despite the fact that not all specimens were measured (see Material and Methods), we have compiled a large amount of data on morphometrics. These data are summarized in table 1.

**INGUINAL BLOTCH** (fig. 9): This character was used for the first time in *Chiasmocleis* taxonomy by Dunn (1949) to describe a "rather vague and irregular" mark in the inguinal region of the holotype of *C. bassleri*. These black or brownish marks can vary widely in form and shape, from a small round spot on the dorsolateral region to a larger and more irregularly shaped blotch that extends from the groin to the dorsum (fig. 9). Although often referred to as an *inguinal spot*, we feel that this character is better designated as *inguinal blotch*.

The presence or absence of the inguinal blotch proved to be a taxonomically informative character. Three species present conspicuous inguinal blotches: *Chiasmocleis bassleri*, *C. shudikarensis*, and *C. superciliarba*. Some specimens of *C. bassleri* and *C. superciliarba* also have additional blotches/spots on the lateral region (fig. 9B). A very faint blotch in the inguinal region of *C. avilapiresae* is present in a more limited number of specimens, all from a single locality (Maués, Amazonas, Brazil). The blotch in *C. avilapiresae* is, however, limited to the inguinal region and does not extend dorsolaterally.

**LIGHT STRIPES ON MIDDORSUM AND POSTERIOR SURFACE OF THIGH (*FEMORAL LINE*):** The presence and shape of a light

TABLE 1  
 Summary of morphometric data for the *Chiasmocleis* species studied<sup>a, b</sup>  
 Abbreviations are listed in the Material and Methods

Species	Sex	Sample size	SVL	HL	HW	ED	IOD	IND	END	THL	TBL	FL2	4TD
<i>C. anantipes</i>	Male	N=2	18.4-21.2	3.8-50.3	4.6-6.3	1.6-1.8	3.0-3.7	1.3-1.6	1.7-1.8	8.9-9.2	8.9-9.6	12.8-14.7	0.5-0.6
	Females	N=1	24.9	5.4	6.6	1.9	4.2	2.0	2.3	10.1	10.2	16.0	0.7
<i>C. antenori</i>	Females	N=3	12.4 ± 1.1	3.3 ± 0.2	3.6 ± 0.3	1.4	2.2 ± 0.1	1.0 ± 0.2	1.0 ± 0.1	5.3	5.7 ± 0.4	8.6 ± 0.4	
			(11.4-13.6)	(3.2-3.5)	(3.3-3.9)		(2.2-2.3)	(0.9-1.2)	(0.9-1.0)		(5.3-6.0)	(8.3-9.0)	
<i>C. avilapitresae</i>	Males	N=28	24.8 ± 1.8	5.4 ± 0.3	6.6 ± 0.6	1.7 ± 0.2	4.0 ± 0.3	1.7 ± 0.2	1.9 ± 0.2	11.4 ± 0.8	11.4 ± 0.7	17.4 ± 1.1	1.0 ± 0.1
			(22.2-28.0)	(4.8-6.0)	(5.8-7.7)	(1.3-2.3)	(3.5-4.5)	(1.4-2.0)	(1.6-2.3)	(1.6-2.3)	(9.6-13.1)	(10.4-12.9)	(16.1-19.9)
<i>C. avilapitresae</i>	Females	N=82	32.0 ± 3.3	6.5 ± 0.6	7.9 ± 0.8	1.9 ± 0.2	4.8 ± 0.4	2.0 ± 0.2	2.4 ± 0.3	13.5 ± 1.2	13.8 ± 1.3	20.8 ± 1.9	1.1 ± 0.2
			(23.6-37.8)	(5.2-8.1)	(6.1-9.6)	(1.4-2.3)	(3.9-5.7)	(1.5-2.9)	(1.7-3.0)	(1.7-3.0)	(10.8-16.4)	(10.9-16.5)	(17.0-25.5)
<i>C. bassleri</i>	Males	N=11	20.3 ± 1.0	4.9 ± 0.3	5.8 ± 0.3	1.4 ± 0.2	3.5 ± 0.2	1.5 ± 0.2	2.0 ± 0.1	9.9 ± 0.5	10.0 ± 0.5	14.4 ± 0.4	0.8 ± 0.1
			(19.2-22.1)	(4.5-5.6)	(5.4-6.3)	(1.2-1.7)	(3.0-3.8)	(1.1-1.8)	(1.8-2.1)	(1.8-2.1)	(9.1-10.6)	(9.5-10.9)	(13.3-15.5)
<i>C. bassleri</i>	Females	N=20	25.6 ± 2.2	5.6 ± 0.4	6.6 ± 0.6	1.6 ± 0.2	4.1 ± 0.3	1.8 ± 0.2	2.3 ± 0.2	11.8 ± 1.1	11.9 ± 1.1	16.8 ± 1.8	0.8 ± 0.1
			(21.2-28.8)	(4.7-6.5)	(5.4-7.5)	(1.3-1.9)	(3.4-4.4)	(1.4-2.0)	(1.8-2.7)	(1.8-2.7)	(9.7-13.8)	(10.1-13.5)	(12.9-19.5)
<i>C. carvalhoi</i>	Females	N=14	11.4 ± 0.4	2.9 ± 0.3	3.1 ± 0.1	1.4 ± 0.2	2.1 ± 0.2	0.9	1.1 ± 0.1	5.1 ± 0.1	4.9 ± 0.3	6.7 ± 0.8	0.4
			(11.1-11.8)	(2.7-3.2)	(3.1-3.2)	(1.3-1.6)	(1.9-2.3)	0.9	(1.0-1.2)	(5.0-5.1)	(4.7-5.3)	(6.1-7.6)	0.4
<i>C. haddadi</i>	Males	N=12	16.1 ± 1.7	4.1 ± 0.3	4.8 ± 0.5	1.5 ± 0.1	3.1 ± 0.2	1.4 ± 0.1	1.4 ± 0.1	7.2 ± 0.7	7.5 ± 0.6	11.3 ± 1.0	0.7 ± 0.1
			(13.7-18.2)	(3.5-4.5)	(4.1-5.4)	(1.4-1.7)	(2.8-3.4)	(1.2-1.6)	(1.2-1.5)	(6.1-8.2)	(6.8-8.8)	(10.1-13.0)	(0.4-0.8)
<i>C. hudsoni</i>	Males	N=20	18.2 ± 2.8	4.3 ± 0.7	5.0 ± 0.7	1.5 ± 0.2	3.0 ± 0.4	1.6 ± 0.2	1.5 ± 0.5	8.3 ± 1.1	9.0 ± 1.3	13.3 ± 2.0	0.7 ± 0.1
			(14.1-23.4)	(2.9-5.4)	(4.1-6.3)	(1.0-1.9)	(2.4-3.7)	(1.0-1.8)	(1.2-1.8)	(7.1-10.6)	(7.3-11.5)	(10.7-17.2)	(0.5-0.9)
<i>C. hudsoni</i>	Females	N=40	21.5 ± 2.7	4.7 ± 0.5	5.5 ± 0.7	1.6 ± 0.2	3.3 ± 0.4	1.6 ± 0.2	1.6 ± 0.2	9.5 ± 1.2	10.2 ± 1.1	15.3 ± 1.9	0.9 ± 0.1
			(17.2-28.4)	(3.8-6.1)	(4.5-6.8)	(1.3-1.9)	(2.7-4.0)	(1.2-1.9)	(1.3-2.0)	(6.5-12.6)	(8.1-13.1)	(11.8-19.1)	(0.7-1.2)
<i>C. magna</i>	Female	N=1	16.7	3.8	4.1	1.7	2.7	1.1	1.1	6.9	7.8	11.5	0.4
<i>C. papachibe</i>	Male	N=1	24.8	4.7	5.3	1.8	4.1	1.8	2.0	9.0	9.4	15.4	0.4
<i>C. papachibe</i>	Females	N=2	28.8-32.6	5.7-6.5	6.8-7.5	1.8-1.9	4.5-4.8	2.1-2.2	2.3-2.9	10.8-11.7	11.4-11.5	18.6-18.9	0.4-0.6
<i>C. royi</i>	Males	N=24	21.3 ± 1.1	4.4 ± 0.3	4.8 ± 0.2	1.5 ± 0.1	3.2 ± 0.2	1.4 ± 0.1	1.6 ± 0.2	8.3 ± 0.6	5.5 ± 0.4	13.8 ± 0.6	0.6 ± 0.1
			(18.8-23.1)	(3.2-4.6)	(4.2-5.3)	(1.2-1.9)	(2.7-3.4)	(1.1-1.7)	(1.3-1.8)	(7.1-9.4)	(7.5-9.2)	(12.1-15.2)	(0.4-0.7)
<i>C. royi</i>	Females	N=16	24.2 ± 2.0	4.8 ± 0.5	5.3 ± 0.4	1.5 ± 0.1	3.4 ± 0.3	1.5 ± 0.1	1.7 ± 0.2	9.3 ± 0.6	9.4 ± 0.7	15.2 ± 1.1	0.7 ± 0.7
			(20.7-27.6)	(4.2-5.8)	(4.7-6.1)	(1.3-1.8)	(2.9-3.9)	(1.3-1.8)	(1.4-2.0)	(8.2-10.4)	(8.4-10.6)	(13.3-17.7)	(0.5-0.8)
<i>C. shudikaresis</i>	Males	N=22	22.2 ± 1.3	5.1 ± 0.3	6.1 ± 0.4	1.7 ± 0.2	3.6 ± 0.2	1.5 ± 0.1	1.8 ± 0.1	10.0 ± 0.9	10.1 ± 0.9	15.3 ± 1.3	0.8 ± 0.1
			(18.7-24.5)	(4.6-5.7)	(5.3-6.9)	(1.4-2.1)	(3.2-4.1)	(1.2-1.9)	(1.6-2.0)	(8.1-11.7)	(8.3-11.6)	(12.4-17.3)	(0.6-1.0)
<i>C. shudikaresis</i>	Females	N=11	26.7 ± 2.3	5.6 ± 0.4	6.9 ± 0.6	1.9 ± 0.1	4.2 ± 0.2	1.7 ± 0.2	2.2 ± 0.2	11.7 ± 1.2	11.9 ± 1.0	17.9 ± 1.6	0.8 ± 0.1
			(20.9-29.7)	(4.8-6.4)	(5.5-7.6)	(1.7-2.1)	(3.9-4.7)	(1.5-2.0)	(1.6-2.5)	(8.8-13.4)	(9.2-12.9)	(13.4-19.2)	(0.6-0.9)
<i>C. venrimaculata</i>	Females	N=3	25.5 ± 3.7	5.1 ± 0.6	5.4-0.3	1.6 ± 0.1	3.8 ± 0.5	0.7 ± 0.1	2.1 ± 0.2	10.9 ± 1.1	10.5-0.8	16.3 ± 1.4	0.8 ± 0.1
			(21.7-29.1)	(4.5-5.6)	(5.1-5.6)	(1.5-1.7)	(3.4-4.3)	(1.6-1.8)	(1.9-2.3)	(9.8-12.0)	(9.7-11.3)	(14.8-17.5)	(0.7-0.9)

<sup>a</sup> Table summarizes only material examined by us (literature data excluded) for which we took measurements. Not all specimens examined were measured.  
<sup>b</sup> The specimen of *Chiasmocleis magna* examined, AMNH 103550, was not sexed via dissection. We infer specimen is a female based on the distribution of dermal spines and the absence of a vocal slit.

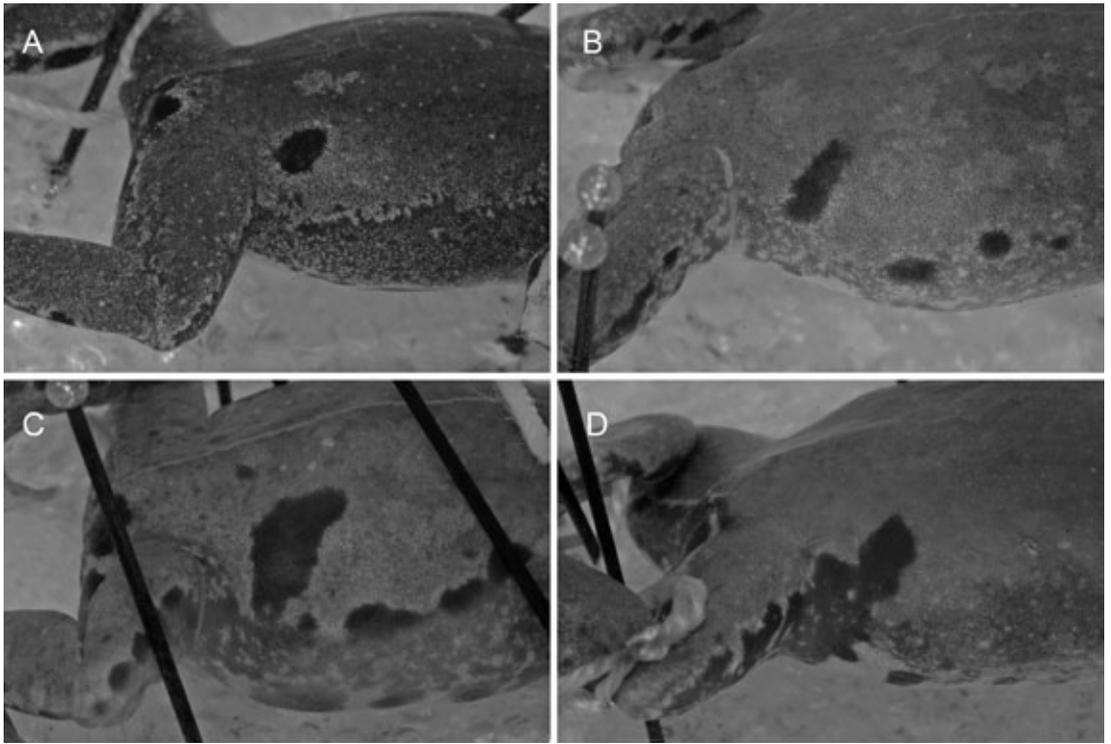


Fig. 9. Variation in size and shape of the inguinal blotch in species of *Chiasmocleis*. (A–C) *C. bassleri*; (A) MPEG 27766, (B) UFAC-RB 3872, and (C) UFAC-RB 1251. (D) *C. shudikarensis*, INPA 278.

stripe on the dorsum varies within populations and proved to be of no taxonomic utility in *Chiasmocleis* (fig. 10 illustrates this character's variation).

On the other hand, a lightly colored (white or cream) line on the posterior surface of the thigh, extending to the knee and over the cloacal opening, is consistently either present or absent within populations, proving to be a useful diagnostic character. We label this character as *femoral line*. All examined specimens of *C. avilapiresae*, *C. shudikarensis*, and *C. royi*, sp. nov. (described below), present femoral lines, whereas the line is absent in all other Amazonian/Guiana Shield species of *Chiasmocleis*. The femoral line can sometimes be connected, and perpendicular, to the dorsal line. The femoral line is present in non-Amazonian *Chiasmocleis* such as *C. capixaba* and *C. leucosticta*.

A different stripe on the posterior surface of thigh and flanks is present in *Chiasmocleis bassleri* and *C. superciliarba*. These lines, called here *split stripes*, are distinct from the

femoral line described above—the limits of the split stripe are not so well defined, but they usually mark a separation (or split) between the dorsal and ventral color patterns. Split stripes are not necessarily a line, but can be formed by a series of irregular light-colored stains (fig. 9A, C). Split stripes may also be evident on the lateral region (fig. 9A, C), and extend throughout the hind limbs. This is treated in more detail ahead (see variation under *C. bassleri*). Split stripes are present in other microhylids (e.g., *Ctenophryne*, *Hamptophryne*, and *Hypopachus*) and can be white as in *Chiasmocleis* and *Ctenophryne* or black as in some *Hamptophryne* and *Hypopachus*. Split stripes are present in most of the specimens of *C. bassleri* and *C. superciliarba*, whereas a few specimens do not show a clear differentiation between dorsal and ventral patterns.

**DERMAL SPINES** (fig. 11): Several authors had acknowledged the importance of dermal spines in microhylid systematics (see Nelson, 1972; Zweifel and Myers, 1989; Cruz et al.,

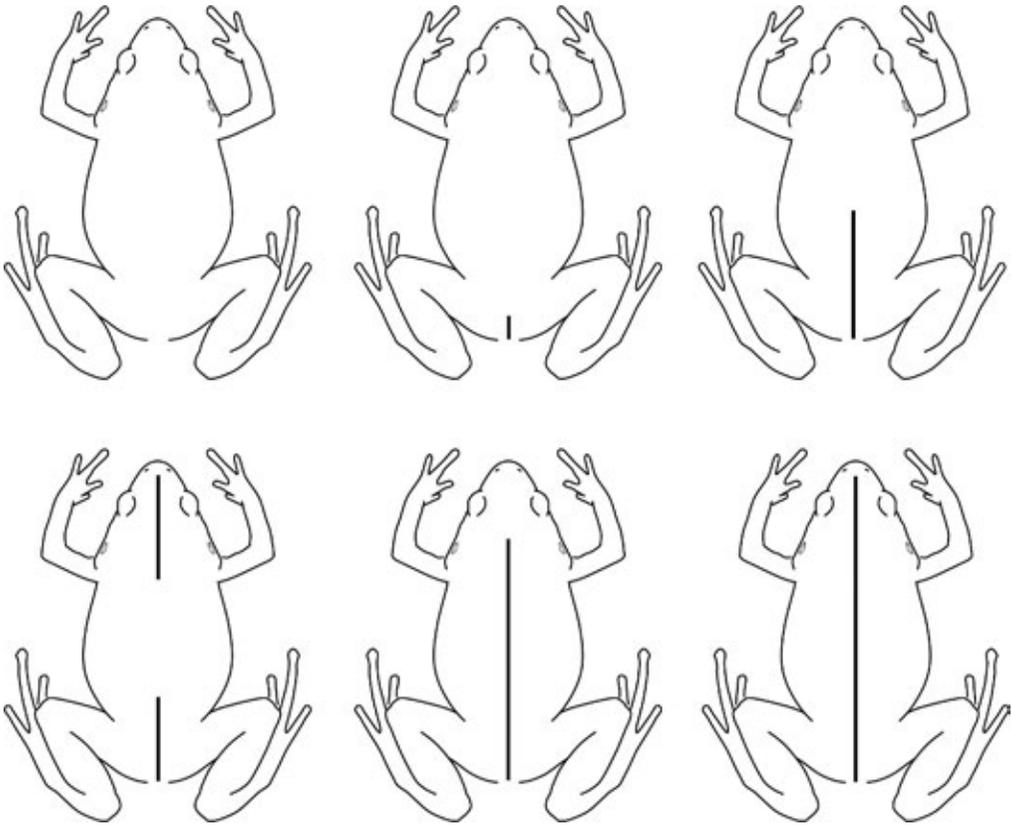


Fig. 10. Schematic drawing of variation in presence and extent of dorsal white lines in *Chiasmocleis*.

1997; Lehr and Trueb, 2007). They have also, however, indicated that the distribution and development of spines may vary sexually and taxonomically. Spines, when present, are usually more evident in reproducing specimens; therefore, the character may also vary

seasonally. At this point it is not clear whether even the spines are homologous structures among all gastrophrynines, or whether different lineages evolved spines independently (e.g., the spines in the chin of *Chiasmocleis hudsoni* are much larger and less numerous than in *C. shudikarensis*). The function and morphological nuances of the spines were never studied in detail, but some authors have related the presence and development of dermal spines to reproductive activity or as a defensive strategy against predators (Lehr and Trueb, 2007).

For the reasons above, although we use the presence/absence and distribution of spines to diagnose species, this character should be evaluated with care. The presence of dermal spines in Microhylidae is well illustrated in Lehr and Trueb (2007: figs. 5–6), Peloso and Sturaro (2008: fig. 6), and Cruz et al. (2007a); spines are also illustrated here, in figure 11.

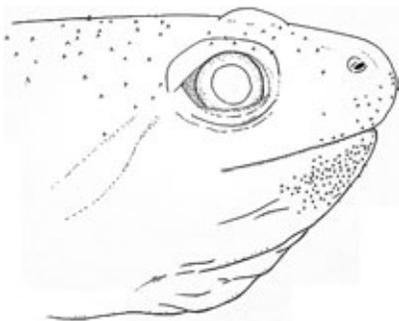


Fig. 11. Example of distribution of dermal spines on the head of *Chiasmocleis*.

In *Chiasmocleis*, the distribution, size, and density of spines vary both taxonomically and sexually. Spines are usually more common in males than in females. At least five species have males with many spines spread over the dorsum, chin, cloacal region, limbs, and digits: *C. anapetes*, *C. avilapiresae*, *C. royi*, sp. nov. (described ahead), *C. shudikarensis*, and *C. ventrimaculata*. Spines are rare, but sometimes present, in *C. albopunctata*, *C. bassleri*, and, although slightly more common, in *C. superciliarba*. *Chiasmocleis hudsoni* also shows some spines on the chin (in males) and in the cloacal region (more commonly in males, but also present in females). The low number of specimens available for *C. magnova* makes it difficult to define the distribution pattern of spines in males; females have many spines in the dorsolateral region and scattered spines on the tarsus and TV (Moravec and Köhler, 2007). Spines are unknown in *C. devriesi* (known only from the female holotype, but see remarks in species accounts), *C. haddadi*, sp. nov. (described below), and *C. papachibe*, sp. nov. (described below). Several *Chiasmocleis* from the Atlantic Rainforest also show a conspicuous presence of dermal spines (Cruz et al., 2007a; Cruz et al., 2007b).

**TOE WEBBING:** This character varies widely between sexes. When present, webbing is much more common and extensive in males than in females, and thus comparisons should be limited to specimens of the same sex. Marked sexual dimorphism is present in *Chiasmocleis avilapiresae* and *C. shudikarensis*, e.g., males generally have fully webbed toes, whereas those in females are only basally webbed or show no web at all (fig. 5). Toes of females *Chiasmocleis anapetes* are reported to be widely webbed (Rodríguez and Duellman, 1994), but examination of a few female specimens refutes this observation (see Remarks under *C. anapetes*). In some taxa, both sexes lack webbing completely (e.g., *C. antenori* and *C. hudsoni*).

There have been several attempts to standardize the description of variation in webbing among frogs (Savage and Heyer, 1967; Myers and Duellman, 1982), but we decided not to apply any notation to the present work for the following reasons: (1) some species present digit reduction, especially in TI and TV (e.g., *Chiasmocleis antenori*, *C.*

*carvalhoi*, *C. haddadi*, sp. nov., *C. hudsoni*, *C. magnova*, and *C. tridactyla*), so they are not directly comparable to species with more developed digits (given that the formula correlates the extent of webbing to digit phalanges); (2) time is constrained when visiting collections—even with experience, taking webbing notation is very time consuming and in many cases would come at the expense of the amount of material examined, since time in several collections was limited. Given the complexity of the group, we decided to prioritize volume of material examined over describing in detail variation in webbing. Instead, variation in webbing was noted solely as absent, basal, or extensive (fig. 5).

Our approach will certainly draw criticism and we are aware that some degree of subjectivity is inserted when not following “standardized recipes” for describing variation. However, we feel that the approach used is of sufficient reliability for diagnosing the currently known diversity in *Chiasmocleis*.

**VENTRAL COLOR PATTERN** (fig. 12): Color pattern of the ventral region (throat, chest, belly, and undersurfaces of limbs) were highly variable both within and among species. Nonetheless, it is a useful diagnostic character to differentiate species. As with dermal spines, although used in all diagnoses, this character should be examined with care, bearing in mind that variation does exist. Whenever a good series of specimens was available variation of the ventral and dorsal color patterns are provided in the variation section. Some clarifications to terminology are, however, needed. We define the ventral patterns observed in *Chiasmocleis* as follows (adapted from Kok and Kalamandeen, 2008):

**Uniform.** We refer to a uniform pattern when no spots, blotches, or vermiculations are present. Most specimens examined, however, do show some pattern of markings on the venter.

**Spots or Stains.** Small to medium-sized roughly round markings (herein called *spots*) or irregularly shaped ones (*stains*) may be light or dark in contrast to with the background color.

**Blotches.** Medium to large-sized irregular, light or dark markings contrasting with the background color. A blotch may show more than one shade of color (e.g., darker outline with a lighter center).

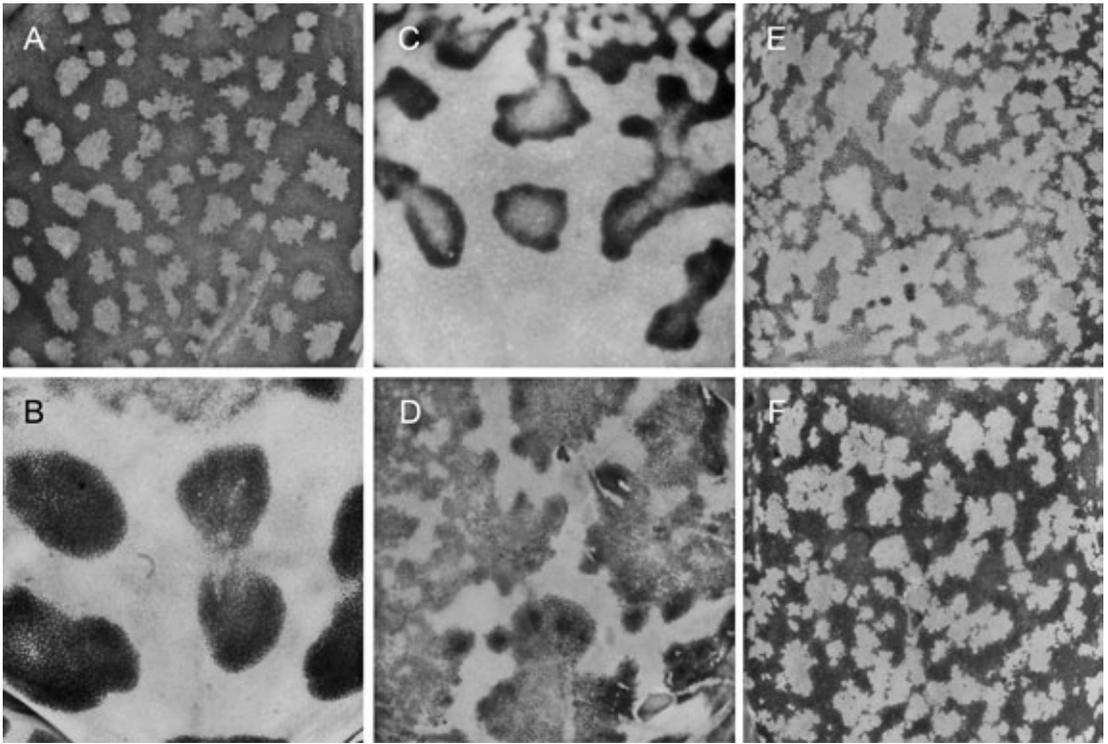


Fig. 12. Terminology used in this paper to describe ventral color pattern: (A) small light spots and stains over a dark background; (B) large dark spots over a light background; (C) dark blotches and stains over a light background; (D) large dark blotches over light background; or alternatively light vermiculations over a dark background; (E) dark vermiculations or reticulation over a light background; (F) intense dark vermiculations over a light background.

**Vermiculations, Reticulations, or Anastomoses.** Dark or light network of lines or elongated stains contrasting with the background color.

It should be noted that some specimens might show a combination of different patterns, for example, a uniform dark throat followed by a reticulation of dark stains on the chest and small spots on the belly. Again, a small level of subjectivity occurs with this character as, for example, different authors may interpret dark vermiculations against a light background as a dark background with many small irregular stains, and vice versa.

**ADVERTISEMENT CALLS:** The calls of all species examined consist of repetitive series of relatively short, multipulsed, notes. This call structure has been argued to be a putative synapomorphy uniting members of *Chiasmocleis* (Hartmann et al., 2002), but Santana et al. (2009) found the call structure to be very different in *C. mantiqueira* (unfortunately

*C. mantiqueira* was never included in a phylogeny of the genus). Up to this point, the calls of several species remain unknown and further investigation is needed to assess whether call structure is a synapomorphy of *Chiasmocleis* or the call found in *C. mantiqueira* is a single exception (autapomorphy).

The duration of notes, intervals between them, as well as number of pulses vary between species and among populations of the same species. A summary of advertisement call parameters found by our analysis of recordings is given in table 2.

#### SPECIES ACCOUNTS

*Chiasmocleis albopunctata* (Boettger, 1885)  
Figure 13, plate 1A–B

*Engystoma albopunctatum*: (Boettger, 1885).  
*Chiasmocleis albopunctata*: (Méhely, 1904).

TABLE 2  
**Summary of acoustic data from advertisement calls of *Chiasmocleis* examined for this study**  
 A review of data from literature is available in Santana et al. (2009)

Call accession number	Taxon	Voucher	Population	Metadata		Call rate (Notes / Min)	Dominant frequency (Hz)	Note duration (sec)	Interval between notes	
				(Date / Time <sup>a</sup> / Air Temperature)					(sec)	Pulses / Note
FNJV 30715	<i>C. bassleri</i>		Ilha da Pedra, Rondônia, Brazil	12, March, 2010 20h00m – 26.4°C		2702.6 ± 87.2 (2584.0–2928.5)	0.05 ± 0.01 (0.02–0.16)	0.03 ± 0.01 (0.01–0.17)	5.4 ± 1.5 (2.0–16.0)	
FNJV 30716	<i>C. bassleri</i>		Rio Madeira, Rondônia, Brazil	February, 2011 21h25m		2697.7 ± 81.8 (2584–2756.2)	0.06 ± 0.005 (0.04–0.07)	0.07 ± 0.02 (0.02–0.15)	5.1 ± 0.4 (4–6)	
FNJV 30717	<i>C. bassleri</i>	MZUFV 8507	Aripuanã, Mato Grosso, Brazil	05, March, 2008 23h41m – 23°C		3068.9 ± 26.15 (3000–3125)	0.06 ± 0.01 (0.04–0.07)	0.08 ± 0.03 (0.04–0.30)	4.7 ± 0.6 (3–6)	
FNJV 30712	<i>C. hudsoni</i>	MPEG 28895	Rondônia, Brazil			4721.9 ± 841.9 (3962.1–8373.8)	0.12 ± 0.01 (0.11–0.18)	0.020 ± 0.002 (0.021–0.038)	6.4 ± 0.7 (6–10)	
USNM Tape 254 Cut 7	<i>C. hudsoni</i>	INPA 3353	Barro Vermelho, Rio Juruá, Amazonas, Brazil	27, October, 1991 24.4°C		4643.9 ± 24.8 (4478.9–4651.2)	0.12 ± 0.01 (0.11–0.20)	0.028 ± 0.001 (0.024–0.032)	6 ± 0.2 (6–8)	
FNJV 30713–30714	<i>C. hudsoni</i>	Two Specimens, Not Collected	Reserva Florestal Adolpho Ducke, Manaus, Amazonas, Brazil	03, March, 2005 25°C		5028.2 ± 141.4 (4823.4–5340.2)	0.07 ± 0.002 (0.07–0.1)	0.022 ± 0.004 (0.015–0.072)	5 ± 0.06 (5–6)	
FNJV 30718	<i>C. haddadi</i>	Not Collected	Mont Kotika, French Guiana		164	4146.5 ± 60.1 (4125.0–4312.5)	0.33 ± 0.04 (0.15–0.445)	0.06 ± 0.02 (0.02–0.17)	10.6 ± 4.07 (5–22)	
USNM Tape 269 Cut 14	<i>C. royi</i>	USNM 343268	Tambopata, Madre de Dios, Peru	12, December, 1990 17h30m – 23.4°C	503.2	7629.1 ± 1204.0 (5512.5–13953.5)	0.09 ± 0.05 (0.08–0.10)	0.02 ± 0.04 (0.015–0.041)	14.6 ± 0.7 (12–16)	

<sup>a</sup> Time of recording refer to data provided by the collector or by collection databases and likely conform to local times at the time of recording.

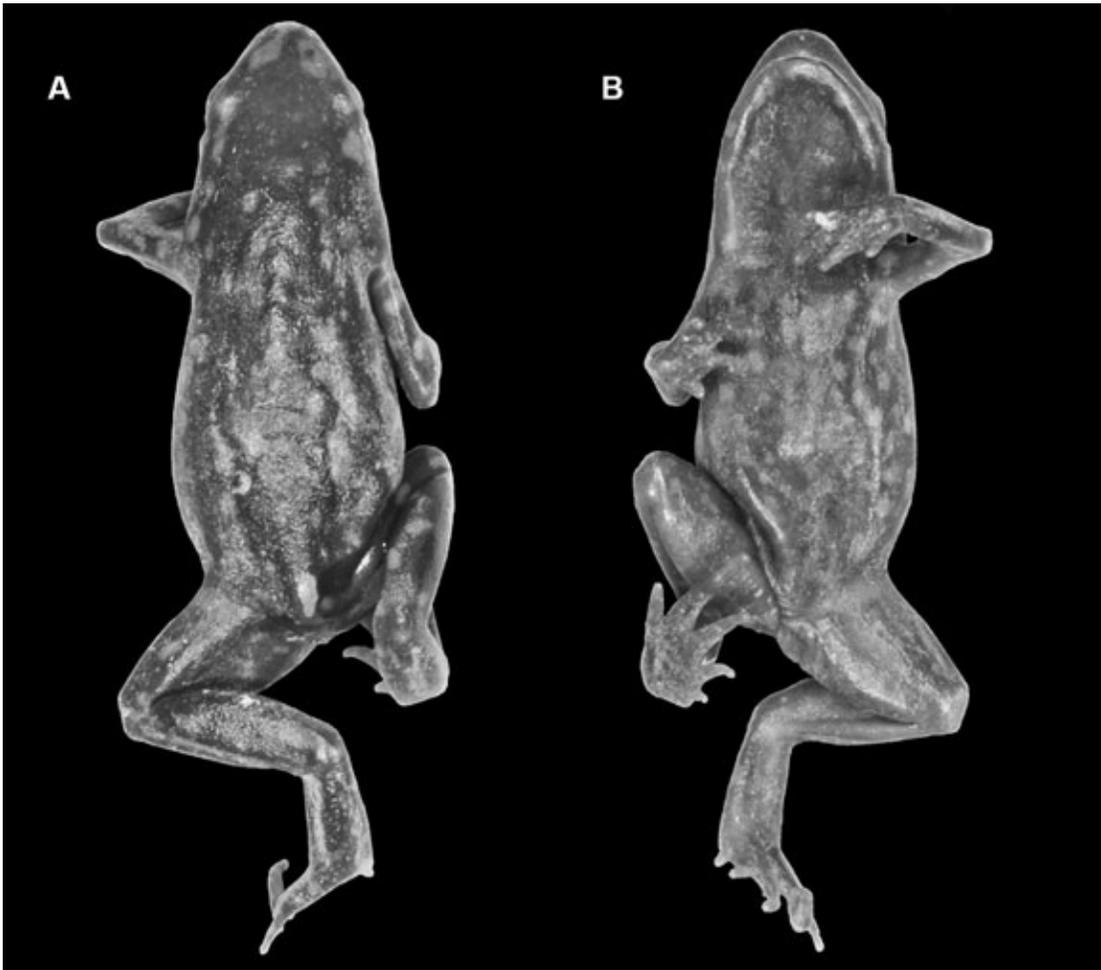


Fig. 13. Holotype of *Chiasmocleis albopunctata* from Paraguay (ZMB 10588) in (A) dorsal and (B) ventral views. SVL = 25 mm.

*Gastrophryne albopunctata*: (Stejneger, 1910).  
*Chiasmocleis bicegoi*: (Miranda-Ribeiro, 1920);  
 synonymy by Cruz et al. (1997).

**HOLOTYPE**: ZMB 10588 (fig. 13) according to Bauer et al. (1966). An adult specimen, examined from photographs; in very good state of preservation.

**TYPE LOCALITY**: Paraguay, Amer[ica]. Merid[ional].

**DIAGNOSIS**. A large species for the genus; SVL in males 23.2–32.2 mm, in females 28.2–38.0 mm (SVL data from Caramaschi and Cruz, 1997). Body ovoid and robust; snout rounded in dorsal and lateral views. Four distinctive fingers, all but FI slightly fringed

in both sexes; fingers not webbed; FI well developed with a distinct, well-developed subarticular tubercle between the proximal phalanges; subarticular tubercles present on all fingers; adpressed FI does not reach the subarticular tubercle of FII; adpressed FIV reach but do not pass distal margin of proximal tubercle of FIII; palmar tubercles protuberant, divided; relative finger lengths  $I < IV < II < III$ . Five distinctive, well-developed toes present; toes fringed in both sexes; toes free of webbing; TI with a distinct, well-developed subarticular tubercle; adpressed TI touch or barely touch subarticular tubercle of TII; adpressed TV does not touch or reaches the middle of the middle subarticular tubercle

of TIV; toes lack terminal discs; relative toe lengths I < II < V < III < IV. Males may present few, small dermal spines on hands. Femoral line absent. Dorsum usually grayish or dark brown with white spots and stains, especially on snout and dorsolateral region; venter (belly and undersurfaces of thigh) usually brownish or grayish with many white spots.

VARIATION: Number of specimens examined in detail is insufficient to present conclusive data on geographic variation. Forlani et al. (2011: fig. 1) reported significant variation in dorsal color pattern between distinct populations along the species' range, but did not comment further on it. Dorsal white spots vary in number, but are always present.

CALL AND TADPOLE: The call of *Chiasmocleis albopunctata* was described twice, first from a population in Bolivia (De la Riva et al., 1996) and then from a population in southeastern Brazil (Oliveira-Filho and Giaretta, 2006). De la Riva et al. (1996) reported a call with a fast series (584.4–907.7 notes/min) of multipulsed notes (5–8 pulses/note) with a mean dominant frequency of 4311.0–4664.4 Hz. Oliveira-Filho and Giaretta (2006) reported a slower call rate (423–501 notes/min), with more pulses per call (9) and a very similar dominant frequency (4306 Hz). Unlike Oliveira-Filho and Giaretta (2006: 67–68), we consider these differences trivial. A larger series of calls from distinct populations is needed to further assess variation in the species.

The tadpole of *Chiasmocleis albopunctata* was described and illustrated by Oliveira-Filho and Giaretta (2006). External morphology is similar to other species of *Chiasmocleis* (McDiarmid and Altig, 1999), but differs from known larvae in having wartlike ornamentations on the oral flaps.

REMARKS. Genetic distances between all specimens of *Chiasmocleis albopunctata* included in the phylogenetic analysis are given in table 3.

DISTRIBUTION: This species is common in open habitats and its distribution in the Amazon is restricted to transitional Cerrado/Amazonia. The species is widely distributed in open areas in Paraguay, Bolivia, and central and northern Brazil. Forlani et al. (2011) recently discussed the range of the species, provided an updated map, and

TABLE 3  
Uncorrected pairwise distances between 16S sequences of *Chiasmocleis albopunctata*

Locality	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 Bolivia: Santa Cruz (AS 0256)														
2 Bolivia: Santa Cruz (AS 0257)	0.002													
3 Bolivia: Santa Cruz (AS 0258)	0.000	0.002												
4 Bolivia: Santa Cruz (AS 0259)	0.000	0.002	0.000											
5 Bolivia: Santa Cruz (AS 0260)	0.002	0.000	0.002	0.002										
6 Brazil: São Paulo (C 572)	0.017	0.019	0.017	0.017	0.019									
7 Brazil: São Paulo (C 621)	0.017	0.019	0.017	0.017	0.019	0.000								
8 Brazil: São Paulo (C 565)	0.017	0.019	0.017	0.017	0.019	0.000	0.000							
9 Brazil: Minas Gerais (CHUNB 44451)	0.013	0.015	0.013	0.013	0.015	0.004	0.004	0.004						
10 Brazil: Maranhão (CHUNB 51830)	0.019	0.022	0.019	0.019	0.022	0.011	0.011	0.011	0.006					
11 Bolivia: No locality data (JMP 218)	0.004	0.006	0.004	0.004	0.006	0.017	0.017	0.017	0.013	0.015				
12 Bolivia: Santa Cruz (MJ 1212)	0.004	0.006	0.004	0.004	0.006	0.017	0.017	0.017	0.013	0.015	0.000			
13 Bolivia: Santa Cruz (MJ 1266)	0.000	0.002	0.000	0.000	0.002	0.017	0.017	0.017	0.013	0.019	0.004	0.004		
14 Bolivia: Santa Cruz (MJ 1372)	0.000	0.002	0.000	0.000	0.002	0.017	0.017	0.017	0.013	0.019	0.004	0.004	0.000	
15 Brazil: Tocantins (MPEG 29414)	0.019	0.022	0.019	0.019	0.022	0.011	0.011	0.011	0.006	0.004	0.015	0.015	0.019	0.019

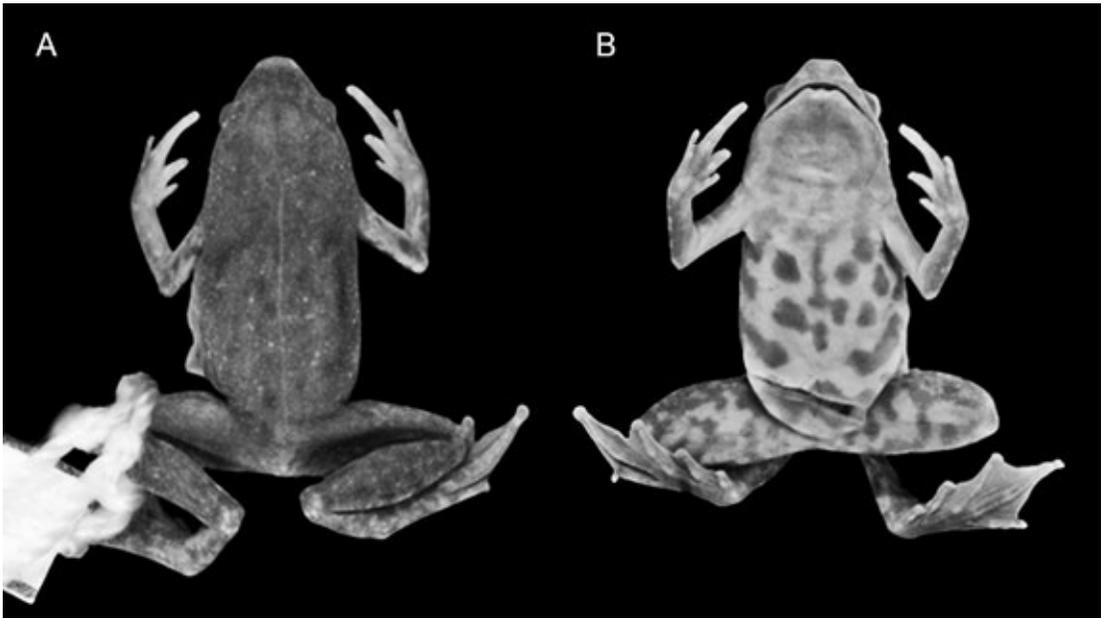


Fig. 14. Holotype of *Chiasmocleis anatipes* (KU 146035) in (A) dorsal and (B) ventral views. SVL = 19.0 mm. Photo M. Bustamante- AmphibiaWebEcuador (see Ron et al., 2014).

commented on a dubious record of a specimen from Pará, Brazil. We have no additional information on the distribution of this species and refer to Forlani et al. (2011) for data on this matter. The species is common in the Rio Tocantins basin with several records in the state of Tocantins, Brazil (Forlani et al., 2011).

*Chiasmocleis anatipes* Walker and Duellman, 1974

Figure 14, plate 1C–H

**HOLOTYPE:** KU 146035 (fig. 14); adult male, examined from photographs; in very good state of preservation.

**TYPE LOCALITY:** Santa Cecília, Província Napo, Ecuador. Coordinates not given in the original. We used the following coordinates, from Paynter (1993): 00°03'N / 76°58'W.

**DIAGNOSIS:** A medium-sized species for the genus; SVL in males 18.0–24.2 mm (Walker and Duellman, 1974; our data), sole female examined 24.9 mm. Body moderately slender; snout rounded in dorsal and lateral views. Four distinctive fingers, all but FI fringed; fingers not webbed; FI well developed with a subarticular tubercle present

between the proximal phalanges; tubercles present on all fingers; adpressed FI surpasses the subarticular tubercle of FII; adpressed FIV does not touch distal tubercle of FIII; palmar tubercles visible, divided; relative finger lengths  $I < IV < II < III$ . Five distinctive, well-developed toes present; toes fringed and extensively webbed in males (see remarks for comments on females); TI with a distinct well-developed subarticular tubercle; adpressed TI does not touch or barely reaches subarticular tubercle of TII; adpressed TV reaches the middle of the middle subarticular tubercle of TIV; TII–V with terminal discs; relative toe lengths  $I < II < V < III < IV$ . Many dermal spines on dorsum and cloacal region in both sexes; spines on chin of males present, absent in females; spines always more abundant and developed in males. Inguinal blotch and femoral line absent. Venter, belly, and under-surfaces of thigh cream colored with large dark brown irregular spots or blotches.

**VARIATION:** The number of specimens analyzed do not allow for a detailed analysis of variation. Intensity of marbling on dorsum may vary and a dorsal midline may be absent or present (pl. 1C–H). Number and shape of ventral dark spots vary among specimens

(figs. 14–15, pl. 1F, H), being almost entirely absent in the specimen depicted in plate 1F. Detailed description of color in life was given by Walker and Duellman (1974).

**CALL AND TADPOLE:** The call of *Chiasmocleis anatypes* was never described; reported to consist of a “short buzz” (Rodríguez and Duellman, 1994). A recording and a brief sonogram are available at from Ron et al. (2014), but the recording seems to be unsuitable for a detailed bioacoustic analysis. From the sonogram published by Ron et al. (2014) it is clear that the call consists of a short series of multipulsed notes.

The tadpole of *Chiasmocleis anatypes* was first described by Walker and Duellman (1974) and briefly redescribed by Duellman (1978) and Rodríguez and Duellman (1994). According to those descriptions the tadpole of *C. anatypes* presents paired spiracles located ventrolaterally and a dextral vent tube, a character state present only in pipoids (Orton, 1953; Haas, 2003). Duellman apparently noticed the mistake, but the correction never appeared in print; the following is taken from Donnelly et al. (1990): “Duellman (1978) described paired ventral spiracles in *C. anatypes* but the spiracle is single and midventral (W.E. Duellman, personal commun. to R. Altig).” Note, however, that Ronn Altig was not an author of the Donnelly et al. paper, but likely acted as a reviewer for the manuscript. We have not examined the mentioned specimens and cannot provide further clarification on the issue. Nonetheless, it is clear that the tadpoles of *C. anatypes* need to be accurately redescribed.

**REMARKS:** Walker and Duellman (1974) described *Chiasmocleis anatypes* based on a series of seven specimens, all males, collected at the type locality. The species was diagnosed based mostly on the amount of toe webbing, extending “to the bases of the terminal phalanges of each digit” (Walker and Duellman, 1974). Females were unknown at that time. Rodríguez and Duellman (1994) reported a population of *C. anatypes* from northern Peru (Iquitos region), including males and females, and reinforced in their diagnosis that “the toes are fully webbed” (Rodríguez and Duellman, 1994: 73). We examined two of the female specimens from

Iquitos (MHNSM 15697, 15700, from photographs only: fig. 15A, B) and they clearly do not show full webbing on toes. From the photos it is impossible to discern, however, whether webbing is basal or even totally absent. One of those specimens (MHNSM 15700) shows a ventral pattern very similar to that of the holotype of *C. ventrimaculata* (fig. 38) and agrees with the description given by Andersson (1945). The other specimen (MHNSM 15979), however, shows a ventral pattern intermediate between the holotype of *C. devriesi* (MHNSM 21540, not examined, but see figs. 15D, pl. 5G) and that of a specimen of *C. ventrimaculata* (MHNSM 21539: fig. 15C) from the same region. Both the holotypes of *C. ventrimaculata* and *C. devriesi* are females. We had access to a series of specimens from two localities in Napo, Ecuador, that we refer to *C. anatypes*. All have ventral color patterns very similar to examined types (holotype examined only from photographs; see fig. 14). Most of specimens of this series from Napo (LACM specimens) are juveniles and cannot be unambiguously identified, but two are adults, one male (QCAZ 51042), and one female (QCAZ 51041). The toes of the male specimen are fully webbed and it is unambiguously identified as *C. anatypes*. The female specimen is not fully webbed, but webbing can be easily seen between TII–TIII, TIII–TIV, and TIV–TV (see also pl. 1G). The two adult specimens (QCAZ 51041–51042) were also included in the genetic analyses and they have identical sequences for 16S and only two SNPs in the COI sequence. These two specimens are sister terminals in the phylogenetic analysis, and therefore we confirm that the female specimen is unambiguously assigned to *C. anatypes*, clearly showing that full webbing is not a diagnosis of the species as a whole, but solely of its males (contra Rodríguez and Duellman, 1994). In addition to the specimens from Napo, two specimens from Orellana, Ecuador, were also examined for morphology and included in the phylogenetic analyses (QCAZ 44341–44342). These are juvenile specimens (sex could not be determined), but basal webbing is present in both. They would, therefore, be assignable to *C. anatypes*. In the phylogeny, these two specimens cluster with the single representative of

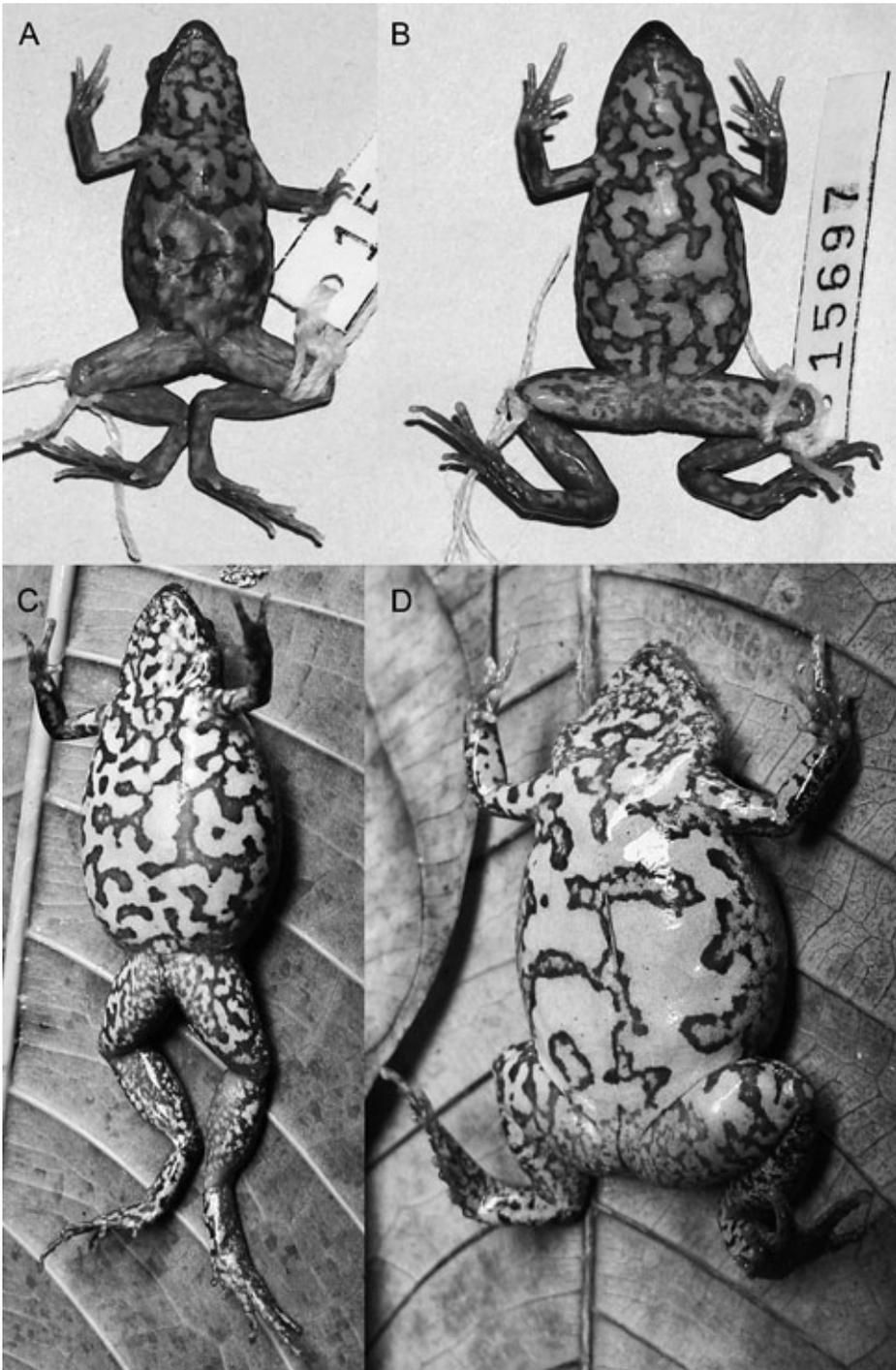


Fig. 15. Ventral views of *Chiasmocleis* specimens from the Iquitos region, Loreto, Peru. (A) Female, SVL 20.0 mm (MHNSM 157000: L. Rodriguez); (B) Female, SVL 28.8 mm (MHNSM 15697: L. Rodriguez); (A–B) Identified as *C. anatis* by Rodriguez and Duellman (1994). (C) Female, SVL 34.4 mm of *C. ventrimaculata*. (D) Female holotype of *C. devriesi* (MHNSM 21540: C. Funk). Not to scale.

TABLE 4  
Uncorrected pairwise distances between 16S sequences of *Chiasmocleis anatipes* and *C. devriesi*

Locality	1	2	3	4	5
1 <i>C. anatipes</i> – Peru: Loreto (MNCNADN 27460)					
2 <i>C. anatipes</i> – Ecuador: Orellana (QCAZ 44341)	0.006				
3 <i>C. anatipes</i> – Ecuador: Orellana (QCAZ 44342)	0.006	0.004			
4 <i>C. anatipes</i> – Ecuador: Napo (QCAZ 51041)	0.006	0.008	0.008		
5 <i>C. anatipes</i> – Ecuador: Napo (QCAZ 51042)	0.006	0.008	0.008	0.000	
6 <i>C. devriesi</i> – Peru: Loreto (MHNSM 21540)	0.004	0.002	0.002	0.006	0.006

*C. devriesi* (MHNSM 21540, from Genbank). Genetic distances in the 16S sequences between all specimens of *C. anatipes*, as well as *C. devriesi*, is given in table 4.

DISTRIBUTION (fig. 16): Known from northeastern Ecuador, at Santa Cecilia, Provincia Sucumbios (type locality), and at the neighboring provinces of Orellana and Napo. Rodríguez and Duellman (1994) reported the species from the Iquitos region, Peru, but we consider the record questionable (see Remarks). Reports of this species for the Manaus region are based on misidentified specimens (P.L.V.P., personal obs.).

*Chiasmocleis antenori* (Walker, 1973)

*Syncope antenori*: (Walker, 1973).

Figure 17, plate 2A–D

HOLOTYPE: KU 124009; adult female, examined from photographs (fig. 17). Specimen well preserved, although a very large incision was made on the belly region. Color pattern only slightly discernible on the venter; cream venter with small whiteish spots.

TYPE LOCALITY: Puerto Libre, Río Aguarico, 570 m, Provincia Napo, Ecuador.

DIAGNOSIS: A small species for the genus; SVL in females 12.4–13.6 mm, no data collected for males. Body slender to slightly robust, snout rounded in dorsal and lateral views. FI very much reduced without subarticular tubercle, tip slightly pointed; FII and FIII well developed with hardly visible subarticular tubercles on FIII, one on FII and two on FIII; FIV reduced but clearly visible, without subarticular tubercles; palmar tubercles not present; relative finger lengths I<IV<II<III. Four distinctive toes present; TI lost, TV reduced but clearly

distinguishable; toes not webbed; tip of toes III–IV rounded with terminal discs present. Relative toe lengths II<V<III<IV. No dermal spines. No femoral stripe present. Venter (belly and undersurfaces of thighs) beige with small light spots.

VARIATION: Despite adding several specimens of *Chiasmocleis antenori* into the genetic analysis, the number of specimens analyzed for morphological characters is fairly limited, restricted to three paratypes and a few specimens collected by P.L.V.P. in Serra do Divisor, Acre, Brazil. The specimens from Acre show variable amount of white spots on dorsum. Color of the iris color varies from golden to orange and red (see pl. 2A–D).

CALL AND TADPOLE: Call is unknown. *Chiasmocleis antenori* has endotrophic larvae developing inside terrestrial bromeliads (Krügel and Richter, 1995). The tadpole was described in detail, including several developmental stages, by Krügel and Richter (1995).

REMARKS: This species is similar in color pattern and external morphology to *Chiasmocleis magna*, from which it differs in having an external tympanum visible (not visible in *C. magna*: Moravec and Kohler, 2007), by its smaller size (maximum recorded SVL 13.6 mm, versus 18.3 mm in *C. magna*), and in having seven presacral vertebrae (eight in *C. magna*).

Phylogenetic analysis found two clades within *Chiasmocleis antenori*, one with three specimens from Ecuador (Orellana and Pastaza) and the other with all of the syntopic samples from Brazil and a sample labeled as *C. carvalhoi* (as *Syncope carvalhoi* in de Sá et al., 2012) from San Martín, Peru. Genetic distances between specimens of *C. antenori* vary from 0%–11.4%, with as much as 9.1% distance between syntopic specimens from Acre, Brazil. Genetic distances between

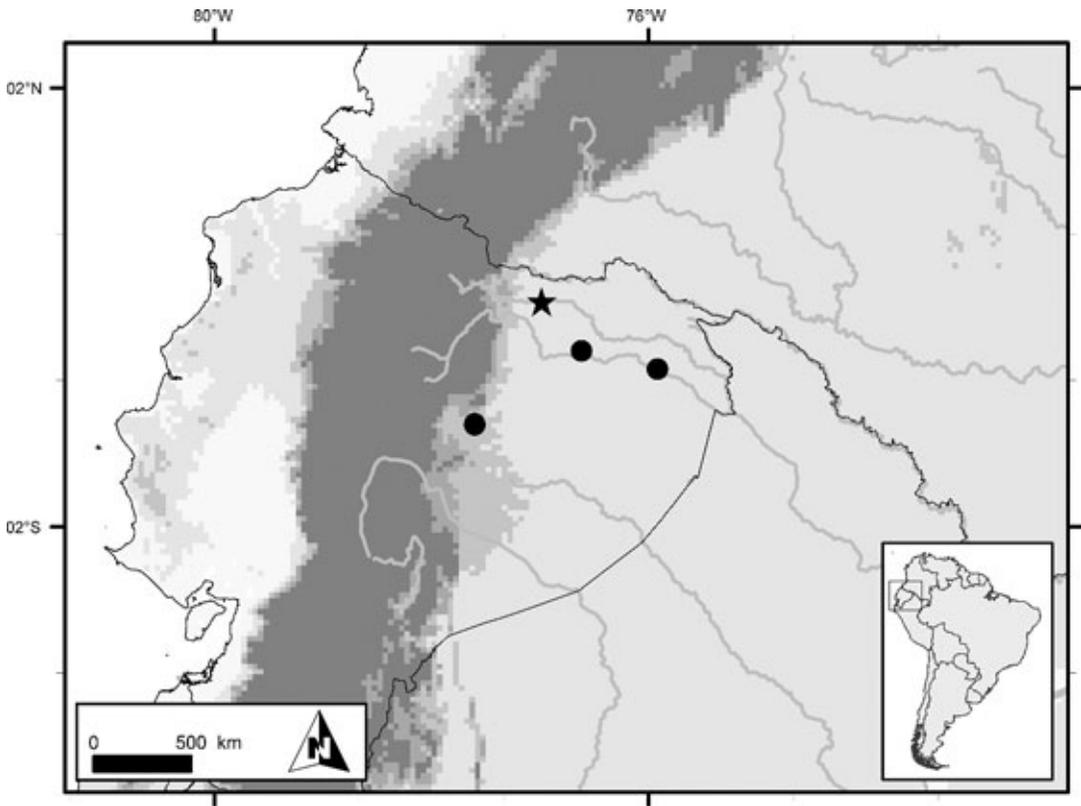


Fig. 16. Distribution of *Chiasmocleis anatipes*. Star = type locality; circle = examined specimens.

all specimens of *C. antenori* included in the phylogenetic analysis are given in table 5.

Unfortunately, we have not examined the Ecuadorian or the Peruvian specimens, making any taxonomic conclusions about the status of these populations unattainable at present.

**DISTRIBUTION** (fig. 18): Ecuador (Napo, Orellana, and Pastaza), and western Brazil (Acre). Coloma et al. (2004) gave a wider distribution and included a large portion of northeastern Peru. A specimen identified as *Chiasmocleis carvalhoi* from San Martín, Peru (de Sá et al., 2012), was found inside our samples of *C. antenori* and is regarded as a confirmed record of the species for Peru.

*Chiasmocleis avilapiresae* Peloso and Sturaro, 2008

Figures 19–20, plates 2E–H, 3

**HOLOTYPE** (fig. 19): MPEG 23299; adult female, in very good state of preservation.

**TYPE LOCALITY:** Estação Científica do Programa Pró-Biodiversidade da Amazônia (PPBio) (aprox. 01°59'S, 51°39'W), Floresta Nacional Caxiuanã, Municipality of Portel, state of Pará, Brazil.

**DIAGNOSIS:** A large species for the genus; SVL in males 22.2–28.0 mm ( $N = 28$ ), in females 23.6–37.8 mm ( $N = 82$ ). Body ovoid and robust; head triangular, snout rounded in dorsal and lateral views. Four distinctive fingers, all but FI fringed in males, less fringed in females; fingers not webbed; FI well developed, with a distinct, well-developed subarticular tubercle present between the proximal phalanges; distinctly visible subarticular tubercles present on all fingers; adpressed FI reaches or surpasses the subarticular tubercle of FII; adpressed FIV does not reach or barely reaches distal tubercle of FIII; palmar tubercles protuberant, divided; relative finger lengths  $I < II < IV < III$ . Five distinctive and well-developed toes present;

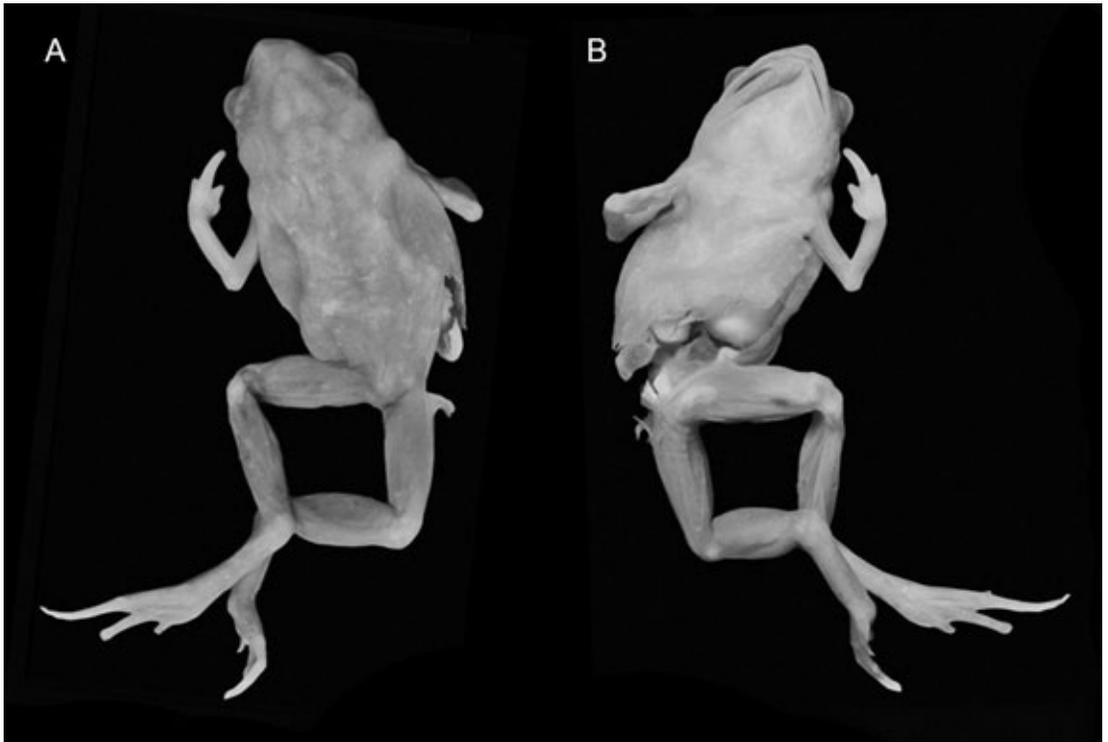


Fig. 17. Holotype of *Chiasmocleis antenori* (KU 23299) in (A) dorsal, and (B) ventral views. SVL = 12.3 mm. Photo M. Bustamante- AmphibiaWebEcuador (see Ron et al. 2013).

toes fringed, less distinct in females; toes usually extensively webbed in males, only basally webbed in females; TI with a distinct, well-developed subarticular tubercle; adpressed TI does not touch or barely touches subarticular tubercle of TII; adpressed TV does not touch or reaches only to the middle of subarticular tubercle of TIV; TII–IV with terminal discs, usually more developed in females, but also present in males; relative toe lengths  $I < II < V < III < IV$ . Males with many dermal spines on fingers and toes; both sexes may show dermal spines, but they are much more numerous and developed in males; males with many spines on anterior portion of chin, absent in females. Inguinal blotch usually absent. Femoral line present. Color pattern given in the variation section.

**VARIATION:** Ventral (throat and belly) color pattern can vary from almost entirely uniform (cream, white, brown, or black) to densely reticulated (fig. 20; see also Peloso and Sturaro, 2008). A single specimen, out of 206 examined, showed strong dark vermiculations

on the venter (fig. 20D). Western populations (west of the state of Amazonas, Mato Grosso and Rondônia) have, in general, fewer spots on the ventral region than those from eastern populations (eastern Amazonas and all Pará). Additionally, the specimens from Aripuanã, Mato Grosso, are slightly smaller than those of remaining populations. A dorsal midline is usually absent, but is present in some specimens, commonly in contact with the femoral line posteriorly (pl. 3D).

The dorsum of *Chiasmocleis avilapiresae* shows a great degree of color variation in life (see pls. 2E–H and 3). In general individuals have a dark, grayish dorsum (pl. 2E, G) while the dorsal surfaces of limbs are usually brightly colored—yellow, orange, or red. In several specimens the flanks are reddish (pls. 2G, 3G) and in a few specimens the reddish pattern extends through most of the dorsum of specimens (pls. 2H, 3H). Some specimens from Mato Grosso (pl. 3E) and Rondônia (pl. 3A, C, F) have golden yellow or orangeish dorsums.

TABLE 5  
Uncorrected pairwise distances between 16S sequences of *Chiasmocleis antenori*

Locality	1	2	3	4	5
1 Brazil: Acre (MTR 28350)					
2 Brazil: Acre (MTR 28373)	0.080				
3 Brazil: Acre (MTR 28416)	0.080	0.005			
4 Ecuador: Pastaza: (QCAZ 38506)	0.065	0.092	0.087		
5 Ecuador: Orellana: (QCAZ 38719)	0.072	0.095	0.090	0.007	
6 <sup>a</sup> Peru: San Martín (KU 215720)	0.065	0.087	0.087	0.067	0.065

<sup>a</sup> This specimen is labeled as *Chiasmocleis "carvalhoi"* in the phylogenetic tree (figs. 6, 7). Sequences for it derive from Genbank and we did not examine the specimen for phenotypic characters.

The snout may be whitish or follow the general dorsal pattern. For additional notes on variation, see Peloso and Sturaro (2008).

**CALL AND TADPOLES:** The advertisement call of *Chiasmocleis avilapiresae* was recently described by Barros et al. (2010). The call consists of a fast series (295.4 notes / min) of multipulsed notes (7–18 pulses/note). Mean

note duration was  $98.0 \pm 9.8$  ms, and mean interval between notes  $111.1 \pm 0.1$  ms. Mean dominant frequency of was  $3368.2 \pm 73.2$  kHz. Tadpoles are unknown.

**DISTRIBUTION** (fig. 21): Brazil, widespread in rainforest areas south of the Rio Amazonas and west of the Rio Tocantins. Known in the states of Acre, Amazonas, Rondônia, Mato

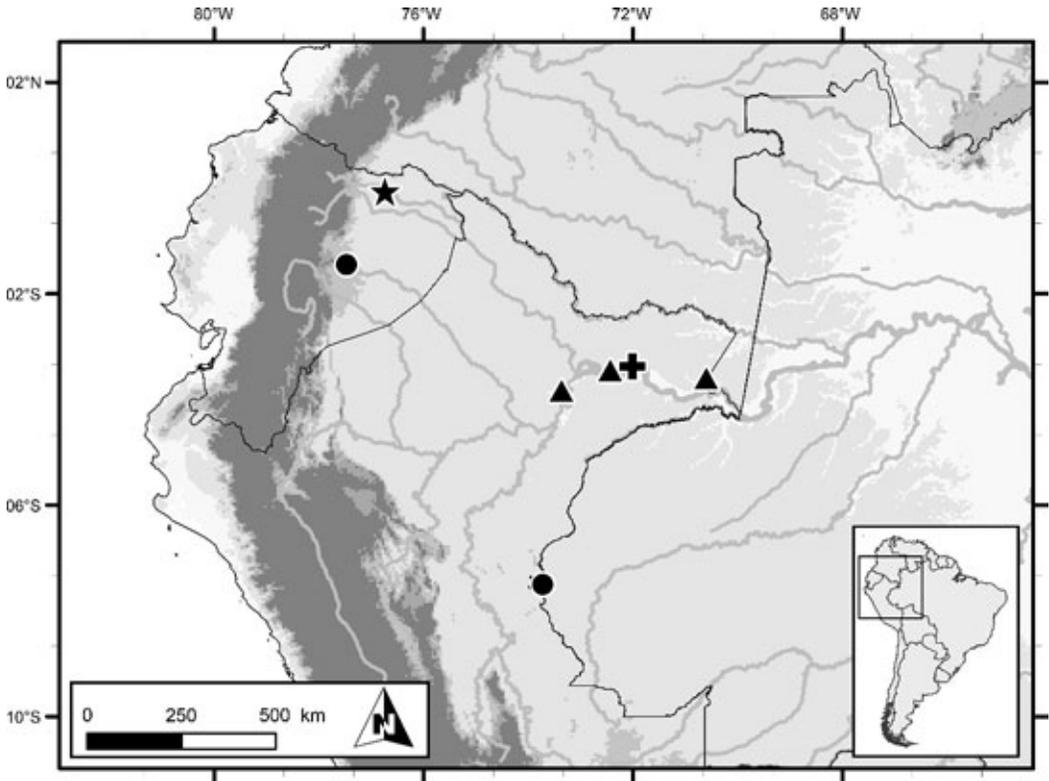


Fig. 18. Distribution of *Chiasmocleis antenori* and *C. carvalhoi*. Star = type locality of *C. antenori*. Circles = examined specimens of *C. antenori*; cross = type locality of *C. carvalhoi* (see text for details). triangles = examined specimens of *C. carvalhoi*.

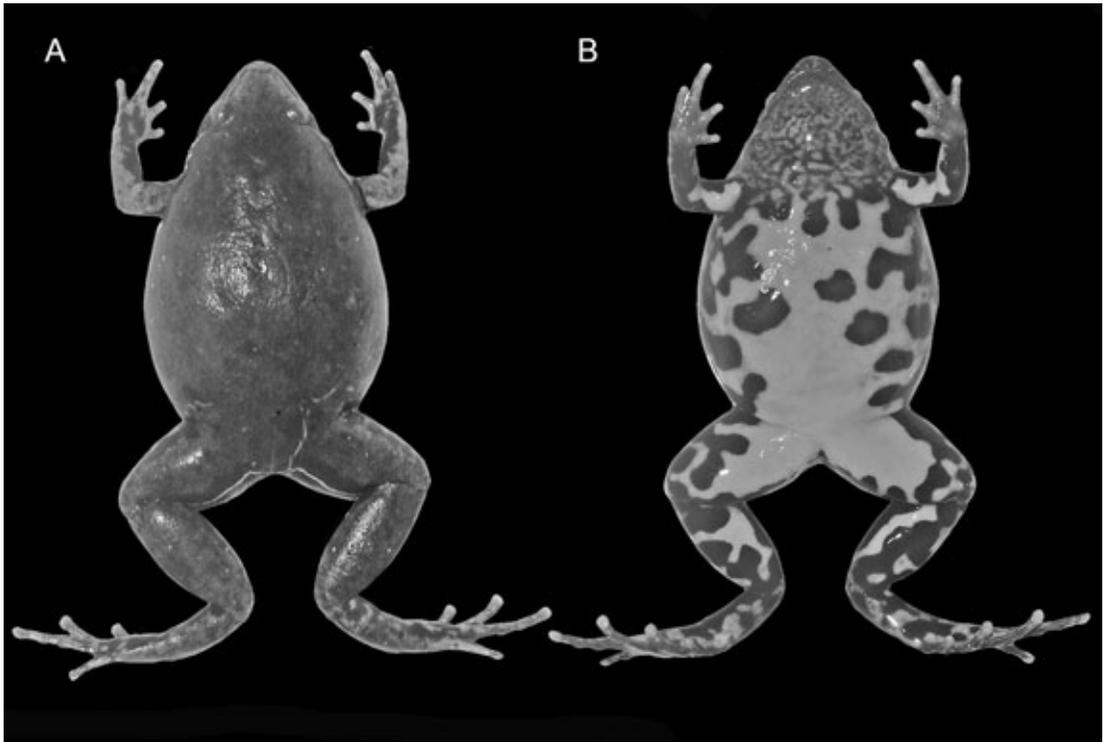


Fig. 19. Holotype of *Chiasmocleis avilapiresae* (MPEG 23299) in (A) dorsal, and (B) ventral views. SVL = 34.9 mm.

Grosso, and Pará. We are unaware of records of this species in adjacent Bolivia and Peru.

**REMARKS:** In the list of paratypes given by Peloso and Sturaro (2008: 42), collection numbers from MNRJ were mistyped. The publication reads MNRJ 14231–80, but the correct collection numbers for that lot are MNRJ 44231–44280. We thank M. Targino for pointing out this mistake to P.L.V.P.

Genetic distances between all specimens of *C. avilapiresae* included in the phylogenetic analysis are given in table 6.

*Chiasmocleis bassleri* Dunn, 1949

Figures 22–23, plate 4

*Syncope bassleri*: (de Sá et al., 2012).

**HOLOTYPE** (fig. 22): AMNH 42699; poorly preserved, portions of limbs destroyed, and color completely faded.

**TYPE LOCALITY:** Type locality given by Dunn (1949) as “Río Utoquinia to Río Tapiche, Peru (near the Brazilian border).”

Peloso and Sturaro (2008) considered the type locality of *Chiasmocleis bassleri* as “vague.” Despite that, Rodrigues et al. (2011) gave an “approximate” coordinate for the type locality of *C. bassleri*, based on unclear arguments. In an attempt to solve this issue, we revisited Harvey Bassler’s field notes (deposited at the AMNH) and several hydrographic maps of eastern Peru.

From the field notes, it seems that the holotype (AMNH 42699) was collected at the region where the Río Utoquinia would meet the Río Tapiche. However, from the maps we analyzed, it is not clear whether there is a water connection between the rivers. It is possible that minor waterways are present, thus providing a connection point between the rivers, but it is also possible that the only connection is by land. Regardless, this putative connection must be somewhere near the borders of departamentos of Ucayali and Loreto (both in Peru) and the state of Acre (Brazil)—this region being roughly 120 km east of the city of Contamana, Peru, and

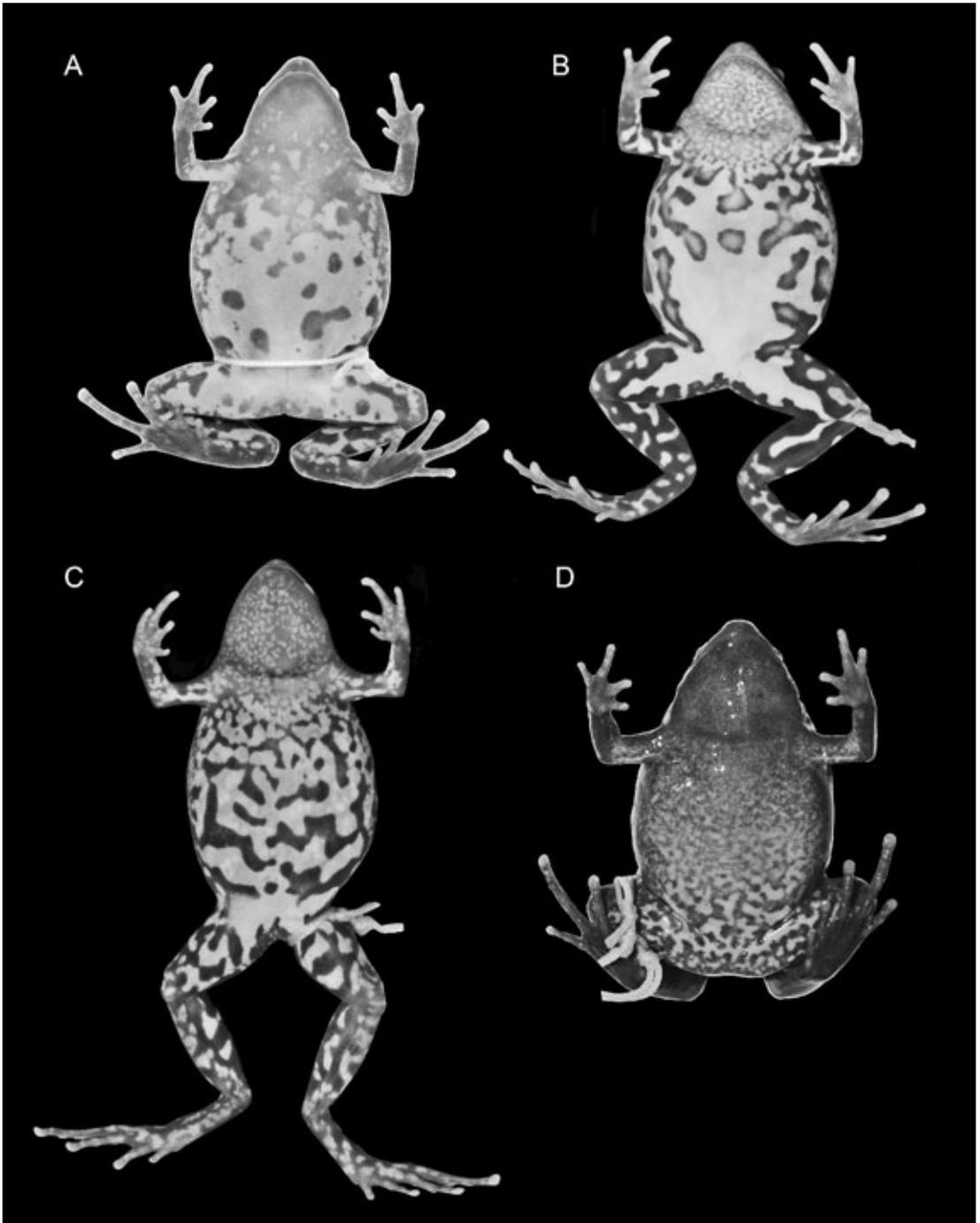


Fig. 20. Variation of ventral color pattern in *Chiasmocleis avilapiresae*. (A) Aripuanã, Mato Grosso, Brazil (UFMT 7124). (B–C) Floresta Nacional Caxiuanã, Pará, Brazil (MPEG 23315, and MPEG 23317, respectively, both paratypes). (D) Resex do Alto Juruá, Rio Juruá, Amazonas, Brazil (INPA 17259, paratype).

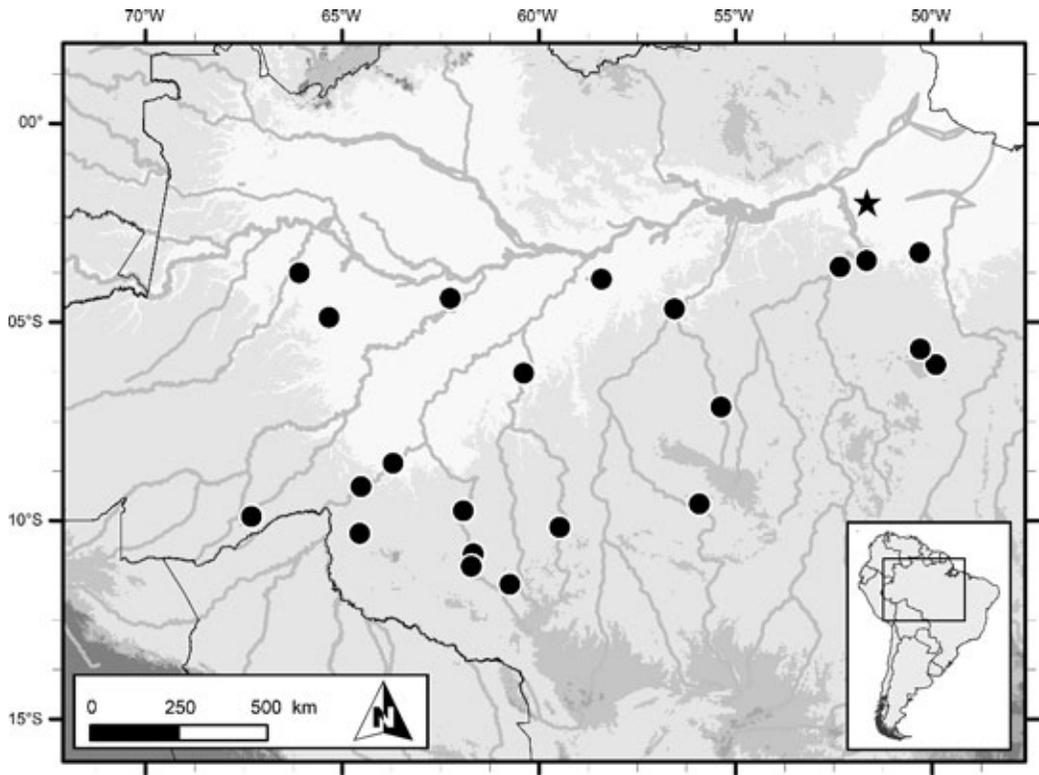


Fig. 21. Distribution of *Chiasmocleis avilapiresae*. Star = type locality, solid circle = examined specimens.

140 km west of Cruzeiro do Sul, Brazil. Dunn (1949) likely used the position of the Utoquinia and Tapiche to draw his map (Dunn, 1949: fig. 4). The locality shown in Rodrigues et al.'s map (Rodrigues et al., 2011: fig. 2) is, however, clearly far from the one presented by Dunn (1949: fig. 4) and certainly does not correspond to any point along the course of either the Río Tapiche or the Río Utoquinia. Coordinates given by Rodrigues et al. (2011) are ca. 450 km southeast of the locality where the distance between the Utoquinia and the Tapiche is at its minimum. After examination of maps and satellite images, we use the following coordinates as a proxy for the type locality of *C. bassleri* (07°32'30"S / 73°59'35"W: see fig. 25).<sup>9</sup>

**DIAGNOSIS:** A medium-sized species for the genus; SVL in males 19.2–22.1 mm ( $N =$

11), in females 21.2–28.8 mm ( $N = 20$ ). Body ovoid to elongate; head triangular; snout rounded in dorsal and lateral views. Four distinctive fingers; FI may be reduced in some specimens, but always clearly visible; tubercle on FI may be absent or present; subarticular tubercles present on all remaining fingers; adpressed FI never extends beyond the distal margin of subarticular tubercle of FII; adpressed FIV does not reach distal tubercle of FIII; palmar tubercles present, not divided; relative finger lengths  $I < II < IV < III$ . Five distinctive toes present, first may be much reduced; toes may be slightly fringed; toes not webbed; TI lacks tubercle; adpressed TI does not touch subarticular tubercle of TII; adpressed TV does not touch or reaches only to the middle of the middle subarticular tubercle of TIV (touches in the holotype); TII–IV with terminal discs, usually more developed in females, but also present in males; relative toe lengths  $I < II < V < III < IV$ . An inguinal blotch, variable in

<sup>9</sup>Coordinates taken from direct observation of satellite images in the interactive software Google Earth, release 6.2.2 for Mac (Google Inc., 2012).

TABLE 6  
Uncorrected pairwise distances between 16S sequences of *Chiasmocleis avilapiresae*

Locality	1	2	3	4
1 Brazil: Pará (MPEG 18571)				
2 Brazil: Pará (MPEG 22787)	0.007			
3 Brazil: Amazonas (MPEG 27768)	0.007	0.007		
4 Brazil: Amazonas (MPEG 27769)	0.009	0.009	0.002	
5 Brazil: Pará (MPEG 28121)	0.007	0.000	0.007	0.009

shape, is always present. There is usually a marked contrast in color pattern between the dorsum and the venter that can be delimited by a split stripe.

VARIATION: We have found a high degree of variation in external characters of *Chiasmocleis bassleri*, especially in color pattern.

The original description reports a “belly white with five large circular black spots” (Dunn 1949: 9). We have examined sympatric specimens that vary in spot counts, from just a couple to several (over five) well-defined

circular spots (see, for example, fig. 23A). Some specimens do not have circular spots, but show elongated stains or, sometimes, a reticulated pattern (fig. 23F; this pattern is common in some specimens from Amazonas and Mato Grosso, Brazil, but is also present in some specimens from Ecuador).

Chest and throat usually consist of dark vermiculations against a light background (fig. 23A, B), but in some specimens the throat is uniformly dark colored, especially in males (fig. 23C, E–F). Few specimens show a



Fig. 22. Holotype of *Chiasmocleis bassleri* (AMNH 42699) in (A) dorsal, and (B) ventral views. SVL = 18.5 mm.

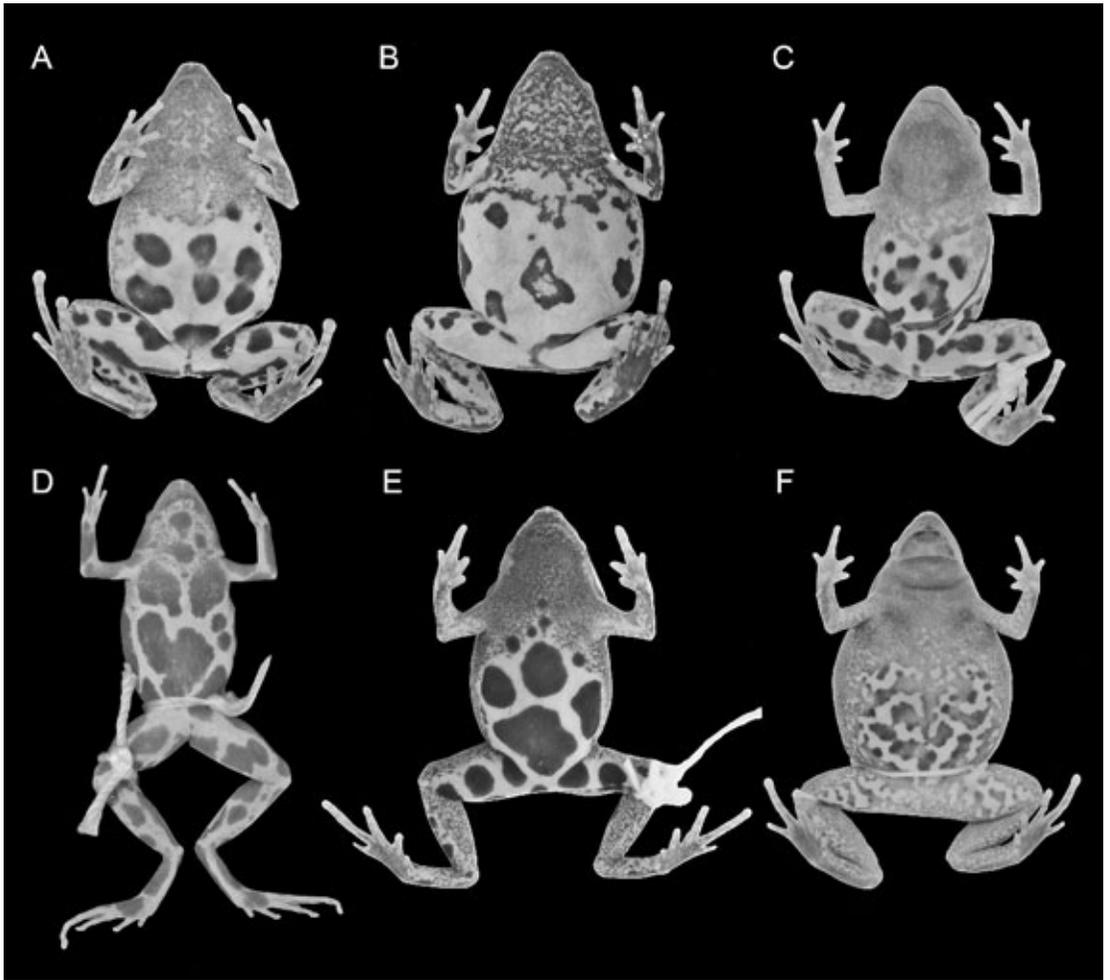


Fig. 23. Variation of ventral color pattern in *Chiasmocleis bassleri*. (A) Parque Nacional da Serra do Divisor, Acre, Brazil (UFAC-RB 1611). (B) Via Tarapacá, Leticia, Amazonas, Colombia (ICN 50249). (C) Porto Walter, Acre, Brazil (OMNH 34829). (D) Rio Curanja, Balta, Ucayali, Peru (KU 197036). (E) Floresta Nacional do Pau-Rosa, Rio Paraconi, Maués, Amazonas, Brazil (MPEG 27766). (F) Aripuanã, Mato Grosso, Brazil (UFMT 7136). Not to scale.

uniform pattern (whitish with black spots or stains) over the entire ventral surface (fig. 23D); this pattern is common in specimens from Peru. There is also extensive variation in length ratios between fingers and toes, especially length of FI, FIII/FIV ratio, length of TI, and TIV/TV ratio.

Color in life varies strikingly among specimens (pl. 4), but data are limited and prevent a detailed analysis of geographic variation. Dorsum can have a uniform color pattern, varying between tones of black, dark brown, purple, reddish, and pink. Several specimens

may show blotches on the dorsum, usually lighter than the dorsum and varying between shades of red, orange, green, yellow, and pinkish. A specimen from Vaupés, Colombia, shows a bizarre dorsal pattern, with the left side dark reddish brown and the right side light cream with dark brown mottling (pl. 4G).

Most specimens show a well-marked differentiation between dorsal and ventral pattern, evidenced by a split stripe. In some specimens, the stripe is wide and black, extending from the posterior corner of the eye to the inguinal region (pl. 4B). The split

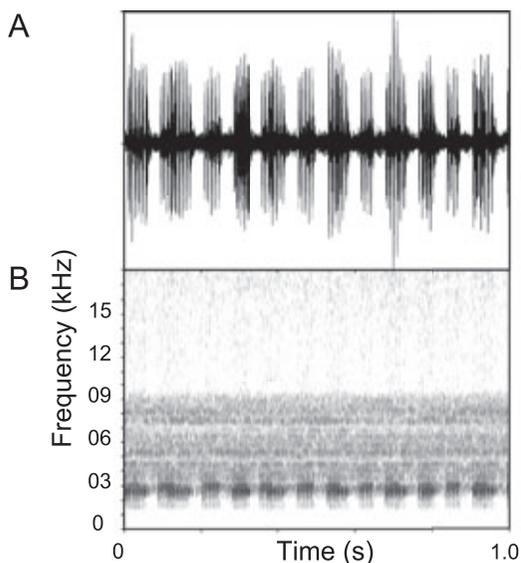


Fig. 24. Advertisement call of *Chiasmocleis bassleri*. (A) Oscillogram and (B) spectrogram of two consecutive multipulsed notes. Recorded at Ilha da Pedra, Rondônia, Brazil; recorded on 12 March 2010 at 26.4° C air temperature (no voucher specimen; recorded by A. Lima, recording number FNJV 30715).

is, however, absent in a few specimens (pl. 4D), but we found no clear pattern of geographical variation in this character. Sympatric specimens can show the absence or presence of the split (e.g., in Porto Walter, Acre, Brazil).

**CALL AND TADPOLES:** The advertisement call of *C. bassleri* has been previously described by Santana et al. (2009). The description here is based on the combined calls of three specimens from different populations, including a reanalysis of Santana et al.'s (2009) recording. Acoustic parameters for each individual call are listed in table 2. The call is composed of a fast, repetitive series of multipulsed notes (mean  $5.2 \pm 1.2$  pulses per note, 2–16,  $N = 764$ ), emitted at a rate of 568.2 notes/min. Mean note duration  $53.3 \pm 11.1$  ms (15.0–163.0,  $N = 786$ ) and mean interval between notes  $49.0 \pm 26.3$  ms (11.0–302.0,  $N = 783$ ). Mean dominant frequency was  $2747.0 \pm 145.8$  Hz (2584–3125,  $N = 786$ ). Pulse duration was  $6.9 \pm 1.6$  ms (4.0–11.0,  $N = 368$ ). A call from Rio Madeira, Rondônia, Brazil, is illustrated in figure 24.

Tadpoles are unknown.

**REMARKS:** The phylogenetic position of *Chiasmocleis bassleri*, given our results, is strikingly distinct from that found by de Sá et al. (2012), represented in his analysis by a single specimen from Loreto, Peru, also included here. We have included several samples of *C. bassleri* from throughout its distribution in the phylogenetic analysis, and although two well-supported clades were found, we did not find any phenotypic evidence to diagnose the clades as separate taxa. The levels of genetic distance within *C. bassleri* are generally low (0–6.8%). Genetic distances between all specimens of *C. bassleri* included in the phylogenetic analysis are given in table 7.

**DISTRIBUTION** (fig. 25): Distributed in western Brazil (Acre, Amazonas, Mato Grosso, Pará, and Rondônia), eastern and northern Peru, southwest Colombia, and Ecuador. Icochea et al. (2004) presented a much wider distribution for the species in Peru, and mention the occurrence of the species in Bolivia.

*Chiasmocleis carvalhoi* (Nelson, 1975)

Figures 26, plate 5A–F

*Syncope carvalhoi*: (Nelson, 1975).

**HOLOTYPE:** MZUSP 36429; an adult male, in very good state of preservation.

**TYPE LOCALITY:** Río Ampí-Yacú (= Ampiyacú), Estirón, Loreto, Peru. No coordinates given in the original. We found at least three different localities in Loreto named Estirón. Because the original explicitly states the specimens were collected along in the Río Ampiyacú river, we assume the type locality refers to Estirón del Cuzco, for which we provide the following approximate coordinates 03°22'S / 72°00'W.<sup>10</sup>

**DIAGNOSIS:** A small species for the genus; SVL of the male holotype 9.4 mm (Nelson, 1975) and 10.9–11.7 mm in the two female paratypes ( $N = 2$ ; Nelson, 1975). Body relatively robust, snout round in dorsal and lateral views. Tympanum is usually not visible. FII–IV much reduced; FI not visible; FIII well developed with subarticular tubercle

<sup>10</sup>Coordinates taken from direct observation of satellite images in the interactive software Google Earth, release 6.2.2 for Mac (Google Inc., 2012).

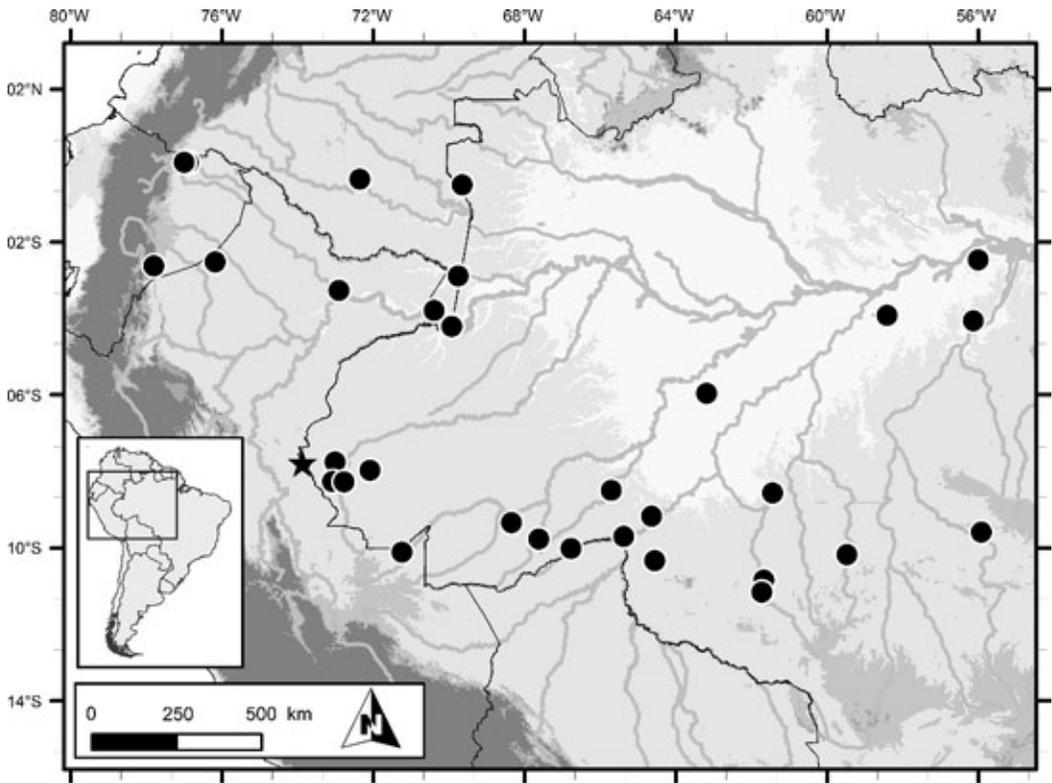


Fig. 25. Distribution of *Chiasmocleis bassleri*. Star = type locality, solid circle = examined specimens.

barely visible, tip of FIII pointed; FIV almost not distinguishable; fingers slightly fringed; palmar tubercles not present; relative finger lengths  $IV < II < III$ . Four toes visible, TI not visible; toes only slightly fringed, not webbed; tips of toes slightly expanded, especially in TIII–TIV, tips of TIII–TIV pointed. Relative toe lengths  $II < V < III < IV$ . Dermal spines absent. No femoral stripe present. In preservative, venter (belly and undersurfaces of thigh) beige with white spots or blotches. In life, dorsum brownish or orangish with darker (brown to dark brown blotches); cream-colored canthal stripe that may end at the shoulder region or extend all the way to the inguinal regions, becoming wider and more irregularly defined posteriorly; belly with large anastomosing cream-colored large blotches (brown area forms an irregularly reticulated pattern).

**VARIATION:** Number of specimens examined in detail ( $N = 7$ ) is much reduced to present data on variation, but we provide a

few remarks on color in life, based on examination of photographs (pl. 5A–F). Two syntopic species, from Umarital, Rio Ampiyacú region, Loreto, Peru (~ 30 km from the type locality) vary markedly in dorsal pattern; JMP 1499 (pl. 5C–D) has a more uniform dorsum (brown) and a canthal stripe extending to the shoulder, while JMP 1451 (pl. 5A–B) has dark brown blotches over a brown dorsum and the stripe extends all the way to the inguinal region. Because these two specimens were examined only from photographs, we do not know whether this difference is due to sex or ontogeny or by chance.

**CALL AND TADPOLE:** Call is unknown. Nelson (1975) reported large unpigmented ovarian eggs for the species suggesting endothermic larvae (e.g., direct development or nonfeeding tadpoles that develop in water or moist soil). Nothing more is known about its reproductive behavior and, at this point, there is no evidence that a tadpole phase even exists.

TABLE 7  
Uncorrected pairwise distances between 16S sequences of *Chiasmocleis bassleri*

Locality	1	2	3	4	5	6	7	8	9	10	11	12
1 Brazil: Amazonas (ALP 14940)												
2 Peru: Loreto (MHNSM 21576)	0.039											
3 Peru: Loreto (MNCNADN 27334)	0.042	0.007										
4 Colombia: Vaupés (MNCNADN 47166)	0.044	0.033	0.037									
5 Colombia: Vaupés (MNCNADN 47167)	0.042	0.031	0.035	0.037								
6 Brazil: Amazonas (MEPEG 27764)	0.035	0.029	0.029	0.026	0.035							
7 Brazil: Amazonas (MEPEG 27765)	0.035	0.029	0.029	0.026	0.035	0.000						
8 Brazil: Pará (MEPEG 28326)	0.041	0.044	0.046	0.041	0.048	0.017	0.017					
9 Brazil: Acre (MTR 28345)	0.041	0.004	0.007	0.033	0.035	0.029	0.029	0.044				
10 Brazil: Acre (MTR 28391)	0.039	0.002	0.006	0.031	0.033	0.028	0.028	0.042	0.002			
11 Brazil: Acre (MTR 28402)	0.039	0.002	0.006	0.031	0.033	0.028	0.028	0.042	0.002	0.000		
12 Ecuador: Orellana (QCAZ 17515)	0.041	0.007	0.007	0.031	0.035	0.029	0.029	0.044	0.007	0.006	0.006	
13 Ecuador: Orellana (QCAZ 24565)	0.042	0.006	0.002	0.035	0.037	0.031	0.031	0.046	0.006	0.004	0.004	0.006

DISTRIBUTION (fig. 18): Known from east Loreto, Peru, and west Colombia (see Acosta-Galvis, 2000, for the Colombian record). Ortega-Andrade and Valencia (2010) provided a record of *Chiasmocleis tridactyla* (as *Syncope tridactyla*) for Lorocachi, Pastaza, Ecuador. We have not examined these specimens, but from the figures in their publication it seems those specimens should be tentatively identified as *C. carvalhoi* based on reduced number of fingers (three) and toes (four) and ventral color pattern (large white blotches) versus small spots in *C. tridactyla*. The only ambiguous character is the presence of a tympanum (barely visible) in both specimens reported by the authors (QCAZ 9577, 9520; tympanum absent in the types of *C. carvalhoi*).

REMARKS: Two specimens from Rio Nanay, Loreto, Peru, included in de Sá et al. (2012) as *Syncope* sp. were found nested within our *Chiasmocleis carvalhoi* clade. These specimens show 0.0% genetic distance from specimen MNCNADN 27392, collected near Iquitos, Loreto, Peru. Pending examination of a larger series of *C. carvalhoi* and the vouchers of the specimens sequenced by de Sá et al. (2012), we include those specimens in *C. carvalhoi*. Genetic distances between all specimens of *C. carvalhoi* included in the phylogenetic analysis are given in table 8.

*Chiasmocleis devriesi* Funk and Cannatella,  
2009

Figure 15D, plate 5G–H

HOLOTYPE (figs. 15D, pl. 5G–H): MHNSM 21540; examined only from the photographs in the original publication (Funk and Cannatella, 2009).

TYPE LOCALITY: Amazon Conservatory for Tropical Studies (ACTS) Field Station, 65 km NE of Iquitos, 1 km N of the Río Napo, and 1.3 km SSE of the ACTS Field Station (3°15'34"S, 72°54'10"W), Departamento Loreto, Peru.

DIAGNOSIS: Since we have not examined the sole specimen of *Chiasmocleis devriesi* (except from the photographs published in the original description), readers should refer to the original description (Funk and Cannatella, 2009) for a diagnosis of the species.

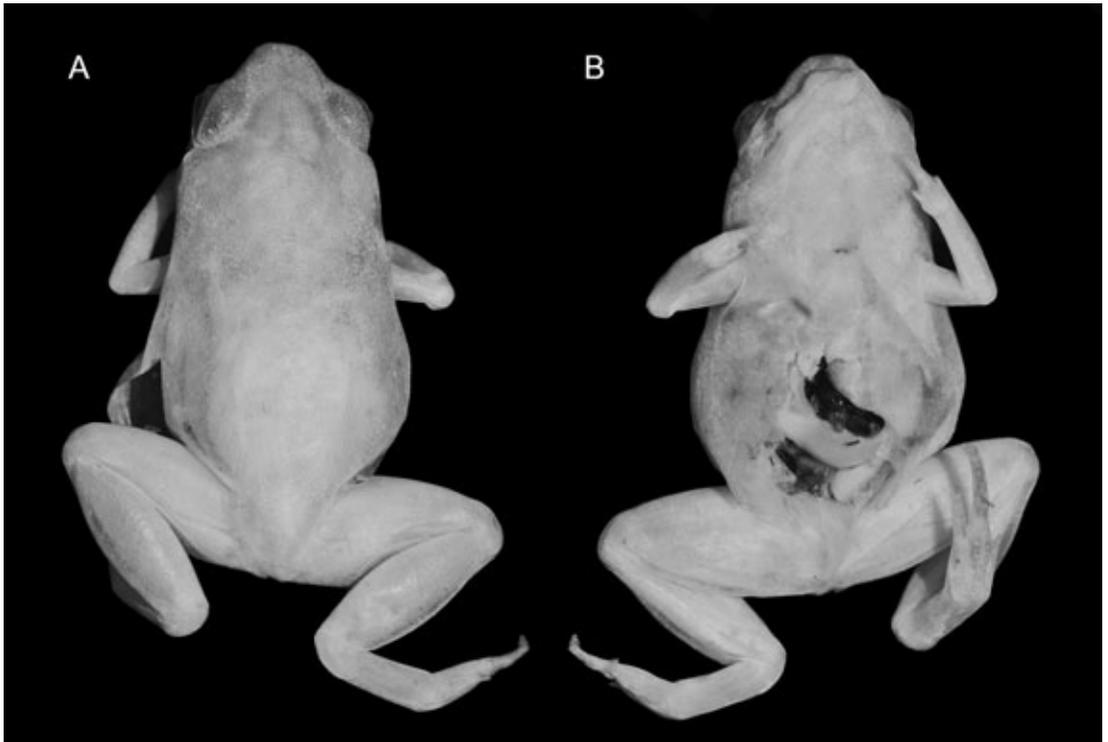


Fig. 26. Paratype of *Chiasmocleis carvalhoi* (AMNH 88065) from Estirón, Rio Ampí-Yacú (type locality) in (A) dorsal, and (B) ventral views. SVL = 11.1.

**VARIATION:** Known only from the female holotype.

**CALL AND TADPOLES:** Call and tadpoles are unknown.

**REMARKS:** Funk and Cannatella (2009) described the species on the basis of a single female specimen, which renders any evaluation of morphological variation unattainable. Additionally, many diagnostic characters in *Chiasmocleis* are present only or are more pronounced in males (i.e., webbing, fringes of digits, and dermal spines). The ventral pattern of the holotype (fig. 15D, pl. 5H) is similar to some specimens of *C. anatis*, *C.*

*avilapiresae*, and *C. ventrimaculata* and cannot be unambiguously set apart from those on the basis of this character. *Chiasmocleis devriesi* differs from all species by its larger size (SVL 42.4 mm in *C. devriesi*; rivaled only by *C. avilapiresae*, with a maximum recorded SVL, according to our sample, of 37.8 mm) and its moderately pointed snout. The absence of a femoral line further differentiates *C. devriesi* from *C. avilapiresae* (femoral line present). From our phylogenetic analysis, it seems clear that the relationship of the sole specimen of *C. devriesi* lies with populations assigned to *C. anatis* and not with *C.*

TABLE 8  
Uncorrected pairwise distances between 16S sequences of *Chiasmocleis carvalhoi*

Locality	1	2	3
1 Peru: Loreto (MNCNADN 26570)			
2 Peru: Loreto (MNCNADN 26618)	0.000		
3 Peru: Loreto (MNCNADN 27392)	0.011	0.011	
4 Peru: Loreto (MNCNADN 27503)	0.007	0.007	0.007

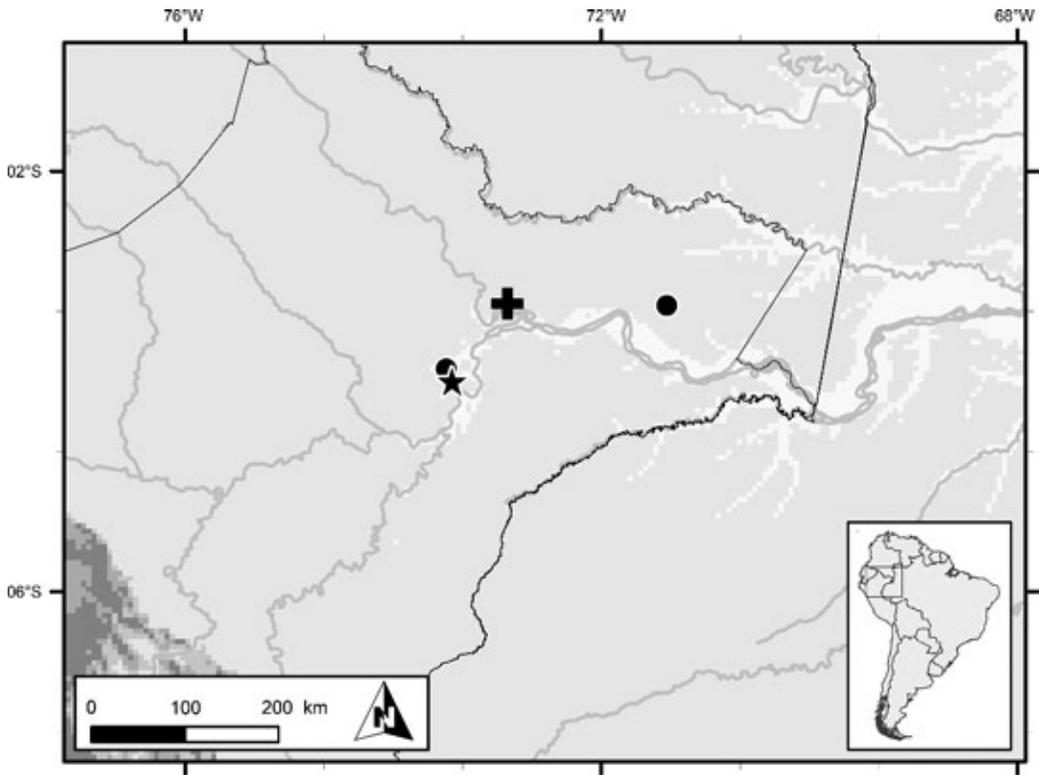


Fig. 27. Distribution of *Chiasmocleis devriesi* and *C. magna*. Star = type locality of *C. magna*; solid circle = examined specimens of *C. magna*; cross = type locality of *C. devriesi*.

*avilapiresae* or *C. ventrimaculata* (fig. 8). The holotype is related to a couple of specimens from Orellana, Ecuador, forming a well-supported sister clade to another three specimens, unambiguously assigned to *C. anatypes*. Because the specimens from Orellana are juveniles they cannot be unambiguously assigned to *C. anatypes* nor do they fit precisely the diagnosis of *C. devriesi*. For the purpose of our phylogenetic analysis, we have labeled the specimens from Orellana as *C. anatypes*, but they clustered with the holotype of *C. devriesi*. There is zero genetic distance in the 16S between the sole specimen of *C. devriesi* and each of the specimens of *C. anatypes* included in our analysis (see table 4). We have examined only the holotype of *C. devriesi* from photographs published in the original description (Funk and Cannatella, 2009; also reproduced here as fig. 15D and pl. 5H). Due to the lack of evidence supporting or falsifying the status of *C. devriesi* as a valid taxon, we chose not to

synonymize it with *C. anatypes*, but highlight that this issue deserves close attention in the future. For the phylogenetic analysis, for example, only the 16S fragment is present for the holotype of *C. devriesi* (which shows no genetic differentiation among populations; table 4). Given the phylogenetic proximity of these populations, it would be wise to expand character sampling for these taxa in the future.

**DISTRIBUTION** (fig. 27): Known only from the type locality.

*Chiasmocleis hudsoni* Parker, 1940  
 Figures 28–29, plate 6

*Chiasmocleis jimi*: (Caramaschi and Cruz, 2001).  
 Holotype, MNRJ 14549, figure 28C–D, **new synonymy**.

*Syncope jimi*: (de Sá et al., 2012).

*Syncope hudsoni*: (de Sá et al., 2012).

**HOLOTYPE** (fig. 28A–B): BM 1939.1.1.3; adult male (according to the original publi-

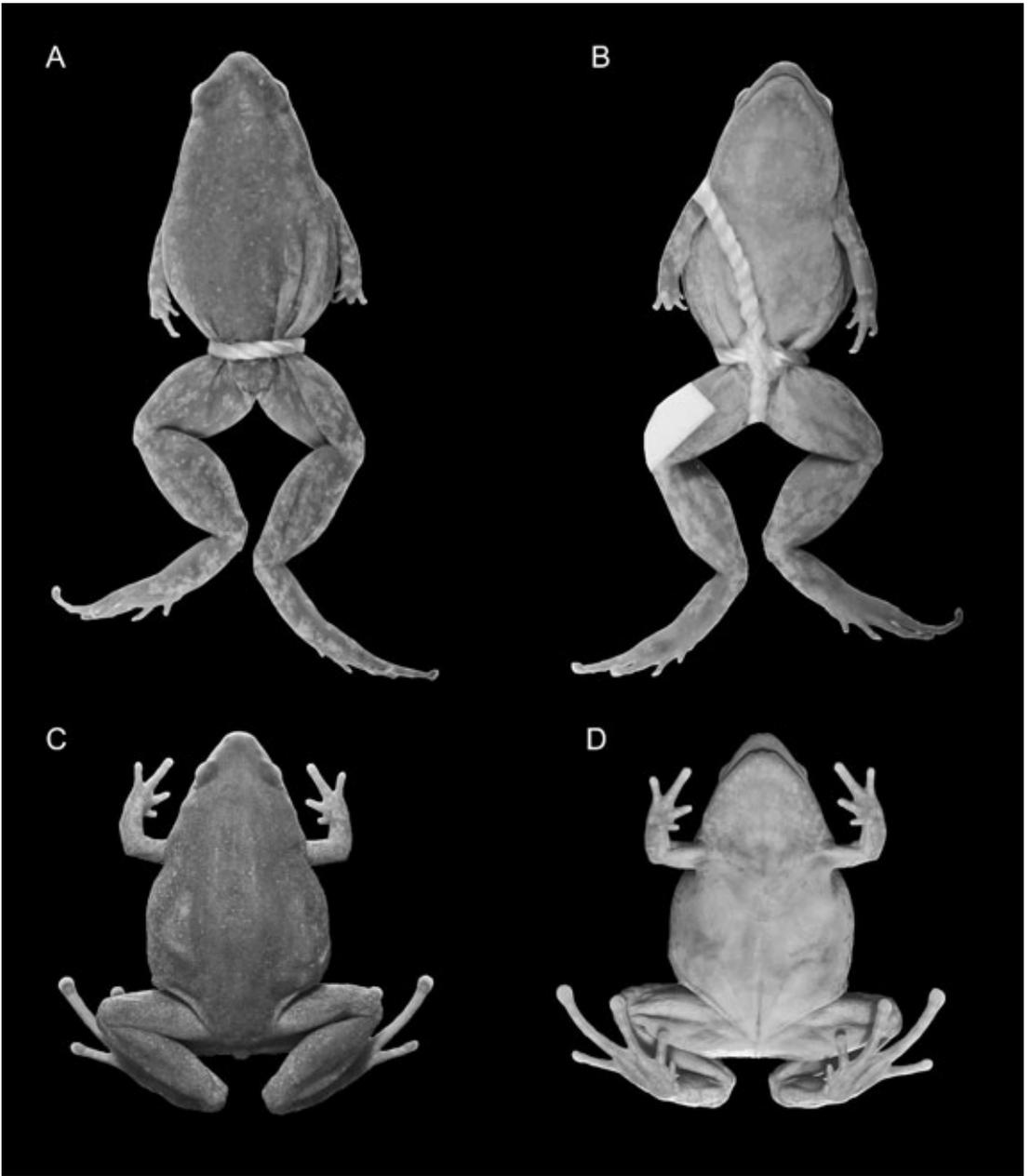


Fig. 28. Holotypes of (A–B) *Chiasmocleis hudsoni* (BMNH 1939.1.1.3: photos: G. Bitencourt), in dorsal and ventral views respectively; and (C–D) *Chiasmocleis jimi* (MNRJ 15459: photos I. Nunes), in dorsal and ventral views respectively.

cation: Parker, 1940) in very good state of preservation (examined from photographs).

**TYPE LOCALITY:** The type locality was given in the original publication as New River, British Guiana—no geographic coor-

dinates given (Parker, 1940). Frost (1985), based on a personal communication from M.S. Hoogmoed, reported that the locality is in SW Suriname. The New River, however, is in an area of territorial dispute (the New

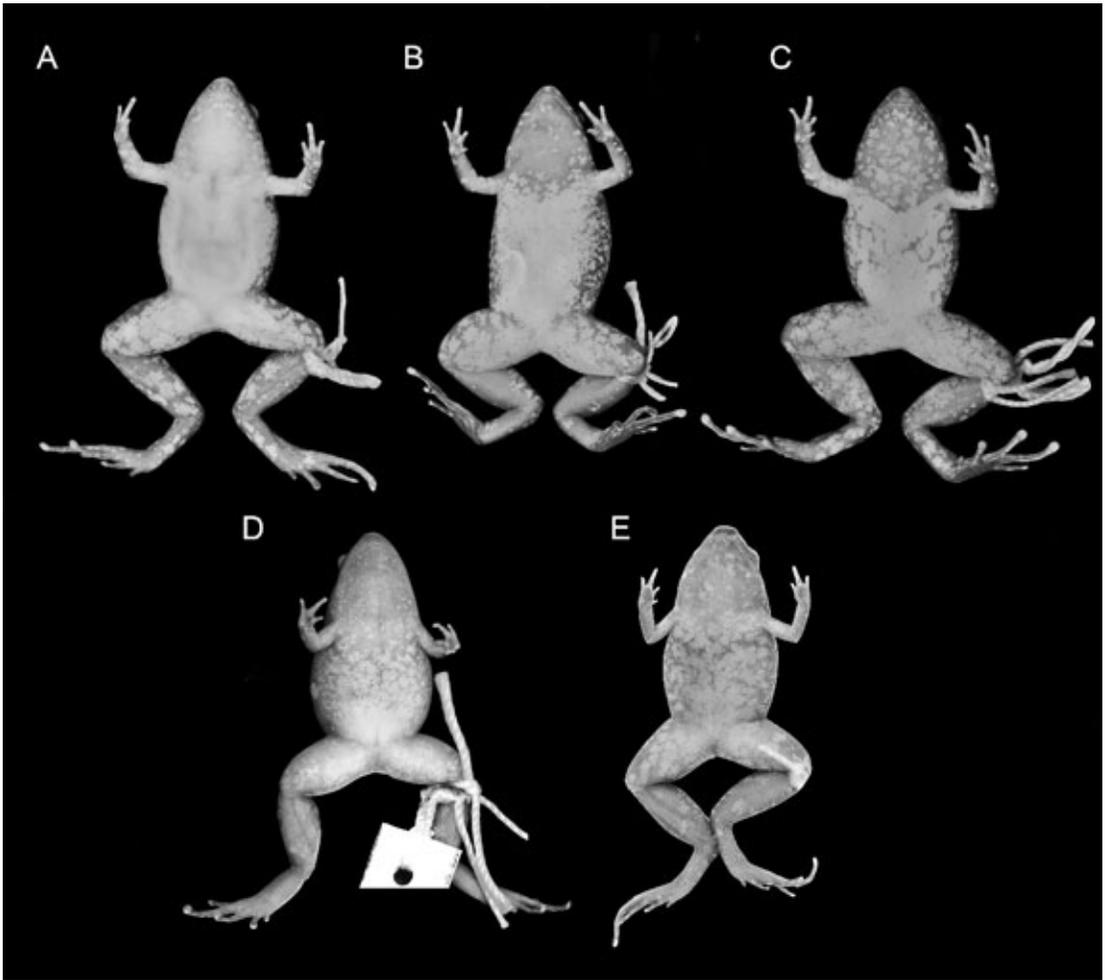


Fig. 29. Variation of ventral color pattern in *Chiasmocleis hudsoni*. (A–C) Parque Nacional da Amazônia, Itaituba, Pará, Brazil (MPEG 18479, MPEG 18511, and MPEG 18554, respectively). (D) Berbice River 18 mi SW Kwakwani, Guyana (AMNH 166437). (E) Estação Ecológica Grão Pará, Alenquer, Pará, Brazil (CN 1881).

River Triangle) between the Co-operative Republic of Guyana (former British Guiana) and the Republic of Suriname (former Dutch Guiana). The issue is unresolved at present, but historical documents indicate the British Guiana should have precedence over the territory (Donovan, 2003). Although irrelevant to the species distribution, based on the interpretation of ancient and current resolutions (see Donovan, 2003, for a historical perspective), we consider the type locality to be New River, Co-operative Republic of Guyana.

**DIAGNOSIS:** A small species for the genus; SVL in males 14.1–23.4 mm ( $N = 20$ ); in

females 17.2–28.4 mm ( $N = 40$ ). Body ovoid, robust; head much narrower than body, snout rounded in dorsal and lateral views. Four distinctive fingers; all but FI slightly fringed, less fringed in females; fingers not webbed; FI reduced with a rounded or slightly pointed tip, lacking subarticular tubercle; finger tips of FII–IV rounded, tips of FII and III swollen, may present discs; adpressed FI does not reach subarticular tubercle of FII; adpressed FIV reach middle or distal margin of distal tubercle on FIII; palmar tubercles protuberant, divided; relative finger lengths  $I < IV < III < II$ . Five distinctive

toes, first slightly reduced; toes slightly fringed, less distinct in females; toes not webbed in either sex; TI usually without subarticular tubercle (limited to a swelling in some specimens but also may be only slightly visible in few others); adpressed TI does not touch subarticular tubercle of TII; adpressed TV does not touch or reaches only up to the middle of the subarticular tubercle of TIV; TII–IV with terminal discs; relative toe lengths  $I < II < V < III < IV$ . Some males with few well-developed dermal spines on chin. Color pattern given in under the variation section.

**VARIATION:** Ventral pattern (throat, chest, and belly) varies between almost completely unpigmented (fig. 29A) to having different amounts of mottling that can extend from the anterior portion of the chin to the hind limbs (fig. 29B–E). Throat is usually more heavily pigmented in males, sometimes completely pigmented. Ventral pigmentation varies from brown to grayish. Most of the variation in this species is with coloration. The rostral region may vary from a completely uniform brown (fig. 29E) to showing a conspicuous pigmentation of orange (fig. 29B, D), cream (fig. 29C, F), or whitish (fig. 29A) extending from the snout to above the eye. In some specimens the colored pigmentation can extend posteriorly to the eye to the inguinal region (fig. 29B–D) becoming more (fig. 29C) or less (fig. 29B, D) faint posteriorly. Dorsal surface of the hind limbs and sometimes the posterior surface of the dorsum may show a variable amount of minute spots of mottling that vary in color among white, golden, purple, and bright orange (fig. 29).

Some males possess few, but large, dermal spines on the chin.

**CALL AND TADPOLE:** The advertisement call and a sporadic call of *Chiasmocleis hudsoni* were described by Rodrigues et al. (2008). The advertisement calls described here (fig. 30) are based on the combined calls of three specimens each belonging to a different population, including one specimen also analyzed by Rodrigues et al. (2008). The call is composed of a repetitive series of multipulsed notes. An introductory note was observed in three calls, with more pulses per note (mean  $17.3 \pm 2.6$  pulses per note, 15–20,

$N = 3$ ) and longer duration ( $427.3 \pm 81.6$  ms, 360.0–518,  $N = 3$ ) than subsequent call notes. The introductory note had a mean dominant frequency of  $4249.2 \pm 263.1$  Hz (3962.1–4478.9,  $N = 3$ ), and pulse duration was  $7.6 \pm 1.8$  ms (4.0–11.0,  $N = 50$ ). The chorus notes are shorter (mean  $5.6 \pm 0.6$  pulses per note, 5–10,  $N = 1108$ ), emitted at a rate of 498.0 notes/min. Mean note duration was  $95.4 \pm 2.2$  ms (7.0–19.8,  $N = 1108$ ) and mean interval between notes was  $24.8 \pm 3.9$  ms (15.0–72.0,  $N = 1106$ ). Mean dominant frequency was  $4845.2 \pm 379.0$  Hz (3962.1–6373.8,  $N = 1108$ ), and the pulse duration was  $7.2 \pm 2.9$  ms (2.0–14.0,  $N = 357$ ). Harmonics could be observed in one call, one with a lower frequency than the dominant frequency ( $2584.0 \pm 114.3$  Hz, 1894.9–2756.2,  $N = 51$ ) and two with frequencies higher than the dominant.

The sporadic call is also composed of a repetitive series of multipulsed notes (mean  $11.8 \pm 4.7$  pulses per note, 7–30,  $N = 107$ ) emitted at a rate of 294.5 notes/minute. Mean note duration was  $158.3 \pm 27.8$  ms (121.0–292.0,  $N = 108$ ) and mean interval between notes was  $32.3 \pm 9.0$  ms (22.0–78.0,  $N = 105$ ). Mean dominant frequency was  $4726.1 \pm 928.5$  Hz (3789.8–6373.8,  $N = 108$ ), and the pulse duration was  $6.8 \pm 1.5$  ms (3.0–12.0,  $N = 282$ ).

The tadpole of *Chiasmocleis hudsoni* was described by Rodrigues et al. (2008) and the external morphology is similar to that of other tadpoles described in the genus. The absence of an arc shape around the interocular region, a light line between the eyes, and a flagellated tail tip differentiate the tadpole of *C. hudsoni* from those of *C. royi* (Schlüter and Salas, 1991).

**REMARKS:** The status of *Chiasmocleis jimi* Caramaschi and Cruz, 2001. Caramaschi and Cruz (2001) described *C. jimi* based on a series of preserved specimens from Humaitá, Amazonas, and Parque Nacional da Amazônia, Pará, both in Brazil. Caramaschi and Cruz (2001) likely did not examine any specimens of *C. hudsoni*—no list of specimens examined is provided—and therefore based their comparisons solely on the description by Parker (1940). The authors considered *C. jimi* to differ from *C. hudsoni* by the swollen tips of fingers III and IV and toes II–V and

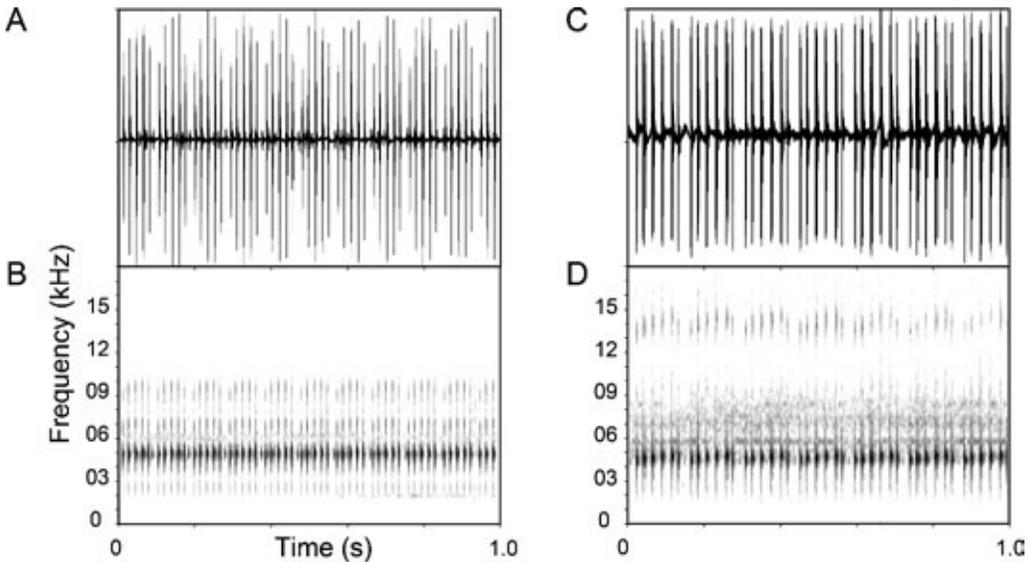


Fig. 30. Advertisement call of *Chiasmocleis hudsoni*. (A) Oscillogram and (B) spectrogram of 11 consecutive notes (last one incomplete) emitted by calling male from Reserva Ducke, Amazonas, Brazil (not collected; recorded by M. Menin; recording number FNJV 30713). (C) Oscillogram and (D) spectrogram of seven consecutive notes emitted by a calling male from Barro Vermelho, Rio Juruá, Amazonas, Brazil; recorded on 27 October 1991, at 24.4° C air temperature (INPA 3353; recorded by C. Gascon; recording number USNM tape 254, cut 7).

by color pattern (Caramaschi and Cruz, 2001: 6). We find that additional discussion of both of these characters is warranted.

**Swollen digital tips.** Caramaschi and Cruz (2001) argue that “tips of all digits not expanded in the other [*Chiasmocleis anatis*, *C. bassleri*, *C. hudsoni*, *C. shudikarensis*, *C. ventrimaculata*] species,” but this statement is inaccurate. The original descriptions of *C. anatis*, *C. bassleri*, *C. hudsoni*, *C. shudikarensis* all report discs on at least some digits (Parker, 1940; Dunn, 1949; Walker and Duellman, 1974). This was confirmed by our observations of larger series of specimens, including a large series of specimens of both *C. hudsoni* and *C. jimi* (including both holotypes). We found no differences in the morphology of hands and feet of the types of *C. hudsoni* and *C. jimi* (fig. 28).

**Color in life.** The description of the color in life of *Chiasmocleis jimi* was based on field notes by Celso Morato de Carvalho (Caramaschi and Cruz 2001: 7). Considering only the original descriptions of both species (Parker 1940; Caramaschi and Cruz, 2001), they can be distinguished only by (1)

“dorsum purple brown with some fine lighter stipplings white forming an indefinite light zone from the tip of snout above canthus rostralis, along the edge of upper eyelid... flanks and limbs with large areas of light pink stippling” in *C. hudsoni* (Parker, 1940), while “dorsum of body, arms and legs uniform reddish brown with minute irregular white dots” in *C. jimi* (Caramaschi and Cruz, 2001); (2) “under surfaces white with brown stippling on gular region” in *C. hudsoni* (Parker, 1940), while “ventrolateral region and venter cream, heavily grayish spotted” in *C. jimi* (Caramaschi and Cruz, 2001). Apparently the specimen described by Carvalho lacks the “light zone on the snout” (hereinafter, white snout). Color pattern is a variable character and examination of recently collected specimens assigned to both *C. jimi* or *C. hudsoni* showed a great degree of variation in the color of live specimens and that the snout may or not be white (pl. 6). The ventrolateral and ventral regions of a *C. jimi* population from Parque Nacional do Amazonas, Pará, Brazil (where some of the paratypes were collected), are brownish and

TABLE 9  
Uncorrected pairwise distances between 16S sequences of *Chiasmocleis hudsoni*

Locality	1	2	3	4	5	6	7	8
1 Brazil: Roraima (AMNHFS 20082)								
2 Colombia: Amazonas (JMP 2286)	0.019							
4 Brazil: Pará (MPEG 23206)	0.006	0.021						
5 Brazil: Pará (MPEG 18545)	0.021	0.024	0.026					
6 Brazil: Pará (MPEG 18547)	0.019	0.023	0.024	0.002				
7 Brazil: Pará (MPEG 23283)	0.009	0.024	0.011	0.026	0.024			
8 Brazil: Pará (MPEG 23285)	0.009	0.024	0.011	0.026	0.024	0.000		
9 Brazil: Pará (MPEG 24527)	0.011	0.026	0.013	0.028	0.026	0.002	0.002	
10 Brazil: Amazonas (MPEG 27763)	0.015	0.030	0.017	0.032	0.030	0.006	0.006	0.008

not grayish (M.S. Hoogmoed, field notes), therefore agreeing with the description of *C. hudsoni* by Parker (1940).

**Advertisement calls.** The call of *Chiasmocleis hudsoni* was described by Rodrigues et al. (2008) from Reserva Florestal Adolpho Ducke, in Manaus, state of Amazonas, Brazil. The authors recognized two call types for *C. hudsoni*, and named them an *advertisement call* and a *sporadic call* (Rodrigues et al., 2008). We had access to two calls of *Chiasmocleis* from Rondônia, Brazil, that are referable to *C. jimi* (based on the original description of the species). In the recording, we detect both the advertisement and sporadic call types and all acoustic parameters are very similar to those of *C. hudsoni* from Amazonas (Rodrigues et al., 2008). Unfortunately, no calls of topotypes of *C. jimi* are available.

**Phylogenetic evidence.** The phylogenetic analysis did not recover monophyly of specimens identified (by the collectors) as *Chiasmocleis jimi* or *C. hudsoni*. Despite uncertainty about the relationships among populations, together all specimens form a well-corroborated clade, sister to *C. haddadi*, sp. nov. The amount of uncorrected genetic distance between populations is considerably variable (0%–11.4%), with up to 2.3% distance between syntopic species. Genetic distance values between all specimens of *C. hudsoni* included in the phylogenetic analysis are given in table 9.

**THE STATUS OF *CHIASMOCLEIS JIMI*:** Given the above discussion and character analyses, we feel that the present evidence is overwhelming and our conclusion is that *C.*

*jimi* Caramaschi and Cruz, 2001, must be regarded a junior synonym of *C. hudsoni* Parker, 1940.

**DISTRIBUTION** (fig. 31): Most of the Amazon basin in Brazil, west of the Rio Tocantins. Although we have not examined specimens from several populations in the Guiana Shield countries, there are known records of the species in Colombia, Venezuela, Guyana, Surinam, and French Guiana (Barrio-Amorós and Schargel, 2003; Rodrigues et al., 2004a). Possibly present in Peru, although we are unaware of any records.

*Chiasmocleis magnova* Moravec and Köhler, 2007

Figures 32, plate 6G–H

*Syncope magnova*: (de Sá et al., 2012).

**HOLOTYPE:** MHNSM 19993, not examined.

**TYPE LOCALITY:** The type locality is 31 km on the road from Iquitos to Nauta, ca. 40 km straight SW of Iquitos (04°00' S, 73°26' W), Departamento Loreto, Peru.

**DIAGNOSIS:** A small species for the genus; SVL in females 16.7–18.3 mm (Moravec and Köhler, 2007). We had no access to male specimens. Body slender, snout rounded in dorsal and lateral views. FI much reduced without subarticular tubercle, tip slightly pointed; FII and FIII well developed with hardly visible subarticular tubercles, one on FII and two on FIII; FIV reduced, without subarticular tubercles; fingers only slightly fringed according to Moravec and Köhler (2007), not fringed in the sole specimen examined (AMNH 103550); palmar tubercles not present; relative finger lengths I<IV<II<III.

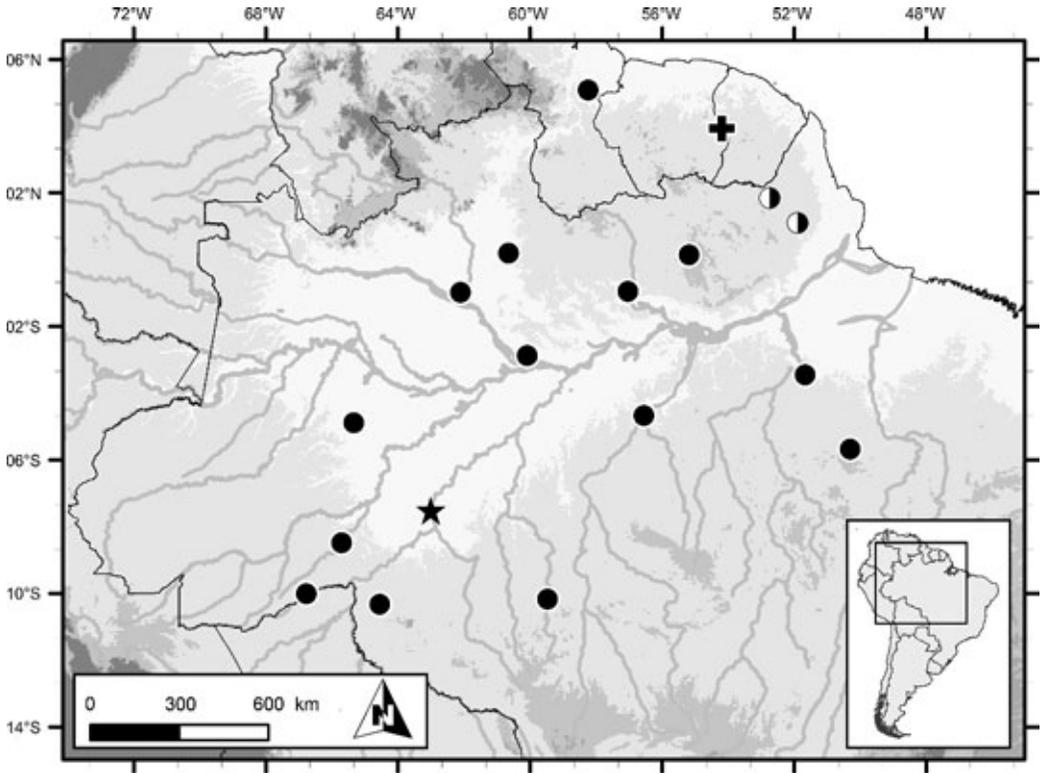


Fig. 31. Distribution of *Chiasmocleis hudsoni* and *C. haddadi*. Star = type locality of *C. jimi* (considered here as a synonym of *C. hudsoni*); circles = examined specimens of *C. hudsoni*; cross = type locality of *C. haddadi*; half circles = examined specimens of *C. haddadi*.

Five distinctive toes present; TI reduced, tip does not reach tubercle of TII by a wide margin; toes only slightly fringed, not webbed; tips of TI pointed, TII–IV rounded with terminal discs present. Relative toe lengths  $I < II < V < III < IV$ . Dermal spines present on dorsum, posterior surface of thighs, toes, and tarsus; absent on fingers. No femoral stripe present. Venter (belly and undersurfaces of thighs) beige with small light spots. Few large unpigmented eggs (Moravec and Köhler, 2007).

CALL AND TADPOLES: Unknown.

REMARKS: Moravec and Köhler (2007), when describing the species, suggested that this species might be associated with the genus *Syncope* (all former members of *Syncope* are now included in our *Chiasmocleis hudsoni* clade). This was based mostly on the basis of the presence of few large eggs (a condition also present in *Syncope*: Krügel and Richter, 1995; Silva and Meinhardt, 1999) and the significant digit reduction.

In our analysis, the sole specimen of *Chiasmocleis magnova* (sequence from de Sá et al., 2012) is well supported as the sister to a clade containing *C. antenori*, *C. carvalhoi*, and *C. tridactyla* while they all form the sister clade to *C. hudsoni* plus *C. haddadi*, sp. nov. Studies on the ecology of *C. magnova* can provide useful insights on the evolution of the group as a whole, as it seems *C. magnova* can be a transitional form between the more general *Chiasmocleis* body plan, and the miniaturized *C. antenori*, *C. carvalhoi*, and *C. tridactyla*.

DISTRIBUTION (fig. 27): Known from the vicinities of the type locality, in Iquitos, Departamento Loreto, Peru.

*Chiasmocleis shudikarensis* Dunn, 1949

Figures 33, plates 7, 14

HOLOTYPE (fig. 33): AMNH 43674; adult, probably female specimen. The chest is cut open. Both hands are partially destroyed and

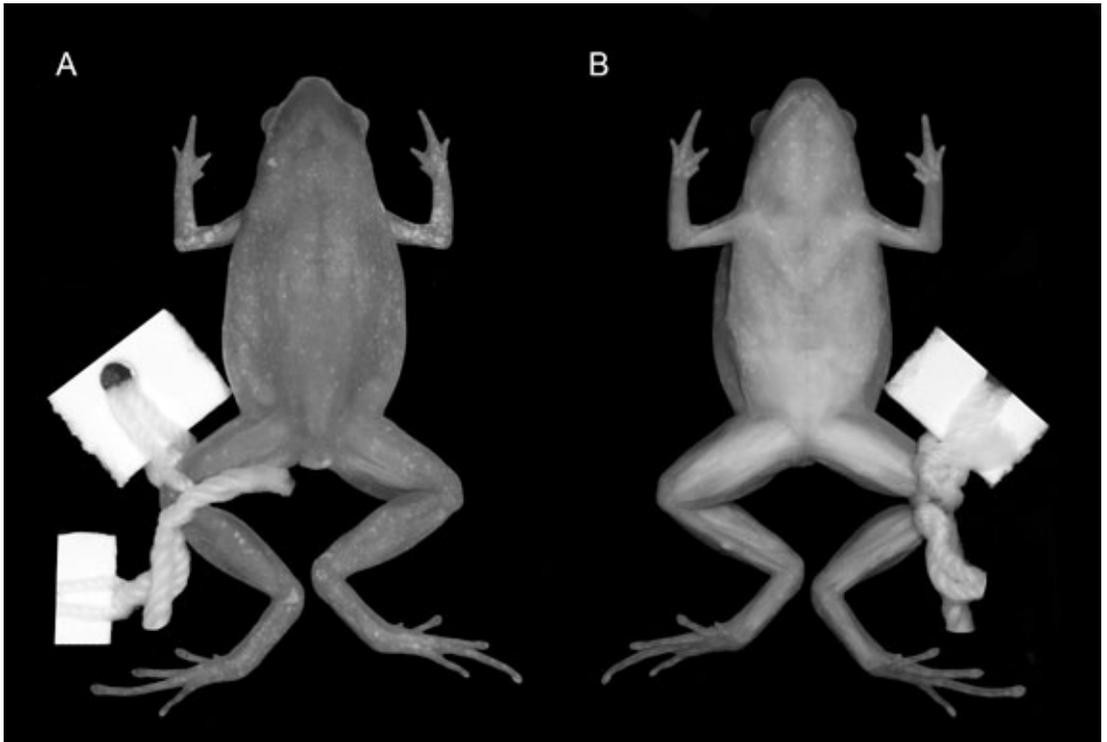


Fig. 32. *Chiasmocleis magnova* (AMNH 103550) from Iquitos, Peru, in (A) dorsal, and (B) ventral views. SVL = 16.7 mm.

so is the dorsal portion of the left foot. Other than that, the specimen is well preserved and some details of color pattern are still clearly visible.

**TYPE LOCALITY:** Shudikar-Wau, Upper Essequibo River, British Guiana (now the Co-operative Republic of Guyana). No geographic coordinates were given in the original description.

**DIAGNOSIS:** A medium-sized species for the genus; SVL in males 18.7–25.5 mm ( $N = 22$ ); in females 20.9–29.7 mm ( $N = 11$ ). Body ovoid, robust; head triangular, snout rounded in dorsal and lateral views. Four distinctive fingers, all but FI fringed in males, much less fringed in females; fingers not webbed; FI well developed with a distinct well-developed subarticular tubercle present between the proximal phalanges; distinctly visible subarticular tubercles present on all fingers; adpressed FI reaches or extends beyond the subarticular tubercle of FII; adpressed FIV does not reach or barely reaches distal tubercle of FIII; palmar tubercles protuberant,

divided; relative finger lengths  $I < IV < II < III$ . Five distinctive and well-developed toes present; toes fringed, less distinct in females; toes usually extensively webbed in males (fig. 5C) and only basally webbed in females (fig. 5B); TI with a distinct well-developed subarticular tubercle; adpressed TI does not touch or barely touches subarticular tubercle of TII; adpressed TV does not touch or reaches only the middle of subarticular tubercle of TIV; TII–V with terminal discs; relative toe lengths  $I < II < V < III < IV$ . Males with many dermal spines on fingers and toes; both sexes may show dermal spines on dorsum, fingers, and toes, much more numerous and developed in males; males with many spines on anterior portion of chin, lacking in females. Femoral line is always present (see pl. 7E).

**VARIATION:** In almost all populations where large series of both males and females were examined (e.g., FLONA do Amapá, Amapá, and Manaus, Amazonas), marked sexual dimorphism in fringes on hands was

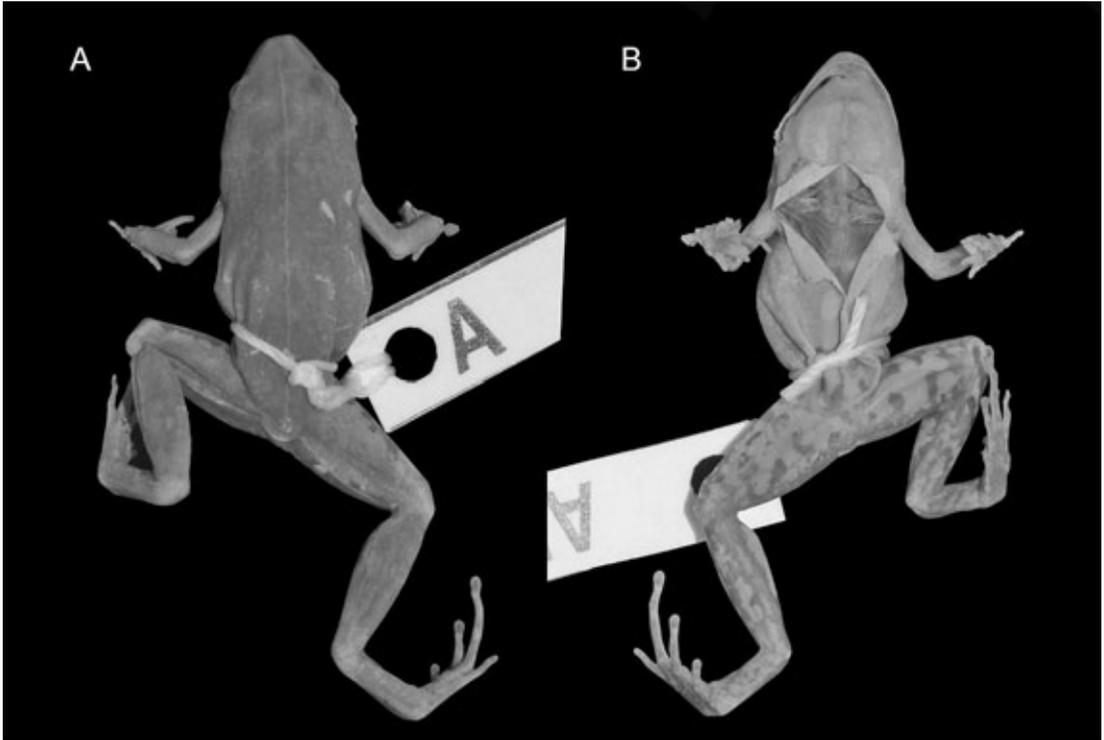


Fig. 33. Holotype of *Chiasmocleis shudikarensis* Dunn, 1949 (AMNH 43674), in (A) dorsal, and (B) ventral views. SVL = 23.3 mm.

observed, with males having conspicuously more developed fringes than females. The fringes in males are usually ornamented with numerous dermal spines. Males from Petit Saut, French Guiana, also show more developed fringes in fingers than females, but the difference is not as conspicuous as in other populations (e.g., Manaus and Amapá).

In life, the dorsum of males is usually reddish or grayish but is commonly marbled in shades of yellow or orange (pl. 7). Dorsum of females is usually more uniformly colored, gray or blackish. Snout follows the same general pattern of the dorsum, or is whitish (pl. 7A, C). A dorsal line may be present, varying in extent (as shown in fig. 10). Hind limbs of males and females usually yellow, orange, or reddish. Forelimbs grayish, yellow, or reddish, being uniform in females and usually marbled (as in the dorsum) in males. Venter color pattern varies in much the same way as it does in *C. avilapiresae* (illustrated in

fig. 20). An inguinal blotch is invariably present, although variable in shape and size.

**CALL AND TADPOLE:** The advertisement call of *Chiasmocleis shudikarensis* was described by Zimmerman and Bogart (1988) from Manaus, Amazonas, Brazil; and by Lescure and Marty (2000) from French Guiana. Both calls presented distinct acoustic parameters: Manaus, Brazil—"frequency range" 5890–7510 Hz; note duration 10–60 ms; interval between notes 10–30 ms (Zimmerman and Bogart, 1988); French Guiana—call rate 360 notes/min; dominant frequency 3380–3750 Hz; note duration 98 ms (Lescure and Marty, 2000). The difference in dominant frequency is striking and deserves further scrutiny as it suggests the possible that at least two distinct taxa are present.

The tadpole of *Chiasmocleis shudikarensis* was supposedly illustrated but not described by Hero (1990). The illustrations were later reported to belong to another microhylid, *Ctenophryne geayi* (Menin et al., 2011).

TABLE 10  
Uncorrected pairwise distances between 16S sequences of *Chiasmocleis shudikarensis*

Locality	1	2	3	4	5
1 Brazil: Amazonas (AMNHFS 20018)					
2 Brazil: Amazonas (AMNHFS 20039)	0.000				
3 Brazil: Amazonas (AMNHFS 20040)	0.000	0.000			
4 Suriname: Sipaliwini (JIW 458)	0.004	0.004	0.004		
5 Brazil: Pará (MPEG 28328)	0.002	0.002	0.002	0.002	
6 Guyana: Brokopondo (MVZ 247574)	0.004	0.004	0.004	0.004	0.002

Tadpoles of *C. shudikarensis* were recently described in detail by Menin et al. (2011).

REMARKS: Ávila-Pires et al. (2010) referred to a presumably undescribed species from the portion of the state of Pará north of the Amazon River. P.L.V.P. was present on a fieldtrip where two of the specimens were collected (Estação Ecológica Grão Pará: CN2112, CN2185—MPEG 28327, MPEG 28328, respectively; see pl. 7A) and we have carefully examined some additional specimens from the series mentioned by Ávila-Pires et al. (2010) at the MPEG collection. We disagree with Ávila-Pires et al. (2010) and consider the populations to be unambiguously assignable to either *C. shudikarensis* or *C. hudsoni* (see appendix 1 for identifications). The *C. shudikarensis* specimens from “Calha Norte” do have a smaller SVL than specimens from French Guiana and Amazonas, but they agree with the variation we observed in larger samples of *C. shudikarensis*, and also agree with the original description of the species (Dunn, 1949) and the general morphology with the holotype (AMNH 43674).

Despite distinct advertisement call parameters, we have decided not to name an additional species of *Chiasmocleis* allied to *C. shudikarensis* at this time for the following reasons: we have examined specimens of the population assigned to the “Manaus call type” (INPA 245, 277–78, 289, 320), but have not examined the vouchers for the “French Guiana call type.” The specimens from Manaus agree with the original description and with the holotype *C. shudikarensis*. We have examined a series of specimens from Petit Saut, French Guiana (MPEG 5106–5107, 5121, 5029–5033, 5060) and the only morphological differences are that male

specimens from Sinnamary River show considerably less fringed fingers than those from Manaus, Amazonas, Brazil, and females from French Guiana are slightly more robust. Therefore, the population from French Guiana is also unambiguously assignable to *C. shudikarensis*. In this particular case, examination of specimens and advertisement calls from the vicinities of the type locality (Essequibo River) is advisable before nomenclatural actions are taken. Genetic distances between 16S sequences included in our analysis very low and are given in table 10.

DISTRIBUTION (fig. 34): Restricted to the Guiana Shield in Guyana, Surinam (we have not examined any specimens from Surinam), French Guiana, and Brazil, north of Rio Amazonas (Amapá, Amazonas, Pará, and Roraima). Rodrigues et al. (2004b) provided a map that likely overestimates the distribution of the species, extending south of Rio Amazonas (Acre, Mato Grosso, and Rondônia). All of the specimens previously identified as *Chiasmocleis shudikarensis* in collections from southern Amazonia were identified by us as either *C. avilapiresae* or *C. bassleri*.

*Chiasmocleis superciliarba* Morales and McDiarmid, 2009  
Figure 35, plate 8

*Chiasmocleis superciliarbus* (Morales and McDiarmid, 2009). Incorrect spelling in the original description (see Peloso et al., 2013).  
*Syncope superciliarbus* (de Sá et al., 2012).

HOLOTYPE: MHNSM 16174; examined solely from a photograph, in life (not shown).

TYPE LOCALITY: Pakitza, Reserve Zone, Manu National Park, ca. 57 km northwestern from the mouth of Rio Manu (11°56'47"S

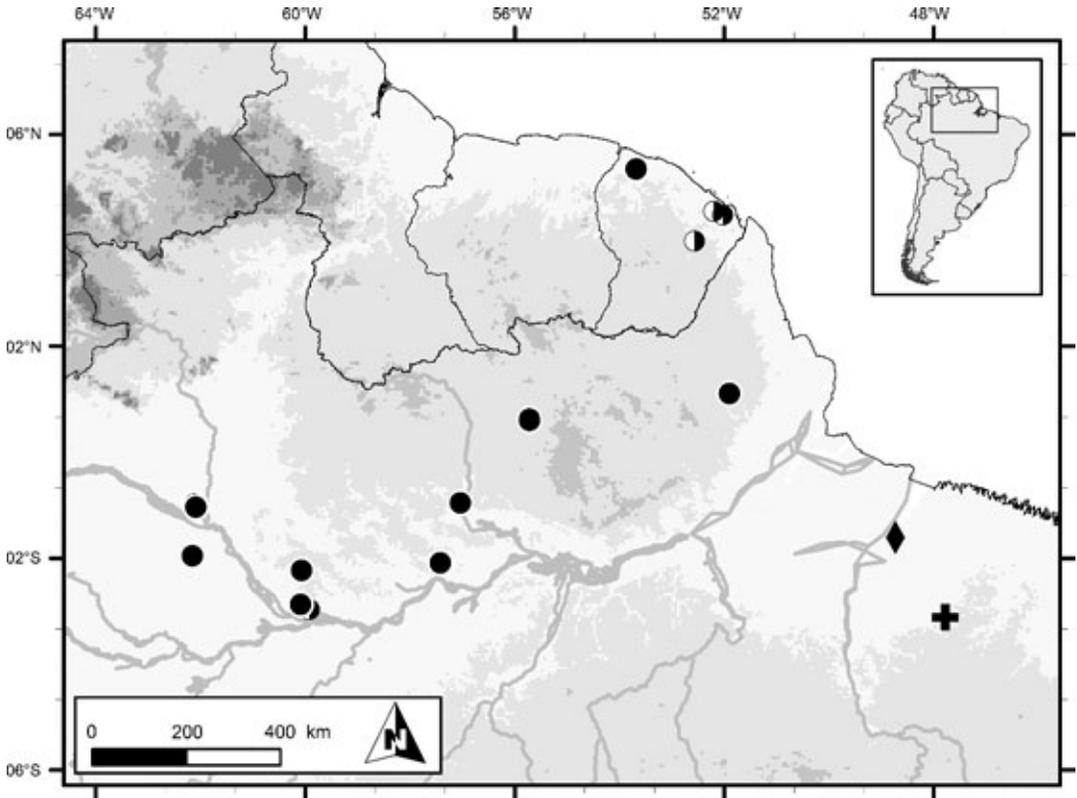


Fig. 34. Distribution of *Chiasmocleis shudikarensis* and *C. papachibe*. Circles = examined specimens of *C. shudikarensis*; half circles = specimens of *C. shudikarensis* examined solely from live photographs; cross = type locality of *C. papachibe*; diamond = examined specimens of *C. papachibe*.

/ 71°17'00"W), on Rio Manu, Departamento Madre de Dios, Peru.

**DIAGNOSIS:** A medium-sized species for the genus; SVL in males 18.4–18.7 mm (Morales and McDiarmid, 2009). Females unknown. Body ovoid to elongate; head triangular, snout rounded in dorsal and lateral views. Four distinctive fingers; FI well developed, subarticular tubercle may be absent or present; subarticular tubercles present on all remaining fingers, sometimes hardly visible; adpressed FI never extends past the distal margin of subarticular tubercle of FII; adpressed FIV does not reach distal tubercle of FIII; palmar tubercles present, not divided; relative finger lengths I<II<IV<III. Five distinctive toes present, first may be much reduced; toes may be slightly fringed; toes not webbed; TI lacks tubercle; adpressed TI does not touch subarticular tubercle of TII; adpressed TV does not touch

middle subarticular tubercle of TIV; TII–IV with terminal discs, usually more developed in females, but also present in males; relative toe lengths I<II<V<III<IV. An inguinal blotch of varied shape is always present. Venter (belly and under surfaces of thighs) usually white or cream with black or dark brown irregular spots.

**VARIATION:** Some variation in color pattern was observed from photos of live specimens (pl. 8) and examination of a paratype (USNM 342862: fig. 35). The dorsum can be dark brown, to almost uniformly whitish (silver) and may show reddish blotches and white spots (when not entirely whitish). A wide white stripe is almost invariably present from the snout to past the eyelids, sometimes extending to the inguinal region (forming the split stripe). A very narrow dorsal white line commonly present, extending from the occipital region



Fig. 35. Paratype of *Chiasmocleis superciliarba* Morales and McDiarmid, 2009 (USNM 342862), paratype in (A) dorsal, and (B) ventral views. SVL = 18.8 mm.

to the cloacal region. Dorsal surfaces of forearm yellowish, orange or red, while dorsal surfaces of hind limbs usually follow the general dorsal pattern. As reported by Morales and McDiarmid (2009) the shape and number of inguinal and lateral blotches (or spots) is variable, but commonly dark brown. Throat region with intense brown reticulation over a white (or cream-colored) background. Chest, belly, and undersurfaces of limbs with large, dark brown spots or irregular blotches (fig. 35, pl. 8D, F, H).

**CALL AND TADPOLE:** The advertisement call of *C. superciliarba* was described by Morales and McDiarmid (2009). Call consists of a fast series of multipulsed notes (mean note duration 31.0 ms; mean interval between notes 37.0 ms) with dominant frequency between 2985.8–3205.0 Hz. Number of pulses per note not given. Tadpoles are unknown.

**REMARKS:** A population from Rio Formoso, state of Rondônia, Brazil (OMNH 37204–37206, 37308–37309, 37319), present

dermal spines on dorsum, upper lips, cloacal region, fingers, and toes. The specimens also show well-developed fringes on the fingers and toes, and the toes are basally webbed. These specimens, therefore, agree (in part) with the diagnosis of *Chiasmocleis superciliarba* (see Morales and McDiarmid 2009, and text above). We tentatively assign the Rio Formoso specimens to *C. superciliarba*.

**DISTRIBUTION** (fig. 36): Southern Peru (Madre de Dios) and western Brazil (Acre and Rondônia).

*Chiasmocleis tridactyla* (Duellman and Mendelson III, 1995)  
Figures 37, plate 9A–D

*Adelophryne tridactyla*: (Duellman and Mendelson III, 1995).

*Syncope tridactyla*: (Silva and Meinhardt, 1999).

**HOLOTYPE:** URP-WED 59935. Not examined. Numbers are W.E. Duellman field numbers. According to the original publication,

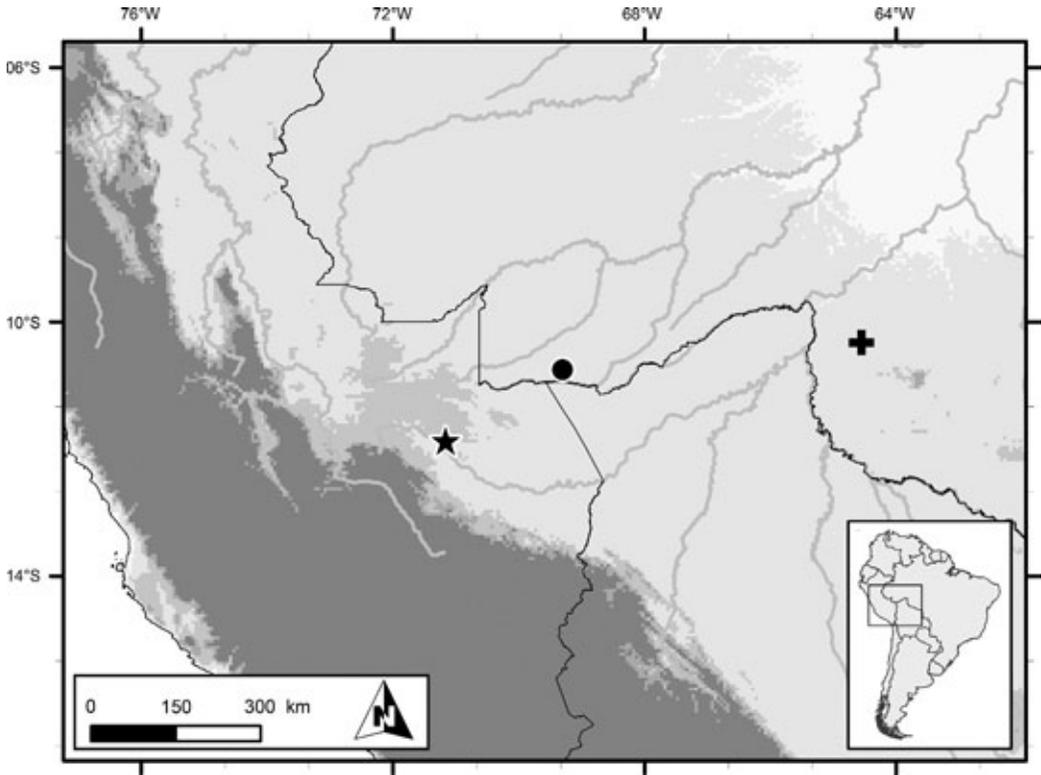


Fig. 36. Distribution of *Chiasmocleis superciliarba*. Star = type locality; circle = additional specimens examined; cross = specimens from Rondônia, Brazil, tentatively labeled as *C. cf. superciliarba*.

the specimens were to be deposited at the Museo de Historia Natural, Ricardo Palma, Lima, Peru (Duellman and Menselson III, 1995)

**TYPE LOCALITY:** San Jacinto, Departamento Loreto, Peru (02°18'45"S / 75°51'46"W, 180 m).

**DIAGNOSIS:** A small species for the genus; SVL in females 11.1–12.4 mm (Duellman and Menselson III, 1995). Body relatively robust, snout round in dorsal and lateral views. A distinct tympanum is visible. FI–IV much reduced; FI almost completely lost; FIV reduced but clearly identifiable, with tip round; FIII well developed with two sub-articular tubercles, tip pointed; FIV much reduced, without subarticular tubercles, tip round; fingers slightly fringed; palmar tubercles not present; relative finger lengths I<IV<II<III. Four toes visible, TI not visible; toes only slightly fringed; not webbed; tips toes pointed, discs absent. Relative toe lengths II<V<III<IV. Dermal spines ab-

sent. No femoral stripe present. In preservative, venter (throat, chest, belly, and undersurfaces of thigh) beige with small light spots. In life, dorsum brownish with light flecking (very small spots) and a cream-colored canthal stripe. Throat, chest, and belly brown with small spots (larger and more irregular posteriorly). Iris is red.

**VARIATION:** Number of specimens examined in detail ( $N = 6$ ) is much reduced to present data on variation, but we provide a few remarks on color in life, based on examination of photographs (pl. 9A–D). Duellman and Mendelson III (1995) reported a dorsolateral cream-colored stripe in specimen KU 221992 (from Teniente Lopez, Loreto, Peru) but the specimens from Leticia, Colombia, lack the dorsolateral portion of the stripe. In those specimens, the stripe ends on the posterior edge of the eyelid. Spots on the dorsum seem to be more numerous and larger in the specimen from Teniente Lopez.

**CALL AND TADPOLES:** Unknown.

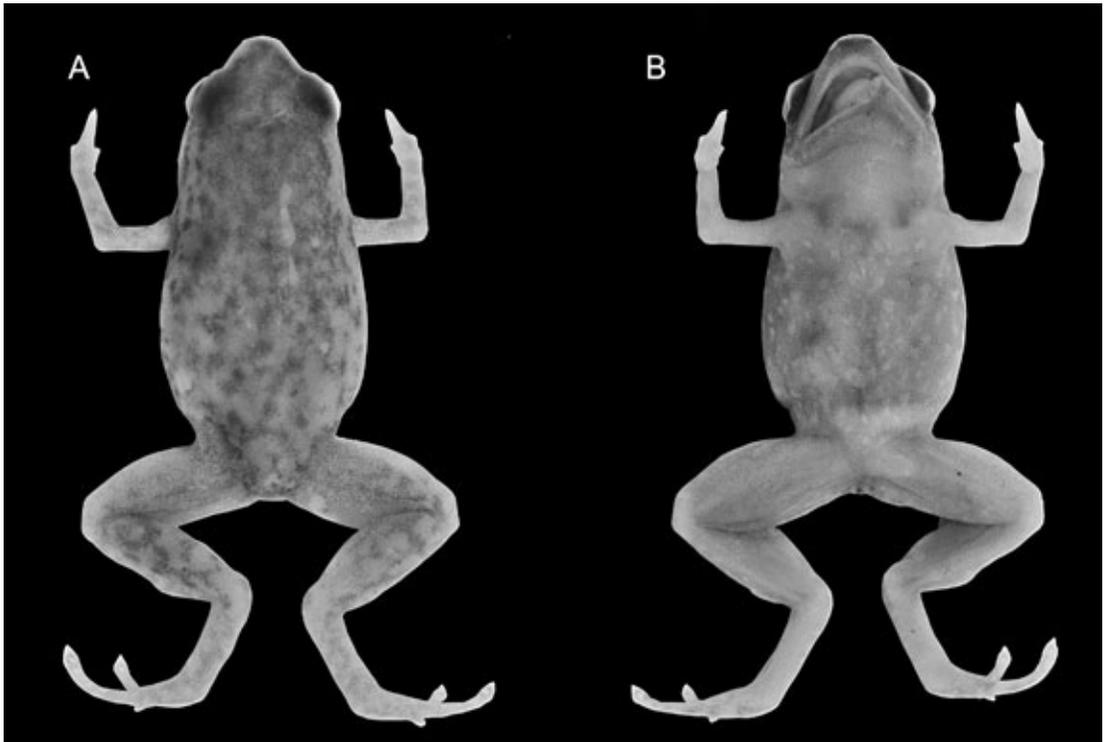


Fig. 37. *Chiasmocleis tridactyla* (MPEG 5637) from Tabatinga, Amazonas, Brazil, in (A) dorsal, and (B) ventral views. SVL = 11.5.

**DISTRIBUTION** (fig. 38): Known from Loreto, Peru (San Jacinto, the type locality, and Teniente López), and from the vicinities of the Brazil-Colombia border near the cities of Leticia (Colombia, Amazonas) and Tabatinga (Brazil, Amazonas).

**REMARKS:** Silva and Meinhardt (1999), when transferring the species to the genus *Syncope*, provided a detailed osteological description of the species based on a specimen from the same population examined by us (Tabatinga, Brazil: RMNH 26812). The specimens examined here, as well as the one examined by Silva and Meinhardt (1999) were listed by Duellman and Mendelson III (1995) “as tentatively referred to *A.[delo-phryne] tridactyla*.” We have not examined the types of *Syncope tridactyla* and therefore follow Duellman and Mendelson III (1995) to refer to the Tabatinga specimens as *Chiasmocleis tridactyla*. The specimens from Leticia, Colombia (JMP 1948, 2057, 2231: examined through photographs, see pl. 9A–D)

agree with the original description and resemble the specimens we have examined from Tabatinga. The specimens from Leticia were, however, collected just around 15 km away from the city of Tabatinga. Genetic distances between the three specimens of *C. tridactyla* included in the phylogenetic analysis are given in table 11.

*Chiasmocleis ventrimaculata*  
(Andersson, 1945)

Figures 39–40, plate 9E–H

*Engystoma ventrimaculata*: (Andersson, 1945).  
*Chiasmocleis ventrimaculata*: (Dunn, 1949).

**HOLOTYPE:** NRM 1943; adult female, examined from photographs (fig. 39). Specimen desiccated, but still preserving overall morphological features and some of the color pattern.

**TYPE LOCALITY:** Río Pastaza, Ecuador. No geographic coordinates given in the original description (Andersson, 1945). The

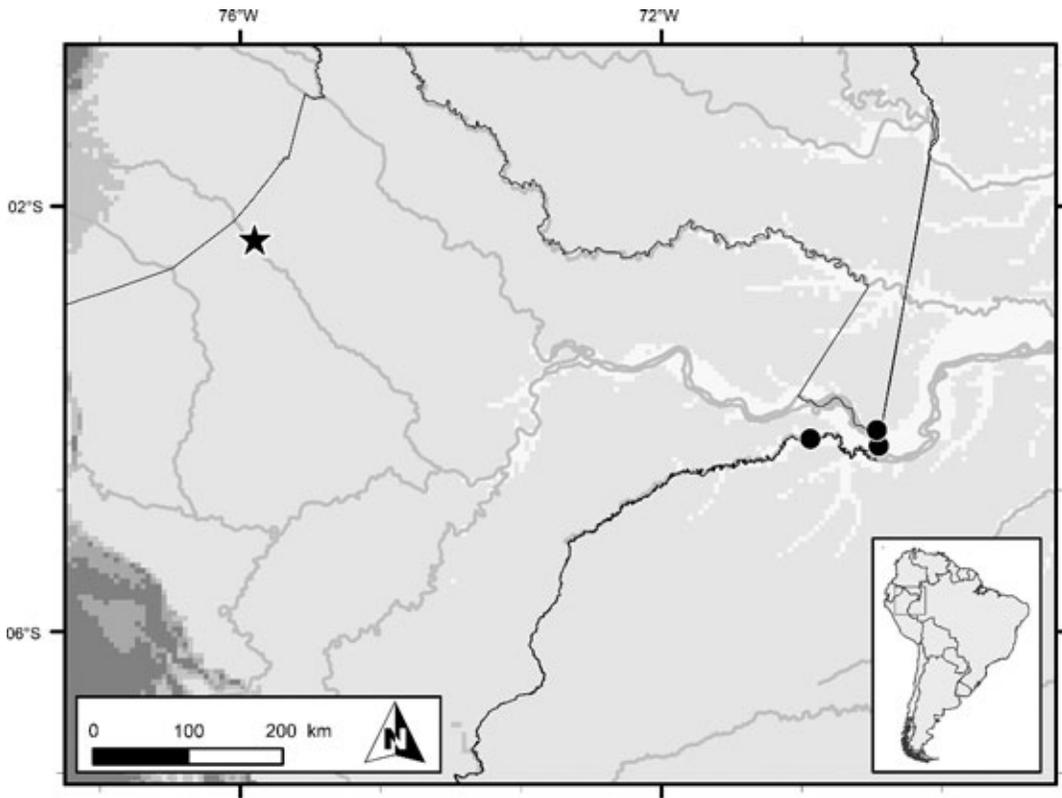


Fig. 38. Distribution of *Chiasmocleis tridactyla*. Star = type locality; circles = examined specimens.

Pastaza River is one of the major rivers in Ecuador, running through a large portion east of the country in the Provinces of Chimborazo, Morona-Santiago, Pastaza, and Tungurahua. It then runs into Peru, where it merges with the Marañon River. The type locality is, therefore, not precise.

DIAGNOSIS: A medium-sized species for the genus; SVL in males 20.0–23.0 mm (Rodriguez and Duellman, 1994; Funk and Cannatella, 2009); in females 21.0–33.4 mm (Rodriguez and Duellman, 1994; Funk and Cannatella, 2009). Body slender; snout

rounded in dorsal and lateral views. Four distinctive fingers, all but FI slightly fringed in males; fingers not webbed; FI well developed with a subarticular tubercle present between the proximal phalanges; sub-articular tubercles usually present on all fingers; adpressed FI may reach, but never reaches beyond, the subarticular tubercle of FII; adpressed FIV may reach distal tubercle of FIII; palmar tubercles visible, divided; relative finger lengths  $I < IV < II < III$ . Five distinctive and well-developed toes present; toes fringed without webbing or with only basal webbing present between TIII–TIV and TIV–TV; TI with a distinct well-developed subarticular tubercle; adpressed TI barely touches subarticular tubercle of TII; adpressed TV reaches the tip of subarticular tubercle of TIV; TII–IV with terminal discs; relative toe lengths  $I < II < V < III < IV$ . Males with many dermal spines on chin, fingers, toes, and dorsum; spines less abundant in females, more common on cloacal region.

TABLE 11  
Uncorrected pairwise distances between 16S sequences of *Chiasmocleis tridactyla*

Locality	1	2
1 Colombia: Leticia (JMP 1948)		
2 Colombia: Leticia (JMP 2057)	0.002	
3 Colombia: Leticia (JMP 2231)	0.002	0.000

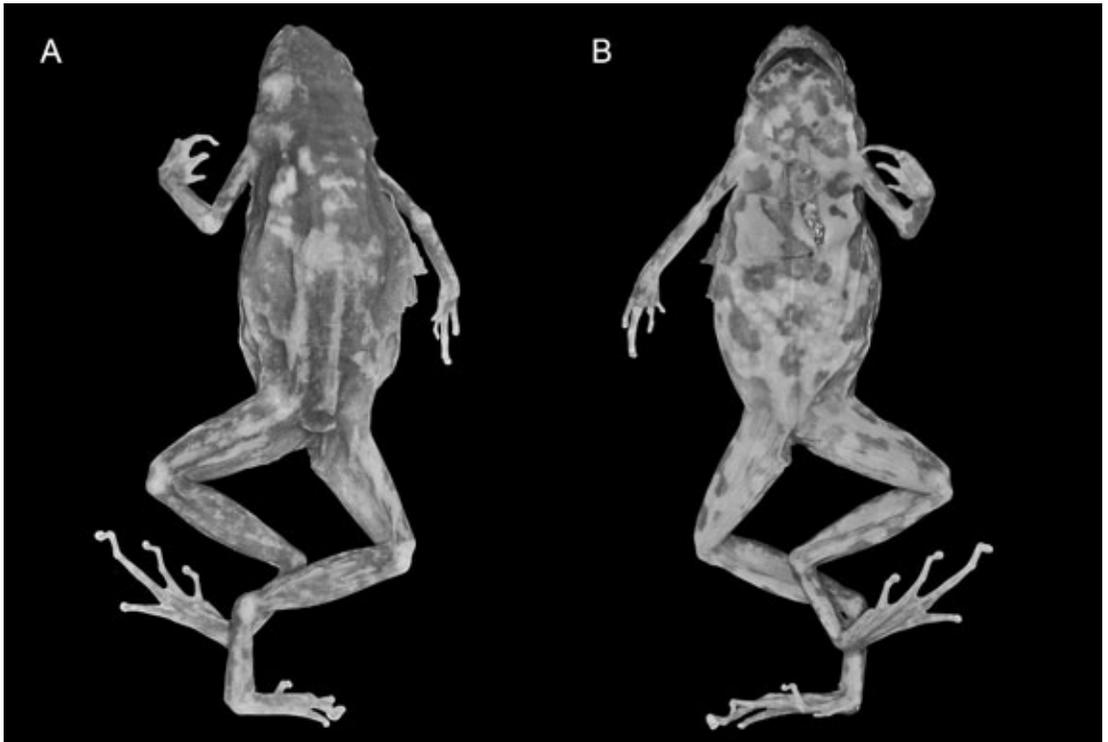


Fig. 39. Holotype of *Chiasmocleis ventrimaculata* (Andersson 1945) (NRM 1943, holotype) in (A) dorsal, and (B) ventral views (photos: J.M. Padial).

Inguinal blotch absent. Femoral stripe on posterior thighs absent. Venter, throat, belly, and undersurface of thighs white or cream colored with large dark brown, irregular blotches; blotching commonly more dense on throat; in preservative, dorsal surface of arms with large white or cream-colored stains.

**VARIATION:** Venter is usually light colored, white, or cream, with brown to black stains and blotches, sometimes forming a slightly reticulated pattern, extending from chin through the throat, chest, belly, and undersurfaces of limbs (fig. 40). In life, the dorsum is almost uniformly dark brown, but may show minute whitish spots (pl. 9E–H). Snout is sometimes golden or whitish, while dorsal surfaces of limbs may show orange or yellow stains of irregular shape (pl. 9E, H).

**CALL AND TADPOLE:** Calls assigned to *Chiasmocleis ventrimaculata* were described twice in the past, once by Nelson (1973) from a population from Colombia, and again by Schlüter (2005) from Panguana, Peru. We

consider the call described by Schlüter (2005) to represent a distinct species, *C. royi*, sp. nov. (described below). The call described by Nelson (1973) has a mean dominant frequency range of  $3562 \pm 110$  Hz (3350–3700 Hz). Attempts to find the recordings analyzed by Nelson (1973), for potential reanalysis, were unfruitful. Tadpole is unknown.

**REMARKS:** Several populations from southern Peru and Bolivia have been called *Chiasmocleis ventrimaculata* in the past (De la Riva, 1995; Schlüter, 2005; Peloso and Sturaro, 2008; Von May et al., 2009). After examination of photographs of the holotype of *C. ventrimaculata* (fig. 39) and a large sample of specimens from throughout the taxon's distribution, we concluded that two species, one of which we describe below (*C. royi*, sp. nov.), are currently associated with the name. Our phylogenetic analysis corroborates this, and the two species are not even sister to each other. Instead, *C. royi*, sp. nov., is sister to *C. papachibe*, sp. nov., + *C. ventrimaculata*.

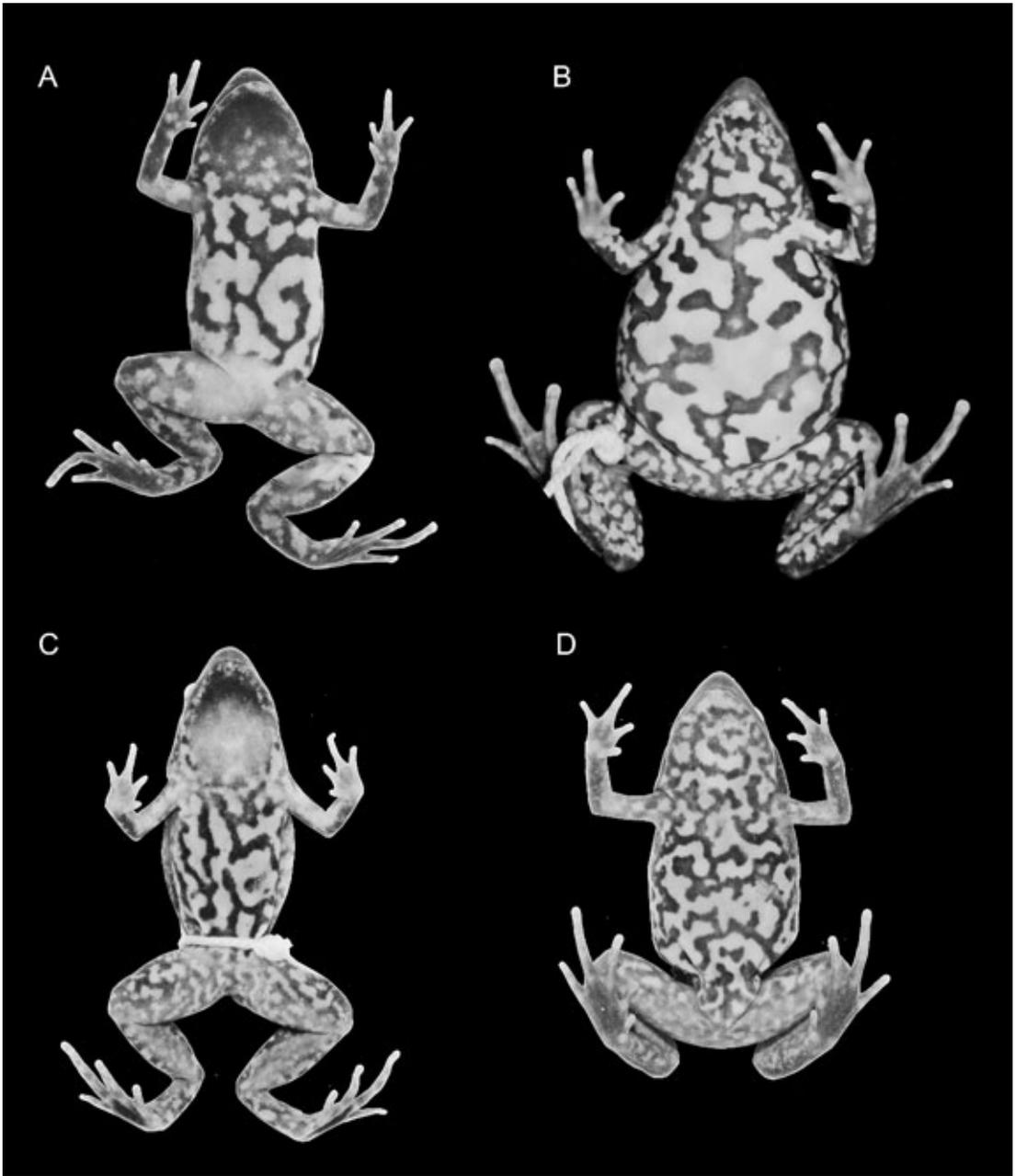


Fig. 40. Variation of ventral color pattern in *Chiasmocleis ventrimaculata*. (A) Cantadera Tacaná, Leticia, Colombia (ICN 50245). (B) Reserva Extrativista do Alto Juruá, Cruzeiro do Sul, Acre, Brazil (UFAC RB 2252). (C–D) Reserva Extrativista Riozinho da Liberdade, Tarauacá, Acre, Brazil (UFACF 641, and UFACF 910, respectively).

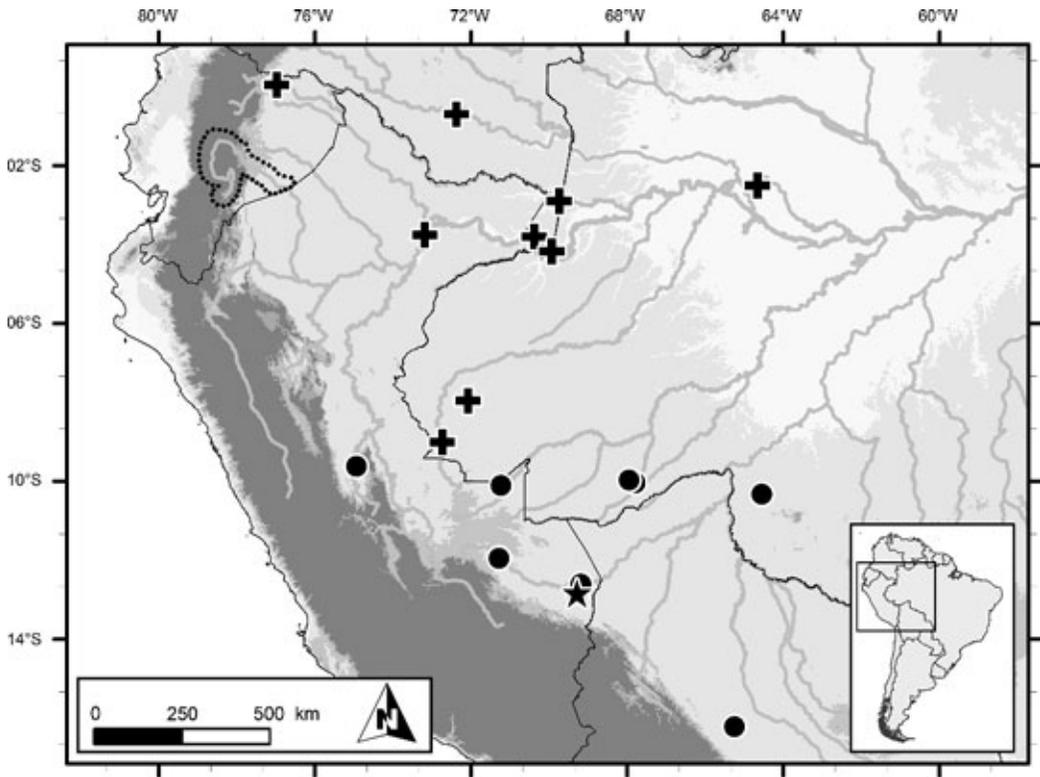


Fig. 41. Distribution of *Chiasmocleis ventrimaculata* and *C. royi*. Crosses = examined specimens of *C. ventrimaculata*. Dashed area refers to the extension of the Río Pastaza (= Pastaza River), inside the territory of Ecuador, given as the type locality of *C. ventrimaculata* by Andersson (1945). Star = type locality of *C. royi*; circles = additional examined specimens of *C. royi*.

Genetic distances between the three specimens of *Chiasmocleis ventrimaculata* is zero.

**DISTRIBUTION** (fig. 41): Colombia, Ecuador, northern Peru, and western Brazil (Acre and western Amazonas).

#### DESCRIPTIONS OF NEW SPECIES

##### *Chiasmocleis haddadi*, new species

Figures 42–43, plate 10

**HOLOTYPE** (fig. 42, pl. 10A–B): MNHNP 2011.0139 (field number PG 403), an adult male, collected by P. Gaucher, on February 21, 2005.

**TYPE LOCALITY**: Montagne Kotika (03°56'00"N / 54°11'05"W, 700 m), French Guiana.

**PARATYPES**: MNHNP 2011.0140, MNHNP 2011.0143–2011.0145, all collected with the holotype. IEPA (FL 453–455, FL 511–513),

Igarapé Santo Antônio, Floresta Nacional do Amapá (1°06'04" N / 51°53'36" W), state of Amapá, Brazil, collected by J.D. Lima and A. Ferreira-Sobrinho in February 28 to March 20, 2005. IEPA (TQ 1036), from Rio Anacuí, Parque Nacional Montanhas do Tumucumaque (1°50'41"N / 52°44'28"W), state of Amapá, Brazil, collected by J.D. Lima and J.R.F. Lima from February 22 to March 11, 2006.

**DIAGNOSIS**: A small sized species for the genus; SVL in males 13.7–18.2 mm ( $N = 12$ ); females unknown. Body ovoid, robust; head much narrower than body, snout rounded in dorsal and lateral views. Four distinctive fingers; all but FI slightly fringed, less fringed in females; fingers not webbed; FI reduced with a rounded or slightly pointed tip, subarticular tubercle usually absent, hardly visible if present; finger tips of FII–IV rounded, tips of FII and III swollen, may



Fig. 42. Holotype of *Chiasmocleis haddadi*, sp. nov. (MNHNP 2011.0139), in (A) dorsal and (B) ventral views. SVL = 14.4 mm.

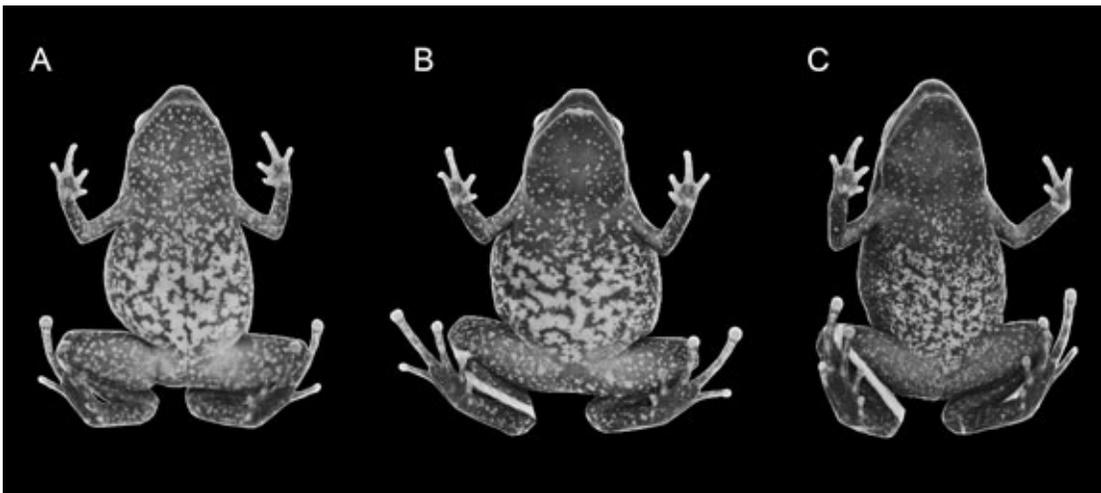


Fig. 43. Variation of ventral color pattern in *Chiasmocleis haddadi*. (A) FL 454; (B) FL 513; (C) FL 512; all from Floresta Nacional do Amapá, Amapá, Brazil. Not to scale.

present discs; adpressed FI does not reach subarticular tubercle of FII; adpressed FIV reaches middle or distal margin of distal tubercle of FIII; thenar tubercle present in most individuals; relative finger lengths  $I < II < IV < III$ . Five distinctive toes, first slightly reduced; toes slightly fringed, less distinct in females; toes not webbed; TI with without subarticular tubercle; adpressed TI does not touch subarticular tubercle of TII; adpressed TV does not reach or reaches only the middle of the middle subarticular tubercle of TIV; TII–IV with terminal discs. Some males with few well-developed dermal spines on chin.

**COMPARISONS** *Chiasmocleis haddadi* differs from *C. antenori* in having four externally evident fingers (FI not evident externally in *C. antenori*), five externally evident toes (TI not evident), toe tips rounded (toe tips pointed), and in having a reticulated venter (dark with scattered light spots). It differs from *C. albopunctata* in having a reduced first finger (well-developed finger in *C. albopunctata*) and by its smaller size, its snout and dorsum lacking large white spots (snout and dorsum with large white spots in *C. albopunctata*), its reduced FI (well-developed in *C. albopunctata*), and its advertisement call. *Chiasmocleis haddadi* differs from *C. anatis* by the absence or much-reduced webbing between toes in males (extensive webbing in males *C. anatis*) and its having a reduced first finger (well-developed finger in *C. anatis*) and a reticulated venter (light colored venter with large brown spots or blotches in *C. anatis*). The new species is distinguished from *C. avilapiresae* by: its smaller size, the absence of a subarticular tubercle on TI (present in *C. avilapiresae*), the absence of or much-reduced webbing between toes in males (extensively webbed in *C. avilapiresae*), its mottled venter (usually blotched in *C. avilapiresae*), the lack of a femoral line (present in *C. avilapiresae*), and its advertisement call. The new species differs from *C. bassleri* in body shape (more robust in *C. bassleri*), in having a mottled venter (usually large dark spots over a light venter in *C. bassleri*), by the absence of an inguinal blotch (present in *C. bassleri*), and by the advertisement call (table 2). The new species differs from *C. carvalhoi* in having four

externally evident fingers (FI not evident externally in *C. carvalhoi*) and five externally evident toes (TI not evident). *Chiasmocleis haddadi* differs from *C. hudsoni* by: its dark brown dorsum (usually light brown or cream dorsum in *C. hudsoni*), dark brown vermiculations on the throat (sometimes largely brown with small white spots), and its advertisement call (table 2). The new species differs from *C. magnova* in having finger IV fully developed, although reduced when compared to most other species (finger VI much reduced in *C. magnova*), and by the dark brown reticulation on throat, chest, and undersurfaces of limbs (belly and undersurfaces of thighs beige with small light spots in *C. magnova*). From *C. royi* the new species differs by having a reduced FI (fully developed in *C. royi*), by the absence of a femoral line (present in *C. royi*) and an externally protruding black vocal sac in males (protruding in *C. royi*), and by its advertisement call (table 2). The new taxon differs from *C. papachibe*, sp. nov., by its smaller size, and in having a reduced first finger (fully developed with a distinct subarticular tubercle in *C. papachibe*). *Chiasmocleis haddadi* is distinguished from *C. shudikarensis* by the absence of or much-reduced webbing between toes in males (males with extensive webbing in *C. shudikarensis*), by the lack of spines on fingers of males (many spines in males of *C. shudikarensis*), a femoral line (well-defined white line in *C. shudikarensis*), and an inguinal blotch (present in *C. shudikarensis*), and by its advertisement call (see text). From *C. superciliarba*, the new taxon differs by having a mottled venter (large dark spots or stains over a light venter in *C. superciliarba*), by the absence of an inguinal blotch (present in *C. superciliarba*), and by its advertisement call (see text). Finally, it differs from *C. tridactyla* in having four externally evident fingers (FI not evident externally in *C. tridactyla*), five externally evident toes (TI not evident), rounded toe tips (toe tips pointed), and a reticulated venter (dark with scattered light spots).

**DESCRIPTION OF THE HOLOTYPE** (fig. 42, pl. 10A–B): Body ovoid, relatively robust. Head short, wider than long (HW  $1.25 \times$  HL); head much narrower than body trunk; snout rounded in dorsal and lateral views;

nostrils not protuberant, positioned antero-laterally, directed laterally. IOD  $2.2 \times$  IND. *Canthus rostralis* indistinct, round in cross section. Eyes are small. Occipital or supra-tympanic folds absent; tympanum not visible. Upper jaw projecting beyond lower; lower lip with truncate, trilobed anterior margin; tongue large, elongate, with free lateral and posterior edges, extended beyond the extent of the jaw; vocal slits present, one on each side of the tongue; choanae small, rounded, widely separated, anterior to eye; vomerine teeth absent. Vocal sac not externally evident.

Forelimb slender; FI reduced, FII, FIII, and FIV well developed; tips of FI and FII rounded; discs on tips of FIII and FIV; all fingers nearly round in cross section; no webbing between fingers; relative finger lengths  $I < II < IV < III$ ; tips rounded, with small discs on FIII and IV. Subarticular tubercles present on all fingers, but inconspicuous on FI; one subarticular tubercle on FII and FIV, two on FIII; all tubercles well developed; no supernumerary tubercles; the- nar tubercle present, rounded; palmar tubercle divided, not prominent. No dermal spines visible on arms, hands, or fingers.

Legs short (combined THL, TBL, and FL  $1.6 \times$  the SVL), relatively robust, lacking tubercles, tibial and tarsal ridges, and warts; toes not webbed; TI weakly developed (tip fails to reach subarticular tubercle on TII), without subarticular tubercle; toe tips rounded with small discs on all except TI. Inner metatarsal tubercle present. Subarticular tubercles present on all toes except TI, large but very weakly developed; no outer metatarsal tubercle. TI barely reaches proximal margin of the tubercle of TII; TV reaches distal margin of proximal subarticular tubercle of TIV; relative toe lengths  $I < II < V < III < IV$ ; toes without dermal spines.

Skin smooth dorsally and ventrally.

MEASUREMENTS OF THE HOLOTYPE: SVL 14.4, HL 3.5, HW 4.1, ED 1.7, IOD 3.0, IND 1.3, END 1.2, THL 6.2, TBL 6.9, FL 10.1, 4TD 0.6.

VARIATION: Dorsum uniform dark brown or mostly dark brown with scattered small white dots. Throat, chest, and ventral surfaces of limbs dark brown with small cream-colored spots; venter varies from dark with white dots to cream colored with intense dark brown vermiculations (fig. 43). In life, lighter

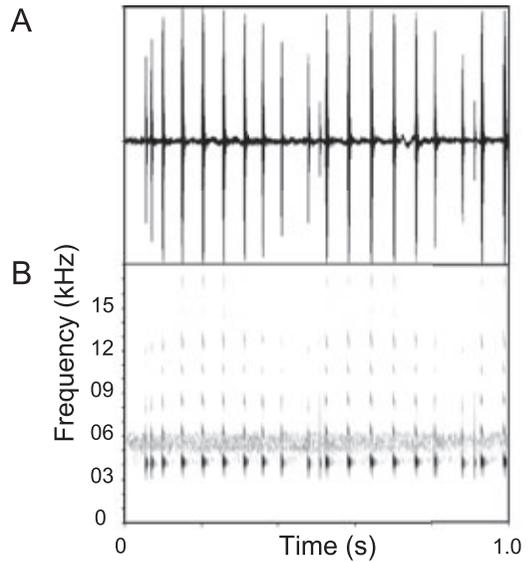


Fig. 44. Advertisement call of *Chiasmocleis haddadi*. (A) Oscillogram and (B) spectrogram of two consecutive multipulsed notes. Recorded at the type locality, Montagne Kotika, French Guiana (recording number FNJV 30718).

portions of venter are blueish (pl. 10B, F) but may show some yellow regions (pl. 10D).

COLOR IN PRESERVATIVE: Dorsum and dorsal surfaces of limbs dark brown with scattered small white spots (usually associated with small warts and more abundant on forelimbs). Throat, chest, and ventral surfaces of limbs dark brown with small cream spots; venter cream colored with intense brown vermiculations.

ETYMOLOGY: The specific epithet is used as a noun in the genitive case and honors Célio F.B. Haddad, friend, amphibian enthusiast, and professor at the Universidade Estadual Paulista, Rio Claro, São Paulo. We honor Célio for his invaluable contribution to South American herpetology, as well as for his continuous help (including on several *Chiasmocleis*-related matters), incentive, and friendship over the years.

CALL AND TADPOLES: The advertisement call of *Chiasmocleis haddadi* (fig. 44) consists of a series (164 notes/minute) of multipulsed notes (mean note duration  $330 \pm 40$  ms; mean interval between notes  $60 \pm 20$  ms) with a mean dominant frequency of  $4146.5 \pm 60.1$  kHz.

TABLE 12  
Uncorrected pairwise distances between 16S sequences of *Chiasmocleis haddadi*

Locality	1	2	3	4
1 French Guiana: Mont Kotika (MNHN 2011.0139)				
2 French Guiana: Mont Kotika (MNHN 2011.0140)	0.000			
3 French Guiana: Mont Kotika (PG 445)	0.000	0.000		
4 French Guiana: Mont Kotika (PG 446)	0.000	0.000	0.000	
5 <sup>a</sup> French Guiana: Mont Bakra (BM 28)	0.042	0.042	0.042	0.042

<sup>a</sup> This specimen is labeled as *Chiasmocleis "hudsoni"* in the phylogenetic tree (figs. 6, 7). Sequences for it derive from Genbank and we did not examine the specimen for phenotypic characters.

**REMARKS:** An individual from Mont Bakra, French Guiana, previously labeled as *C. hudsoni* (Fouquet et al., 2007), included in the phylogeny (voucher specimen not examined) is sister to four samples of *C. haddadi* from Mont Kotika, French Guiana (all paratypes) (fig. 6), and is included in this taxon. Genetic distances between all specimens of *Chiasmocleis haddadi* included in the phylogenetic analysis are given in table 12.

**DISTRIBUTION** (fig. 31): Known from the type locality and from Mont Bakra in French Guiana, and from two localities in the state of Amapá, Brazil.

*Chiasmocleis papachibe*, new species  
Figure 45, plate 11

**HOLOTYPE** (fig. 45, pl. 11A–B): MPEG 30683 (field number PRG 043), an adult

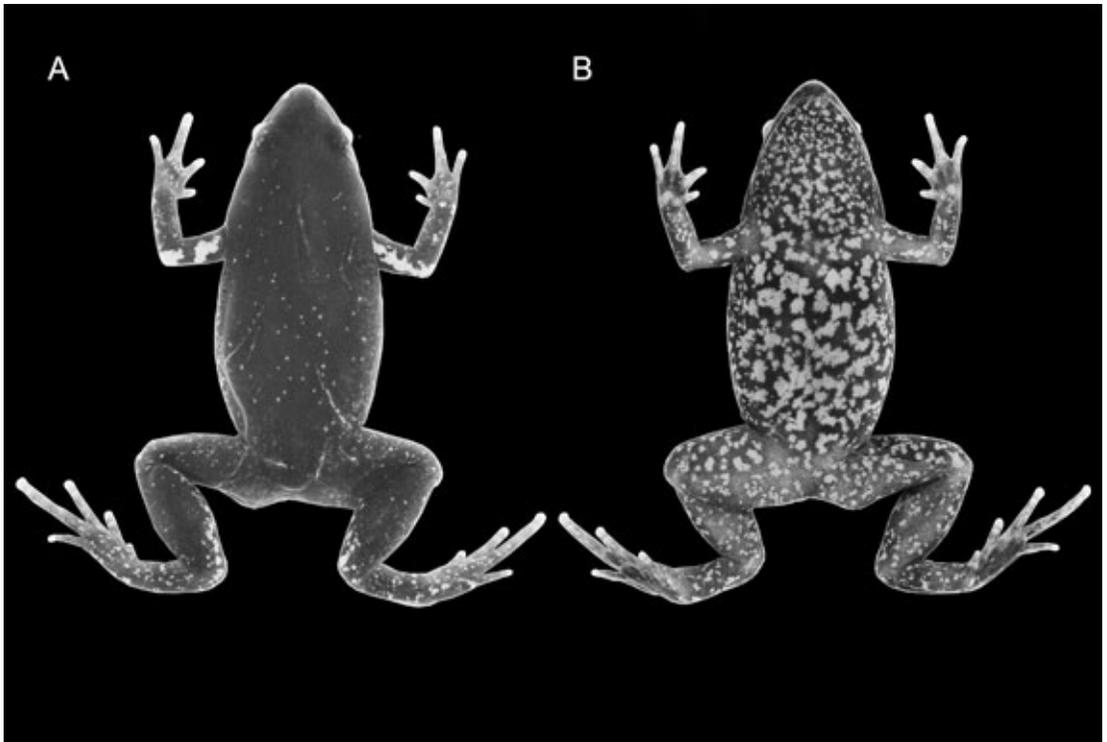


Fig. 45. Holotype of *Chiasmocleis papachibe*, sp. nov. (MPEG 30683), in (A) dorsal and (B) ventral views. SVL = 24.8 mm.

male, collected by M.J. Sturaro and A. D'Angiolella in April 18, 2010.

TYPE LOCALITY: Paragominas (03°06'23" S / 47°46'55" W), municipality of Paragominas, state of Pará, Brazil.

PARATYPE: MPEG 30684 (field number PRG 055), an adult female (pl. 11C–D), from the type locality, collected by M.J. Sturaro and A. D'Angiolella, in April 23, 2010.

DIAGNOSIS: A medium-sized *Chiasmocleis*; SVL of adult male 24.8 mm, of female 32.6 mm. Body ovoid and relatively slender; snout rounded in dorsal and lateral views, IOD about 2.1–2.3 × the IND. Four distinctive fingers present; all but FI fringed in males; FI well developed with a subarticular tubercle usually present between the proximal phalanges; adpressed FI does not touch subarticular tubercle on FII; adpressed FIV touches distal subarticular tubercle of FIII; distinct subarticular tubercles present on all fingers; palmar tubercles protuberant, divided; relative finger lengths I < II < IV < III. Five distinctive and well-developed toes present; toes fringed, less so in female; adpressed TI does not touch or barely touches subarticular tubercle of TII; adpressed TV does not reach or reaches only to the middle of the middle subarticular tubercle on TIV; TII–IV with terminal discs, usually more developed in females; toes basally webbed; relative toe lengths I < II < V < III < IV. Males without dermal spines on fingers and toes; both sexes without dermal spines on dorsum and toes. Vocal sac undeveloped, vermiculated by black and white. Femoral line and inguinal blotch are always absent.

COMPARISONS: *Chiasmocleis papachibe* differs from *C. antenori* by its much larger SVL (maximum recorded SVL 13.6 mm in *C. antenori*) and in having four externally evident fingers (FI not evident externally), five externally evident toes (TI not evident), toe tips rounded (toe tips pointed), and a reticulated venter (dark with scattered light spots).

The new species differs from *Chiasmocleis anatis* in having basal webbing in toes of males (extensive webbing in males of *C. anatis*), and by its vermiculated venter (dark spots in *C. anatis*). The new species is distinguished from *C. avilapiresae* by: its smaller size (SVL of *C. avilapiresae* up to

37.8 mm in females), its basally webbed feet in males (extensively webbed in male *C. avilapiresae*), the absence of a femoral line (present in *C. avilapiresae*), and its venter with intense dark reticulations over a white background (brown stains or blotches in *C. avilapiresae*). The new species differs from *C. bassleri* in having a vermiculated venter (large dark spots or stains over a light venter in *C. bassleri*) and by the absence of an inguinal blotch (present in *C. bassleri*). The new species differ from *C. carvalhoi* by its much larger SVL (maximum recorded SVL 13.2 in *C. carvalhoi*: Nelson, 1975), four externally evident fingers (FI not evident externally), and five externally evident toes (TI not evident). The new species is distinguished from *C. haddadi* and *C. hudsoni* by its larger size (maximum SVL 23.4 mm in *C. hudsoni* and 18.2 mm in *C. haddadi*), fully developed FI (reduced in *C. haddadi* and *C. hudsoni*), and a round finger I tip (tip slightly pointed in *C. haddadi* and *C. hudsoni*). *Chiasmocleis papachibe* differs from *C. magnova* by having all fingers fully developed (fingers I and IV reduced in *C. magnova*), and by its larger size (maximum SVL 18.3 mm in *C. magnova*: Moravec and Köhler, 2007). *Chiasmocleis papachibe* is distinguished from *C. shudikarensis* in having basal webbing on toes of males (males with extensive webbing in *C. shudikarensis*) and in lacking an inguinal blotch (present in *C. shudikarensis*) and dermal spines on dorsum and digits (spines numerous and conspicuous in *C. shudikarensis*). *Chiasmocleis papachibe* differs from *C. ventrimaculata* in having a venter with a heavy amount of brown vermiculations (venter light colored with brown stains or blotches, sometimes forming a weakly defined vermiculated pattern in *C. ventrimaculata*). The new taxon differs from *C. tridactyla* by its much larger SVL (maximum recorded SVL 12.4 mm in *C. tridactyla*; Duellman and Mendelson III, 1995) in by its four externally evident fingers (FI not evident externally in *C. tridactyla*), five externally evident toes (TI not evident), rounded toe tips (toe tips pointed), by its reticulated venter (dark with scattered light spots).

DESCRIPTION OF THE HOLOTYPE: Body ovoid, relatively slender. Head short, wider

than long (HW 1.1 × HL); head slightly narrower than body; snout rounded in dorsal and lateral views; nostrils not protuberant, positioned anterolaterally, directed laterally. IOD 2.3 × the IND. *Canthus rostralis* poorly defined, round in cross section; loreal region slightly convex. Eyes are small. No occipital fold present, supratympanic fold present; tympanum not apparent externally. Upper jaw projecting beyond lower; lower lip with truncate, trilobed anterior margin; spines on chin absent; tongue large, elongated, with free lateral and posterior edges; vocal slits not developed; choanae small, rounded, widely separated, just anterior to eye; vomerine teeth absent. Vocal sac is not developed.

Forelimbs slender; all fingers developed, nearly round in cross section; no webbing between fingers; relative finger lengths I < II < IV < III; tips rounded, with little developed fringes, without discs. FI swollen, no distinct subarticular tubercle visible. Subarticular tubercles on remaining fingers present but not very developed and not prominent; one subarticular tubercle on FII and FIV, two on FIII; both tubercles are equal in size; no supernumerary tubercles; palmar tubercle not visible, thenar tubercle present, large, round prominent; outer metacarpal tubercle present. All fingers without dermal spines laterally.

Legs short (combined THL, TBL, and FL 1.36 × SVL); legs relatively robust, lacking tubercles, lacking tibial and tarsal ridges or warts; toes not webbed (a very rudimentary vestige of web between TIII–TIV and TIV–TV is present and may be considered basal webbing by some observers); TI weakly developed (tip fails to reach subarticular tubercle of TII), without a visible subarticular tubercle; toe tips rounded with little developed lateral fringes and small discs on all but TI. Subarticular tubercles present in all toes; no outer metatarsal tubercle. TI barely reaches proximal margin of the tubercle of TII; TV reaches distal margin of proximal subarticular tubercle on TIV; relative toe lengths I < II < V < III < IV. Toes without lateral dermal spines.

Skin smooth dorsally and ventrally without scattered spines.

MEASUREMENTS OF THE HOLOTYPE: SVL 24.8, HL 4.7, HW 5.3, ED 1.8, IOD 4.1, IND 1.8, END 2.0, THL 9.0, TBL 9.4, FL 15.4.

VARIATION: The species is only known from three specimens (two of which are illustrated in pl. 11) and all have very similar morphology, except for trivial differences in size and body shape between males and females. Additionally, males seem to have more numerous white dots on the dorsum than females.

ETYMOLOGY: The specific epithet, a noun in apposition, refers to the vernacular composite word “Papa-Chibé,” meaning “the one who eats chibé.” *Chibé* is made by soaking manioc (*Manihot esculenta* Crantz) flour—locally known as *farinha de mandioca*—in water. The resulting porridge, or soupy liquid, is then commonly seasoned with salt and hot peppers and eaten, sometimes with fish or game, but often as the only source of nutrients (Murrieta, 1998). *Farinha de mandioca* and its derivatives, including chibé, are an important source of nutrition to several Amazonian populations in the Lower Rio Amazonas region (Murrieta, 1998; Murrieta et al., 2008). The name “Papa-Chibé,” or “Papa-Xibé,” is colloquially used to refer to anyone who is native to the state of Pará, Brazil (Sobral, 2005). *Chiasmocleis papachibe* is, up until now, known only from a couple of localities in Pará, and the name is given as homage to the inhabitants of the Brazilian state of Pará (“paraenses”).

CALL AND TADPOLES: Unknown.

REMARKS: Genetic distances between the three specimens of *Chiasmocleis papachibe* included in the phylogenetic is zero.

DISTRIBUTION (fig. 34): Known from the type locality and from a nearby locality, Barcarena, Pará, Brazil.

### *Chiasmocleis royi*, new species

Figures 46–47, plates 12–13

HOLOTYPE (fig. 46): USNM 343266 (field number USNM-FS 153416), an adult male, collected by R.B. Cocroft on December 12 1990.

TYPE LOCALITY: Explorer’s Inn, 30 km southwest of Tambopata Reserve (12°50’S / 69°17’W; 280 m.a.s.l.), Puerto Maldonado, Departamento Madre de Dios, Peru.

PARATYPES: USNM 269000, adult male, collected by R.B. Cocroft and K. Hambler on 12 July 1986; USNM 269001, adult male,



Fig. 46. Holotype of *Chiasmocleis royi*, sp. nov. (USNM 343266), in (A) dorsal and (B) ventral views. SVL = 20.6 mm.

collected by K. Hambler; USNM 346267–346268, two adult males, collected with the holotype; USNM 343033, adult female, collected by R.W. McDiarmid, in January 10, 1989; USNM 247432, juvenile, anonymous native inhabitant (information taken from label), in August 28, 1983; USNM 247433, juveniles, collected by R.B. Cocroft, on September 13, 1984. All paratypes collected at type locality.

Additional referred (nontype) material listed in appendix 1.

**DIAGNOSIS:** A medium-sized *Chiasmocleis*; SVL in males 18.8–23.1 mm ( $N = 24$ ); females 20.7–29.1 mm ( $N = 16$ ). Body ovoid and relatively slender; snout rounded in dorsal and lateral views. Four distinctive fingers present; all but FI fringed in males, less so in females; fingers not webbed; FI well developed with a subarticular tubercle usually present between the proximal phalanges; distinct subarticular tubercles present on all fingers; palmar tubercles protuberant, divided; relative finger lengths  $I < II < IV < III$ . Five

distinctive, well-developed toes present; toes fringed, less so in female; toes basally webbed in both sexes; TI with a distinct well-developed subarticular tubercle; adpressed TI does not reach or barely reaches subarticular tubercle of TII; adpressed TV does not reach or reaches only to the middle of the middle subarticular tubercle of TIV; TII–IV with terminal discs, usually more developed in females, but also present in males; relative toe lengths  $I < II < V < III < IV$ . Males with dermal spines on fingers and toes, more numerous and more developed in males. Males with few spines on anterior portion of chin (may be absent in some specimens). Vocal sac well developed, black, directed anteriorly when males are actively calling (pl. 12G). The femoral line is always present.

**COMPARISONS:** *Chiasmocleis royi* differs from *C. antenori* by having four externally evident fingers (FI not evident externally in *C. antenori*), five externally evident toes (TI not evident), rounded toe tips (toe tips

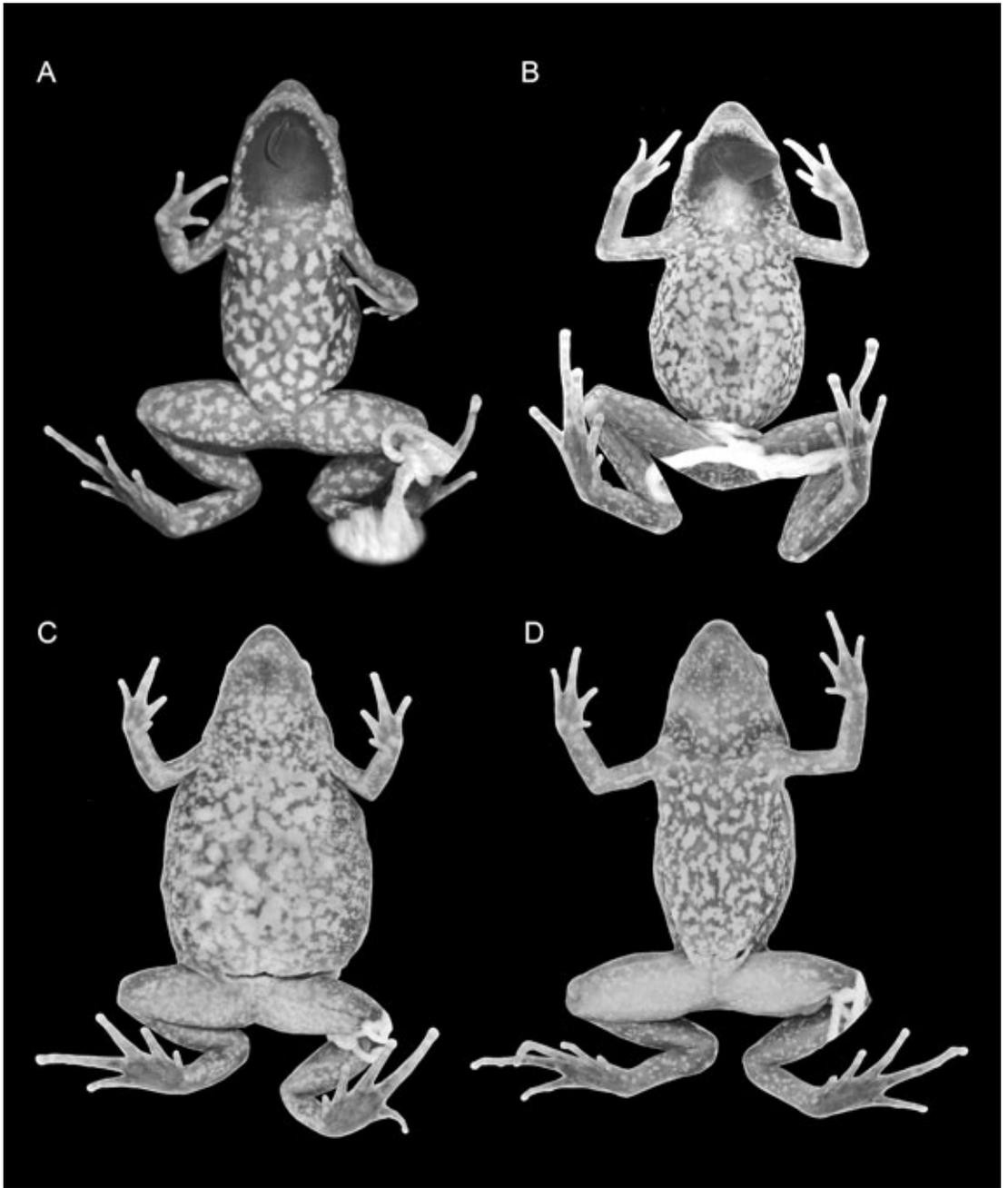


Fig. 47. Variation of ventral color pattern in *Chiasmocleis royi*, sp. nov. (A) Male, from Parque Ambiental Chico Mendes, Rio Branco, Acre, Brazil (UFAC-RB 3539). (B) Male, paratype, from Puerto Maldonado, Madre de Dios, Peru (USNM 343268, paratype). (C–D) Females, Guajará-Mirim, Rondônia, Brazil (CHUNB 23547, 25555, respectively).

pointed), and a reticulated venter (dark with scattered light spots). It differs from *C. albopunctata* by the absence of white blotches on the snout and dorsum (present in *C. albopunctata*), its light venter with dark mottling (dark with white dots and blotches in *C. albopunctata*), and its advertisement call (see text for details). It differs from *C. anatipes* by having basal webbing on toes of males (extensive webbing in males *C. anatipes*) and by its mottled venter (dark spots in *C. anatipes*). The new species is distinguished from *C. avilapiresae* by its smaller size (mean SVL of *C. avilapiresae* 32.0 mm in females), its having basally webbed feet in males (extensively webbed in *C. avilapiresae*), a mottled venter (usually blotched in *C. avilapiresae*), and a slender body (robust in *C. avilapiresae*), and by its advertisement call (table 2). The new species differs from *C. bassleri* in having a mottled venter (large dark spots over a light venter in *C. bassleri*), by the absence of an inguinal blotch (present in *C. bassleri*) and the presence of the femoral line (absent in *C. bassleri*), and by its advertisement call (table 2). The new species differs from *C. carvalhoi* in having four externally evident fingers (FI not evident externally in *C. carvalhoi*) and five externally evident toes (TI not evident). *Chiasmocleis royi* differs from *C. devriesi* by its smaller size (SVL of the holotype *C. devriesi* 42.2 mm), its mottled venter (large dark spots over a light venter in *C. devriesi*), presence of a femoral line (absent in *C. devriesi*), and its slender body (robust in *C. devriesi*). It is distinguished from *C. hudsoni* by a round finger I tip (tip slightly pointed in *C. hudsoni*), the presence of a femoral line (absent in *C. hudsoni*), its having a vocal sac protruding forward when calling (vocal sac round, not protruding forward in *C. hudsoni*), and by its advertisement call (table 2). *Chiasmocleis royi* differs from *C. magnova* in having all fingers fully developed (fingers I and IV reduced in *C. magnova*) and by containing many small, pigmented, eggs in oviduct (few large, unpigmented, eggs in *C. magnova*; Moravec and Köhler, 2007). *Chiasmocleis royi* is distinguished from *C. shudikarensis* by its basal webbing in toes of males (extensive webbing in *C. shudikarensis*), the absence of an inguinal blotch (present in *C. shudikarensis*),

a vocal sac protruding forward when calling (vocal sac round, not protruding forward in *C. shudikarensis*: see pl. 14A–B), and its advertisement call (table 2). *Chiasmocleis royi* differs from *C. superciliarba* by the absence of inguinal blotches (present in *C. superciliarba*), by the mottled venter (with large dark spots), and by its advertisement call (table 2). Finally, it differs from *C. tridactyla* in having four externally evident fingers (FI not evident externally in *C. tridactyla*), five externally evident toes (TI not evident), rounded toe tips (toe tips pointed), and a reticulated venter (dark with scattered light spots).

The new species has been historically confused with *Chiasmocleis ventrimaculata* (Croft and Hamblen, 1989; De la Riva, 1995; Schlüter, 2005; Peloso and Sturaro, 2008), from which it differs by having a smaller, more slender body (usually more robust in *C. ventrimaculata*), ventral pattern usually reticulated, becoming more densely reticulated on ventral thigh (brown spots in *C. ventrimaculata*), longer finger IV, with tip reaching distal tubercle of finger III (finger shorter in *C. ventrimaculata*, finger tip does not pass the distal margin of the proximal tubercle on finger III), and a femoral line present (femoral line not visible in the photos of the holotype and lacking according to M.S. Hoogmoed personal notes: “back of thighs without light line”; also lacking in all other specimens examined).

**DESCRIPTION OF THE HOLOTYPE** (fig. 46): Body ovoid, relatively slender. Head short, wider than long (HW  $1.2 \times$  HL); head slightly narrower than body; snout rounded in dorsal and lateral profiles; nostrils not protuberant, positioned anterolaterally, directed laterally. IOD  $2.2 \times$  IND. *Canthus rostralis* poorly defined, round in cross section; loreal region slightly convex. Eyes small. No occipital fold present, supratympanic fold visible; tympanum not apparent externally. Upper jaw projecting beyond lower; lower lip with truncate, trilobed anterior margin; few spicules on chin present; tongue large, elongated, with free lateral and posterior edges; vocal slits present, extended through most of the extent of the jaw, choanae small, rounded, widely separated, just anterior to eye; vomerine teeth absent. Vocal sac large and prominent, dark colored, directed forward.

Forelimb slender; all fingers developed, nearly round in cross section; no webbing between fingers; relative finger lengths  $I < IV < II < III$ ; tips rounded, without discs. Subarticular tubercle usually not visible in FI; subarticular tubercles on remaining fingers present but not very developed and not prominent; one subarticular tubercle on FII and FIV, two on FIII; proximal tubercle more prominent than distal, which is hardly visible; no supranumerary tubercles; palmar tubercle not visible, thenar tubercle present, large, round not very prominent; outer metacarpal tubercle present. All fingers with many dermal spicules laterally.

Legs short (combined THL, TBL and FL  $1.57 \times$  SVL); relatively robust, lacking tubercles, tibial and tarsal ridges or warts; toes not webbed (a very rudimentary vestige of web between TIII–TIV and TIV–TV is present and may be considered as basal webbing by some observers); TI weakly developed (tip fails to reach subarticular tubercle of TII), without a visible subarticular tubercle; toe tips rounded with small discs on all but TI. Subarticular tubercles present in all toes except TI; no outer metatarsal tubercle. TI barely reaches proximal margin of the tubercle of TII; TV reaches distal margin of proximal subarticular tubercle of TIV; relative toe lengths  $I < II < V < III < IV$ . Toes with few lateral dermal spicules.

Skin mostly smooth dorsally and ventrally, with scattered spines, especially on dorsum, hind limbs, fingers, and toes.

MEASUREMENTS OF THE HOLOTYPE: SVL 20.6, HL 4.0, HW 5.3, ED 1.5, IOD 3.2, IND 1.4, END 1.4, THL 9.0, TBL 8.4, FL2 13.5, 4TD 0.7.

VARIATION: Throat in males is dark brown or black and a vocal sac can be easily observed in adult male specimens. Ventral patterns usually consist of dense grayish or dark brown vermiculations against a light background (figs. 46, 47, pl. 12B), but in some specimens it consists of numerous small dark spots and stains (fig. 47B).

Color in life seems to be variable. Dorsal color varies from brown to blackish or reddish (pl. 12). Dorsum is not uniformly colored and may show white, orange, or black mottling. A middorsal line is present in most specimens examined, but it may be absent, while the

femoral line is always present. Dorsal portion of forelimbs either has the same overall pattern as dorsum, or is either orange or reddish.

ETYMOLOGY: The specific epithet is used as a noun in the genitive case and honors Roy McDiarmid, friend and researcher at the USGS Patuxent Wildlife Research Center and National Museum of Natural History, Washington, DC. Roy has been actively studying frogs in South America for a long time. He was the first one to call the attention of P.L.V.P. to the possibility of a species complex within *Chiasmocleis ventrimaculata* and continuously encouraged us to describe this new form, which he first collected, along with other colleagues, over 20 years ago.

CALL AND TADPOLES: Schlüter (2005) described a call of *Chiasmocleis ventrimaculata* from Panguana, Madre de Dios, Peru. The specimens are actually representatives of *C. royi*. The range of the dominant frequency is 5000–7000 Hz. We had access to additional calls of the species, deposited at the USNM collection, made at Tambopata, Peru, by R. Cocroft (fig. 48). The call is composed of a repetitive series of multipulsed notes (mean  $14.6 \pm 0.7$  pulses per note, 12–16,  $N = 109$ ) emitted at a rate of 503.2 notes/minute. Mean note duration is  $89.5 \pm 5.2$  ms (77.0–104.0,  $N = 109$ ) and mean interval between notes  $21.9 \pm 4.4$  ms (15.0–41.0,  $N = 107$ ). Pulse duration was  $4.0 \pm 0.8$  ms (3.0–7.0,  $N = 201$ ). Mean dominant frequency, belonging to the second harmonic, was  $7629.1 \pm 1204.0$  Hz (5512.5–13953.5,  $N = 109$ ). The fundamental frequency is  $3729.9 \pm 526.1$  (3273.0–4823.4). Two harmonics with frequencies higher than the dominant frequency could be seen.

Tadpoles are unknown.

REMARKS: *Chiasmocleis royi* has been historically confounded with *C. ventrimaculata* (De la Riva, 1995; Morales and McDiarmid, 1996; Peloso and Sturaro, 2008; Von May et al., 2009), and most of the data on ecology published on the latter actually refers to the new taxon named here (Cocroft and Hamblen, 1989; Schlüter and Salas, 1991). The two are not, to our knowledge found in sympatry (fig. 41) with *C. ventrimaculata* showing a more septentrional distribution than *C. royi*.

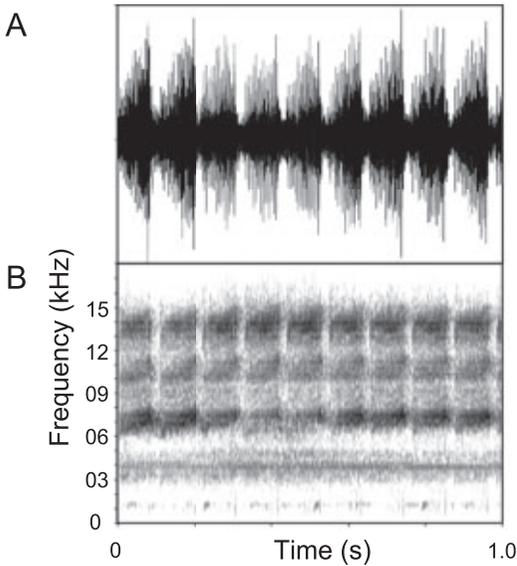


Fig. 48. Advertisement call of *Chiasmocleis royi*. (A) Oscillogram and (B) spectrogram of a series of nine consecutive notes emitted by a calling male from the type locality, at Tambopata, Madre de Dios, Peru; recorded on 12 December 1990, at 23.4° C air temperature (USNM 343268, paratype; recorded by R.B. Cocroft; recording number USNM tape 269, cut 13).

Genetic distances between the three specimens of *C. royi* included in the phylogenetic analysis are given in table 13.

DISTRIBUTION (fig. 41): Known from eastern and southern Peru, northern Bolivia, and western Brazil.

DISCUSSION  
SYSTEMATICS

We provide an overview of the current knowledge and taxonomy of *Chiasmocleis* in the Amazon and Guiana Shield regions. Given the geographical scope we attempted to cover, we regret that many topics and populations could not be included. Nonetheless, this is, by far, the most complete sampling for *Chiasmocleis* systematics in the study area. Our findings are consistent with the recognition of 16 species: *C. albopunctata*, *C. anatipes*, *C. antenori*, *C. avilapiresae*, *C. bassleri*, *C. carvalhoi*, *C. devriesi*, *C. haddadi* (described and named here), *C. hudsoni*, *C. magna*, *C. papachibe* (described and named

TABLE 13  
Uncorrected pairwise distances between 16S sequences of *Chiasmocleis royi*

Locality	1	2
1 <sup>a</sup> Peru: Madre de Dios (KU 215540)		
2 Peru: Madre de Dios (KU 215542)	0.006	
3 <sup>b</sup> Peru: Madre de Dios (ROM 40139) <sup>a</sup>	0.004	0.006

<sup>a</sup> Sequences for KU 215540 derive from Genbank and were originally labeled as *Chiasmocleis* “*ventrimaculata*.” We have examined the specimen and included it in the type series of *Chiasmocleis royi*, sp. nov., and labeled it accordingly in the phylogenetic tree (fig. 8).

<sup>b</sup> Sequences for ROM 40139 derive from Genbank and were originally labeled as *Chiasmocleis* “*ventrimaculata*.” We did not examine the specimen for phenotypic characters and left it labeled as “*C. ventrimaculata*” in our phylogenetic tree (fig. 8). Based on its phylogenetic position and geographic location, we consider this specimen to be a representative of *C. royi* pending examination of the voucher.

here), *C. royi* (described and named here), *C. shudikarensis*, *C. superciliarba*, *C. tridactyla*, and *C. ventrimaculata*. *Chiasmocleis jimi* is considered a junior synonym of *C. hudsoni*. See table 14 for a summary of all taxonomic rearrangements proposed in the present study.

A few new questions and problems arose during this study, and we particularly point to the problematic taxonomy of *Chiasmocleis bassleri* (and its putative relative, *C. superciliarba*), and to the need for further sampling and ecological studies in the *C. hudsoni* clade. It is extremely important that future work on *Chiasmocleis* account for variation among populations and that effort is directed to the collection of tadpoles, the recording of advertisement calls, documentation of reproductive behavior, and the collection of tissue samples to improve coverage of populations in phylogenetic studies. These data are essential for further exploration of systematics, geographical variation, and character evolution in the group.

The *Chiasmocleis bassleri* Clade; a Complex of Species?

Although we assign several populations to *C. bassleri*, this is done tentatively. Some populations referred to *C. bassleri* remain

TABLE 14  
**Summary of nominal taxa associated with *Chiasmocleis***

Review of names associated with *Chiasmocleis* and dealt with in this study. Original author and publication date is given for all specific names related to current and former members of *Chiasmocleis* is given, followed by combination after the review and a justification of taxonomic action taken, if any.

Specific epithet	Original generic combination	Author	Combination after review	Action taken
<i>albopunctata</i>	<i>Engystoma</i>	Boettger, 1885	<i>Chiasmocleis albopunctata</i>	None
<i>anatipes</i>	<i>Chiasmocleis</i>	Walker and Duellman, 1974	<i>Chiasmocleis anatipes</i>	None
<i>anteriori</i>	<i>Syncope</i>	Walker, 1973	<i>Chiasmocleis anteriori</i>	Transferred to <i>Chiasmocleis</i> <sup>a</sup>
<i>avilapitresae</i>	<i>Chiasmocleis</i>	Peloso and Sturaro, 2008	<i>Chiasmocleis avilapitresae</i>	None
<i>bassleri</i>	<i>Chiasmocleis</i>	Dunn, 1949	<i>Chiasmocleis bassleri</i>	Transferred back to <i>Chiasmocleis</i> <sup>a</sup>
<i>boliviana</i>	<i>Chiasmocleis</i>	Parker, 1927	<i>Hamptophryne boliviana</i>	None
<i>carvalhoi</i>	<i>Syncope</i>	Nelson, 1975	<i>Chiasmocleis carvalhoi</i>	Transferred to <i>Chiasmocleis</i> <sup>a</sup>
<i>carvalhoi</i>	<i>Chiasmocleis</i>	Cruz, Carmaschi, Izecksohn, 1997	<i>Chiasmocleis lacrimae</i>	New specific name to avoid secondary homonym
<i>devriesi</i>	<i>Chiasmocleis</i>	Funk and Camatella, 2009	<i>Chiasmocleis devriesi</i>	None
<i>haddadi</i>	<i>Chiasmocleis</i>	This study	<i>Chiasmocleis haddadi</i>	Named here
<i>hudsoni</i>	<i>Chiasmocleis</i>	Parker, 1940	<i>Chiasmocleis hudsoni</i>	Transferred back to <i>Chiasmocleis</i> <sup>a</sup>
<i>jimi</i>	<i>Chiasmocleis</i>	Carmaschi and Cruz, 2001	<i>Chiasmocleis hudsoni</i>	Placed in the synonymy of <i>Chiasmocleis hudsoni</i>
<i>magnova</i>	<i>Chiasmocleis</i>	Moravec and Köhler, 2007	<i>Chiasmocleis magnova</i>	Transferred back <i>Chiasmocleis</i> <sup>a</sup>
<i>papachibe</i>	<i>Chiasmocleis</i>	This study	<i>Chiasmocleis papachibe</i>	Named here
<i>royi</i>	<i>Chiasmocleis</i>	This study	<i>Chiasmocleis royi</i>	Named here
<i>shudikarensis</i>	<i>Chiasmocleis</i>	Dunn, 1949	<i>Chiasmocleis shudikarensis</i>	None
<i>supercilialbus</i>	<i>Chiasmocleis</i>	Morales and McDiarmid, 2009	<i>Chiasmocleis supercilialba</i>	Transferred back to <i>Chiasmocleis</i> <sup>a</sup>
<i>tridactyla</i>	<i>Adelophryne</i>	Duellman and Mendelson, 1995	<i>Chiasmocleis tridactyla</i>	Transferred to <i>Chiasmocleis</i> <sup>a</sup>
<i>ventrimaculata</i>	<i>Engystoma</i>	Andersson, 1945	<i>Chiasmocleis ventrimaculata</i>	None

<sup>a</sup> Transferred from *Syncope*, where the taxon had been placed in the review by de Sá et al. (2012).

with their status undefined because our observations, particularly given the degree of morphological variation observed, do not allow reliable conclusions regarding their taxonomic status. Moreover, sampling included in the phylogenetic analysis is too small for any conclusive observations. Here, we briefly comment on some of these populations and highlight the importance of a directed effort to study variation in the *C. bassleri* complex. Specimens included in what we refer to as the *C. bassleri* complex are easily recognized by the combination of the following characters: presence of an inguinal blotch; venter white or cream with black or dark brown spots or stains; toes usually not fully webbed (webbing basal or absent); and femoral line absent. As described earlier (variation section under *C. bassleri*), the dorsal and ventral color pattern vary extensively (see fig. 23 and pl. 4), and some variation in body shape and measurements also exists (e.g., relative lengths of FIII and IV, and toes I and V; fig. 23). Populations from southern Brazilian Amazonia (Amazonas, Mato Grosso), and some from Colombia and Ecuador show a much more reticulated venter than other populations, including the holotype, which has large black spots on the venter (Dunn, 1949). The variable nature of this character (as observed in sympatric specimens from Peru) complicates any accurate assessments. It is possible that distinct species are syntopic in western Amazonia, further complicating the delimitation of species, but our current approach could not detect any obvious pattern.

Our phylogenetic analysis recovered two well-defined clades within *C. bassleri* (with arguably additional clades found within them; fig. 7). Genetic distances in the 16S between the specimens of *C. bassleri* are, however, relatively low (up to 4.5%: table 7).

A more detailed, integrative approach to taxonomy (including additional morphological, acoustic, and molecular data) is needed to resolve the taxonomic status of the populations here assigned to *Chiasmocleis bassleri* and *C. superciliarba*, as well as of additional populations for which we examined a very limited amount of material (i.e., from Colombia and Ecuador).

When describing *Chiasmocleis superciliarba*, Morales and McDiarmid (2009) proposed the recognition of a “*Chiasmocleis bassleri* group” on the basis of “flanks with one or two dark spots, but if the spots are not present, the flanks show a fine clear line at the junction of the ventral and dorsal pattern coloration; ventral patters with dark spots on a light background.” We find the diagnosis provided by Morales and McDiarmid (2009) for the *C. bassleri* species group inadequate. By their definition, *C. shudikarensis* could be included in the group on the basis that specimens show one dark spot in the inguinal region. The line at the juncture of the ventral and dorsal pattern coloration is what we refer to as a split stripe, but several specimens of *C. bassleri* have neither spots nor a split line on their flanks.

We were unable to sample *C. superciliarba* for our phylogenetic analysis, and although we think that a close relationship exist between *C. bassleri* and *C. superciliarba*, kinship can only be assumed. Nonetheless, the diagnostic characters suggested by Morales and McDiarmid (2009) do not hold, given the material we analyzed.

#### The *Chiasmocleis hudsoni* Clade: Taxonomy and Evolution

**TAXONOMY:** The topology of this clade, is substantially different from that of de Sá et al. (2012). Their specimen of *C. carvalhoi* (as *Syncope carvalhoi* in their analysis; see fig. 2) was found at a basal position, and sister to all remaining species in the clade (which also included *C. bassleri* in their results), while we recovered that same specimen nested within our samples of *C. antenori*. The two specimens labeled as *Syncope* sp. by de Sá et al. (2012) were found here to be part of *C. carvalhoi*. We have included three specimens of *C. tridactyla*, from Leticia, Colombia—this species was not sampled by de Sá et al. (2012). We have also named a new species, which is included in this clade (*C. haddadi*).

**EVOLUTION:** A few members of this clade show an advanced degree of miniaturization, which includes lost of vertebrae and digits (Silva and Meinhardt, 1999). Reproductive biology characters also are of great interest as

at least one species has a derived reproductive mode, with tadpoles developing inside bromeliads. Direct development has been postulated in other members of the clade as well, (Krügel and Richter, 1995; Moravec and Köhler, 2007), but to our knowledge never confirmed by empirical observations.

Unfortunately, limited data on osteology, as well as missing data on ecology and behavior precludes any detailed analysis of evolutionary trend in the clade. Fieldwork directed to collect data on reproduction and behavior of species in this clade can prove useful for understanding the evolution of reproductive biology of this very interesting lineage of frogs.

#### PHENOTYPIC VARIATION

Our results revealed some amount of variation in morphology (see species accounts) and advertisement call parameters (see call descriptions under each species account) in Amazonian and Guiana populations of *Chiasmocleis*. This is also true for non-Amazonian species of the genus (Caramaschi and Cruz, 1997; Cruz et al., 2007a,b). Thus, it is extremely important that population variation among populations of described species be studied for a more accurate definition of diagnostic characters and species boundaries (Frost et al., 1998). The lack of a more complete understanding of variation may lead to inaccuracies in diagnoses and species recognition. As an example, the comparative table presented by Funk and Cannatella (2009: 40, table 1) lacks most of the species of *Chiasmocleis* and the sample of characters is very limited, rendering it unsuitable for diagnosing any species of *Chiasmocleis* (their table was likely based solely on the literature, which is limited for many *Chiasmocleis* species). Although considerably more complete (20 species represented), the table presented by Morales and McDiarmid (2009: 76, table 1) is also not very reliable. Although they compared several species, the authors do not present a list of material examined, and therefore it is impossible to assess whether the table was based on the direct comparison of specimens or on the literature. Furthermore, inaccurate information is given such as: (1) the absence

of toe discs in *C. jimi* (considered here a synonym of *C. hudsoni*; toe discs present in most specimens examined and also reported in the original description, Caramaschi and Cruz, 2001); (2) dorsal pattern uniform in *C. bassleri* and *C. shudikarensis* (clearly not uniform in several specimens of *C. bassleri*, e.g., pl. 4, and in *C. shudikarensis*, e.g., pl. 7); (3) dorsal dermal spines absent in *C. shudikarensis* (conspicuously present in most males examined, indeed absent in most females). These inaccuracies render such comparative tables less reliable and prone to misidentifications. We regard both the tables provided by Funk and Cannatella (2009) and Morales and McDiarmid (2009) as of limited utility for any purpose regarding the taxonomy of *Chiasmocleis* and they should be avoided for the identification of species in the genus.

Many species of *Chiasmocleis* look alike, and the addition of characters is crucial for the progress of taxonomy in the group. We point out that although the degree of webbing on toes, development of fringes, presence/absence of femoral lines, presence/absence and distribution of dermal spines, presence/absence of an inguinal blotch, and general color pattern are useful characters, they should be carefully evaluated and used with caution. Sexual dimorphism—as well as ontogenetic variation—in toe webbing and the presence/distribution of dermal spines should be considered when comparing species. Fringes and dermal spines could be related to reproductive activity and also show some populational variation. Color patterns have been shown to change ontogenetically in several amphibian species including some species of the Microhylidae (Kraus and Allison, 2009), and the nature of this sort of variation within *Chiasmocleis* is, to this point, obscure.

Advertisement calls are also a powerful source of information for anuran systematics and this is no different with the Microhylidae. Despite the similar structure of most *Chiasmocleis* advertisement calls, usually composed of a series of multipulsed notes (Santana et al., 2009; but see Santana et al., 2012, for the peculiar call of *C. mantiqueira*), many diagnostic characters can still be extracted from analyses of well-recorded advertisement calls (i.e., call rate, number of pulses, frequency data).

## CHARACTER EVOLUTION

Optimization of phenotypic characters in the phylogeny of *Chiasmocleis* suggests that all characters evaluated have complex histories, with multiple transformations involved (e.g., multiple losses of dermal spines, and multiple appearances of the femoral line).

The optimization of dermal spines and degree of toe webbing were unambiguous and needed three and four steps, respectively (fig. 49). The presence of dermal spines in *Chiasmocleis* is apparently plesiomorphic and was lost three times, independently, in the group (fig. 49A). Although the presence of extensive webbing is widespread in Anura, including many other microhylids, the absence of extensive webbing is the plesiomorphic state in *Chiasmocleis* with four independent appearances of webbing in the group (fig. 49B). The amount of webbing in *Chiasmocleis* may be related to the ability of males for swimming and/or floating on water, but additional field observations will corroborate or refute this prediction.

Evolutionary history of the femoral lines is more complex and could not be unambiguously optimized. The optimization of this character requires at least four steps and four equally parsimonious alternative scenarios were found (fig. 50). These alternative scenarios are as diverse as the postulation of a single origin with three subsequent losses (fig. 50A) to four independent appearances of the femoral line (fig. 50D). Intermediate scenarios, involving independent appearances and reversals, are shown in figure 50B–C. The function of the femoral line is not known. Although a similar line is present in other gastrophrynine microhylids (e.g., *Hamptophryne boliviana*) the absence of the femoral line is the plesiomorphic state in *Chiasmocleis*.

In an attempt to understand the evolution of reproductive modes in *Chiasmocleis*, we optimized egg clutch size on the tree. Although information is missing for a few species, a single event of decrease in number of eggs per clutch is postulated on the branch leading to *C. magnova*, *C. antenori*, *C. carvalhoi*, and *C. tridactyla* (information on clutch size is not available for *C. tridactyla*; fig. 51).

Mapping of additional reproductive characters on the tree suggest that a complex

evolutionary scenario played out in the *C. hudsoni* clade (fig. 51). In addition to reduction in clutch size, endotrophic but free-swimming tadpoles were reported for *C. antenori* (Krügel and Richter, 1995). The presence of unpigmented eggs in *C. carvalhoi* and *C. magnova* has been associated to the presence endotrophic larvae (perhaps even direct development) in those species (see Nelson, 1975; Krügel and Richter, 1995; Moravec and Köhler, 2007), but this was never confirmed by field or laboratory observations. The amount of missing data on reproductive behavior for *Chiasmocleis*, and especially in this miniaturized species, hinders a better understanding of the transformation series involved in the appearance of endotrophic tadpoles and, potentially, direct development in the group.

Miniaturization and “terrestrialization” (i.e., evolution of endotrophic tadpoles or direct development) have been associated with higher rates of diversification and evolutionary success in frogs, including cophyline (Andreone et al., 2005) and asterophryne (Zweifel, 1972) microhylids, although empirical tests did not find this to be correct in all cases (Gomez-Mestre et al., 2012; Zimkus et al., 2012). It appears that this is also not the case for New World microhylids. Endotrophic tadpoles are present at least in *Chiasmocleis* (see above), *Myersiella* (Izecksohn et al., 1971: monotypic), and *Synapturanus* (Menin et al., 2007: three known species). Although the low number of species can be a result of poor taxonomic knowledge (e.g., we are aware of additional *Myersiella* and *Synapturanus* species awaiting description: P.L.V.P., personal obs.) we do not expect the number of species to increase drastically so as to represent hyperdiverse clades. Notwithstanding the fact that data on ecology are missing for key taxa (fig. 51), it seems clear to us that miniaturization and terrestriality (both conspicuous characteristics of species in the *C. hudsoni* clade) did not have a major impact in the diversification of *Chiasmocleis*. At any rate, only when we have information on egg development for all species in the *C. hudsoni* clade will it be possible to assess the impact of this novelty in the evolution of the group.

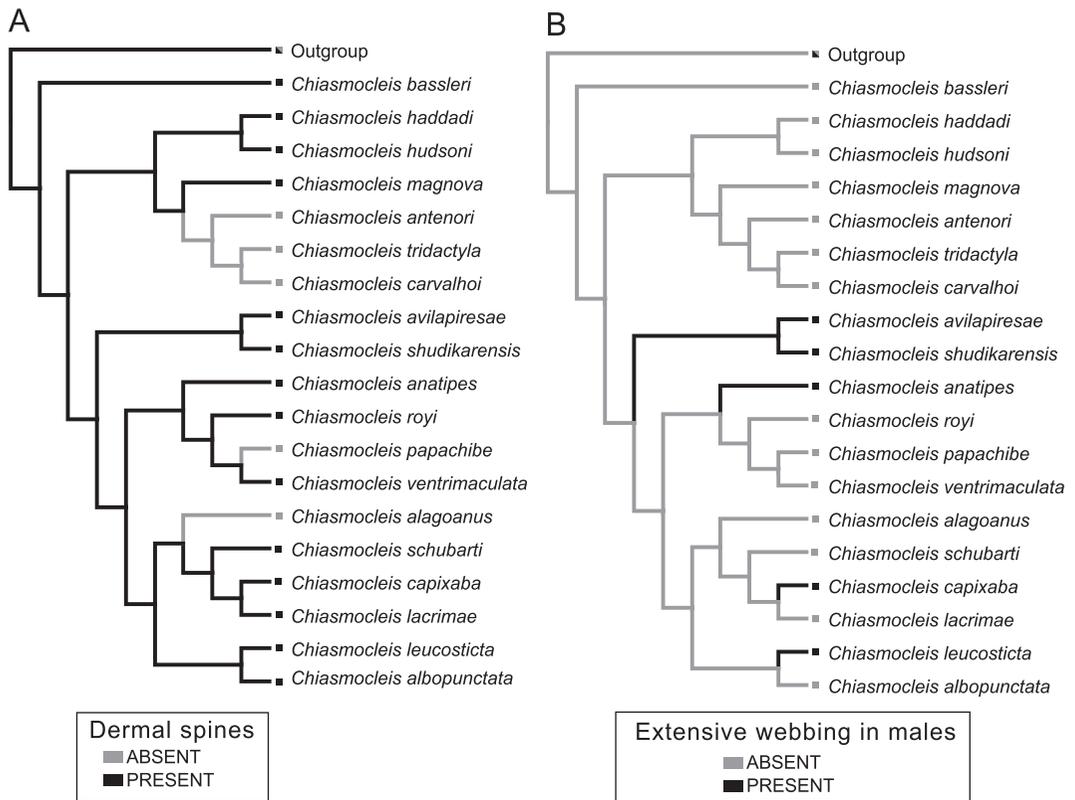


Fig. 49. Optimization of absence (gray) and presence (black) of dermal spines (A, three steps) and of the amount of webbing in males (B, four steps) of *Chiasmocleis*. Optimizations of both characters required three and four steps, respectively for dermal spines and amount of webbing. Presence of spines is the plesiomorphic state, and they were lost three times independently, while the absence of webbing is the plesiomorphic state and it appears four times independently. Taxonomy updated to the one proposed in the present work. *Chiasmocleis devriesi* is nested within *C. anatipes* and is not shown.

### Notes on Reproductive Ecology

Our results suggest that the evolution of reproductive ecology in *Chiasmocleis* did not happen in a trivial manner. The addition of taxa and characters associated with reproduction into the analyses can shed light on this issue in the future. Unfortunately, there is little data available on the natural history of the species in the genus. Here, we summarize some of the data available for *Chiasmocleis* from Amazonia and the Guiana Shield and highlight the need for additional fieldwork aiming to collect natural history data and observations.

Most species are associated with “Terra Firme” habitats and breed in temporary ponds inside the forest (pls. 13, 15). As with

many gastrophrynine microhylids, *Chiasmocleis* are usually explosive breeders. It is not uncommon to find reproductive specimens in large groups, with dozens or even hundreds of individuals calling and breeding simultaneously after heavy rains (Zimmerman and Bogart, 1988; Rodrigues et al., 2008; see also pls. 13–14). Specimens can also often be found calling in isolation from other males, as has been observed at least for *C. bassleri* and *C. hudsoni* (Rodrigues et al., 2008; Santana et al., 2009). Most species usually call from burrows, under fallen logs, stones, or leaf litter, or near bodies of water, but can also call in the open, either on vegetation or free floating on water (Lima et al., 2005; Schlüter, 2005; Peloso and Sturaro, 2008; Santana et al., 2009). Obviously, calling site is

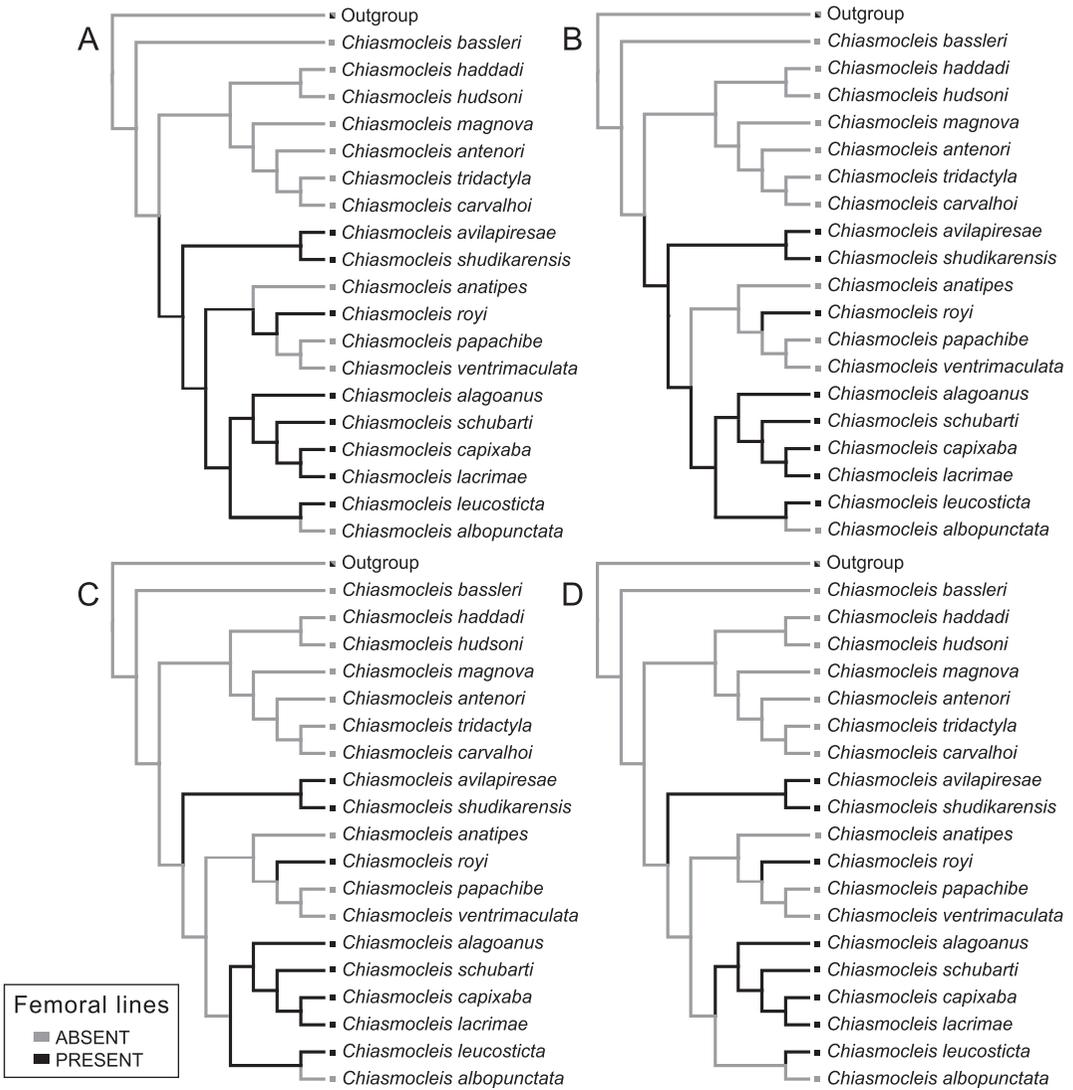


Fig. 50. Optimization of absence (gray) and presence (black) of the femoral line in *Chiasmocleis*. Four equally parsimonious alternative explanations, with four steps each. Scenario (A) shows a single appearance of the femoral line, with three reversals; scenarios (B) and (C) depicts alternative scenarios, involving appearances and reversals to absence; scenario (D) postulates four independent appearances of the femoral line. Taxonomy updated to the one proposed in the present work. *Chiasmocleis devriesi* is nested within *C. anatipes* and is not shown.

likely to vary with microhabitat availability and substrate composition (e.g., number of logs, water availability, presence of rocks, etc). *Chiasmocleis royi* is known to call exposed on floating vegetation of logs, sometimes partially submerged (Schlüter, 2005; see pl. 13), and we have observed *C. shudikarensis* calling either exposed or com-

pletely hidden. At least *C. albopunctata* and *C. shudikarensis* (pl. 14A–B) are known to call both on land and in the water, and in the latter case they call anchored to vegetation with the posterior part of the body submerged (Oliveira-Filho and Giaretta, 2006, for data on *C. albopunctata* and our personal observation for *C. shudikarensis*). Lima et al. (2005)

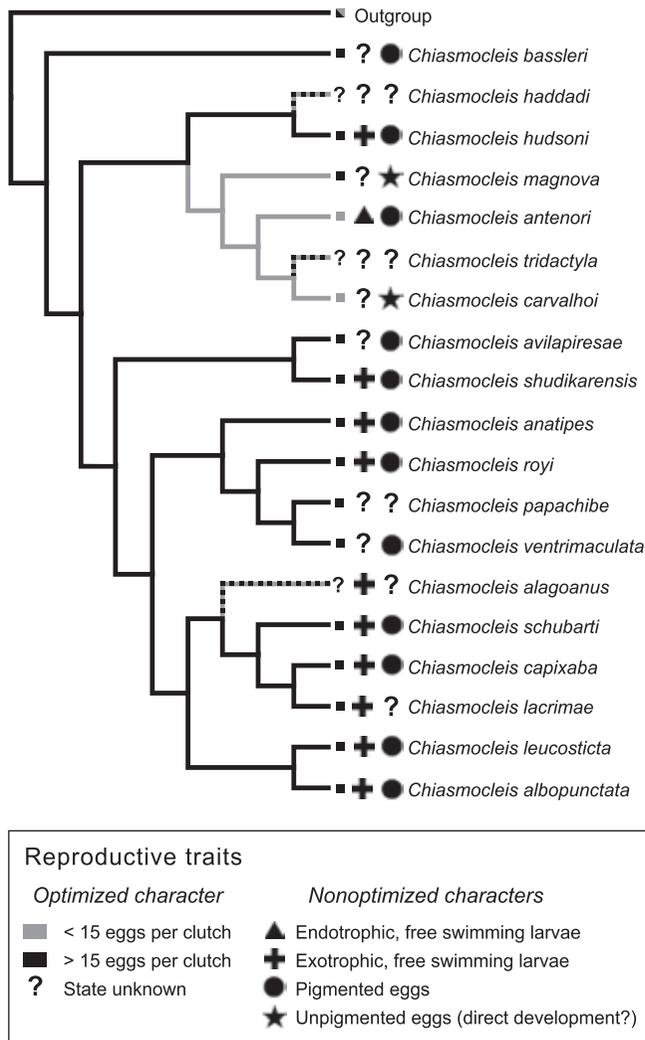


Fig. 51. Optimization (egg clutch size) and distribution (tadpole energy source and egg pigmentation) of some characters associated with reproductive biology of *Chiasmocleis*. Taxonomy updated to the one proposed in the present work. *Chiasmocleis devriesi* is nested within *C. anatipes* and is not shown.

reported specimens of *C. shudikarensis*, from Manaus, Amazonas, Brazil, calling while floating on water. Multiple specimens of *Chiasmocleis bassleri* from Ilha da Pedra, Rondônia, Brazil, were calling syntopically and floating on the water (A.P. Lima, personal commun.), whereas the single specimen observed in Aripuanã was calling on land (D. Santana, personal commun.). Given these observations, it is likely that several *Chiasmocleis* can call both on land and in water, but limited observations impede a generalized assessment of the plasticity of this behavior.

Eggs of most species are laid on the surface of temporary ponds (Zimmerman and Bogart, 1988; Rodriguez and Duellman, 1994; Lima et al., 2005) and usually consist of a gelatinous mass containing a large number of eggs (pl. 15C). Clutch size was reported for *C. hudsoni* (269–412 eggs: Rodrigues et al., 2008), *C. shudikarensis* (around 230 eggs: Lima et al., 2006), and *C. ventrimaculata* (222–248 eggs: Rodriguez and Duellman, 1994). Duellman (1978) reported 151–250 ovarian eggs in *C. bassleri*, and 210 in *C. ventrimaculata*. Peloso and Sturaro (2008)

reported over 1900 eggs (both mature and immature) in the abdomen of a gravid female *C. avilapiresae*.

Noteworthy exceptions to the general trend in reproductive behavior within the group are *C. antenori*, *C. carvalhoi*, and *C. magnova* (and presumably *C. tridactyla*). *Chiasmocleis antenori* has an aquatic endotrophic larvae (Krügel and Richter, 1995), which develops in bromeliads. *Chiasmocleis carvalhoi* and *C. magnova* both have very few but large eggs, and were suggested to reproduce by direct development or in a fashion similar to *C. antenori* (Nelson, 1975; Moravec and Köhler, 2007). The low number of oviductal eggs in *C. antenori*, *C. carvalhoi*, and *C. magnova* suggests that they are not explosive breeders. The complex evolutionary scenario involved in the evolution of reproductive modes in *Chiasmocleis* is depicted in figure 51.

#### CONSERVATION

Of all the species of *Chiasmocleis* treated here, none is listed as threatened by the International Union for Conservation of Nature and Natural Resource's Global Amphibian Assessment (IUCN, 2012). Most species are listed as of "least concern" (LC), while *C. devriesi* and *C. magnova* are listed as "data deficient" (DD). *Chiasmocleis jimi*, listed as DD, is considered here a junior synonym of *C. hudsoni*, which in turn is listed as LC.

The three new species of *Chiasmocleis* described herein require a conservation assessment in this context. *Chiasmocleis haddadi* is known from a few localities in French Guiana and Brazil (fig. 31). The area of potential occurrence of this species is poorly sampled, and although the species occurs within two protected areas in Brazil, we think that current data are insufficient to assess the conservation status of this species and it should therefore be listed as DD. *Chiasmocleis papachibe* is known from only three specimens from two localities in the state of Pará, and so should also be listed as DD. Inventories in the vicinities of the localities of known occurrences of both *C. haddadi* (especially in Brazil) and *C. papachibe* are urgently needed, as the areas are the center of intense habitat degradation, deforestation, mining, and human occupancy.

*Chiasmocleis royi* is known from several localities in Peru, Bolivia, and Brazil, including some protected areas. The species is locally abundant in several areas where it occurs and may be somewhat tolerant of habitat degradation. It also occurs within protected areas in Peru (e.g. Manu National Park) and Brazil (e.g. Parque Estadual Guajará-Mirim). Thus, we consider that this species should be treated as of least concern.

#### FUTURE WORK

Until recently, very little was known about the phylogenetic affinities of the species of *Chiasmocleis*. This began to change with the work by de Sá et al. (2012), and continued with the present work. Despite this recent advance, a complete phylogenetic hypothesis is still lacking as many species have been left out, especially from the Atlantic Rainforest. We expect future contributions to increase taxon and character sampling used for inferring the phylogeny of *Chiasmocleis*. We also envision benefits from the inclusion of phenotypic characters into the phylogenetic estimation. Being a widespread taxon in South America and occurring in several biomes, the genus has the potential to be of great relevance for biogeographic studies (e.g., Tonini et al., 2013) and this should be further explored. The phenotypic diversity that exists within *Chiasmocleis* (for examples, see: Haddad and Hödl, 1997; Canedo et al., 2004; Santana et al., 2012) can also be more deeply explored once a more complete and robust phylogenetic hypothesis is available and ecological knowledge of the group increases.

On the taxonomic front, we expect that more species of *Chiasmocleis* will continue to be named as more populations are evaluated and incorporated into revisionary studies. Integrating additional data, beyond the obvious soft morphology and dominant frequency of advertisement calls, will certainly improve knowledge of diversity and variation within *Chiasmocleis*.

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## APPENDIX 1

LIST OF SPECIMENS EXAMINED FOR  
MORPHOLOGICAL CHARACTERS

For collection and field number acronyms see Material and Methods. Specimens listed here are in addition to any types (holo- or paratypes) listed in the text, for newly described taxa. Types of previously known species are listed here.

*CHIASMOCLEIS ALBOPUNCTATA* (*N* = 8)

**BRAZIL:** **Goiás:** U.H.E. Serra da Mesa, Minaçu (MPEG 9010–9014); **Mato Grosso:** Querência (MPEG 21074); **Tocantins:** Araguatins (MPEG 29414); **PARAGUAY** (ZMB 10588, *holotype*).

*CHIASMOCLEIS ANATIPES* (*N* = 7)

**ECUADOR:** **Napo:** Jatun Sacha, 01°04'S / 77°36'W (QCAZ 51041–51042); Limoncocha, 00°24'S / 76°36'W (LACM 72713–17275, 72718–72719); **Orellana:** Chiroisla, Río Napo, banco sur, 00°34'S / 75°55'W (QCAZ 44341–44342); **Sucumbios:** Santa Cecilia 00°03'N / 76°58'W (KU 146035, *holotype*, examined from photographs, UMMZ 132897, *paratype*).

*CHIASMOCLEIS ANTENORI* (*N* = 7)

**BRAZIL:** **Acre:** Parque Nacional da Serra do Divisor, Rio Mõa, 07°30'S / 73°43'W (MTR 28350, 28373, 28407, 28416).

**ECUADOR:** **Napo:** Puerto Libre, Rio Aguariço, 00°04'S / 76°44'W (KU 124004–06, *paratypes*).

*CHIASMOCLEIS AVILAPIRESAE* (*N* = 206)

**BRAZIL:** **Amazonas:** Reserva Extrativista do Baixo Juruá, Rio Juruá, Juruá, 3°45'S / 66°05'W (INPA 17258–17259, *paratypes*); Porto Urucu, 4°53'S, 65°20'W (MPEG 5169, *paratype*); Lago Ayapuá, Rio Purus, Beruri, 4°24'S / 62°15'W (INPA 14218, 14224, *paratypes*); Igarapé Estrema, left bank of Rio Aripuanã, Aripuanã, 6°17'S / 60°23'W (INPA 13102, *paratype*); Floresta Nacional do Pau-Rosa, Rio Paracopni, Maués, 3°55'08"S / 58°24'20" (MPEG 27768, 27770–72, 27790–27795); **Mato Grosso:** Alta floresta, Rio Cristalino –9°34'38.9"S / 55°55'18.9"W (CHUNB 46802–46851, OMNH 41434); Aripuanã, 10°10'S / 59°28'W (MNRJ 44231–80, *paratypes*, UFMT 7124, 7135, 7142); **Pará:** Parque Nacional da Amazônia, Rio Tapajós, Itaituba, 04°40'S / 56°33'W (MPEG 18571–18573, 23287–23298, *paratypes*); Floresta Nacional de Caxiuanã (MPEG 23299, *holotype*, MPEG 23300–23306, *paratypes*); Tapuama, Rio Xingu, Altamira, 3°36'39"S, 52°20'26"W (MPEG 23280, *paratype*); Fazenda Caracol, Rio Xingu, Anapu, 3°27'10"S / 51°40'31"W (MPEG 23277–23279, *paratype*); Fazenda Riacho, Monte Verde, Portel, 3°15'S / 50°19'W (MPEG 22787, *paratype*); Barragem da Pêra, Serra dos Carajás, Parauapebas, 6°04'S / 49°54'W (MPEG 23388, *paratype*); Novo Progresso, 07°08'S / 55°22'W (CHUNB 34600–34612, 40250); Reserva Biológica de Tapirapé, Marabá, 05°40'32"S 50°18'10"W (MZUSP 139431); Serra dos Carajás, Parauapebas, 06°04'S / 49°54'W (MPEG 23339–23341, *paratypes*); **Rondônia:** Cachoeira

Nazaré, west bank of Rio Ji-Paraná, 09°45'S / 61°55'W (USNM 266139–266141, *paratypes*); Ilha do Búfalo, Rio Madeira 09° 08' 37" S 64° 30'58"W (14868–69); Nova Brasília, 11°09'S / 61°34'W (USNM 284500–284501, 565956, *paratypes*); Nova Colina, Rio Morim, 10°50'S / 61°43'W (USNM 565955, *paratype*); Fazenda Jaburi, Espigão do Oeste, 11°36'S / 60°44'W (CFBH 5132–5133, *paratypes*, UFAC-RB 3235); Parque Estadual Guajará-Mirim, Rio Formoso –10°19'17"S / 64°33'48"W (CHUNB 23798–23800, OMNH 37338, 37340–37342).

*CHIASMOCLEIS BASSLERI* (*N* = 104)

**BRAZIL:** **Acre:** Floresta Estadual do Antimary, Uirapuru, 09°19'S / 68°20'W (UFAC-RB 4303); Parque Nacional da Serra do Divisor, Rio Juruá-Mirim (UFAC-RB 3872); Parque Nacional da Serra do Divisor, Cruzeiro do Sul, 07°30'S / 73°43'W (UFAC-RB 1611, MTR 28353, 28391, 28402); Reserva Extrativista Riozinho da Liberdade, Tarauacá 07°57'20"S / 72°04'37"W (UFACF 623); Reserva Extrativista Porto Dias, Plácido de Castro 10°00'S / 66°46'W (UFAC-RB 1251); Reserva florestal de Humaitá (UFAC-RB 1112); Porto Walter 8°15'31.2"S / 72°46'37.1"W (OMNH 34829, 36506–36507); **Amazonas:** Floresta Nacional do Pau-Rosa, Rio Paraconi, Maués, 3°55'08"S / 58°24'20" (MPEG 27764–27767); Porto Urucu (MPEG 5170); Fazenda Passo Formoso, Manicari, 08°33'S, 61°26'W (MPEG 18574); Madereira Scheffer, Rio Ituxi 8°28'46"S / 65°42'60"W (OMNH 36877–36880, 37301, 37311–37312, 37321); Tabatinga (ICN 50196, examined from photographs); **Mato Grosso:** Alta Floresta, Rio Cristalino –9°34'38.9"S / 55°55'18.9"W (CHUNB 46799–46801, 46873, OMNH 41383–41384); Aripuanã (UFMT 7136, 7548, 7799, 8066); **Pará:** Parque Nacional da Amazônia, Rio Tapajós, Itaituba, 04°40'S / 56°33'W (MPEG 18574); Juruti (MPEG 22557); **Rondônia:** Albumã (UFAC-RB 172); Nova Colina, 10°50'S / 61°43'W (USNM 595567); Ilha da Pedra, Rio Madeira, 09°09'32"S / 64°38'02"W (INPA 14939–14940); Parque Estadual Guajará-Mirim, Rio Formoso, 10°19'17"S / 64°33'48"W (CHUNB 23801–23803); Nova Brasília (USNM 284496, 565957–565962).

**COLOMBIA:** **Amazonas:** Leticia, Cantadera Tancaná (ICN 50207, examined from photographs); Leticia, Comunidad Jitoma (ICN 46845, 50197, examined from photographs); Leticia, Comunidad Monilla Amena Jusie (ICN 50202); Leticia, Casa de Rodolfo Mesa (ICN 50205, examined from photographs); Leticia, Via Tarapacá (ICN 50198, 50209–50211, 50213, 50216, 50220–50223, 50249, examined from photographs); **Caquetá:** Puerto Abeja, Rio Mesay (ICN 42731–42732, examined from photographs); **Vaupés:** Taraira, Estación Caparí (ICN 36458, examined from photographs).

**ECUADOR:** **Orellana:** Estación Científica Yasuní, PUCE, 00°40'S / 76°23'W (QCAZ 17515, QCAZ 24565); **Sucumbios:** Lago Agrio, 00°06'N / 76°55'W (KU 126668); Santa Cecilia, 00°03'N / 76°59'W (KU 124000, 150625, 150627); **Morona-Santiago:** Miazal, 02°37'S / 77°48'W (USNM 236949–236953).

**PERU:** **Loreto:** Rio Utoquinia–Rio Tapiche, near the Brazilian border (AMNH 42699, *holotype*); Junction of Rio Sucusari and Rio Napo (KU

220478) 1.5 km north of Teniente Lopez (KU 222103–07); **Ucayali:** Balta, Rio Curanja, 10°06'S / 71°14'W (KU 197033–197046).

*CHIASCOCLEIS CARVALHOI* (*N* = 7)

**PERU:** **Loreto:** Estirón, Rio Ampiyacú, 03°22'S / 72°00'W (MZUSP 36429, *holotype*; AMNH 88065, *paratype*); Puerto Almendra, Arboreto UNAM, 03°50'S / 73°22'W (JMP 1376); Umarital, Rio Ampiyacu, 03°27'S / 72°26'W (JMP 1499, 1451); Yagua Indian Village, headquarters of Rio Loretoyacu (= Rio Loreto Yacú), 03°36'S / 72°36'W<sup>7</sup> (AMNH 96400–96401).

*CHIASCOCLEIS HUDSONI* (*N* = 75)

**BRAZIL:** **Acre:** Reserva Extrativista Porto Dias, Plácido de Castro (UFAC-RB 1259, 1261); **Amazonas:** Barro Vermelho, Rio Juruá, 06°20'S / 68°46'W (INPA 3353); Igarapé do Banheiro, Humaitá, 07°31'S / 63°00'W (MNRJ 14549, *holotype* of *C. jimi*); Reserva INPA/WWF, near Manaus, 02°52'S / 60°05'W (MZUSP 64565, 64567–64568); Rio Baria, Rio Negro (USNM 562555–562557); Madereira Scheffer, Rio Ituxí 8°28'46"S / 65°42'60"W (OMNH 36884, 36886, 36898, 36903–36904, 36906–36907, 36909–36910, 36913); **Mato Grosso:** Aripuanã (UFMT 8296); **Pará:** Estação Ecológica Grão Pará, Alenquer, 00° 09'N 55°11'W (MPEG [CN] 1881); Parque Nacional da Amazônia, Rio Tapajós, Itaituba, 04°40'S / 56°33'W (MPEG 18479, 18511, 18535, 18540–18560, 18566, 18568, 18577, 19060, 19073; MZUSP 53981, *paratype*); Fazenda Caracol, Rio Xingu, Anapu, 3°27'10"S / 51°40'31"W (MPEG 23281–23285); UHE Cachoeira Porteira, Rio Trombetas (INPA 528–535); Reserva Biológica de Tapirapé, Marabá, 05°40'32"S 50°18'10"W (MZUSP 140085) **Rondônia:** Parque Estadual Guajará-Mirim, Rio Formoso –10°19'17"S / 64°33'48"W (CHUNB 23554); **Roraima:** Vila de Caicubi, Bacaba (MZUSP [GA] 446, 560, 603); Sítio Sr. Domingo, Vicinal 1, Vila do Equador, BR 174, 00°11'46"N / 60°38'55"W (AMNH-FS [INPA] 20082).

**GUYANA:** Berbice River 18 mi SW Kwakwani (AMNH 166437–166439); New River (BMNH 1939.1.1.3, *holotype*, examined from photographs).

*CHIASCOCLEIS MAGNOVA* (*N* = 2)

**PERU:** **Loreto:** 3 km SSW of Mishana, Rio Nanay (AMNH 96398, 103550).

*CHIASCOCLEIS PAPACHIBE* (*N* = 1)

**BRAZIL:** **Pará:** Vila dos Cabanos, Barcarena, 1°36'14"S / 48°43'50"W (MPEG 27788).

*CHIASCOCLEIS PANAMENSIS* (*N* = 2)

**PANAMA:** **Old Panama:** (AMNH 52741, *holotype*; 53764, *paratype*).

*CHIASCOCLEIS ROYI* (*N* = 45)

**BOLIVIA:** **Cochabamba:** 6.5 km N Chipiri, 16°13'S / 65°15'W (KU 136316).

**BRAZIL:** **Acre:** Rio Branco, Parque Ambiental Chico Mendes, 10°02'11"S / 67°47'43"W (UFAC-RB 3539); Rio Branco, Parque Zoológico, Universidade Federal do Acre 09°58'S / 67°57'W (UFAC-RB 3065, 3182); **Rondônia:** Parque Estadual Guajará-Mirim, Rio Formoso, 10°19'17"S / 64°33'48"W (CHUNB 23547–23553, 23555–23560).

**PERU:** **Cuzco:** Kinkariari Creek, Rio Urubamba, 11°48'S / 72°52'W (USNM 538243); **Madre de Dios:** 15 km East of Puerto Maldonado, Cuzco Amazonico, (KU 205776, 206632, 206634–206635, 215540–215542); Manu National Park, Rio Manu, Pakitza, 11°56'S / 71°17'W (USNM 342660, 345292); Rio Yullapichis, Panguana (ZMH 2255–2258, 2260–2263, 2442–2450); **Ucayali:** Balta, Rio Curanja, 10°06'S / 71°14'W (KU 197047, examined from photographs).

*CHIASCOCLEIS SHUDIKARENSIS* (*N* = 55)

**BRAZIL:** **Amapá:** Floresta Nacional do Amapá, Igarapé Santo Antônio, 01°06'04"N / 51°53'36"W (IEPA—not cataloged—[FL] 410, 412–414, 487, 489, 491–492); **Amazonas:** Sítio Tamaga, ZF5, km7 of BR174, 02°13'S / 60°03'W (AMNH-FS 2001); Reserva INPA/WWF, Manaus (MZUSP 60035–60039, 60041–60049, 60051–60052, 60059, 60061–60063); **Pará:** Estação Ecológica Grão Pará, Óbidos, 00°37'N / 55°43'W (MPEG—not cataloged—[CN] 2112, 2185); UHE Cachoeira Porteira, Rio Trombetas (INPA 245, 277–278, 289, 320); **Roraima:** Caracarái (MZUSP—not cataloged—[GA] 464, 466, 519, 563, 592–94, 598–99).

**FRENCH GUIANA:** 20 km Petit Saut, River Sinnamary (MPEG 5029–5033, 5060), Petit Saut, River Sinnamary (MPEG 5106–07, 5121).

**GUYANA:** Shudikar-Wau, Upper Esequibo River, not far from Brazilian border (AMNH 43674, *holotype*).

*CHIASCOCLEIS SUPERCILLIALBA* (*N* = 4)

**BRAZIL:** **Acre:** Reserva Extrativista Chico Mendes, Brasília, 10°45'S / 69°18'W (UFACF 4082–4084). **PERU:** **Madre de Dios:** Manu National Park, Rio Manu, Pakitza 11°56'S / 71°18'W (USNM 342862, *paratype*).

*CHIASCOCLEIS CF. SUPERCILLIALBA* (*N* = 6)

**BRAZIL:** **Rondônia:** Parque Estadual Guajará-Mirim, Rio Formoso, 10°19'17"S / 64°33'48"W (OMNH 37204–37206, 37308–37309, 37319).

*CHIASCOCLEIS TRYDACTYLA* (*N* = 6)

**BRAZIL:** **Amazonas:** Tabatinga, 04°15'S / 69°56' W (MPEG 5304–5305, 5637).

**COLOMBIA:** **Amazonas:** Huallarkaka, Km11 of the road from Leticia-Nazareth 04°11'S / 69°95'W (JMP 1948, JMP 2231); Tanimboca, km 13 of the road from Leticia-Nazareth, 04°06'S / 69°57'W (JMP 2057).

*CHIASCOCLEIS VENTRIMACULATA* (*N* = 30)

**BRAZIL:** **Acre:** Reserva Extrativista Riozinho da Libertade, Tarauacá (UFACF 641, 767, 810, 866, 897, 910, 927); Cruzeiro do Sul, Reserva Extrativista do Alto Juruá, foz do Rio Tejo (UFAC-RB 2252); **Amazonas:** Tabatinga (ICN 50238, examined from photographs).

**COLOMBIA:** **Amazonas:** Leticia, Cantadera Tacaná (ICN 50243–50245, examined from photographs); Leticia, Comunidad Monilla Amena Jusie (ICN 50240–50242, examined from photographs); Leticia, Casa de Rodolfo Mesa (ICN 50246–50247, examined from photographs); Leticia, Via Tarapacá (ICN 50239–50249, examined from photographs).

**ECUADOR:** **Sucumbios:** Santa Cecilia, 00°03'N / 76°59'W (KU 105255, examined from photographs); **No data for Departamento:** Rio Pastaza (NRM 1943, *holotype*, examined from photographs).

APPENDIX 2  
SPECIMENS INCLUDED IN THE PHYLOGENETIC ANALYSIS

The list includes collection numbers (when available), as well as field series numbers (given in parentheses) associated with the specimens; updated taxonomy as shown by our results; locality data; Genbank accession numbers (those in **bold** correspond to sequences retrieved from Genbank, and generated from previous studies); and reference for generation of the sequences. Data for sequences derived from Genbank reflect the original publication as closely as possible. For some terminals retrieved from Genbank it is not clear whether voucher numbers refer to collection, field series, or laboratory ID numbers; these are given as in the original and are, sometimes, not listed in Abbreviations for Collections and Field Series Numbers section.

Voucher	Taxon	Locality	16S	COI	Tyrosinase	Reference
C 2682	<i>C. alagoanus</i>	Brazil: Alagoas: Maceió, Mata do Catolé	<b>KC180026</b>	—	<b>KC180236</b>	de Sá et al. (2012)
C 2683	<i>C. alagoanus</i>	Brazil: Alagoas: Maceió, Mata do Catolé	<b>KC180030</b>	—	<b>KC180237</b>	de Sá et al. (2012)
MNKA 9568 (AS0256)	<i>C. albopunctata</i>	Bolivia: Santa Cruz: Velasco, Caparu (14°54'S / 61°05'W)	<b>JF790155</b>	—	—	Jensen et al. (2011)
MNKA 9569 (AS0257)	<i>C. albopunctata</i>	Bolivia: Santa Cruz: Velasco, Caparu (14°54'S / 61°05'W)	<b>JF790156</b>	—	—	Jensen et al. (2011)
MNKA 9570 (AS0258)	<i>C. albopunctata</i>	Bolivia: Santa Cruz: Velasco, Caparu (14°54'S / 61°05'W)	<b>JF790157</b>	—	—	Jensen et al. (2011)
MNKA 9571 (AS0259)	<i>C. albopunctata</i>	Bolivia: Santa Cruz: Velasco, Caparu (14°54'S / 61°05'W)	<b>JF790158</b>	—	—	Jensen et al. (2011)
MNKA 9572 (AS0260)	<i>C. albopunctata</i>	Bolivia: Santa Cruz: Velasco, Caparu (14°54'S / 61°05'W)	<b>JF790159</b>	—	—	Jensen et al. (2011)
C 565	<i>C. albopunctata</i>	Brazil: São Paulo: Estação Ecológica de Iuirapina	<b>JQ268476</b>	—	<b>KC180238</b>	de Sá et al. (2012)
C 572	<i>C. albopunctata</i>	Brazil: São Paulo: Estação Ecológica de Iuirapina	<b>KC180023</b>	—	<b>KC180239</b>	de Sá et al. (2012)
C 621	<i>C. albopunctata</i>	Brazil: São Paulo: Rio Claro: Mata São José	<b>KC179991</b>	—	<b>KC180240</b>	de Sá et al. (2012)
CHUNB 44451 (GRColli 16850)	<i>C. albopunctata</i>	Brazil: Minas Gerais: Buritizeiro	KF621136	KF621202	KF621256	This study
CHUNB 51830 (PHV 1615)	<i>C. albopunctata</i>	Brazil: Maranhão: Carolina	KF621137	KF621203	—	This study
(JMP 218)	<i>C. albopunctata</i>	Bolivia	<b>KC179990</b>	—	<b>KC180267</b>	de Sá et al. (2012)
SMF 88227 (MJ1212)	<i>C. albopunctata</i>	Bolivia: Santa Cruz: Sara, Buenavista (17°29'S / 631°41'W)	<b>JF790160</b>	—	—	Jensen et al. (2011)
MNKA 9433 (MJ1266)	<i>C. albopunctata</i>	Bolivia: Santa Cruz, Nuflo de Chavez, San Sebastián (16°21'S / 62°00'W)	<b>JF790161</b>	—	—	Jensen et al. (2011)
MNKA 9361 (MJ1372)	<i>C. albopunctata</i>	Bolivia: Santa Cruz, Nuflo de Chavez, San Sebastián (16°21'S / 62°00'W)	<b>JF790162</b>	—	—	Jensen et al. (2011)
MPEG 29414 (DT 1780)	<i>C. albopunctata</i>	Brazil: Tocantins: Araguatins	KF621138	KF621204	KF621257	This study
MNCN/ADN 27460 (IDLAR 8158)	<i>C. anatipes</i>	Peru: Loreto: Arboretum de la UNAM, camino hacia Puerto Almendras	KF621145	KF621210	KF621263	This study
QCAZ 44341	<i>C. anatipes</i>	Ecuador: Orellana: Río Napo, Chiroisla, Banco sur (00°34'S / 75°55'W)	KF621146	KF621211	KF621264	This study
QCAZ 44342	<i>C. anatipes</i>	Ecuador: Orellana: Río Napo, Chiroisla, Banco sur (00°34'S / 75°55'W)	KF621147	KF621212	KF621265	This study
QCAZ 51041	<i>C. anatipes</i>	Ecuador: Napo: Jatun Sacha (01°04'S / 77°36'W)	KF621143	KF621208	KF621261	This study
QCAZ 51042	<i>C. anatipes</i>	Ecuador: Napo: Jatun Sacha (01°04'S / 77°36'W)	KF621144	KF621209	KF621262	This study

APPENDIX 2  
(Continued)

Voucher	Taxon	Locality	16S	COI	Tyrosinase	Reference
MZUSP (MTR 28416)	<i>C. antenori</i>	Brazil: Acre: Parque Nacional da Serra do Divisor, (07°30'S / 73°43'W)	KF621141	KF621207	KF621260	This study
MZUSP (MTR 28350)	<i>C. antenori</i>	Brazil: Acre: Parque Nacional da Serra do Divisor, (07°30'S / 73°43'W)	KF621139	KF621205	KF621258	This study
MZUSP (MTR 28373)	<i>C. antenori</i>	Brazil: Acre: Parque Nacional da Serra do Divisor, (07°30'S / 73°43'W)	KF621140	KF621206	KF621259	This study
QCAZ_23824	<i>C. antenori</i>	Ecuador: Orellana: Estación Científica Yasuni	<b>KF621254<sup>a</sup></b>	—	<b>KC180286</b>	This study
QCAZ 38506	<i>C. antenori</i>	Ecuador: Pastaza: Alrededores de Villano, campamento petrolero de AGIP	KF621142	—	—	This study
QCAZ 38719	<i>C. antenori</i>	Ecuador: Pastaza: Alrededores de Villano, campamento petrolero de AGIP	KF621148	KF621213	KF621266	This study
MPEG 18571 (MSH 8120)	<i>C. avilapiresae</i>	Brazil: Pará: Itaituba, Parque Nacional da Amazonia, Rio Tapajós (04°40'S / 56°33'W)	KF621149	KF621214	KF621267	This study
MPEG 22787 (MV 363)	<i>C. avilapiresae</i>	Brazil: Pará: Portel, Monte Verde, Fazenda Riacho (03°15'S / 50°19'W)	KF621153	KF621218	KF621271	This study
MPEG 27768 (FPR 015)	<i>C. avilapiresae</i>	Brazil: Amazonas: Maués, FLONA Pau-Rosa, Rio Paraoní (03°55'S / 58°24'W)	KF621150	KF621215	KF621268	This study
MPEG 27769 (FPR 057)	<i>C. avilapiresae</i>	Brazil: Amazonas: Maués, FLONA Pau-Rosa, Rio Paraoní (03°55'S / 58°24'W)	KF621151	KF621216	KF621269	This study
MPEG 28121 (MA 169)	<i>C. avilapiresae</i>	Brazil: Pará: Carajás, ALPA	KF621152	KF621217	KF621270	This study
(ALP_14940)	<i>C. bassleri</i>	Brazil: Amazonas	KF621154	KF621219	KF621272	This study
MHNSM 21576	<i>C. bassleri</i>	Ecuador: Loreto: 65 km NE of Iquitos (03°15'34" S / 72°54'10" W)	<b>GQ891752</b>	—	—	Funk and Cannatella (2009)
MNCN/ADN 27334 (IDLAR 8030)	<i>C. bassleri</i>	Peru: :Loreto: Arboretum de la UNAM, camino hacia Puerto Almendras	KF621164	KF621222	—	This study
MNCN/AND 47166 (AJC 2429)	<i>C. bassleri</i>	Colombia: Vaupés: Comunidad Puerto Vaupes, rio Vaupes	KF621155	—	KF621273	This study
MNCN/AND 47167 (AJC 2430)	<i>C. bassleri</i>	Colombia: Vaupés: Comunidad Puerto Vaupes, rio Vaupes	KF621156	—	KF621274	This study
MPEG 27764 (FPR 092)	<i>C. bassleri</i>	Brazil: Amazonas: Maués, FLONA Pau-Rosa, Rio Paraoní (03°55'S / 58°24'W)	KF621157	KF621220	KF621275	This study
MPEG 27765 (FPR 100)	<i>C. bassleri</i>	Brazil: Amazonas: Maués, FLONA Pau-Rosa, Rio Paraoní (03°55'S / 58°24'W)	KF621158	—	KF621276	This study
MPEG 28326 (JUR 707)	<i>C. bassleri</i>	Brazil: Pará: Juruti, ALCOA	KF621165	—	—	This study

APPENDIX 2  
(Continued)

Voucher	Taxon	Locality	16S	COI	Tyrosinase	Reference
MZUSP (MTR 28345)	<i>C. bassleri</i>	Brazil: Acre: Parque Nacional da Serra do Divisor, Rio Móa (07°30'S / 73°43'W)	KF621159	—	KF621277	This study
MZUSP (MTR 28391)	<i>C. bassleri</i>	Brazil: Acre: Parque Nacional da Serra do Divisor, Rio Móa (07°30'S / 73°43'W)	KF621160	—	KF621278	This study
MZUSP (MTR 28402)	<i>C. bassleri</i>	Brazil: Acre: Parque Nacional da Serra do Divisor, Rio Móa (07°30'S / 73°43'W)	KF621161	KF621221	KF621279	This study
NMPGV 71148	<i>C. bassleri</i>	Peru: Loreto: Puerto Almendras, 17 KM SW of Iquitos	<b>KF621255<sup>a</sup></b>	—	<b>KCI80284</b>	This study
QCAZ 17515	<i>C. bassleri</i>	Ecuador: Orellana: Estación Científica Yasuni PUCE (00°40'S / 76°23'W)	KF621162	—	KF621280	This study
QCAZ 24565	<i>C. bassleri</i>	Ecuador: Orellana: Estación Científica Yasuni PUCE (00°40'S / 76°23'W)	KF621163	—	KF621281	This study
C 1437	<i>C. capixaba</i>	Brazil: Espírito Santo: Linhares	<b>KCI180044</b>	—	<b>KCI180234</b>	de Sá et al. (2012)
C 1438	<i>C. capixaba</i>	Brazil: Espírito Santo: Linhares	<b>KCI179977</b>	—	<b>KCI180235</b>	de Sá et al. (2012)
KU 215720	<i>C. carvalhoi</i>	Peru: San Martín: San Juan de Pacaysapa	<b>KCI179972</b>	—	<b>KCI180275</b>	de Sá et al. (2012)
MNCNI/ADN 26570 (JMP 1451)	<i>C. carvalhoi</i>	Peru: Loreto: Umanital, Río Ampiyacu	KF621166	KF621223	KF621282	This study
MNCNI/ADN 27503 (JMP 1376)	<i>C. carvalhoi</i>	Peru: Loreto: Arboretum de la UNAM, camino hacia Puerto Almendras	KF621167	KF621224	KF621283	This study
MNCNI/ADN 26618 (JMP 1499)	<i>C. carvalhoi</i>	Peru: Loreto: Umanital, Río Ampiyacu	KF621168	—	—	This study
MNCNI/ADN 27392 (IDLAR 8090)	<i>C. carvalhoi</i>	Peru: Loreto: Hacienda Zamora, km 52.5 de la carretera Iquitos-Nauta	KF621169	KF621225	KF621284	This study
MHNSM 21540	<i>C. devriesi</i>	Ecuador: Loreto: 65 km NE of Iquitos (03°15'34" S / 72°54'10" W: type locality)	<b>GQ891750</b>	—	—	Funk and Cannatella (2009)
MNHN 2011.0139 (PG 403)	<i>C. haddadi</i>	French Guiana: Mont Kotika: Plateau Mare N° 1 (03°56'00"N / 54°11'05"W: type locality)	KF621170	KF621226	KF621285	This study
MNHN 2011.0140 (PG 443)	<i>C. haddadi</i>	French Guiana: Mont Kotika: Plateau Mare N° 1 (03°56'00"N / 54°11'05"W: type locality)	KF621171	—	—	This study
(PG 445)	<i>C. haddadi</i>	French Guiana: Mont Kotika: Plateau Mare N° 1 (03°56'00"N / 54°11'05"W: type locality)	KF621172	KF621227	—	This study
(PG 446)	<i>C. haddadi</i>	French Guiana: Mont Kotika: Plateau Mare N° 1 (03°56'00"N / 54°11'05"W: type locality)	KF621173	—	—	This study
28bm	<i>C. haddadi</i>	French Guiana: Mont Bakra (03°81'08"N / 52°56'73"W)	<b>EU201099</b>	—	—	Fouquet et al. (2007)
INPA-H 31276 (AMNH-FS 20082)	<i>C. hudsoni</i>	Brazil: Roraima: Floresta approx. 3 Km de casa del Sr Domingo (00°11'46"N / 60°38'55"W)	KF621174	KF621228	—	This study

APPENDIX 2  
(Continued)

Voucher	Taxon	Locality	16S	COI	Tyrosinase	Reference
(JMP 2286)	<i>C. hudsoni</i>	Colombia: Amazonas: Senda Zafire-Takana al Norte de la carretera Leticia	KF621175	KF621229	—	This study
MAD 116	<i>C. hudsoni</i>	Guyana: Iwokrama Forest: Muri Scrub Camp	<b>KC180060</b>	—	<b>KC180280</b>	de Sá et al. (2012)
MPEG 23206 (CN 0268)	<i>C. hudsoni</i>	Brazil: Pará: Faro, Floresta Estadual de Faro (1°42'50.44"S, 57°12'47.88"W)	KF621176	KF621230	KF621286	This study
MPEG 18545 (MSH 8252)	<i>C. jimi</i>	Brazil: Pará: Itaituba, Parque Nacional da Amazonia, Rio Tapajós (04°40'S / 56°33'W)	KF621177	KF621231	KF621287	This study
MPEG 18547 (MSH 8059)	<i>C. jimi</i>	Brazil: Pará: Itaituba, Parque Nacional da Amazonia, Rio Tapajós (04°40'S / 56°33'W)	KF621178	KF621232	KF621288	This study
MPEG 23283 (BML 1327)	<i>C. jimi</i>	Brazil: Pará: Rio Xingu, Fazenda Caracol (03°27'S / 51°40'W)	KF621181	KF621235	KF621289	This study
MPEG 23285 (BML 1441)	<i>C. jimi</i>	Brazil: Pará: Rio Xingu, Fazenda Caracol (03°27'S / 51°40'W)	KF621182	KF621236	KF621290	This study
MPEG 24527 (MAR 881)	<i>C. jimi</i>	Brazil: Pará: Portel, Plot PPBio, Floresta Nacional de Caxuanã (01°59'S / 51°39'W)	KF621179	KF621233	—	This study
MPEG 27763 (FPR 096)	<i>C. jimi</i>	Brazil: Amazonas: Maués, FLONA Pau-Rosa, Rio Paraconi (03°55'08"S / 58°24'20")	KF621180	KF621234	—	This study
C 73	<i>C. lacrimae</i>	Brazil: São Paulo: Picinguaba, Ubatuba	<b>KC180040</b>	—	<b>KC180241</b>	de Sá et al. (2012)
C 76	<i>C. lacrimae</i>	Brazil: São Paulo: Picinguaba, Ubatuba	<b>KC180063</b>	—	<b>KC180242</b>	de Sá et al. (2012)
T5	<i>C. leucosticta</i>	Brazil (no additional data given by de Sá et al., 2012)	<b>KC180039</b>	—	<b>KC180243</b>	de Sá et al. (2012)
7	<i>C. magnova</i>	Peru: Loreto: 31 KM SW of Iquitos (04°00' S, 73°26' W: type locality)	<b>KC180062</b>	—	<b>KC180248</b>	de Sá et al. (2012)
MPEG 27788	<i>C. papachibe</i>	Brazil: Pará: Barcarena (01°36'S / 48°43'W)	KF621185	—	—	This study
MPEG 30683 (PRG 43)	<i>C. papachibe</i>	Brazil: Pará: Paragominas (03°6'23" S / 47°46'55"W: type locality)	KF621183	—	—	This study
MPEG 30684 (PRG 55)	<i>C. papachibe</i>	Brazil: Pará: Paragominas (03°6'23" S / 47°46'55"W: type locality)	KF621184	KF621237	KF621291	This study
KU 215542 (WED 59347)	<i>C. royi</i>	Peru: Madre de Dios: 15km E of Puerto Maldonado	KF621186	KF621238	KF621292	This study
ROM 40139	<i>C. royi</i>	Peru: Madre de Dios: Tambopata	<b>KC180041</b>	—	<b>KC180304</b>	de Sá et al. (2012)
KU 215540	<i>C. royi</i>	Peru: Madre de Dios: Puerto Maldonado	<b>KC180059</b>	—	<b>KC180274</b>	de Sá et al. (2012)
CFBH 9331	<i>C. schubarti</i>	Brazil: Espírito Santo: Espírito Santo: Reserva Biológica de Sooretama	<b>KC180071</b>	—	<b>KC180246</b>	de Sá et al. (2012)
MNRJ (AMNH-FS 20018)	<i>C. shudikarensis</i>	Brazil: Amazonas: Tamaga, CF 5 Km 7, BR 174 approx. Km 85 (02°13'S / 60°03'W)	KF621187	KF621239	—	This study
INPA-H 31274 (AMNH-FS 20039)	<i>C. shudikarensis</i>	Brazil: Amazonas: Tamaga, CF 5 Km 7, BR 174 approx. Km 85 (02°13'S / 60°03'W)	KF621188	KF621240	—	This study
INPA-H 31275 (AMNH-FS 20040)	<i>C. shudikarensis</i>	Brazil: Amazonas: Tamaga, CF 5 Km 7, BR 174 approx. Km 85 (02°13'S / 60°03'W)	KF621189	KF621241	—	This study

APPENDIX 2  
(Continued)

Voucher	Taxon	Locality	16S	COI	Tyrosinase	Reference
JIW 458	<i>C. shudikarensis</i>	Suriname: Sipaliwini District: Lely Mts	<b>KC180008</b>	—	<b>KC180266</b>	de Sá et al. (2012)
MPEG 28328 (CN 2185)	<i>C. shudikarensis</i>	Brazil: Pará: Estação Ecológica Grão Pará	KF621190	KF621242	—	This study
MVZ-247574	<i>C. shudikarensis</i>	Guyana: Brokopondo District: Mazaroni Rd., 0.3 km from junction with Brownsberg Rd., Brownsberg Nature Park	KF621191	—	—	This study
31	<i>C. sp. (carvalhoi)</i>	Peru: Loreto: Villa Anguilla at Río Nanay	<b>KC180065</b>	—	<b>KC180306</b>	de Sá et al. (2012)
63	<i>C. sp. (carvalhoi)</i>	Peru: Loreto: Villa Anguilla at Río Nanay	<b>KC180074</b>	—	<b>KC180307</b>	de Sá et al. (2012)
(JMP 1948)	<i>C. tridactyla</i>	Colombia: Amazonas: Letícia, Kilometro 11 Tanimbooca, senda frente a la reserva (04°07'08"S / 69°57'03"W)	KF621192	KF621243	—	This study
(JMP 2057)	<i>C. tridactyla</i>	Colombia: Amazonas: Letícia, Kilometro 13 (04°06'43"S / 69°57'39"W)	KF621193	KF621244	—	This study
(JMP 2231)	<i>C. tridactyla</i>	Colombia: Amazonas: Letícia, Huallarkaka	KF621194	KF621245	—	This study
ANDES-A (JMP 1943)	<i>C. ventrimaculata</i>	Colombia: Amazonas: Letícia, Kilometro 11 Tanimbooca, senda frente a la reserva (04°07'S" / 69°57'W)	KF621195	KF621246	—	This study
ANDES-A (JMP 1944)	<i>C. ventrimaculata</i>	Colombia: Amazonas: Letícia, Kilometro 11 Tanimbooca, senda frente a la reserva (04°07'S" / 69°57'W)	KF621196	KF621247	—	This study
MHNSM 21539	<i>C. ventrimaculata</i>	Ecuador: Loreto: 65 km NE of Iquitos (03°15'34" S / 72°54'10" W)	<b>GQ891751</b>	—	—	Funk and Cannatella (2009)
No voucher	<i>Ctenophryne barbatula</i>	Peru: Pasco: Oxapampa: Parque Nacional Yanachaga-Chemillen	<b>KC179994</b>	—	<b>KC180205</b>	de Sá et al. (2012)
MPEG 25397	<i>Ctenophryne geayi</i>	Brazil: Pará: Rio Xingu, Faz. Caracol (03°27'10"S, 51°40'31"W)	KF621197	KF621248	KF621293	This study
MPEG 29412	<i>Dermatonotus muelleri</i>	Brazil: Maranhão: Dom Pedro	KF621198	KF621249	KF621294	This study
MPEG 29419	<i>Elachistocleis heliannae</i>	Brazil: Pará: Belém, Terra Firme	KF621199	KF621250	KF621295	This study
(AJC 988)	<i>Elachistocleis panamensis</i>	Panama: Panamá: Peninsula Gigante, Lake Gatún (09°07'N / 79°52')	<b>KC179980</b>	KF671188 <sup>b</sup>	<b>KC180232</b>	de Sá et al. (2012)
CAS 214349	<i>Gastrophryne carolinensis</i>	USA: Florida: Camel Lake	KF621200	KF621251	KF621296	This study
MPEG 27797	<i>Hamptophryne boliviana</i>	Brazil: Amazonas: Maués, FLONA Pau-Rosa, Rio Paracomi (03°55'S / 58°24'W)	KF621201	KF621252	—	This study
No voucher	<i>Katophrynus interlineatus</i>		<b>AB611916</b>	<b>AB611913</b>	<b>AB611911</b>	Kurabayashi et al. (2011)
AMNH-A 163850	<i>Microhyla heymonsi</i>	Vietnam: Ha Gieng Province: Yeh Mihn 22.54.24N, 105.13.52E	<b>DQ283382</b>	KF621253	<b>DQ282992</b>	This study

<sup>a</sup> This sequence had no Genbank accession number, but was included in the dataset published by de Sá et al. (2012) and was retrieved from Tree Base (www.treebase.org; Study ID: 13478). We have submitted the sequence and although we provide an accession number for it, we are not responsible for its generation.

<sup>b</sup> Sequence generously provided by A.J. Crawford.

# PLATES



Plate 1. *Chiasmocleis albopunctata* (A–B)—*Chiasmocleis anatipes* (C–H) (voucher specimen: photographer in parentheses). (A) Araguatins, Tocantins, Brazil (MPEG 29414: P.L.V. Peloso). (B) Departamento Santa Cruz, Bolivia (no number: M. Jensen). (C–D) Santa Cecilia, Napo, Ecuador, type locality; (C) male paratype (KU 146034: W.E. Duellman) and (D) male holotype (KU 146035: W.E. Duellman). (E–H) Jatun Sacha, Napo, Ecuador; (E) dorsal and (F) ventral views of a male (QCAZ 51042: M. Read); (G) dorsal and (H) ventral views of a female (QCAZ 51041: M. Read). Not to scale.



Plate 2. *Chiasmocleis antenori* (A–D)—*Chiasmocleis avilapiresae* (part: E–H) (voucher specimen: photographer in parentheses). (A–D) Syntopic specimens from Parque Nacional da Serra do Divisor, Acre, Brazil, evidencing intrapopulation variation in color pattern (A, MTR 28407; B, MTR 28350; C, MTR 28373; D, MTR 28416: all photos P.L.V. Peloso). (E–H) Rondônia, Brazil; (E) dorsal and (F) ventral views of a female (JPC 15378; J.P. Caldwell); (G–H) Two syntopic females with very distinct coloration (no number: C. Cintra). Not to scale.



Plate 3. *Chiasmocleis avilapiresae* (part: A–H) (voucher specimen: photographer in parentheses). (A–D) Syntopic specimens from Porto Velho, Rondônia, Brazil: (A–B) and (C–D) dorsal and ventral views of two specimens of unknown sex (no number: R. Gaiga). (E) Aripuanã, Mato Grosso, Brazil (no number: R. Ávila). (F) Amplexant pair from Amazonas, Brazil (JPC 15752 – male; JPC 15750 – female: J.P. Caldwell); (G) Female paratype from Vitória do Xingu, Pará, Brazil (MPEG 23279: P.V.L. Peloso). (H) Floresta Nacional de Pau Rosa, Amazonas, Brazil (no number: P.L.V. Peloso). Not to scale.

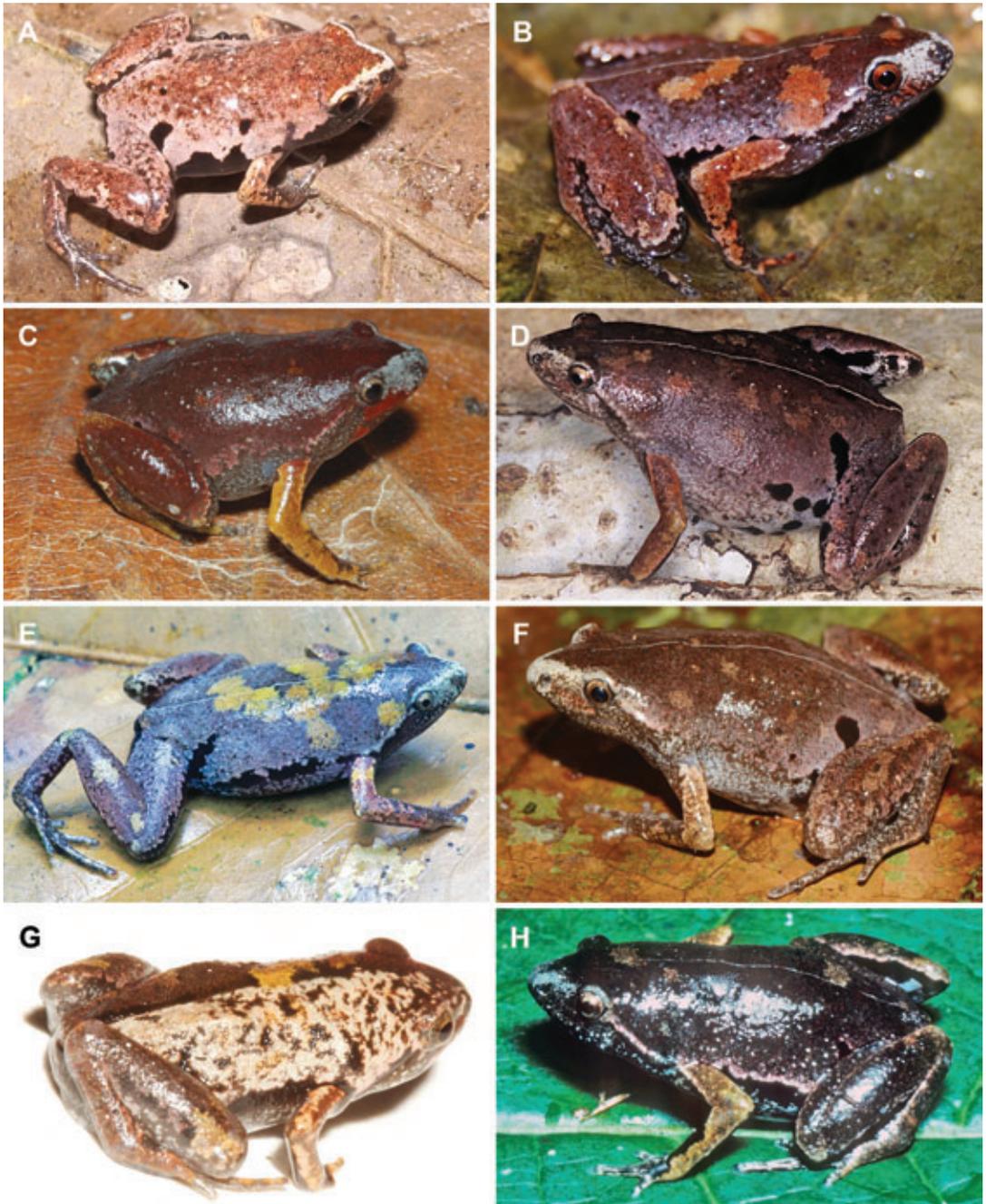


Plate 4. *Chiasmocleis bassleri* (A–H) (voucher specimen: photographer in parentheses). (A) Aripuanã, Mato Grosso, Brazil (no number: R. Ávila). (B) UHE Jirau, Rondônia, Brazil (no number: C. Cintra). (C) Floresta Nacional de Pau Rosa, Amazonas, Brazil (no number: P.L.V.P.). (D) Porto Walter, Acre, Brazil (JPC 12825: J.P. Caldwell) (E) Lower Rio Cristalino, Mato-Grosso/Pará border, Brazil (F) Serra do Divisor, Acre, Brazil (MTR 28391: P.L.V.P.). (G) Strikingly odd dorsal pattern on a specimen from Vaupés, Colombia (no number: S. Castroviejo-Fisher). (H) Explornapo, Loreto, Peru (KU 220478: W.E. Duellman). Not to scale.



Plate 5. *Chiasmocleis carvalhoi* (A–D)—*Chiasmocleis devriesi* (G–H) (voucher specimen: photographer in parentheses). (A–D) Two syntopic specimens from Umarital, Río Apiyacu, Loreto, Peru evidencing striking differences in color pattern; (A) dorsal and (B) ventral views (JMP 1451: J.M. Padial); (C) dorsal and (D) ventral views (JMP 1944: J.M. Padial). (E) Dorsal and (F) ventral views of specimen from Puerto Almendra, Arboreto UNAM (JMP 1376: J.M. Padial). (G) Dorsal and (H) ventral views of female holotype from Departamento Loreto, Peru (MHNSM 21540: C. Funk). Not to scale.



Plate 6. *Chiasmocleis hudsoni* (A–F)—*Chiasmocleis magnova* (G–H) (voucher specimen: photographer in parentheses). (A) Vitória do Xingu, Pará, Brazil (no number; P.L.V. Peloso). (B) Rio Jufari, Caracaraí, Roraima, Brazil (no number; M.C.Forlani). (C) Reserva Ducke, Manaus Amazonas, Brazil (no number; A.P. Lima). (D) Roraima, Brazil (AMNH-FS 20082; P.L.V. Peloso). (E) UHE Jirau, Rondônia, Brazil (MPEG 28895; C. Cintra). (F) Rondônia, Brazil (no number; R. Gaiga). (G) Male and (H) female from Iquitos, Peru (no number, both photos: P.P. Peña). Not to scale.



Plate 7. *Chiasmocleis shudikarensis* (A–H) (voucher specimen: photographer in parentheses). (A) Estação Ecológica Grão Pará, Pará, Brazil (MPEG 28327: P.L.V. Peloso). (B) Reserva Ducke, Manaus Amazonas, Brazil (no number; A.P. Lima). (C–F) Two syntopic specimens from Rio Jufari, Caracaraí, Roraima; (C) Dorsal, (D) ventral and (E) posterior view (note white femoral line) of a female and (F) different female with a marbled dorsum (no numbers: C–F, M.C.Forlani). (G) Porto Trombetas, Pará, Brazil (no number: V. São Pedro). (H) Amplexant pair at Nouragues Reserve, French Guiana (no number: A. Fouquet). Not to scale.



Plate 8. *Chiasmocleis superciliarba* (A–H) (voucher specimen: photographer in parentheses). (A) Acre, Brazil (no number: M.A. Freitas). (B–H) Syntopic specimens from Reserva Comunal Purus, Peru; (B) Amplexant pair (no number: S. Castroviejo); (C) dorsal (D) and ventral views of a male (no number: J.M. Padial); (E) dorsal and (F) ventral views of a female (no number: J.M. Padial); (G) dorsal and (H) ventral views of a specimen of unknown sex (no number: J.M. Padial). Not to scale.

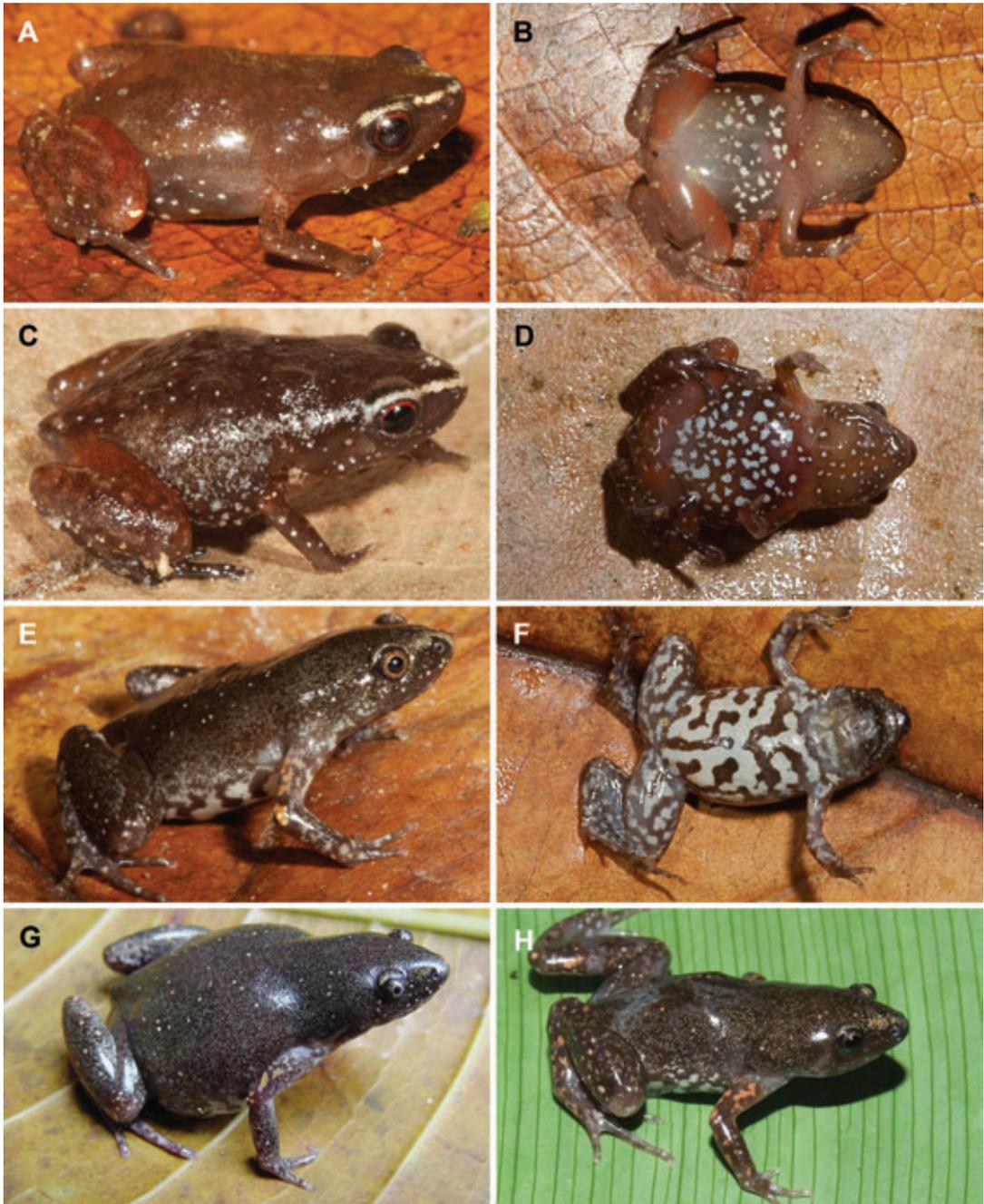


Plate 9. *Chiasmocleis tridactyla* (A–D)—*Chiasmocleis ventrimaculata* (E–H) (voucher specimen: photographer in parentheses). (A) Dorsal and (B) ventral views of specimen from Tanimboca, Leticia, Colombia (JMP 2057: S. Castroviejo-Fisher). (C) Dorsal and (D) ventral views of specimen from Huallarkaka, Leticia, Colombia (JMP 2231: J.M. Padial). (E) Dorsal and (F) ventral views of a male from Leticia (no number: J.M. Padial). (H) Female from Departamento Loreto, Peru (MHNSM 21539: C. Funk). (H) Floresta do Baixo Rio Moa, Cruzeiro do Sul, Acre, Brazil (no number: P.S. Bernarde). Not to scale.

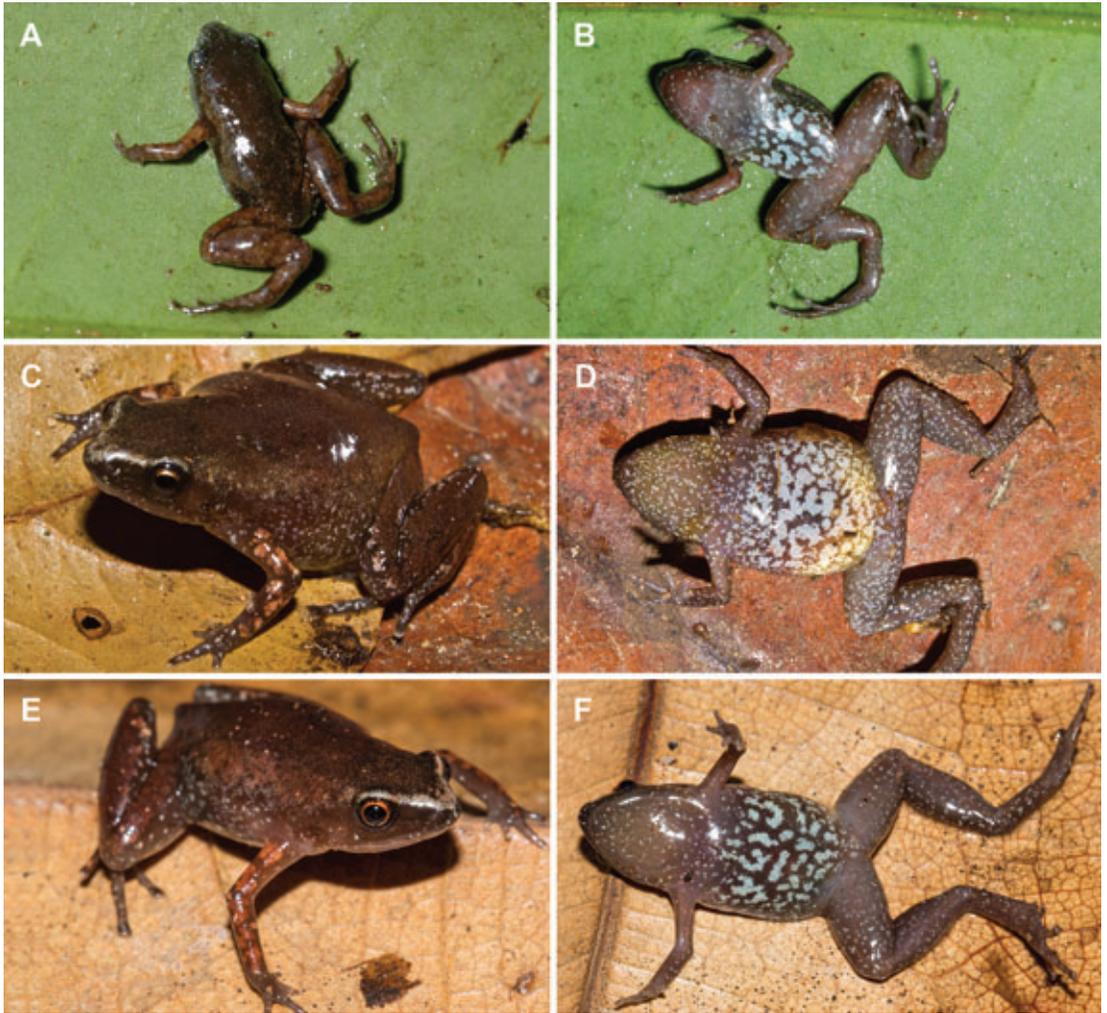


Plate 10. *Chiasmocleis haddadi*, sp. nov. (A–F) (voucher specimen: photographer in parentheses). (A) Dorsal and (B) ventral views of male holotype from Montagne Kotika, French Guiana (MNHNP 2011.0139). (C) Dorsal and (D) ventral views of specimen from Oiapoque, Amapá, Brazil (MTR 24296: A. Fouquet). (E) Dorsal and (F) ventral views of specimen from Lourenço Amapá, Brazil (MTR 24274: A. Fouquet). Not to scale.

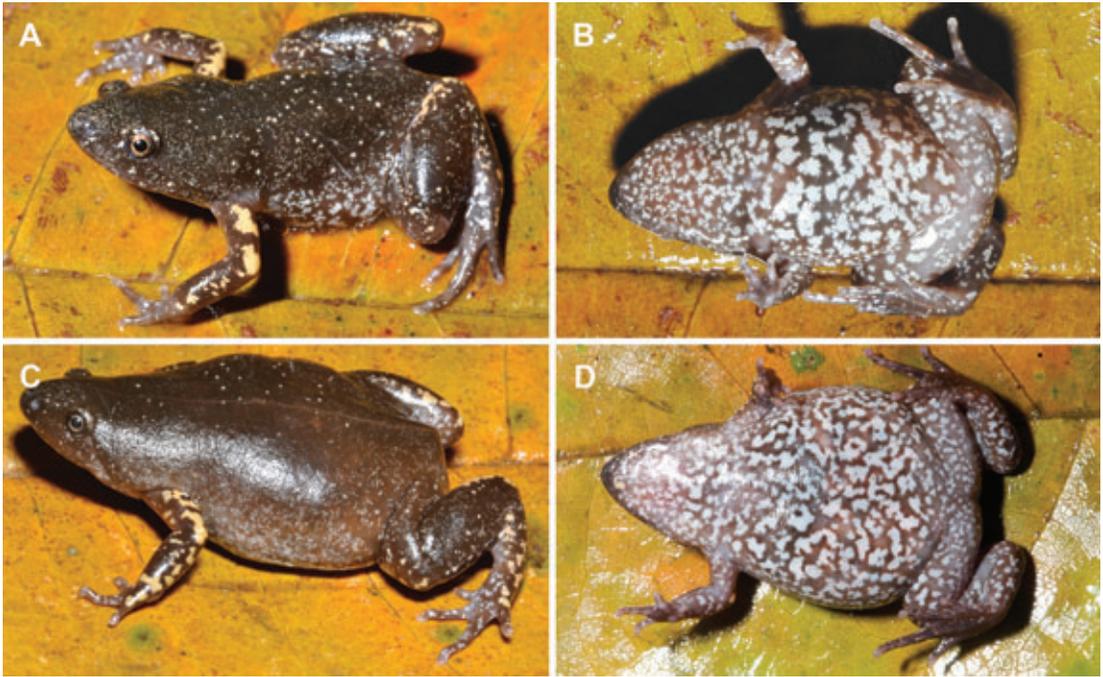


Plate 11. *Chiasmocleis papachibe*, sp. nov. (A–D) (voucher specimen: photographer in parentheses). All from the type locality at Paragominas, Pará, Brazil. (A) Dorsal and (B) ventral views of male holotype (MPEG 30683; M.J. Sturaro). (C) Dorsal and (D) ventral views respectively of female paratype (MPEG 30684; M.J. Sturaro). Not to scale.

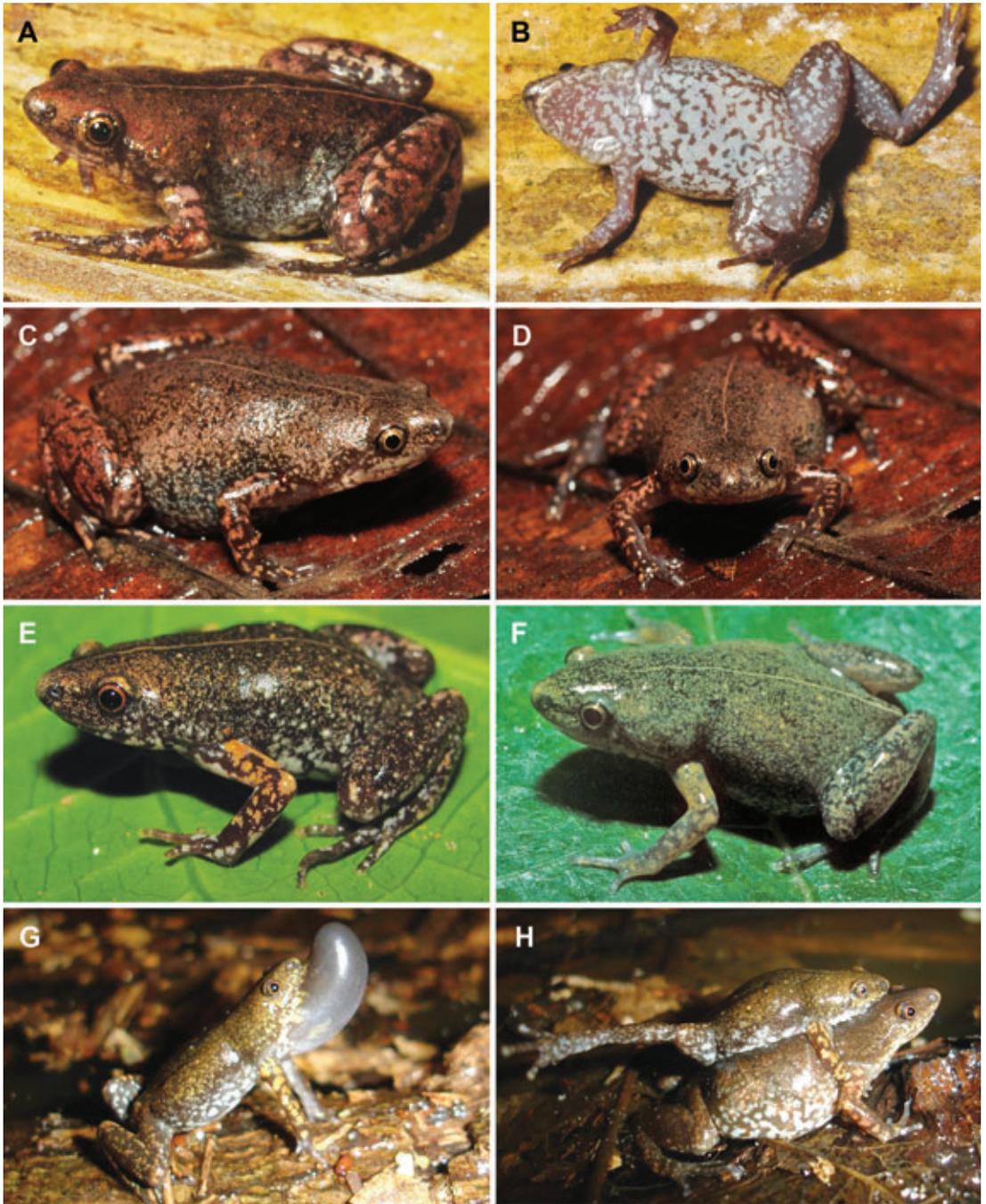


Plate 12. *Chiasmocleis royi*, sp. nov. (A–H) (voucher specimen: photographer in parentheses). (A–D) Porto Velho, Rondônia, Brazil; (A) dorsal and (B) ventral views of a female (no number: R. Gaiga); (C) Dorsal and (D) frontal views another female (no number: R. Gaiga). (E) Male from Parque Zoobotânico, Universidade Federal do Acre (UFAC-RB 5160: P. Melo-Sampaio). (F) Male from the type locality in Madre de Dios, Peru (KU 215542: W.E. Duellman). (G) Calling male and (H) amplexant pair from Panguana, Peru (no number: V. Flechas). Not to scale.

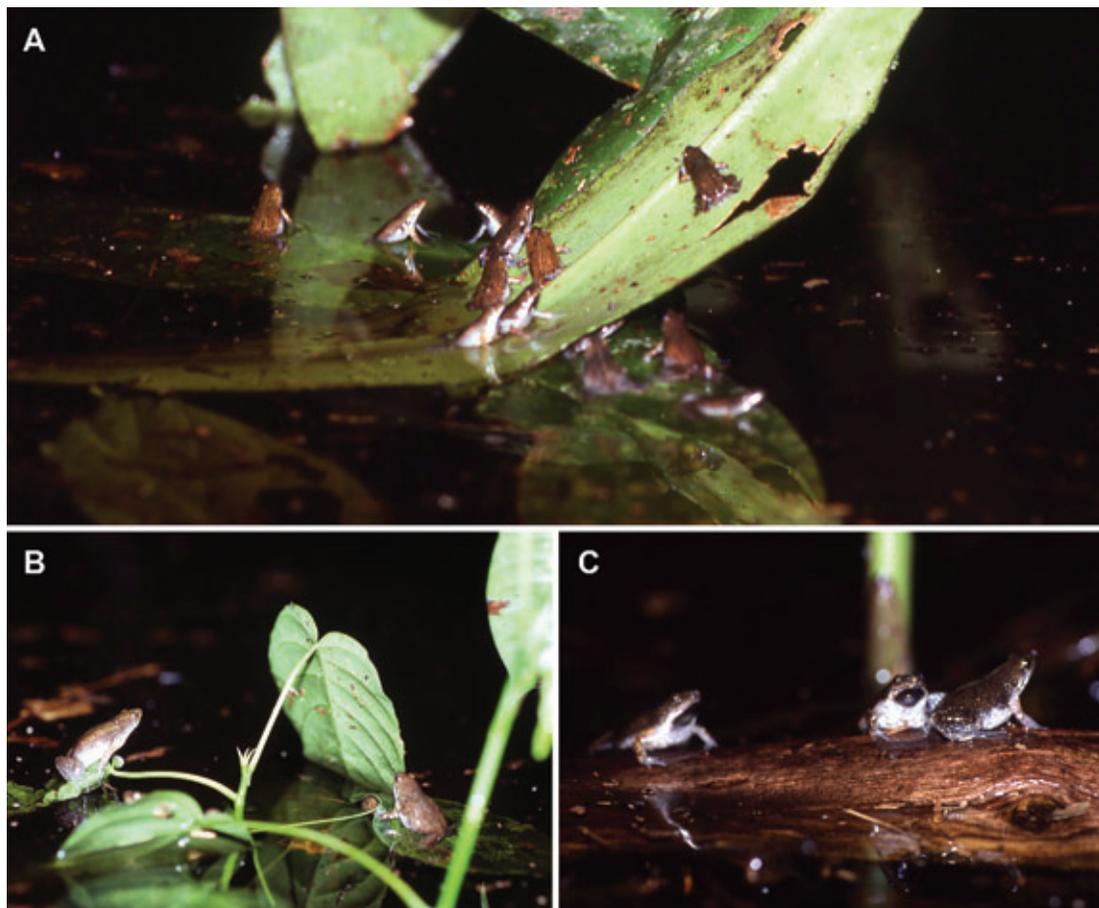


Plate 13. *Chiasmocleis royi*, sp. nov. (A–C) (all photos A. Schlüter). Congregation of breeding specimens in a temporary pond inside the forest at Panguana, Peru. (A) Specimens perching on the vegetation, completely outside the water or partially submerged. Males may call from the vegetation, on floating logs and debris or may call partially submerged. (B) Two specimens hanging on to the vegetation. (C) Three calling males on a small floating log.



Plate 14. Reproductive behavior of *Chiasmocleis shudikarensis* (photographer in parentheses). (A–B) Calling males from French Guiana. (A) Male calling partially submerged, hanging onto vegetation at Mare Arataie, French Guiana (W. Hödl: no number). (B) Male calling from the ground at Arlésienne, French Guiana (P. Gaucher: no number). (C) Aggregation of reproductive specimens in a temporary pond at Petite Mare, Kaw, French Guiana. Hundreds of specimens can be observed breeding simultaneously (P. Gaucher). (D) Aggregation of tadpoles of *C. shudikarensis* at Montagne de Kaw, French Guiana (T. Montford). Not to scale.

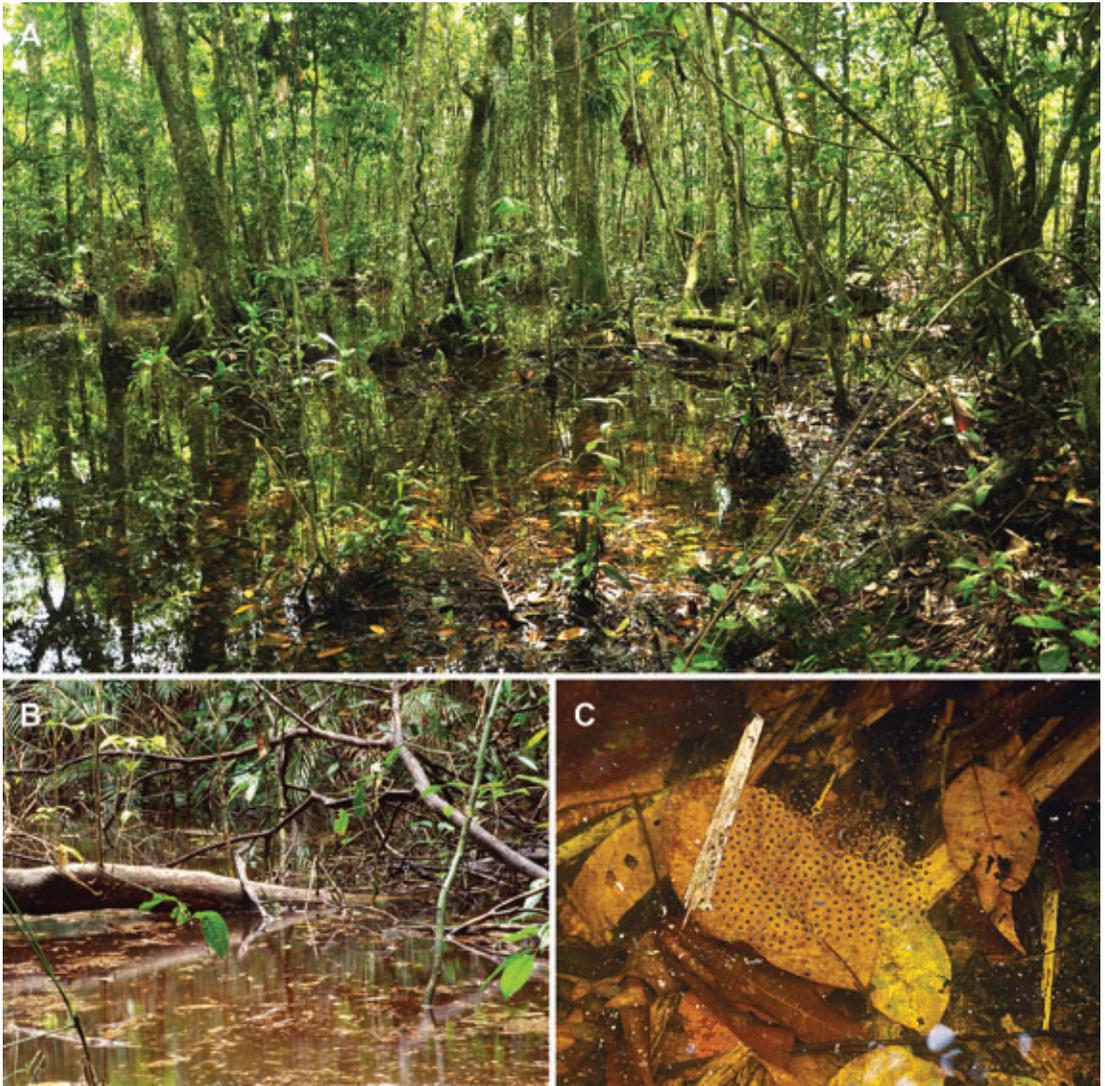


Plate 15. Habitat and eggs of *Chiasmocleis* (A–C). (A) Temporary pond inside the forest in Rondônia, Brazil (R. Gaiga). (B) Breeding site of *Chiasmocleis bassleri* and (C) eggs mass found in the same pond at Rio Ituxí, Amazonas, Brazil (J.P. Caldwell).