UNIVERSIDADE FEDERAL DE PERNAMBUCO

CENTRO DE BIOCIÊNCIAS

PROGRAMA DE PÓS GRADUAÇÃO EM BIOLOGIA ANIMAL

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REVISÃO TAXONÔMICA DO COMPLEXO *IPHISA ELEGANS* GRAY, 1851 (SQUAMATA:GYMNOPHTHALMIDAE)

RECIFE

2019

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REVISÃO TAXONÔMICA DO COMPLEXO *IPHISA ELEGANS* GRAY, 1851 (SQUAMATA:GYMNOPHTHALMIDAE)

Dissertação apresentada ao Programa de Pós-Graduação em Biologia Animal, da Universidade Federal de Pernambuco, como requisito parcial para a obtenção do título de Mestre em Biologia Animal.

Orientador: Prof. Dr. Pedro M. Sales Nunes

Coorientador: Dr. Renato Sousa Recoder

Recife

2019

Catalogação na fonte:
Bibliotecária Claudina Queiroz, CRB4/1752

Mello, Anna Virginia Albano de
Revisão taxonômica do complexo *Iphisa elegans* GRAY, 1851 (Squamata:Gymnophthalmidae) / Anna Virginia Albano de Mello - 2019.
88 folhas: il., fig., tab.

Orientador: Pedro M. Sales Nunes
Coorientador: Renato Sousa Recoder
Dissertação (mestrado) – Universidade Federal de Pernambuco. Centro de Biociências. Programa de Pós-Graduação em Biologia Animal. Recife, 2019.

Inclui referências e anexo.

1. Lagartos 2. Diversidade críptica 3. Amazônia
I. Nunes, Pedro M. Sales (orient.) II. Recoder, Renato Sousa (coorient.) III.Título

597.95 CDD (22.ed.) UFPE/CB-2019-354

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Aprovada em 31 de Julho de 2019

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Às minhas sobrinhas, Maria Alice e Bela, que cresçam mergulhadas em sua curiosidade e criatividade e que com isso, desbravem o mundo.

AGRADECIMENTOS

Agradeço primeiramente a minha mãe e meu pai, que sempre acreditaram em mim e me ensinaram a ser uma pessoa melhor, não importa o que aconteça. Ao meu irmão, pelos ensinamentos da vida e por me ensinar a sempre enfrentar os problemas sendo gentil com todos. À minha sobrinha, Maria Alice, pelas brincadeiras, risadas e por sempre me lembrar que ser curiosa é muito divertido. E as minhas cachorras, Youka e Lilo, pela companhia e por me darem um amor incondicional. Agradeço ao meu orientador, por sempre acreditar em mim, confiar e pela infinita paciência ao repetir 3.674 vezes a mesma coisa até que eu REALMENTE entenda. Agradeço por sempre ouvir meus áudios e mensagens sobre alguma curiosidade ou descoberta a respeito do meu trabalho, mesmo quando isso acontecia as 23:59 da noite de uma sexta-feira. Agradeço também pela amizade, brincadeiras, palhaçadas e pela disponibilidade em ajudar sempre que precisei. Agradeço também ao meu co-orientador, Recoder "Reco" pela infinita paciência, pelas brincadeiras, risadas e por compartilhar todo o conhecimento que podia no tempo que estive em São Paulo. Agradeço a todas as curadores e curadores que permitiram minha visita às coleções para analisar os espécimes que estudei: INPA, MPEG e MZUSP; e todas as que puderam fazer o envio os espécimes, muito obrigada! Agradeço a banca, que também sempre me apoiaram e se mostraram dispostos a ajudar sempre que necessário: Diego Astúa, Pedro Ivo, Sérgio Marques e Roberta Pinto. Agradeço infinitamente aos meus amigos do laboratório de herpetologia, Pati, Bruna, Lucas, Osmar, Thaís, Marcos, Mauro, Luiza, Tamires, Antonio, Natallia e Bili por sempre me apoiarem; por tentarem fazer silêncio enquanto eu estava concentrada, por mais divertida que a conversa em grupo estivesse; por confiarem em mim para tirar dúvidas e compartilhar conhecimentos; pelas brincadeiras, risadas e pelo companheirismo. Agradeço à Pati e Bruna, pela amizade, por sempre estarem comigo nos momentos mais difíceis, por confiarem em mim, pelos conselhos, pelo carinho e pelas danças em campo. Agradeço a Lusca por sempre se preocupar comigo, por ter me ajudado com o meu mestrado desde que comecei e pelas caronas, principalmente em dias que a asma não estava a fim de me deixar em paz. E agradeço imensamente a Antônio Moraes, por sempre compartilhar suas experiências e ensinamentos e por me mostrar que Ciência é difícil mesmo, mas a gente gosta, né? Tem que fazer! Agradeço a John John por sempre me ajudar com análises, sempre me visitar no lab, junto com Haggy e Victor, algumas vezes atrapalhando, mas TODAS as vezes, me fazendo rir e ficar tranquila. Agradeço também a todas as minhas amigas e amigos da faculdade, por fazer meus dias mais felizes e tornar a vida mais simples e fácil, seja por

almoçar comigo na copa, ou só ficar jogando conversa fora em qualquer lugar. Obrigada também aos amigos que fiz em São Paulo nos dois meses que fiquei, pelo carinho, pela ajuda, pelo abrigo e pelas dicas de como sobreviver ao frio. Em especial, agradeço a Regina, por me abrigar a maior parte do tempo que fiquei em São Paulo, pelas risadas, conselhos e conversas matinais. E também ao Bogão e Agustin, por me abrigarem por mais um tempo em São Paulo, pelas conversas, brincadeiras e pelas pizzas e sushi! Agradeço também ao Miguel Trefaut por me deixar trabalhar no laboratório, risadas e pelos ensinamentos, assim como a Ju e Neto! Agradeço imensamente a Fernanda Ito, por sempre me ensinar de tudo um pouco, pela disponibilidade e por ser uma das melhores amigas que já tive. Pela diversão e ensinamentos eu agradeço aos meus amigos da Pós-Graduação em Biologia Animal e aos professores que alguma vez me apoiaram e me ensinaram coisas. Agradeço também a Marcos, Tamí e Tetê da UFAL e a Manô que me recebeu em Manaus, carinhosamente com a Mel e seus cinco gatos. Agradeço a todos os curadores que disponibilizaram material e visitas técnicas para a realização desse mestrado. Agradeço a todos que me ajudaram de qualquer forma, direta ou indiretamente nos dois anos de mestrado. Agradeço a Bruno, namorado de Pati, pela tatuagem free que marcou o meu mestrado. Agradeço também a todas as mulheres da ciência que me inspiram, em especial: Robertinha, Bruna Bezerra, Nicole Malinconico, Tainá Lacerda, Pati Marques, Bruna Morais, Bruna Teixeira, Radha Recinos, Jennifer e Fer Ito.

Agradeço a Capes, pela bolsa concedida para a realização desse mestrado.

"Nada na vida deve ser temido, somente compreendido. Agora é hora de compreender mais para temer menos. "

Marie Curie (1977)

RESUMO

Iphisa é um gênero de lagarto monotípico, com duas subespécies. De ampla distribuição amazônica e morfologia bastante conservada. Estudos anteriores analisando dados genéticos e a morfologia do hemipênis, identificaram cinco linhagens evolutivas indicando que uma diversidade de espécies ainda não descritas ocorre sob o nome *Iphisa elegans* Gray, 1851. Visando ampliar amostragens anteriores em busca de uma hipótese filogenética mais abrangente e adequar a taxonomia à nova proposta sistemática, se necessário, com base em um conjunto de caracteres, foram analisados 766 espécimes e, dentre esses, 71 hemipênis. A partir dessa amostragem foram analisados 25 caracteres morfológicos de e marcadores mitocondriais (*16S; Cytb*) e nucleares (*C-MOS; PRLR*), totalizando 1327 pares de bases. Com base em árvores filogenéticas geradas por inferência Bayesiana e em evidências morfológicas, cinco Unidades Taxonômicas Operacionais (UTO) foram propostas: UTO 1 (Noroeste da América do Sul); UTO 2 (Sul da Amazônia); UTO 3 (Equador/margens do Rio Içá); UTO 4 (Amazônia central); UTO5 (Peru/Acre). Análises de variância apontam diferenças em tamanho, distinguindo as UTOs 1 e 2, mas não as UTOs 3, 4 e 5. O número de supralabiais diagnosticam a UTO4; poros femorais e escamas ventrais as UTOs 2, 3 e 5 e a ausência de pré-frontais a UTO5. As UTOs 1 e 5 apresentam morfotipos hemipenianos exclusivos. Dessa forma, informações genéticas e de diferentes complexos morfológicos independentes (caracteres morfométricos, merísticos ou categóricos) suportaram as cinco UTOs propostas que devem ser consideradas espécies plenas. O nome *Iphisa elegans* Gray, 1851 fica associado à UTO 1, enquanto *Iphisa soinii* Dixon, 1974 fica associado à UTO 5. As espécies correspondentes às outras três UTOs não apresentam nomes disponíveis, necessitando assim a criação e atribuição de novos nomes. Os resultados confirmam a diversidade críptica anteriormente revelada para o gênero, elevando *Iphisa e. soinni* à categoria de espécie e propondo três novos táxons dentro do gênero.

Palavras-chave: Amazônia. Diversidade críptica. Filogenia. Hemipênis. Morfologia.

ABSTRACT

Iphisa is a monotypic lizard genus with two subspecies. Contrasting with its wide Amazonian distribution, it presents conserved external morphology. Previous studies analyzing genetic data and hemipenes morphology, identified five evolutionary lineages indicating a diversity not yet identified under the name *Iphisa elegans* Gray, 1851. In order to extend previous assessments and aim at a more comprehensive phylogenetic hypothesis while adapting current taxonomy to this new systematic proposal, if necessary, based on a set of characters, I analyzed 766 specimens and, among them, 71 hemipenis. From these samples, 25 morphological characters of mitochondrial (*16S; Cytb*) and nuclear (*C-MOS; PRLR*) markers were analyzed, totaling 1327 base pairs. Based on the trees generated by Bayesian inference and morphological evidence, five Operational Taxonomic Units (OTU) were proposed: UTO 1 (Northwest of South America); UTO 2 (Southern Amazonia); UTO 3 (Ecuador / Içá River banks); UTO 4 (central Amazonia); UTO5 (Peru / Acre). Analyzes of variance indicated differences in size, distinguishing between UTOs 1 and 2, but not UTOs 3, 4 and 5. The number of supralabials diagnoses UTO4; femoral pores and ventral scales UTOs 2, 3 and 5 and the absence of pre-frontal UTO5. UTOs 1 and 5 present unique hemipenial morphotypes. Thus, genetic information and of different independent morphological complexes (morphometric, meristic or categorical characters) supported the five proposed UTOs that should be considered full species. The name *Iphisa elegans* Gray, 1851 is associated with UTO 1, while *Iphisa soinii* Dixon, 1974 is associated with UTO 5. The other three of these species do not have names available, thus requiring the creation and assignment of new names. The results presented here corroborate the cryptic diversity previously revealed for the genus, raising *Iphisa e. soinni* to the category of species and proposing three new taxa within the genus.

Keywords: Amazon. Cryptic diversity. Phylogeny. Hemipenes. Morphology.

SUMÁRIO

1 INTRODUÇÃO

Por décadas, a família Gymnophthalmidae foi considerada como parte da família Teiidae, apesar de, desde muito cedo, ser reconhecida em grupos separados dos demais táxons da família. Boulenger (1885) propôs a alocação dos gêneros que compõem a família Teiidae em quatro subgrupos, com base em caracteres de morfologia externa. MacLean (1974) reconheceu, dentro dos grupos de Teiidae propostos por Boulenger, as subfamílias Teiinae e Gymnophthalminae que, posteriormente, foram elevadas aos status de famílias com base em caracteres de fisiologia, morfologia cromossômica e anatomia (Ávila-Pires, 1995, 1980; Gorman, 1970) e reconhecidos como "*macroteídeos"* e "*microteídeos*", respectivamente.

Com cerca de 260 espécies e 51 gêneros, Gymnophthalmidae é considerada uma das famílias de lagartos neotropicais mais diversas (Uetz & Hosek, 2019), com distribuição ampla desde o sul do México, ilhas do Caribe, até a Argentina (Pellegrino et al., 2001; Doan & Castoe, 2005). Ocupam desde áreas abertas e de altitude a regiões de baixada em florestas úmidas. É uma família de lagartos com hábitos variados, com espécies terrestres, arborícolas, semiaquáticas e também fossoriais (Vanzolini et al., 1980; Avila-Pires, 1995; Rodrigues, 1995; Pellegrino et al., 2001; Kohlsdorf & Wagner, 2006; Kohlsdorf et al., 2010; Marques-Souza et al., 2018). A sistemática dos lagartos microteídeos vem se mostrando complexa ao longo dos anos, muito devido às dificuldades na resolução das relações filogenéticas entre os diversos grupos da família, repleta de convergências adaptativas como, por exemplo, o alongamento do corpo, redução dos membros, perda das pálpebras e/ou abertura externa dos ouvidos e presença ou ausência de algumas escamas da cabeça observadas em espécies de hábitos fossoriais não relacionadas (Pellegrino et al., 2001).

Em sua maioria, os gimnoftalmídeos são diagnosticados através de poucos caracteres de morfologia externa, como número, formato e disposição de escamas, além da proporção entre o tamanho dos membros e corpo (Peloso & Avila-Pires, 2010; Colli et al., 2015). Apesar disso, o conhecimento a respeito dessa família apresentou avanços consideráveis nas últimas décadas (Murphy et al., 2019), com a utilização de um conjunto de ferramentas investigativas com abordagens mais integrativas, combinando dados de morfologia externa, interna e dados moleculares (Torres-Carvajal et al., 2015; 2016; Sanchéz-Pacheco et al., 2017). Abordagens integrativas permitem um refinamento maior dos padrões observados, uma vez que a eventual congruência de diversas fontes de dados sustenta com mais robustez as relações inter e

intragenéricas, permitindo um avanço considerável na sistemática dos grupos (Padial et al., 2010). Contudo, ainda persistem diversas questões em aberto, principalmente quanto às relações entre as espécies de Gymnophthalmidae (Peloso & Avila-Pires, 2010), mas também envolvendo o monofiletismo de alguns gêneros e da família como um todo (Hernandez-Morales et al., no prelo).

Nas primeiras abordagens moleculares incluindo o gênero *Iphisa* Gray, 1851 dentre outros 26 gêneros de Gymnophthalmidae, Pellegrino et al. (2001) reconhecem duas novas tribos dentro da subfamília Gymnophthalminae (Heterodactylini e Gymnophthalmini), e alocam o gênero *Iphisa* como relacionado a *Colobosaura* e como grupo irmão de *Heterodactylus* e *Colobodactylus*, todos pertencentes a tribo Heterodactylini. Castoe et al. (2004) baseados em dados moleculares, modificam a topologia da família Gymnophthalmidae posicionando o gênero *Colobosaura* como parafilético em relação a *Iphisa*. Além disso, os autores reúnem as duas tribos propostas por Pellegrino et al. (2001) na subfamília Gymnophthalminae, sem divisões em tribos. Rodrigues et al. (2007) descrevem o gênero monotípico *Alexandresaurus* e o gênero *Acratosaura* (para acomodar *A. mentalis*, anteriormente no gênero *Colobosaura*) baseados em dados moleculares e morfológicos. *Alexandresaurus*, é descrito como táxon irmão de *Colobosaura modesta* e *Iphisa elegans*, considerados pelos autores como membros da tribo Heterodactylini, seguindo a proposta de Pellegrino et al. (2001).

Rodrigues et al. (2009) descrevem o novo gênero *Caparaonia*, relacionado à *Colobodactylus* e *Heterodactylus*, pertencentes à tribo Heterodactylini. Entretanto, a tribo Heterodactylini é recuperada em dois clados bem suportados, contendo os gêneros (i) *Colobodactylus, Heterodactylus* e *Caparaonia*; (ii) *Alexandresaurus, Iphisa, Colobosaura, Acratosaura e Stenolepis*. Baseados nessa topologia, os autores decidem por incluir o segundo clado em uma nova tribo: Iphisiini (grafia correta Iphisini: Colli et al., 2015). Colli et al. (2015) descrevem o novo gênero *Rondonops*, com duas novas espécies, dentro de Iphisini e posicionam o novo gênero como o novo grupo-irmão do gênero *Iphisa*.

Dentro da tribo Iphisini, seis gêneros são atualmente conhecidos: *Acratosaura*, *Alexandresaurus*, *Colobosaura*, *Iphisa*, *Rondonops* e *Stenolepis.* A tribo se distribui por toda a América do Sul cisandina, pelos biomas da Amazônica, Caatinga, Cerrado e Mata Atlântica com indivíduos de pequeno porte, hábitos semifossoriais e geralmente habitando o folhiço, com

corpo alongado, cauda duas ou três vezes maior que o corpo habitando regiões secas e úmidas. O gênero *Iphisa* é atualmente considerado monotípico, incluindo apenas a espécie nominal *Iphisa elegans*, que foi descrita com localidade-tipo imprecisa, no estado do Pará, e reconhecida por apresentar escamas lisas e amplas, dorso e ventre cobertos com duas fileiras de escamas lisas, corpo alongado, cabeça comprimida e escamas em forma de escudo. A espécie foi, por muitos anos, compreendida como amplamente distribuída através da Planície Amazônica, nos estados brasileiros do Amapá, Pará, Maranhão, Amazonas, Acre, Rondônia e Mato Grosso, além de regiões no Peru, Bolívia, Equador, Suriname, Guiana, Guiana Francesa e Colômbia (Dixon, 1974; Nunes et al., 2012; Recoder, 2016).

Dixon (1974) apresentou a única revisão taxonômica ampla para o gênero *Iphisa* até o presente momento, analisando a maior parte dos espécimes disponíveis em coleções que, na época, incluíam poucas dezenas de indivíduos. Dixon utilizou, além da análise de caracteres morfológicos externos, dados de osteologia e de morfologia hemipeniana de poucos espécimes na sua amostra. Algumas variações são apontadas por Dixon na quantidade de escamas supralabiais e nos poros femorais em fêmeas, além de variações na presença e posição das escamas pré-frontais. Com base em variações de escamas pré-frontais (ausência e presença), Dixon (1974) decide organizar a espécie nominal em duas subespécies: *Iphisa elegans elegans* e *Iphisa elegans soinii* Dixon, 1974, sendo essa última restrita ao Peru e Bolívia.

Em um estudo envolvendo caracteres moleculares e de morfologia do hemipênis, Nunes et al. (2012), revelaram a existência de uma diversidade ainda não reconhecida sob o táxon *Iphisa elegans*. Apesar dos indivíduos da espécie apresentarem uma morfologia externa aparentemente bastante conservada, a análise de caracteres hemipenianos de indivíduos provenientes de diversos pontos da distribuição da espécie e a inclusão de caracteres genéticos, até então não utilizados em um contexto de diferenciação populacional dentro da espécie, revelaram a existência de, ao menos, cinco linhagens crípticas sob o nome *Iphisa elegans*. Recoder (2016), em sua tese de doutoramento, abordou padrões morfológicos e moleculares na tribo Iphisini e, além de corroborar as linhagens crípticas já definidas por Nunes et al. (2012), revelou a existência de ao menos mais duas linhagens ainda sem nome para o gênero *Iphisa*. Dessa forma, esses autores concluem que o gênero *Iphisa* abrigaria uma diversidade críptica subestimada até então, representando um complexo de espécies ainda não nomeadas.

Dentro desse contexto, fica evidente a necessidade de uma ampla revisão dos espécimes de *Iphisa elegans* disponíveis nas coleções herpetológicas, de forma a verificar a congruência entre dados genéticos e morfológicos buscando a delimitação precisa das linhagens reveladas por estudos recentes (Nunes et al., 2012; Recoder, 2016). Além disso, é bastante importante investigar a existência de caracteres de morfologia externa que permitam diagnosticar essas linhagens e adequar a taxonomia do grupo a esta diversidade, de forma a descrever a diversidade do gênero de maneira precisa. Dessa forma, este trabalho teve como objetivos: (I) revisar os espécimes sob ao nome *Iphisa elegans* disponíveis em coleções herpetológicas brasileiras e estrangeiras, de forma a identificar caracteres de morfologia externa que permitam a diagnose das linhagens previamente reveladas por estudos anteriores e, eventualmente, identificar novas linhagens ainda não identificadas; (II) Ampliar o conhecimento acerca das variações morfológicas no gênero, incluindo a morfologia hemipeniana, e ampliar o conhecimento genético sob à luz de dados moleculares de dois genes mitocondriais e dois genes nucleares, que se mostraram particularmente informativos na delimitação de linhagens em estudos anteriores; (III) Adequar a taxonomia do grupo aos resultados obtidos, atribuindo nomes já disponíveis e propondo novos nomes às espécie candidatas reveladas.

O estudo desenvolvido e apresentado como dissertação de mestrado junto ao PPGBA-UFPE está organizado a seguir, em forma de manuscrito redigido em língua inglesa e segue a formatação sugerida pelo *Zoological Journal of the Linnean Society*.

2 INTEGRATIVE TAXONOMY REVEALS HIDDEN DIVERSITY IN THE COMPLEX *Iphisa elegans* (SQUAMATA:GYMNOPHTHALMIDAE)

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ABSTRACT

Iphisa is a monotypic lizard genus with two subspecies. Contrasting with its wide Amazonian distribution, it presents conserved external morphology. Nunes et al. (2012), with hemipenian and genetic data, identified five lineages indicating a diversity not yet described. Aiming to expand previous samples, we present a phylogenetic hypothesis and adapt the taxonomy, 25 morphological characters and 71 hemipenis of 766 specimens and mitochondrial (*16S; Cytb*) and nuclear (*C-MOS; PRLR*) markers were analyzed. Based on the trees generated by Bayesian inference and morphological evidence, five Operational Taxonomic Units (OTU) were proposed: OTU 1 (Northwest of South America); OTU 2 (Southern Amazonia); OTU 3 (Ecuador / Içá River banks); OTU 4 (central Amazonia); OTU 5 (Peru / Acre). Analyzes of variance point out differences in size, distinguishing between OTUs 1 and 2, but not OTUs 3, 4 and 5. The number of supralabials diagnoses OTU 4; femoral pores and ventral scales OTUs 2, 3 and 5 and the absence of pre-frontal OTU 5. OTUs 1 and 5 present exclusive hemipenis. Thus, genetics and morphology (morphometric, meristic or categorical characters) support the five proposed OTUs, being considered full species. Three of these OTUs require the assignment of new names; the name *Iphisa elegans* is associated with OTU 1 and *Iphisa soinii* is associated with OTU 5. With subtle variation, the results corroborate the cryptic diversity of the genus, revealing three new taxa and the elevation of *Iphisa e. soinni* to the species category.

Keywords: Cryptic diversity; Amazonia; Morphology; Hemipenis. Phylogeny.

INTRODUCTION

The monotypic genus *Iphisa* Gray, 1851 was created to include *Iphisa elegans* Gray, 1851, described with inaccurate-type locality on the Brazilian state of Pará. The species presents small body-size, semi-fossorial and diurnal habits and tends to forage on the leaf litter (Avila-Pires, 1995; Vitt, 2008). It is widely distributed throughout the Amazon, in the Brazilian states of Amapá, Pará, Maranhão, Amazonas, Acre, Rondônia and Mato Grosso, as well as regions in Peru, Bolivia, Ecuador, Suriname, Guyana, French Guiana and Colombia (Dixon, 1974; Peters & Donoso-Barros, 1986). The genus can be readily diagnosed from other Gymnophthalmidae genera by having two parallel rows of smooth scales in dorsal and ventral surfaces; a large pair of mentonians forming a shield shape; elongate body with short limbs; narrow tail, lanceolate in shape, long, cylindrical and strongly pointed.

In the original description of the genus, Gray (1851) mentioneds the type was collected by Wallace and Bates in an expedition around 300 miles from Pará [probably referring to the city of Belém, Pará (Hoogmoed, 1973)] and then deposited at the Natural History Museum in London. Gray (1851) noted that the individual collected had a very distinct body shape, so different from the other species previously observed, that he proposed a new family to allocate the monotypic genus: Iphisadae. Later, Boulenger (1885) analysed a female specimen from Demerara Falls (Guyana) adding a few more details regarding the number and arrangement of the head scales. Hoogmoed (1973) compiled data from expeditions in Suriname, and adds details on the number of pores (present in males and females) and gives a much more detailed description for the species and describes the species' habitat as the leaf-litter on the floor of humid tropical forests.

Dixon (1974) carried out the only taxonomic review for the genus *Iphisa* to date, involving around 50 specimens. The author analysed characters of external morphology, and includeddata on osteology and hemipenial morphology improving the original description of Gray (1851). He also mentioned populational variation regarding the presence and position of prefrontal scales. Furthermore, the author pointed out some variations in the number of supralabials scales and in the number of femoral pores in females. Based on these variations, Dixon proposed the organization of the nominal species into two subspecies: *Iphisa elegans*

elegans and *Iphisa elegans soinii* Dixon, 1974, the latter being restricted to Peru and Bolivia and characterized by the lack of the prefrontals scales.

In the first molecular approach including *Iphisa* and 26 additional Gymnophthalmidae genera, Pellegrino et al. (2001) recognized two new tribes within the Gymnophthalminae subfamily (Heterodactylini and Gymnophthalmini). The authors allocated *Iphisa* as the sister clade to *Colobosaura* and *Iphisa* + *Colobosaura* as the sister group to *Heterodactylus* + *Colobodactylus*, all belonging to Heterodactylini tribe. Castoe et al. (2004) based on molecular data, present a different topology for the family Gymnophthalmidae. The authors recognized the subfamily Gymnophthalminae without tribal divisions and recognize the genus *Colobosaura* as paraphyletic with respect to *Iphisa*. Rodrigues et al. (2007) described the new genus *Alexandresaurus* as the sister taxa of the clade including *Colobosaura modesta* and *Iphisa elegans*, within the tribe Heterodactylini. Furthermore, in the same study, the authors recognized *Colobosaura* as paraphyletic and creates the new genus *Acratosaura* to allocate *Colobosaura mentalis*.

Rodrigues et al. (2009) described *Caparaonia*, and place it in the Heterodactylini tribe. However, in this study Heterodactylini was recovered in two well-supported clades, containing the genera (i) *Colobodactylus, Heterodactylus* and *Caparaonia;* (ii) *Alexandresaurus, Iphisa, Colobosaura, Acratosaura* and *Stenolepis*. Based on their topology, the authors decide to split the second clade into a new tribe: Iphisiini (Iphisini: Colli et al., 2015). Subsequently, Colli et al. (2015) described the new genus *Rondonops* within Iphisini, placing the new taxa as the sister group to *Iphisa*.

More recently, Nunes et al. (2012) revealed a hidden diversity in *Iphisa elegans* based on hemipenial morphology and molecular evidence. The author recovered five evolutionary lineages that matched with five hemipenial morphotypes. The lack of shared mtDNA (*Cytb)* haplotypes among morphotypes, suggested reproductive isolation between populations, and five candidate species were hypothesized. Although nominal specimens present an apparently conserved external morphology, the variation found in hemipenial characters in individuals from different geographic regions and population-level genetic differentiation revealed the existence of at least five cryptic lineages. Recoder (2016), in an unpublished PhD dissertation, addressed morphological and molecular patterns in the Iphisini tribe and, expanding the

geographic sampling of molecular data for *Iphisa elegans*, corroborated the cryptic lineages defined by Nunes et al. (2012), and revealed the possibility of two additional lineages within the genus. Although earlier studies had already identified independent lineages under the name *I. elegans* and recognized the need of nomenclatural changes with the proposition of new specific names, such modifications were postponed awaiting a comprehensive revision with more extensive sampling and more detailed morphological and molecular analyses (Nunes et al., 2012).

In this scenario, aiming at delimiting the boundaries between of such lineages, diagnosing them based on morphological and molecular characters and at adequating the taxonomy to the current understanding of the diversity in the genus, we carried out detailed morphological (hemipenes, pholidosis and morphometrics) and molecular analyses on specimens of *Iphisa*, including the holotypes of each subspecies and additional specimens collected throughout their distribution. We provide a systematic review of the genus *Iphisa* based on an integrative dataset after analysing a sample over ten times larger than the last revision (Dixon, 1974). Finally, we propose a new taxonomic arrangement for the genus, presenting and discussing intraspecific variations.

MATERIAL AND METHODS

Molecular data

For the molecular analysis, tissue samples we used 156 *Iphisa elegans* liver or muscle tissue samples stored in 95% ethanol. Genomic DNA was extracted from samples following the protocol described in Fetzner (1999). We obtained sequence fragments of the mitochondrial *16S* rRNA (*16S*) gene, of the mitochondrial protein coding gene Cytochrome b (*Cytb*), and the nuclear exons oocyte maturation factor Mos (*C-mos*) and prolactin receptor gene (*PRLR*) (Table 1). Samples encompassed specimens collected in 53 localities (Table 2), covering the entire geographic distribution of the genus and representing both nominal subspecies and the hemipenial morphotypes defined in Nunes et al. (2012). Samples of *Rondonops xanthomystax* Colli, Hoogmoed, Cannatella, Cassimiro, Gomes, Ghellere, Sales-Nunes, Pellegrino, Salerno, Marques De Souza & Rodrigues 2015; *Colobosaura modesta* (Reinhardt & Lütken, 1862); *Acratosaura mentalis* (Amaral, 1933) and *Stenolepis ridleyi* Boulenger, 1887 were used as external groups in the molecular analyses.

Amplification of the DNA fragments was done in a final volume solution of 15µl containing 5.95µl H2O of milli-Q water, 1.5µl of 10x reaction buffer, 0.9µl of MgCl2, 0.15µl of Taq Polymerase (0.01 u / µl), 1.5 µl total dNTPs (0.2mM each), 1.5 µl of each primer specific for foward (F) and reverse (R) and 2 µl of diluted solution of DNA. In the thermal cycler they followed the basic PCR protocol with initial denaturation of 94ºC for 5min, followed by 35 cycles with denaturation at 94ºC for 30 seconds, annealing at 51°C for 30 seconds and extension of 72°C for 40 seconds, followed by a final cycle at 72°C for 7 min, terminating the reaction at 4°C. PCR results were subjected to Exonuclease I and Shrimp Alkaline Phosphatase purification (EXO/SAP) and further visualized on 2% agarose gel for quantification. The sequencing was performed in an automatic sequencer at the Instituto de Biociências of the Universidade de São Paulo.

Phylogenetic analyses

Sequences were edited and aligned using GENEIOUS 6.1 software (Kearse et al., 2012). The alignments were made under the CLUSTALW 2.1 algorithm (Larkin et al., 2007) with the software's default parameters. After editing and aligning each marker separately, a concatenated alignment was generated in SEQUENCEMATRIX 1.7 (Vaidya et al., 2011) with the *Cytb, C-mos* and *PRLR* genes. These fragments were successfully amplified from a total XX samples, whereas the *16S* rRNA fragment was left out of the phylogenetic analyses in order to reduce potencial effects of missing data on phylogeny estimation. Thefinal concatenated aligment contained 119 terminals and 1327 bp. To avoid zero-length branches, identical sequences were identified and removed from analysis. The best models of nucleotide substitution for each gene were selected with the software Molecular Evolutionary Genetics Analysis (MEGA X) (Kumar et al, 2018) using the Akaike criteria (Burnham & Anderson, 2002): GTR + I + G for the *16S*, *Cytb* and *PRLR* genes and HKY + I + G for *C-MOS*. A Bayesian inference analysis was run using MRBAYES 3.2 software (Ronquist et al., 2012) for 40 million generations and a sampling rate every 1000 generations. In addition, an haplotype network was inferred based on 134 sequences of mtDNA (*Cytb*) using the statistical parsimony method of Templeton, Crandall and Sing (TCS) (Clement et al. 2000) with PopArt 1.7 (Leigh & Bryant 2015) and DNAsp 5.1 (Librado & Rozas 2009).

Morphological data

A total 774 *Iphisa* specimens were analysed morphologically: 432 males, 258 females and 84 juvenile or non-sexed individuals, from 208 different locations (Fig. 1), including the holotypes of *Iphisa e. elegans* and *Iphisa e. soinii*, which are deposited in The Natural History Museum, London and at the Smithsonian National Museum of Natural History, respectively. The remaining specimens are housed in the following institutions (acronyms in parenthesis): American Museum of Natural History (AMNH), Centro de Ornitología y Biodiversidad (CORBIDI), Institute of Natural Sciences of Belgique (IRSNB), Instituto de Ciencias Naturales (ICN), Instituto Nacional de Pesquisas da Amazônia (INPA), Louisiana State University Museum of Natural Science (LSUMZ), Museo de Historia Natural, Universidad de San Marcos (MHNSM), Museu de Zoologia da Universidade de São Paulo (MZUSP), Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ), Museu Paraense Emílio Goeldi (MPEG), Muséum National d'Histoire Naturelle (MNHN), The Natural History Museum, London (BMNH), Museum of Comparative Zoology (UH-MCZ), Universidade Federal de Rondônia (UFRO), Universidade Bandeirantes de São Paulo (UNIBAN), Pontifícia Universidade Católica do Rio Grande do Sul (PUCRS), Smithsonian National Museum of Natural History (USNM), Universidade Federal de Minas Gerais (UFMG), Universidade Federal do Acre (UFAC), Universidade Federal do Mato Grosso (UFMT), Universidade Federal do Oeste do Pará (UFOPA) and University of Kansas Natural History Museum (KU).

We obtained data for 28 external morphological characters. Of these, twelve characters were meristic (scale and pore counts): LFH, subdigital lamella of the fourth finger; LFF, subdigital lamella of the fourth toe; POR, femoral pores; DOR, rows of dorsal scales; GUL, rows of gular scales; SAM, scales around midbody; VEN, rows of ventral scales; PA, scales on anal plate; SL, supralabials; IL, infralabiais; SO, supraocular; SC, supraciliar. Six were qualitative characters: MSL, largest supralabial; SUE, supralabial under the eye; MIL, largest infralabials; ICH, infralabials in contact with the chin; FRO, condition of presence or absence of the frontoparietal; PF, condition of presence or absence of the prefrontal. And eight were morphometric characters: SVL, snout-vent length; TRL, trunk length between limbs; HW, head width; HL, head length; TL, tail length; ED, eye diameter; END, eye-nostril distance; ND, distance between nostrils.

Most characters were taken using a binocular stereomicroscope and a digital calliper with a precision of 0.1 mm. Tail measurement was made using a cotton thread in case of curved tails and later measured with a ruler with precision of 1 mm. Sex of the specimens was verified by the presence of hemipenes, evident gonads or eggs.

Hemipenial morphology

We analysed 71 hemipenes of specimens from all the taxonomic units and throughout the genus distribution. We accessed some of the organs already analysed by Nunes et al. (2012) and added specimens from new localities. Some subtly distinct characteristics were observed, but those were not suggestive of different patterns or morphotypes. As Nunes et al. (2012) provide the brief descriptions of the five hemipenial morphotypes, here we only complement their results by adding information on unreported variations.

Hemipenial preparations followed techniques proposed by Manzani and Abe (1988), and modifications proposed by Pesantes (1994) and Zaher and Prudente (2003). The retractor muscle was manually separated and the everted organ filled with stained petroleum jelly. The organs were immersed in an alcoholic solution of Alizarin Red for 24 hours in order to stain eventual calcified structures (e.g., spines or spicules), in an adaptation proposed by Nunes et al. (2012) on the procedures described by Uzzell (1973) and Harvey and Embert (2008).

Statistical analyses

For the qualitative characters, a visual inspection of the raw data was done through *boxplot* and *barplot* graphs, and non-normal individuals (outliers) and missing data were excluded from the analysis. In addition, small-bodied individuals with SVL < 40mm were considered as juveniles, and were removed from analysis (Dixon, 1974). The *Shapiro-Wilks* and *Levene* homoscedasticity tests were used to analyse the behaviour of the data distribution and variance. The tail length data were excluded from multivariate analysis because many of individuals with regenerated or broken tails. Significant sexual dimorphism was tested for each group using a one-way analysis of variance (ANOVA) and significant morphometric differences among groups were tested with multivariate analysis of variance (MANOVA). When sexual dimorphism was identified, sexes were analysed separately. *Kruskal-Wallis* non-parametric statistical test was used for data with non-normal distribution. For the morphometric data (treated separately) a multivariate principal component analysis (PCA) was performed for

an exploratory visualization of axes that explain the greatest variation in the data set in a multidimensional space, and discriminant functions (DFs) (Manly, 2004) to detect characters that better differentiate the groups suggested by molecular analyses. For PCAs the entire data set was used, without prior group delimitation, to verify stronger evidence of possible clusters. Unlike PCA, discriminant functions use pre-established groups, based on mitochondrial topology highlighting differences between groups (Manly, 2000). All analyses were performed in R (R Core Team, 2016) and Paleontological statistics software (PAST) (Hammer, et al. 2001) using 0.05 of significance.

Delimitation of UTO's

For the prior definition of the Operational Taxonomic Units (OTU) groups were delimited based on the results of molecular analyses due the highly conservative external morphology of the specimens. We based the definition of the OTUs using exclusively the tree obtained in a Bayesian inference of mitochondrial gene (*Cytb*). The choice for this tree (Fig. 2) was based in the representativeness of the genus distribution for this gene that is not well represented for other molecular markers. Based on the clades defined in the phylogenetic analyses, we included in the same OTU specimens with congruent morphology (external and hemipenial), considering the geographic distribution (i.e., avoiding disjoint distributions). Since the analysis of hemipenial morphology revealed the presence of more than one morphotype in some clades, information on genital morphology was not firstly considered for the definition of OTUs (Fig. 3).

RESULTS

Molecular Analyses

The phylogenetic tree based on Bayesian phylogenetic inference based on mtDNA (*Cytb*) and nuDNA (*C-mos* and *PRLR*) of 119 specimens (Fig. 4), recovered a monophyletic genus *Iphisa* with four major groups, reciprocally monophyletic and strongly supported, nested in an unresolved polytomy. The clade A (Fig. 4) includes 41 specimens from southern Amazon, in the Brazilian states of Mato Grosso, Rondônia and Amazonas, in the interfluve between the rivers Madeira and Aripuanã.

Clades B and C received strong support, and were recovered as nested in a more inclusive, weakly supported (Fig. 4). Clade B includes six samples from Ecuador and from the Içá River, in Brazil. Although strongly supported, some genetic structure was found within clade C, which encompassed four monophyletic groups nested in a polytomy. One of these clades, C1, clusters samples from Peru and from northwestern Brazil (state of Acre). The other three groups, jointly designated as group C2, encompassed 19 samples from a wider geographic range, including the Guiana Shield and north-western Brazil, in the interfluve between rivers Purus and Madeira (Fig. 4).

Finally, Clade D (Fig. 4) is a well-supported group, clustering 50 samples from right bank of Amazonas River, in central Amazon, with six samples from margins of Abacaxis River, in the interfluvium of Madeira and Tapajós River, and samples from right margin of Aripuanã River, at the mouth of Rio Juma (Fig. 4) as sister taxa of all other samples in a larger but not supported clade.

OTU 1 corresponds to the clade C2 in Figure 2. Although this clade presents a reduced support (pp = 0.7), all the specimens with hemipenial morphology accessed in this group presented a unique morphotype, suggesting the group as an independent lineage. This unit included 230 specimens, distributed along the left bank of the Amazon River through lower Japurá and upper Solimões Rivers, and on the right bank of the Amazon River in lower Purus River and Juruá River and far as upper Madeira River in Rondônia State. The OTU 2 corresponds to the clade A in Fig. 2 and includes 306 specimens, occurring on the Madeira-Aripuanã and Juruena-São Manuel interfluves and in the Madeira-Aripuanã Interfluve. OTU 3 corresponds to the clade B in Fig. 2 and includes 27 individuals, with distribution in Ecuador, on the interfluve of Napo, Aguarico and Içá River. The OTU 4 corresponds to the clade D in Fig. 2 and includes 161 specimens distributed in the central Amazonia through the interfluves Purus-Madeira, Aripuanã-Juruena, Madeira-Tapajós, and on the right and left banks of the Tapajós River. The OTU 5 corresponds to the clade C1 in Fig. 2 and included 43 specimens distributed by the Peruvian Amazon, in the districts of Loreto, Huànuco, Cusco, San Martín and Genaro Herrera, and in northwestern Brazil, in the state of Acre, in the municipality of Porto Walter and in Parque Nacional da Serra do Divisor.

A total of 72 haplotypes were recovered in the mtDNA (*Cytb*) haplotype network (Fig. 5). The configuration of the haplotype network recovered five structured clusters, distant from each other by more than 30 evolutionary steps (except between OTU 1 and OTU 5 with 24 evolutionary steps) with no haplotype sharing and a high haplotype diversity (H_d = 0.983). The amount of evolutionary steps between haplotypes of the same cluster ranges from one to more than 30 steps.

External Morphology

The specimens of *Iphisa elegans* analysed throughout its geographic distribution revealed a conservative external morphology with only subtle differences within OTUs. Therefore, we present a general description of the external morphology for the whole genus and proceed to present specific features exclusive of each taxonomic unit.

Specimens in genus *Iphisa* are small sized lizards (maximum snout-vent length = 58 mm) with elongated bodies, robust and short heads, pentadactyl limbs, and smooth body scales. Two rows of paired and imbricated, wider than long scales are present on dorsum, ranging from twenty-five to thirty-four in each row. Dorsum scales may be spotted black or dark brown, with stains forming undefined shapes (Fig. 6A) or well-defined dots (Fig. 6B). Two paired rows of gular scales are present, ranging from seven to nine pair, usually eight (87.4% of specimens). Two rows of ventral scales ranging from fourteen to twenty-two pair, yellowish and lacking pigmented areas. Anal plate usually with five scales, always the median scale longer than the others. Rostral scale wide and in contact with a nasal scale on each side. Frontonasal is single, frontal, frontoparietals, interparietal and parietals are present. When present, the paired prefrontals can be slightly triangular in shape (Fig. 7B) or hexagonal with midline broadly in touch (Fig 7C).

Frequently, three supraoculars and four supraciliarieis are present. Six (32%) or seven (67%) supralabials. When seven supralabials are present (Fig. 8A), the fifth labial is frequently the largest and the third and fourth supralabials are positioned below the eye; When six supralabials are present (Fig. 8B), the fourth supralabial is frequently the largest and the third supralabial positioned below the eye. Small and numerous temporals; Ear opening rounded and deeper in the posterior region, surrounded by small granules. Usually six infralabials (92%) third the longest. Mental wider than long, shell shape, in contact with postmental, first

supralabials and rostral. Postmental single, wide and shield shaped. A pair of large mentonians, shield shaped, occupy more than a half of the length of the head, usually in contact with the second to fourth infralabials. Femoral pores vary between males and females (Table 3), males usually with more femoral pores than females, and counts being more variable in females (variation described in Taxonomic accounts, below).

Scales on tail have the same dark colours of the dorsum and venter and are very different in shape from those on the rest of the body, being small and lanceolate. Lateral scales on trunk (between fore and hindlimbs) are smaller than scales on dorsum and venter; with three to five transversal scales, usually four (86%). The sides of the body vary colour the pattern : with stains may appear as round and well-defined forms, overlapping on the dorsal region and more scattered on median region of the body (Fig. 6C). Also, as a colour gradient, in which the dorsal region of the flank is brown to dark brown, towards the ventral region (Fig. 6D).

Morphological variation

Scale counts are significantly different between sexes, with females presenting more dorsal and ventral scales, and a smaller number of femoral pores (Kruskal-Wallis test, $p < 0.01$). Across geographic regions for both sexes, significant differences are found for all scale counts except for the number of subdigital lamellae on the finger of males, the number of dorsal scales in females and the number of infralabials for both sexes (Table 3). The number of femoral pores in OTU 3 is higher than in other populations (Table 3, Fig. 9) whereas it is significantly smaller in populations of OTU 2 (Table 3, Fig. 9). The number of supralabials is six in more than 90% of specimens in OTU 4 ($\chi^2 = 289.2$, $P < 0.01$, Fig 10A), and seven in more than 80% of the specimens in the other taxonomic units (Fig. 10A). A pair of prefrontal scales is absent in more than 50% of the specimens in OTU 5 (Table 4, Fig. 10B), whereas it is present and in contact in over 80% of samples in the other OTUs (Table 4, Fig. 10B). Male specimens in OTU 1 and 5 present exclusive hemipenial morphotypes (Morphotype 4 and Morphotype 5, respectively). Morphometric differences among males of the different OTUs are significant in all characters analysed ($P < 0.05$ in all tests) except for distance between eyes (MANOVA, $F= 1.79$, $P = 0.13$, Table 5) and for females, except for trunk length between legs (MANOVA, $F = 1.63$, $P = 0.16$, Table. 5) and distance between eyes (MANOVA, $F = 1.93$, $P = 0.108$).

The hemipenial patterns identified herein corroborate with the five morphotypes earlier revealed in Nunes et al. (2012). The analyses of the hemipenial morphology revealed polymorphisms within some OTUs. The hemipenial Morphotype 1 is found in OTU 2 (N=15) and OTU 3 (N=2), two taxonomic units completely allopatric. On the other hand, the Morphotypes 2 (N=14) and 3 (N=7) are found only in individuals of OTU 4, in the same margin of the Abacaxis River. The Morphotype 4 (N=12) was recorded exclusively in individuals of OTU 1 and Morphotype 5 (N=5) exclusively in individuals of OTU 5.

Principal component analysis was done separately for males and females, since significant dimorphism was recovered in some morphometric characters. The two principal components estimated for males explained 76.8% of the variation, being 64.2% explained by first principal component. For females, the first principal component explains 96.6% and the second 2.6%, total of 99.2% of the variation (Fig. 11B). For males, the measurements of body head and eyes presents positive loadings in the first component (Table 6), while head and body measurements show negative loadings in second component. Thus, there is an axis of contrast between body size and eye measurements. For females, the same correlations are observed in the first component for head and body, while head length, snout-vent length, eye diameter and distance between nostrils have negative loadings in the second component. However, male and female specimens in all OTUs overlap in the multivariate space limited by the two first principal components (Fig. 11)

Discriminant analysis with male specimens produced the first discriminant function explained 76.4% of the variation, while the second explained, 13.1% (Fig. 11C). Opposite signs of correlation between coefficients presented in the second component indicate that measurements of head length, trunk length between members and eye diameter increase inversely proportional to head width, snout-vent length, eye-nostril distance and distance between nostrils. Discriminant analysis with female specimens produced the first discriminant function explaining 96.6% of the variation and a second function explaining 2.6% (Fig. 11D); trunk length increases inversely to eye diameter and distance between nostrils (Table 7). The classification matrix (Table 8) of groups indicates low percentages of correctly classifications to all groups. To original data, 44% of females and 46.6% of males were correctly classified, while in the cross-validated data, 38% of females and 43.7% of males were correctly classified.

The overall low percentage of correct classifications among groups indicates low morphometric differentiation among groups and sexes. OTU 2 presented the most correctly classified individuals, yet with relatively low percentage (< 40%) of correct classifications (Table 8).

The differences observed here in scale counts (Table 2), morphometry (Table 7), hemipenial morphology (Fig. 3: numbers 1, 2, 3, 4 and 5), in congruence with mtDNA genetic structure and the phylogenetic three of concatenated mtDNA and nuclear genes (Figs. 4 and 5) indicate the five OTUs analysed as independent lineages and, therefore, reveal the need for the creation of three new specific names in the genus and the elevation of *Iphisa e. soinii* to species status.

TAXONOMIC ACCOUNTS

Iphisa elegans GRAY, 1851 (Fig. 3) – OTU 1

Synonym: Gray 1851, p. 39*;* Amaral 1937a, p. 1740; 1937b, p. 191;1949, p. 111; Ávila-Pires 1995, p. 383 (part); Boulenger 1885, p. 424*;* Burt & Burt 1933, p. 66; Cunha 1961, p 153; Dixon 1974, p. 136 (part); Hoogmoed 1973; p. 279 (part); 1975, p. 158; 1979, p. 278; 1989, p. 168; Nunes et al. 2012 (part); Peters et al. 1970, p. 150*;* Vanzolini 1972, p. 105; ; Ribeiro-Júnior et al., 2017, p. 169-170 (part).

Holotype: BMNH 1946.9.1.1, adult male, British Museum of Natural History; collected by A. R. Wallace and H. W. Bates; type locality within 300 miles from Pará (Gray, 1851). Hoogmoed (1973) restricted the locality to a radius of 300 miles from the city of Belém, Pará, Brazil.

Diagnosis: Iphisa elegans is characterized by: (1) femoral pores usually present in females (0-23 pores, modal value = 0; absent in 30%); (2) Seven supralabials present in most specimens(78.5%); frequently the fifth supralabial is the largest (71.5%); frequently, the third and fourth supralabials are located under the eye (74.3%); (3) prefrontal scales always present and frequently in contact (92.5%).

Measurements of holotype (in mm): Snout-vent length 53.3 mm; Trunk length between members 27.9 mm; Head length 11.4 mm; Head width 5.7 mm.

Variation: Iphisa elegans is sexually dimorphic with males having larger heads in relation to body size, if compared to females (ANCOVA, $F_{1,168} = 39.9$ $P < 0.01$). Males present head measurements (HL, HW, ED, ND, END) larger than those of females, although snout-vent length does not show significant differences between sexes and females (ANOVA, $F_{1,168} = 0.08$ $P > 0.05$). Females presented slightly longer TRL than males (ANCOVA, $F_{1,168} = 11.9$ $P < 0.01$) and have less pores than males, with a modal value of 0 pores, while males have a modal value of 20 pores. Males also present a smallernumber of dorsal and ventral scales when compared to females (Kruskal-wallis, $P < 0.01$). Six supralabials are present in 21% of the specimens, which were collected in Igarapé Camaipi (Amapá), Moiobamba (Amazonas) and a few individuals from Lake Chaviana and Laranjal do Jari (Amazonas), Mazagão and Serra do Navio (Amapá) and Porto Velho (Rondônia). Only a few specimens (7%) have prefrontals no contact with each other. Prefrontals. Although hemipenial morphotype 4 is the most commom morphotype for *Iphisa elegans* (86% of males), three individuals of Manaus, Oriximiná and Urucará have a different hemipenis morphotype, similar to Morphotype 3 (more frequent in males of *Iphisa* sp. nov. 1) distinct from it by the presence of two additional parallel longitudinal rows of spicules in the assulcate face.

Comparisons: Iphisa elegans differs from *Iphisa* sp. nov. 2 in the number of femoral pores, females with modal value of 0 pores and males with modal value of 20 pores (0 and 18, respectively in *Iphisa* sp. nov. 2) and differs from *Iphisa* sp. nov. 3 with females having less femoral pores (modal value 18in *Iphisa* sp. nov. 3). *Iphisa elegans* differs in size only from *Iphisa* sp. nov. 2 presenting larger individuals, with snout-vent length of the largest male 58 mm and the largest female 56.7 mm (51.3 mm and 51.6 in male and female *Iphisa* sp. nov. 2, respectively). Females of *Iphisa elegans* also have more subdigital lamellae in the fourth finger of the hand (11-17) and less in the fourth finger of the foot (15-20) than the females of *Iphisa* sp. nov.2 [(10-14) and (13-24)]. Also, is readily diagnosed from *Iphisa* sp. nov. 1 by having seven supralabials 78% of specimens (6.7% in *Iphisa* sp. nov. 1). Differs from *Iphisa soinii* by having 92% of presence and contact of prefrontals (usually absent in *Iphisa soinii*, 57.1%). *Iphisa elegans* is easily distinguished from the others species by having an exclusive morphotype of hemipenes (Morphotype 4).

Distribuition: Iphisa elegans is distributed throughout northern South America, in the GuianaShield region, with the exception of the Venezuelan Amazon Forest. Is distribution

extends south, along the entire left bank of the Amazon River, and southwest to the Purus River basin. West of the Amazon, individuals are distributed in the municipality of Coari and, in the right bank of the Amazon River. Near the mouth of the Juruá River. The distribution extends to the south Amazon to, the boundary of the states of Rondônia and Amazonas, in Brazil, along the Madeira River, near the site of the hydroelectric power plant of Jirau, in the municipality of Porto Velho.

Remarks: The holotype of *Iphisa elegans* is here taken as part of OTU 1 due the occurrence of seven supralabials, the most common condition in specimens in the left margin of the Amazon River (OTU 1 range), contrasting with the reduced probability (6.7%) of occurrence of its characteristic in the other OTU with occurrence in the Wallace and Bates route (OTU 4).

Iphisa soinii **(Fig. 3) – OTU 5**

Synonym: Dixon, 1974, p. 138.*;* Avila-Pires 1995, p. 383; Nunes et al. 2012 (part); Ribeiro-Júnior et al., 2017, p. 169-170 (part).

Holotype: USNM 193623, Dixon (1974), an adult male, National Museum of Natural History, from Nuevo Tocache, Rio Huallaga, Departamento of San Martín, Peru (8°11'03.1"S, 76°30'45.0"W). Collected by Wade C. Sherbrooke, 1967.

Diagnosis: Iphisa soinii is characterized by: (1) femoral pores in females frequently present (0-16 pores, average = 7.4; absent in 20%); (2) seven supralabials (93.3%), frequently fifth supralabials is the largest (88.8%) and frequently third and fourth supralabial under the eye (96.1%); (3) prefrontal usually absent (57.1%), when present, in contact (32.1%) and separate (10.7%).

Variation: Males and females in *Iphisa soinii* does not variate in size. Nevertheless, a sexual dimorphism exists in number of femoral pores with females usually presenting less pores (Kruskal-Wallis, $P < 0,01$) and more ventral scales than males (Kruskal-Wallis, $P < 0,01$). *Iphisa soinii* looks subdivided in two populations by prefrontal condition (present and absent). The northern region of Peru, near Rio Corriente, Rio Maniti and Rio Orosa (Peru) and a specimen from the municipality of Porto Walter (Acre, Brazil) have the condition of presence

of the prefrontals, representing 30% of the condition in *Iphisa soinii*, while the other characters are located within the variation observed for the species.

Comparisons: Iphisa soinii can be readily diagnosed of the other species by presenting individuals with no prefrontals (prefrontals present in more than 80% of individuals of the other species of *Iphisa*). *Iphisa soinii* can also be distinguished from the other species of the genus be having an exclusive hemipenial morphotype (Morphotype 5). Differs from *Iphisa* sp. nov. 2 by their males tend to have a longer head and body, with the largest head having a length of 13 mm and a body 56.7 mm (10.3 mm and 51.3 mm in *Iphisa* sp. nov. 2). *Iphisa soinii* are distinguished from *Iphisa* sp. nov.2 by having females with femoral pores (0-16; no femoral pores in females of *Iphisa* sp. nov. 2); and differs from the females of *Iphisa* sp. nov.3, presenting a smaller number of pores (0-16; 16-20 femoral pores in females of *Iphisa* sp. nov. 3). Futhermore, *Iphisa soinii* can be distinguished from *Iphisa* sp. nov. 1 by presenting seven supralabials 93.33% (six supralabials 93% in *Iphisa* sp. nov. 1).

Distribution: Iphisa soinii occurs in the Acre State, in the municipality of Porto Walter and in the municipality of Cruzeiro do Sul, in the forest of the lower Moa River and in the Serra do Divisor National Park. It is widely distributed in the lowland regions of Peru, comprising the districts of Loreto, Cusco, Huànuco and San Martín.

Comments: An individual coming from Estirón (MZUSP 13964), near the Ampyacu River, in the department of Loreto (Peru) has the Morphotype 1 of the hemipenis, and has the condition of the presence of prefrontals, in contact, being the exception for the population. The absence of molecular data for this specimen removes the accuracy of which OTU is most appropriate to accommodate this specimen. Individuals from Peru, in coloration, resemble individuals of Pará, they are more orange coloured, as well as individuals of Nova Colina and Montenegro/Cacaulândia (Rondônia) (*Iphisa* sp. nov. 2), in contrast of the individuals of the eastern portion of Rondônia in the border with the state of Mato Grosso (dark brown back).

Iphisa sp. nov. 1 (Figs 3 and 12) – OTU 4

Synonym: Nunes et al. 2012 (part); Ribeiro-Júnior et al., 2017, p. 169-170 (part).

Holotype: Field number SMS 648, from Comunidade São Sebastião dos Bargas (3°47'23.5"S 59°02'06.8"W; WGS 84) municipality of Nova Olinda, state of Amazonas, Brazil. Collected on 16 july 2010 by Sérgio Marques de Souza.

Diagnosis: Iphisa sp. nov. 1 is characterized by: (1) femoral pores in females present (0-20 (when presents, modal value = 14); absent in 40%); (2) six supralabials (93.8%), frequently fourth supralabials is the largest (84.9%) and frequently third supralabial under the eye (94.6%); (3) prefrontal always present, usually in contact (94%) and separate (6%).

Description of the holotype (Fig. 12): Adult, male with snout-vent length 46.6 mm. Rostral broad, well seen from above, wider than high, in contact with the first supralabial, nasal and frontonasal. Frontonasal rounded, wider and higher than rostral, contacting the rostral, nasals, loreal, and prefrontal. Prefrontal pentagonal touching broadly each other, contacting the loreal, first and second supraocular, frontal and frontonasal. Frontal hexagonal, higher than wide, marginated laterally by the second supraocular, almost parallel to it, also contacting anteriorly the prefrontal and posteriorly by the frontoparietal. Frontoparietal pentagonal, slightly larger than prefrontal, in contact with third supraocular, frontal, parietals and interparietal. Interparietal longer than wide, as high as parietal, but narrower; in contact with frontoparietal, parietals and the first pair of dorsal scales. Parietal heptagonal, lateral contact with three temporals, previously contacting the third supralabial and frontoparietal, posteriorly in contact with the first dorsal scale. Three supraoculars, the first much smaller than second, in contact with the loreal, second supraocular and first supraciliar; the second is the largest, narrower anteriorly, in broad lateral contact with the frontal, previously in contact with prefrontal, first superocular, first and second superciliar, posteriorly in contact with the third superciliar; the third superocular has medium size, in contact with the second supraocular, third superciliar, parietal, frontopariental and temporal. Nasal above first supralabial, anteriorly wider, becoming narrower in the posterior region, nostril in the lower portion of the center of the scale in contact with the first supralabial, frenocular, loreal, frontonasal and rostral. Frenocular with a very small, square, in contact with nasal, loreal, second supralabials. Six supralabials, fourth the largest, in contact with third and fifth supralabial, subocular and temporal; Third supralabial the longest, under the eye and almost parallel to the third subocular; sixth supralabial the smallest, posteriorly rounded and in contact with granules around the tympanum and with temporal scales. Four supraciliaries, the first larger, in contact with the first and second supraocular,

loreal, subocular, second superciliar and eyelid. Upper and lower eyelid with small rounded scales. Temporal region with rounded scales and irregular size and shape between lateral, dorsal, parietal and supralabial scales. Ear surrounded by a row of small scales and larger scales of lateral and temporal region. Mental wide, shell-shaped, in contact with the postmental and first infralabial. Postmental larger than mental, heptagonal, in contact with mental, first and second infralabials and a pair of mental. A broad pair of mentonian shield-shaped, symmetrical. Six infralabials, third infralabial the larger, sixth smaller, in contact with the granules of the tympanic region. Eight pairs of smooth, intercalated, imbricate and rounded gular scales. Gular scales followed by three interbrachial scales, with the median longer than wide compared to the other two. Scales ventral in pairs, smooth, intercalated and imbricated. Lateral scales smaller than those of the dorsum and ventral, rounded, smooth, imbricate, smaller when surrounded by limbs. Two rows of smooth dorsal, imbricate, intercalate and isometric to the beginning of the tail. Tail scales lanceolate, keeled and smaller than scales on back. Anal plate with five scales, three larger in the central and the mid-one narrower and pointed. Eighteen femoral pores, eight in the right leg and ten in the left leg, a single pore in a rounded scale forming a row of scales in the lower region of the limb. Members with rounded, smooth, imbricate scales, with irregular and smaller sizes between the limb and the body. Interior region of limbs with juxtaposed granules, increasing in size on the sides and upper region. Large and imbricate scales; five fingers on the hind limbs, the fourth finger being the largest with twelve lamellae; imbricate and smooth subdigital lamellae, small and granular palmar scales. Large and imbricate tarsal scales; five fingers on the hind limbs, the second finger being the largest with seventeen lamellae; imbricate and smooth subdigital lamellae, small and granular palmar scales. Alcohol coloration of the light brown dorsum with very light stains. A black strip on the side of the body with white spots on the posterior tip of the scale. Tail brown than the back, with irregular spots and dotted. Ventral cream-colored, no stains.

Measurements of holotype (in mm): Snout-vent length 46.6 mm; Trunk length between members 27.7 mm; Head length 9.3 mm; Head width 7.8 mm.

Variation: Iphisa sp. nov. 1 is sexually dimorphic, males have larger head dimensions (HW, HL, ED, ND, END) with nose distance showing differences in relation to head length between sexes, males have more narrower head (ANCOVA, $F_{1,\ 126} = 29.5$ $P < 0.01$). Futhermore, males have more femoral pores and dorsal than females (Kruskal-Wallis, $P < 0.05$)

while females have more ventral than males (Kruskal-Wallis, $P < 0.05$). Populations of Parque Nacional do Amazonas, municipality of Itaituba, and from Reversa Extrativista Tapajós-Arapiuns, both in left margin of Tapajós River, have seven supralabials (9.4%), it can be found also in two individuals from municipality of Porto velho, in the Hidroeletric Plant of Jirau where an overlapping of populations of *Iphisa elegans* and *Iphisa* sp. nov. 1 occurs. In relation to hemipenial morphology, two morphotypes are found. Morphotype 2 are found in populations from interfluvium Madeira-Purus [Campo Catuquira, Campo Tupana, Comunidade Projó (left and right margin of Aripuanã River)], Itaituba (left margin of Tapajós River), Moiobamba (right margin of Purus River), Porto Velho (Rondônia) and from two margins of Abacaxis River (left margin, Igarapé-açú and right margin, São Sebastião). Morphotype 3 are found in populations from Juruti (PA) and Igarapé-açú (right margin of Abacaxis River, AM).

Comparisons: Iphisa sp. nov. 1 differs from *Iphisa elegans*, *Iphisa* sp. nov.*2, Iphisa* sp. nov. 3 and *Iphisa soinii,* by having six supralabials in 93.4% of specimens (seven supralabiais is most frequent in other groups). Furthermore, *Iphisa* sp. nov. 1 differs from *Iphisa* sp. nov. 2 by its bigger size, with the largest male attaining 53.5 mm and largest females attaining 54.9 mm (51.3 mm and 51.6 mm, respectively in *Iphisa* sp. nov. 2). Differs from *Iphisa* sp. nov. 3 by having males with narrower head; number of femoral pores in females of *Iphisa* sp. nov. 1 (modal value = 14 pores) differs significantly from *Iphisa* sp. nov. 2 (no pores) and from *Iphisa* sp. nov. 3 (modal value = 18 pores). Also, *Iphisa* sp. nov. 1 differs from *Iphisa soinii* by having prefrontals in contact 93.9%. The morphology of hemipenis also differs *Iphisa* sp. nov. 1 from the other species by having the only morphotype with two appendices digitiform (Morphotype 2) and two rows of spicules in the assulcate face arranged in the form of "S" (Morphotype 3).

Distribution: Occurs in the interfluvial regions of Central Amazonia, Purus-Madeira and Madeira-Tapajós, and occurs on the two banks of the Tapajós River. The distribution extends further south of the state of Amazonas, on the right bank of the Aripuanã River, and the left bank of the Juruena River. Although having close distributions, *Iphisa* sp. nov. 1 and *Iphisa* sp. nov. 2 are allopatric species occurring on opposite sides of the Aripuanã, Juruena and Madeira Rivers. (Fig. 13).

Iphisa sp. nov. 2 (Figs 3 and 14) – OTU 2

Synonym: Goicoechea et al. 2016, p. 631; Nunes et al. 2012 (part); Dirksen & De La Riva 1999; Harvey 1998, p. 148; Ribeiro-Júnior et al., 2017, p. 169-170 (part).

Holotype: UFMT 10126, (field number LTJV 60) from 12°44'15.9"S 60°10'12.3"W; WGS 84; Seasonal semidecidual forest municipality of Vilhena, state of Rondônia, Brazil. Collected on 25 October 2007 by Morais, D.

Diagnosis: Iphisa sp. nov. 2 is characterized by: (1) femoral pores frequently absent in females (82%), present (18%); (2) frequently seven supralabials (89.3%), frequently the fifth supralabial is the largest (85.3%) and frequently third and fourth supralabials under the eye (90.4%); (3) prefrontal frequently present, usually in contact (81.1%), separate (11.9%) and absent (6.9%). (4) Small size for the genus, largest male SVL 51.3; largest female SVL 51.6.

*Description of the holotype (Fig. 14):*Adult, male with snout-vent length 41.3 mm. Rostral broad, well seen from above, wider than high, in contact with the first supralabial, nasal and frontonasal. Frontonasal as long as rostral and higher, contacting the rostral, nasal, loreal, prefrontal and frontal. Prefrontal with a shape similar to triangles, separated by a projection in the midline of the frontonasal that comes into contact with frontal, contacting the loreal, first and second supraocular, frontal and frontonasal. Frontal hexagonal, higher than broad, marginated laterally by the second supraocular, anteriorly by the frontal and frontonasal and later by the frontoparietal. Frontoparietal pentagonal, slightly larger than prefrontal, in contact with the second and third supraocular, frontal, parietal and interparietal. Interparietal longer than wide, as high as parietal, but narrower; in contact with frontoparietal, parietal and the first pair of dorsal scales. Parietal heptagonal, lateral contact with three temporals, previously contacting the third supralabial and frontoparietal, later in contact with the first dorsal scale. Three supraoculars, the first much smaller than second, in contact with the loreal, frontal, second supraocular and first supraciliar; the second is the largest, in broad lateral contact with the frontal, previously in contact with prefrontal, first supraocular, first and second superciliar, later in contact with the third superciliar, frontoparietal; the third supraocular has medium size, in contact with the second supraocular, third superciliar, parietal, frontopariental and temporal. Nasal above first supralabial, anteriorly wider, becoming narrower in the posterior region, nostril in the lower portion of the center of the scale in contact with the first supralabial,

frenocular, loreal, frontonasal and rostral. Frenocular with a very similar form of loreal, but smaller, in contact with nasal, loreal, first superciliar and second supralabials. Seven supralabials, fifth the larges, in contact with subocular and temporal; seventh supralabial the smallest, in contact with granules around the tympanum and with temporal scales. Four supraciliaries, the first larger, in contact with the first and second supraocular, loreal, subocular, second superciliar and eyelid. Upper and lower eyelid with small rounded scales. Temporal region with rounded scales and irregular size and shape between lateral, dorsal, parietal and supralabial scales. Ear surrounded by a row of small scales and larger scales of lateral and temporal region. Mental wide shell-shaped, in contact with the postmental and first infralabial. Postmental larger than mental, heptagonal, in contact with mental, first and second infralabials and a pair of mental. A broad pair of mentonian shield-shaped, symmetrical. Six infralabials, second infralabial the larger, sixth smaller, in contact with the granules of the tympanic region. Eight pairs of smooth, intercalated, imbricate and rounded border scales. Gular scales followed by three much larger scales, with the median longer than wide compared to the other two. Scales ventral in pairs, smooth, intercalated and imbricated. Lateral scales smaller than those of the dorsum and belly, rounded, smooth, imbricate, smaller when surrounded by limbs. Two rows of smooth dorsal, imbricate, intercalate and isometric to the beginning of the tail. Tail scales lanceolate, keeled and smaller than scales on back. Less lateral scales than round and juxtaposed scales of the dorsal and ventral, smaller when close to the limbs. Anal plate with five scales, three larger central ones with smaller and pointed mid-scale scales. Sixteen femoral pores, eight in each leg, a single pore in a rounded scale forming a row of scales in the lower region of the limb. Members with rounded, smooth, imbricate scales, with irregular and smaller sizes between the limb and the body. Interior region of limbs with juxtaposed granules, increasing in size on the sides and upper region. Large and imbricate scales; five fingers on the hind limbs, the fourth finger being the largest with twelve lamellae; imbricate and smooth supradigital lamellae, small and granular palmar scales. Large and imbricate tarsal scales; five fingers on the hind limbs, the second finger being the largest with fifteen lamellae; imbricate and smooth subdigital lamellae, small and granular palmar scales. Alcohol coloration of the light brown dorsum with pointed spots on each dorsal scale, losing its shape in the most distal region of the dorsum. Side with rounded black spots juxtaposed. Tail darker than the back, with irregular spots and dotted. Cream-colored ventral, no stains.

Measurements of holotype (in mm): Snout-vent length 41.2 mm; Trunk length between members 23.2 mm; Head length 8.12 mm; Head width 5.5 mm.*:*

Variation: Iphisa sp. nov.2 is sexual dimorphic with males presenting larger head size in relation to the body when compared to females (ANCOVA, $F_{1,221} = 29.7$ $P < 0.01$). Males presents 19-22 while females have no pores (Kruskal-Wallis, $P < 0.001$). Females have a higher number of dorsal and ventral than in males in *Iphisa* sp. nov.2 (Kruskal-Wallis, $P < 0.01$). Few females (25%) of Guarajará-Mirim and Vale de São Domingos have between four and twenty pores being the exception of the female variation in the number of femoral pores. Population from Guarajará-Mirim and a few specimens from Vale de São Domingos and Colniza have six supralabials (13%). Futhermore, part of a population from Vale de São Domingos and Comorodo have the condition of absence of prefrontals (8.5%)

Comparisons: In relation to size, *Iphisa* sp. nov. 2 differs from all other species because it presents the smallest body size for the genus, with the largest male measuring 51.31 mm and the largest female 51.65 mm. *Iphisa* sp. nov.2 can be distinguished from the other species by females without femoral pores. In addition, males in *Iphisa* sp. nov. 2 have less pores (12-22) than males of *Iphisa* sp. nov.1 (16-25). Is readily diagnosed from *Iphisa* sp. nov. 1, *Iphisa elegans* and *Iphisa soinii* for having males with Morphotype 1 of hemipenis.

Distribution: The individuals of this species are distributed in the Madeira-Aripuanã interfluvial, in the municipalities of Itapinima and Santa Maria (AM). The distribution extends further south, already in the state of Mato Grosso, between the Roosevelt and Juruena Rivers, and in the state of Rondônia, on the margins of the Mamoré River. Individuals can also be found in the Juruena-São Manuel river basin and in the region of the Guaporé hydroelectric power station.

***Iphisa* sp. nov. 3 (Figs 3 and 15) – OTU 3**

Synonym: Duellman 1978, p. 215; According to Duellman (1978), Fitch (1968:37) erroneously identifies a specimen of *Iphisa*, from Ecuador, as *Calliscincophis agilis;* Nunes et al. 2012 (part); Ribeiro-Júnior et al., 2017, p. 169-170 (part).

Holotype: Field number MTR 36543, from São Pedro (3°02'06.5"S 68°52'58.6"W; WGS 84) municipality of Santo Antônio do Içá, state of Amazonas, Brazil. Collected on 23 April 2015 by Miguel Trefaut, Mauro Teixeira Jr., Renato Recoder, Marco Sena, Ivan Prates, Francisco dal Vecchio, Pedro Dias, Sérgio Marques, José Mario Guellere.

Diagnosis: Iphisa sp. nov. 3 is characterized by: (1) femoral pores in females always present (16-20, average = 17.8); (2) frequently seven supralabials (92.3%) with the fifth supralabial always the largest (100%) and third and fourth supralabials under the eye (100%); (4) prefrontal always present, usually in contact (92.3%).

Description of the holotype (Fig. 15): Adult, male with snout-vent length 43.6 mm. Rostral broad, well seen from above, wider than high, in contact with the first supralabial, nasal and frontonasal. Frontonasal twice wide as high, contacting the rostral, nasal, loreal, prefrontal and frontal. Prefrontal hexagonals, narrower in the midline, contacting each other, in contact with the loreal, first and second supraocular, frontal and frontonasal. Frontal hexagonal, higher than wide, in contact with prefrontals, second supraocular and frontaparietals. Frontoparietal pentagonal, larger than prefrontal, as long as wide, in broad contact in the midline, contacting frontal, second and third supraocular, parietals and interparietal. Interparietal higher than wide, longer and narrower than frontal and parietals, front part is pointed, in contact with frontoparietal, parietals and the first pair of dorsal scales. Parietal heptagonal, much wider than high, in lateral contact with two temporals, anteriorly contacting third supraocular and frontoparietals, medially with interparietal and posteriorly contacting first dorsal. Three supraoculars, , first the smallest, in contact with prefrontals, loreal, first superciliar and second supraocular; second the largest, in broad contact with frontal, anteriorly in contact with prefrontals, posteriorly in contact with third supraocular and frontoparietals, and the first three superciliar; third supraocular in contact with second supraocular, frontoparietal, parietal, one temporal and third and fourth superciliar. Nasal wider than high, with nostril in the center and bottom of scale, contacting first supralabial, loreal and rostral. Loreal posteriorly to nasal, diagonally oriented, higher than wide, contacting nasal, frontonasal, first supraocular, first superciliar, preocular and frenocular. Frenocular below loreal and preocular, small than preocular, followed by subocular, in contact with loreal, preocular, subocular and second supralabials. Seven supralabials, third and fourth under the eye, fifth the largest in contact with temporals, subocular and postocular; seventh supralabial the smallest, in contact with small

granules around the ear. Lower eyelid granules smaller and more numbers than upper eyelid. Three superciliaries, first the largest, wider laterally, in contact with first and second supraocular, second superciliar, preocular, loreal and eyelid. Upper and lower eyelid with small rounded scales. Temporals smooth, with different size and shape, between parietal and supralabial. Ear opening surrounding by small juxtaposed rounded granules. Lateral scales of the neck smooth, imbricate, shape similar to a shell, larger dorsally. Mental broad, shell-shaped, in contact with the postmental and first infralabial. Postmental heptagonal, higher than mental, in contact with mental, first and second supralabial and followed by a pair of mentonian. Mentonians very larger, posteriorly wider, occupying more than half of the ventral region of the head. Six infralabials, third infralabial the larger, sixth smaller, in contact with the granules of the tympanic region. Eight pairs of smooth, intercalated, imbricate and rounded border gular scales, followed by a peitoral region with three scales larger than gular scales, imbricate and shielded, mid-scale higher than lateral scales. Two rows of ventral scales with eighteen pairs, from interbrachials (not-included) too preanals; same size and shape that dorsal scales and imbricate, beginning at pectoral scales, ending in the pre-anal scales. Lateral scales in shell shape, imbricate, with similar size in the mid-body, becoming smaller, rounded and tight around arm level; Four transversal lateral scale at mid-body. Two rows of smooth dorsal, imbricate, alternated, hexagonal, wider than higher. Tail lanceolate, keeled, imbricate, alternated in the dorsal while ventral scales of tail are mucronate, smooth, imbricate and alternated; more rounded near to anal plate. Anal plate with five lanceolate scales, mid one higher than wider, medial the largest, peripheral scales smaller. Total of femoral pores twenty-two; each pore in a small rounded scale in the bottom of the leg. Limb scales rounded and bigger in the dorsal surface than scales in the margin to femoral pores; interior surface with small granules and juxtaposed. Large and imbricate scales; five fingers on the hind limbs, the fourth finger being the largest with twelve lamellae; imbricate and smooth supradigital lamellae, small and granular palmar scales. Tarsal and carpal surface with rounded, imbricate scales; fingers with juxtaposed and rectangular scales, clawed; palmar surface with small granules; Subdigital lamellae twelve on fourth finger and seventeen on fourth toe. Dorsal and tail surface dark brown, head and dorsal body lighter. Scales of the back with spots without definition and two darker stripes in the margins. Back of head without stains. Side of body and dark brown head almost black, spots juxtaposed near the back and more scattered near vent. Whole vent light cream color, without stains.

Measurements of holotype (in mm): Snout-vent length 43.5 mm; Trunk length between members 28.2 mm; Head length 10.4 mm; Head width 8.4 mm.*:*

Variation: No significant differences was observed between sexes for any meristic or morphometric character in *Iphisa* sp. nov.*3*. In relation to hemipenial morphotype, Morphotype 1 is found in the two margins of Içá River and Morphotype 5 is found in two specimens from Ecuador (Locality of Puerto Libre, Aguarico River and Rampon, near to Chiguaza).

Comparisons: Iphisa sp. nov.*3* can be easily differentiated from *Iphisa* sp. nov.2 by presenting larger individuals (ANOVA, $p < 0.01$) with the largest male measuring SVL 57.1 mm and SVL female 52.1 mm (51.3 mm and 51.6 mm respectively in *Iphisa* sp. nov. 2). *Iphisa* sp. nov.3 differs from others species for presenting females with greater number of femoral pores for the genus. *Iphisa* sp. nov. 3 can also be diagnosed of *Iphisa* sp. nov. 1 with females presenting smaller number of ventral (15-20 in *Iphisa* sp. nov. 3 and 17-22 in *Iphisa* sp. nov. 1). Futhermore, can be distinguished from *Iphisa elegans and Iphisa* sp. nov. 1 by hemipenial morphotype (Morphotype 4 in *Iphisa elegans* and Morphotype 2 and 3 in *Iphisa* sp. nov. 1).

Distribution: Iphisa sp. nov. 3 is distributed on the margins of the Içá River (AM) in the community of Cachoeirinha, Cuiauá Community and Açaí in Santo Antônio do Içá (left margins) and São Pedro, in Santo Antônio do Içá (right margin). They are also distributed further west of the Amazon, in Ecuador in the lowland regions, near the Rio Napo and Cuyabeno, besides Rampon, near Chiguaza and Puerto Libre, Ecuador.

DISCUSSION

The results presented herein revealed three new species and the elevation to species level of subsespecie *Iphisa elegans soinii* in the genus *Iphisa*, supported by the congruence of different sources of characters: molecular data (mitochondrial and nuclear), external morphology (morphometry and pholidosis) and internal morphology (hemipenes). There are only two species-group names available in genus *Iphisa* and, therefore, three new specific names had to be assigned to the remaining lineages identified. Our results mostly corroborate Dixon's (1974) observations and decisions, which attributed a subspecific name for the Peruvian populations of *Iphisa*, based on variation in scale counts of supralabials and infralabials, on the number of femoral pores in females and variation in the presence and

position of prefrontal scales. The results presented herein, based in a sample much larger than Dixon's, found that most of the individuals in OTU 5 lack prefrontal scales (60%) and that counts of femoral pores in females and supralabial scales are important diagnostic characters (Table 4). Therefore, the western populations of *Iphisa*, herein treated as OTU 5, correspond to subspecies *Iphisa elegans soinii* Dixon, 1974 and is also supported by our morphological and molecular data, and is here elevated to the species level (Fig. 4C1).

Attributing of the name *Iphisa elegans* to one of the OTUs proposed herein was more challenging, because of the imprecision of in the geographic location of it type-locality. Based strictly in historical record of the route roamed by the collectors (A. R. Wallace and H. W. Bates), but with no explicit justification, Gray (1851) defined the estimated range of collection of the holotype as "*a circuit of 300 miles of Para* (Brazilian state)". Hoogmoed (1973) understood that Gray (1851) was probably referring to the capital of Pará State, the municipality of Belém. However, after an extensive search in the main herpetological collections of Amazonian samples, including Museu Paraense Emílio Goeldi (MPEG), in Belém, we could not find any specimen collected this specific locality. By projecting a 300 miles radius around Belém (Fig. 3), the only OTU occurring within this area is OTU 1. However, we are aware that Wallace and Bates' routes extrapolate 300 miles from Belém, and hence decided to evaluate OTUs occurring throughout all the historical travel route of the collectors (Wallace, 1889).

Considering the records of Wallace and Bates' travel through the Amazon and Negro Rivers (Wallace, 1889) we recognized two possibilities of allocation for the *Iphisa elegans*' Gray 1851 holotype (Fig. 3): OTU 1, occurring from the Guyana Shield to western Brazil; or OTU 4, distributed in central and eastern Amazonia. Both OTUs are separated by the Amazon River along the most of their distribution (OTU 1 northern and OTU 4 southern), and the Amazon is exactly the main pathway used by Wallace and Bates during their expedition, what prevented us to determine in which bank of the river the holotype was collected. Thus, we decided to base our decision in the morphological similarity between the holotype and the variation described for each OTU. Although the specimens of both OTUs overlap the most of meristic and morphometric characters, the frequency of occurrence of the supralabial scales counts in each OTU is remarkably distinct (Table 4 and Fig. 8A). The specimens in OTU 1 has the largest majority of its specimens with seven supralabial (80 %), whereas the OTU 4 presents six supralabials as the most common condition (93 %). Since the holotype presents seven

supralabials, we decided that to assign the name *Iphisa elegans* to OTU 1 is the most reasonable option.

This study had as a starting point the results presented by Nunes et al. (2012), which indicated the existence of an undescribed diversity under the name *Iphisa elegans*. Thus, although our results corroborate the most of their findings, their assumptions on the hemipenial morphology as a constant characteristic for each clade recovered in their phylogenetic analyses and the remarkably differences in genital anatomy acting as a putative mechanism of prezygotic isolation in the genus were, at least, partially contradicted by our findings. With the increase of the sampling of hemipenes, our analyses found the clades A (*Iphisa* sp. nov. 2), B (*Iphisa* sp. nov. 3) and D (*Iphisa* sp. nov. 1) recovered in our concatenate tree including specimens with hemipenial Morphotypes 1 (clades A and B) and 2 and 3 (clade D). Such results revealed the existence of more than one distinct hemipenial morphotype in the clade D and the presence of the same morphotype in distinct clades (A and B), contrasting with the results presented by Nunes et al. (2012) that suggested the hemipenial morphology as a constant diagnostic for each lineage.

In *Iphisa* sp. nov. 1, the hemipenial Morphotype 2 seems to be dispersed throughout the geographic distribution and restricted to the larger and weakly supported group in the clade D (Fig. 4). On the other hand, the hemipenial Morphotype 3 is also present in specimens attributed to the *Iphisa* sp.nov. 1, but restricted to three specimens from Abacaxis River in a smaller and supported subclade within the *Iphisa* sp. nov. 1 (Fig. 4). The existence of a hemipenial morphotype exclusive to this subclade within the *Iphisa* sp. nov. 1 radiation could be an indicative of a distinct unnamed lineage associated with it. However, the reduced sample for the clade and the lack of hemipenial information for the specimens from Juma River, prevented us to take nomenclatural decisions involving this clade in the present study, keeping it within *Iphisa* sp. nov. 1 until further information is available.

Our sampling of *Iphisa* specimens included the main collections covering the distribution of the genus and, as results, we presented an updated distribution, increasing significantly the information available so far (Dixon, 1974; Avila-Pires, 1995). The delimitation of the five species recognized herein revealed patterns of diversity still not accessed for the genus revealing species mostly allopatric with their distributions in some points apparently influenced

by the Amazonian Rivers. The distribution of *Iphisa* sp. nov. 1 is northern limited by the upper Amazon River, which seems to isolate it from *I. elegans* in the most of its distribution. Sympatry occurs in the southern limit of the distribution of both species and in Moiobamba, in the right margin of middle Purus River (Fig. 13). Nevertheless, regarding the distribution of *Iphisa* sp. nov. 1 (green area, Fig. 13) and *Iphisa* sp. nov. 2 (yellow area, Fig. 13), the Aripuanã and Juruena Rivers seem to restrict the southern limit of the former species to the interfluve of these rivers. Furthermore, apparently the Aripuanã and Juruena Rivers also prevent the sympatry between these species, keeping *Iphisa* sp. nov. 2 in the opposite margins in relation to *Iphisa* sp. nov. 1.

The five species defined herein are supported simultaneously by morphological characters and by the phylogenetic analyses based on molecular data. Despite recovered as a monophyletic unit in the analysis involving the *Cytb* gene isolated (Fig. 2), *Iphisa elegans* sensu stricto was recovered dispersed in a polytomy with the group representing *Iphisa soinii* in the concatenate analyses (Fig. 4). However, although not recovered as a group in the multilocus tree (Fig. 4; group "C2"), *I. elegans* is strongly supported by a set of external (counts of femoral pores, counts of supralabials, and presence of prefrontals scales) and genital morphology, presenting an exclusive hemipenial morphotype, and being promptly diagnosed from *I. soinii*. Therefore, considering its morphological distinction, the evidence of monophyly in *Cytb* topology, the geographical distribution, and the unresolved topology in clade C of the concatenate analysis, we understand to have evidences enough to propose *Iphisa elegans* and *I. soinii* as full independent species.

The genus *Iphisa* has been frequently considered as a morphologically conservative taxon (Dixon, 1974; Avila-Pires, 1995, Nunes et al., 2012) and, consequently, has been treated as a monotypic genus for decades, with a subspecies being recognized by Dixon (1974). Our results partially confirm this overall morphological similarity in the genus once the statistical analyses comparing the most of the meristic and morphometric characters of the different OTUs revealed all the units broadly overlapped (Figs. 7). On the other hand, the analyses of large samples of specimens throughout the full distribution of the genus, integrating external and hemipenial morphologies, revealed specific variations in structure counts and morphometry that together made possible the diagnosis of five independent lineages. Thus, our results reinforces the notion that careful and extensive revisions of museum specimens with the access of multiple sources

of data are frequently effective in revealing not promptly recognizable diagnostic characteristics and making possible the recognition of species earlier considered not distinguishable using morphological features (e.g. Padial and De La Riva, 2009; Taylor et al., 2018). In summary, the results herein presented reveals the importance of the application of many independent lines of evidence in integrative systematic approaches. When in accordance, such characters are efficient and convincing features in solving complexes groups and in diagnosing diversity previously recognizable only through genetic data (Padial and De La Riva, 2009; Padial et al., 2010). Finally, the capacity of to diagnose morphologically species by integration of distinct and independent characters questions if the understanding of "cryptic diversity" is not frequently inadequately used, considering that several of the taxa earlier considered as cryptic ends to be revealed morphologically distinguishable after adequate extensive revisions of its diversity, revealing such taxa as "pseudo-cryptic" in fact (Medina et al., 2012).

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FIGURES

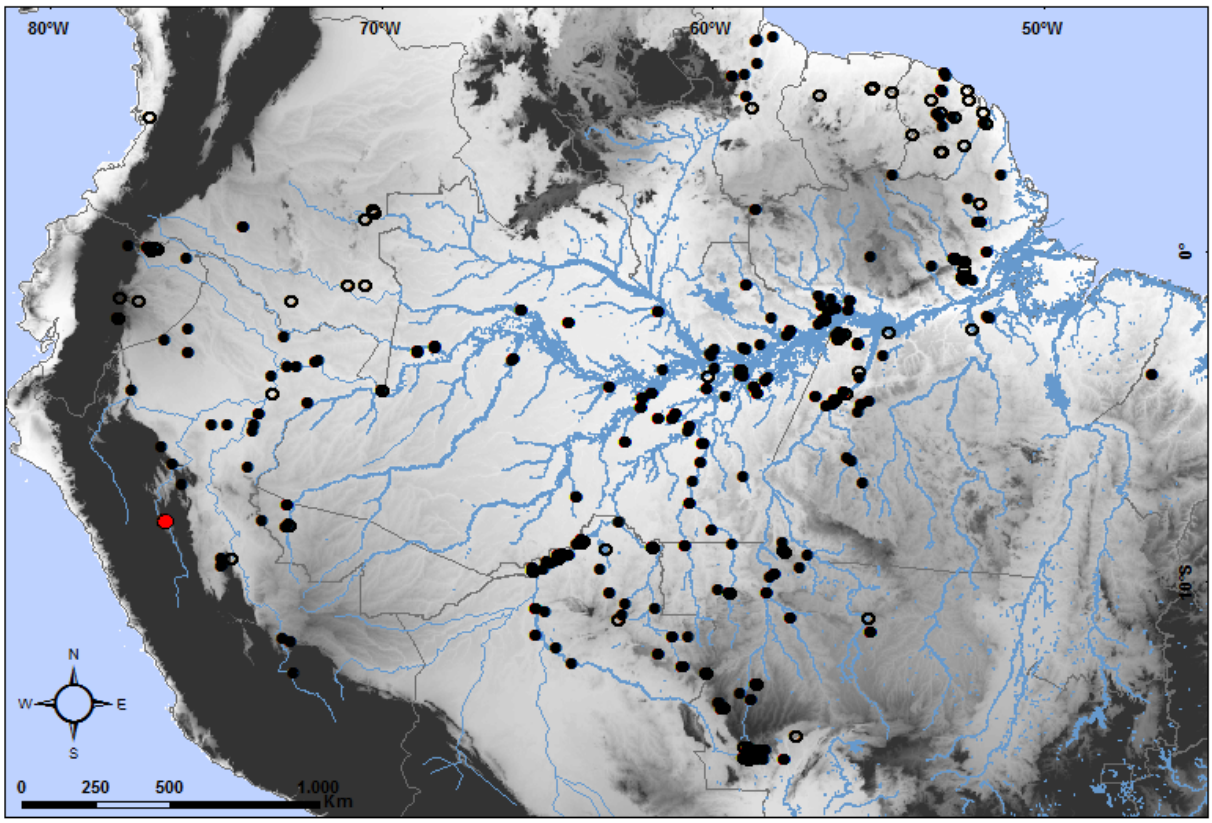

Figure 1. Distribution of the genus *Iphisa* through Amazon in South America. Empty circles indicate literature records; full circles indicates analysed material; red circle is the locality-type of *Iphisa soinii*.

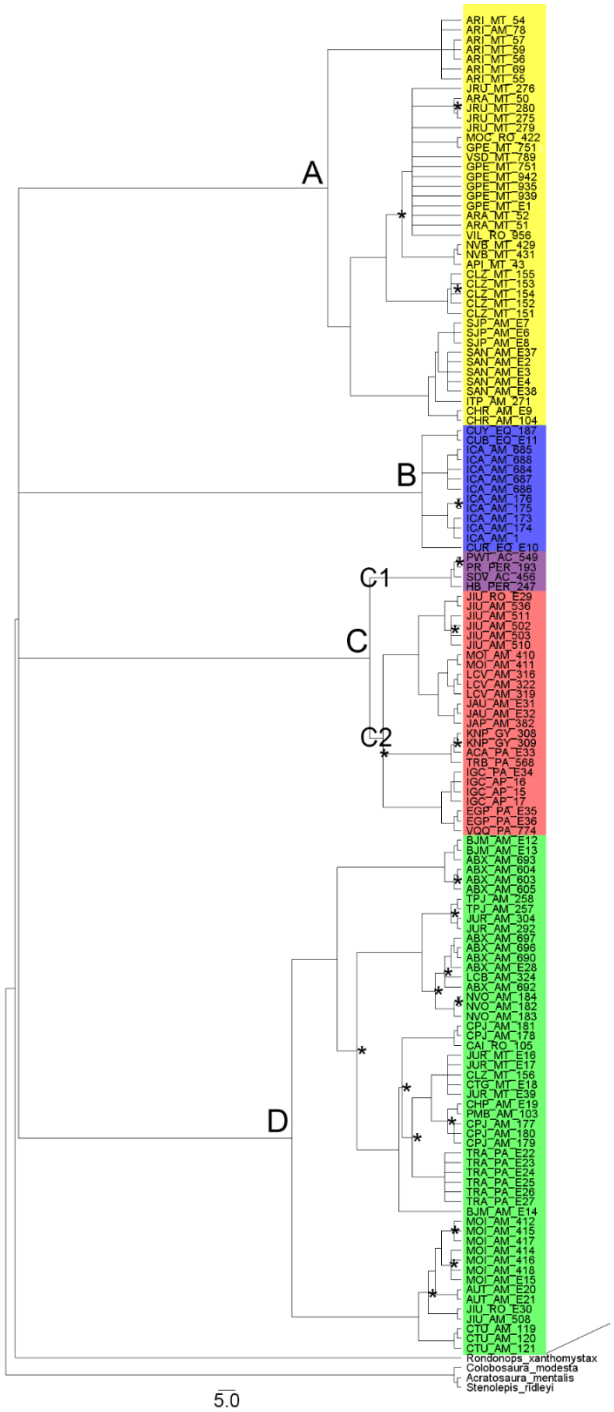

Figure 2. Phylogenetic tree of the genus *Iphisa* based on Bayesian Inference of mtDNA (Cytb) (N = 141). Terminal names shows a short code for the locality (for full details, see Table 2). Nodes with pp < 0.90 are shown with asterisks in the tree. Colours represent the taxonomic units and the species limits proposed here: red: OTU 1; yellow: OTU 2; blue: OTU 3; green: OTU 4; purple: OTU 5.

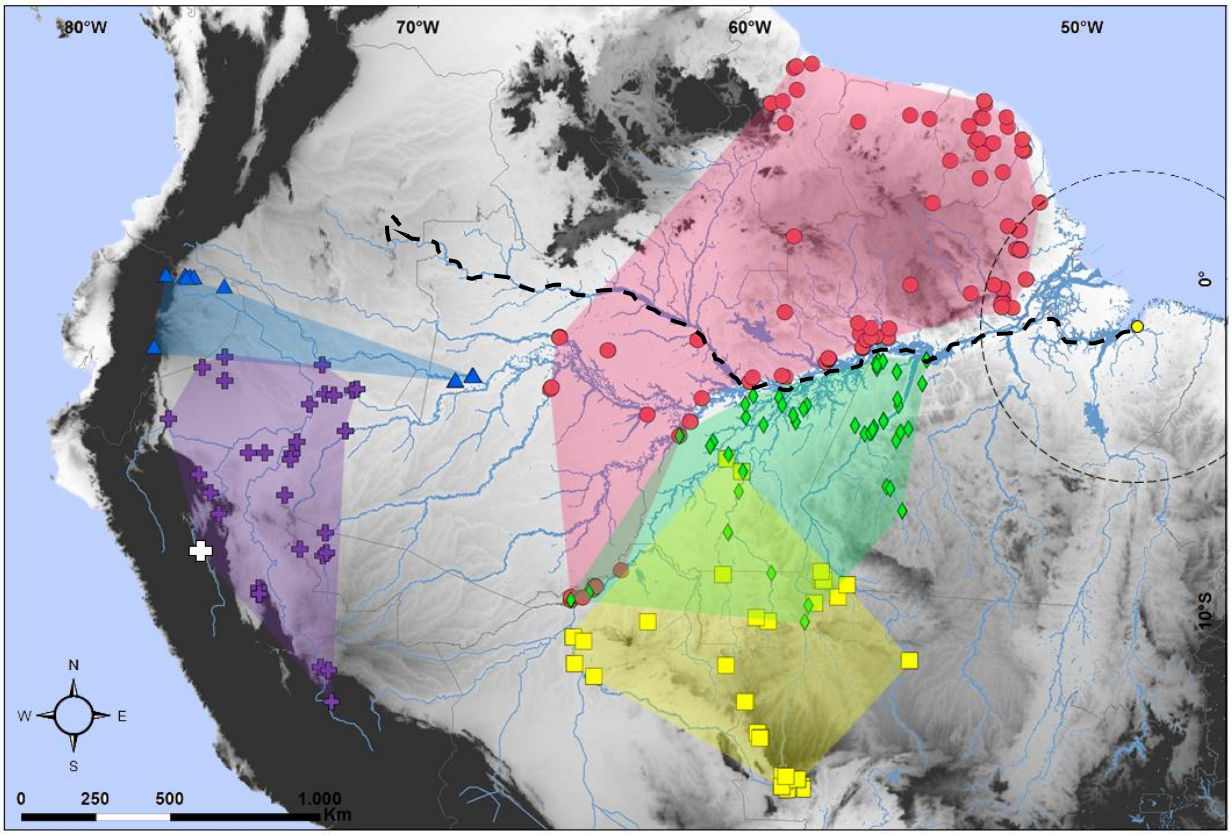

Figure 3. Distribution of Operational Taxonomic Units (OTU) proposed: red circles: OTU 1 – *Iphisa elegans*; yellow squares: OTU 2 – *Iphisa* sp. nov. 2: blue triangles: OTU 3 – *Iphisa* sp. nov. 3: green diamonds: OTU 4- *Iphisa* sp. nov. 1; OTU 5 – *Iphisa soinii*; yellow circle is the locality of Belém, Pará; dashed circle represents a radius of 300 miles from Belém. Dashed line in black represents the trajectory of Wallace and Bates in the Amazon River.

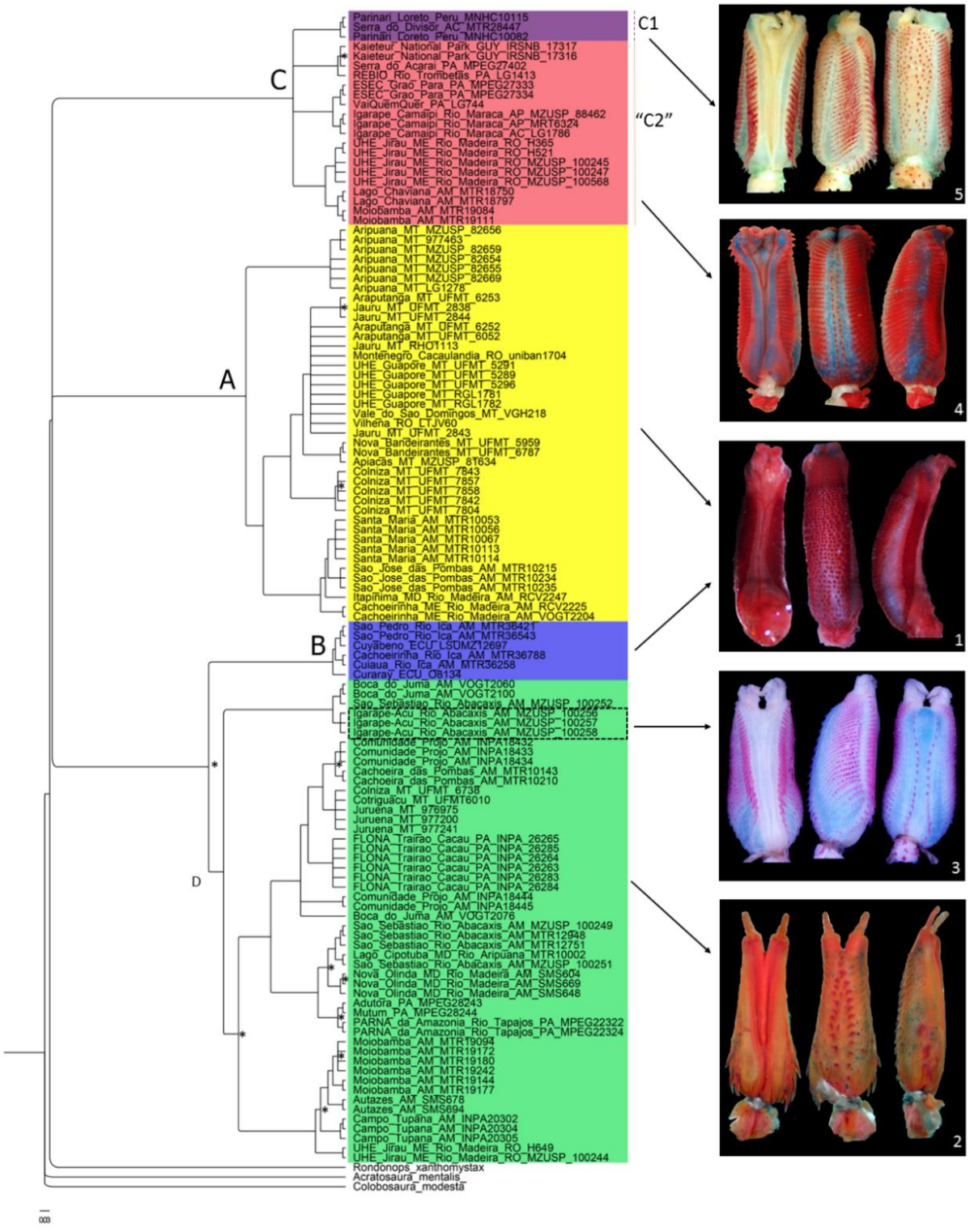

Figure 4. *Iphisa* topology based on Bayesian Inference (N = 119) of mitochondrial (*CYTB*) and nuclear (*C-MOS* and *PRLR)* genes. Terminal names show locality and voucher number. Nodes with pp < 0.90 are show with asterisks in the tree. Colours represent the taxonomic units and the species limits proposed here: red: OTU 1; yellow: OTU 2; blue: OTU 3; green: OTU 4; purple: OTU 5. Number in lower rights represents the number of hemipenial morphotype described in Nunes et al., (2012). Photos of Morphotype 3 and 5 with permission of the authors.

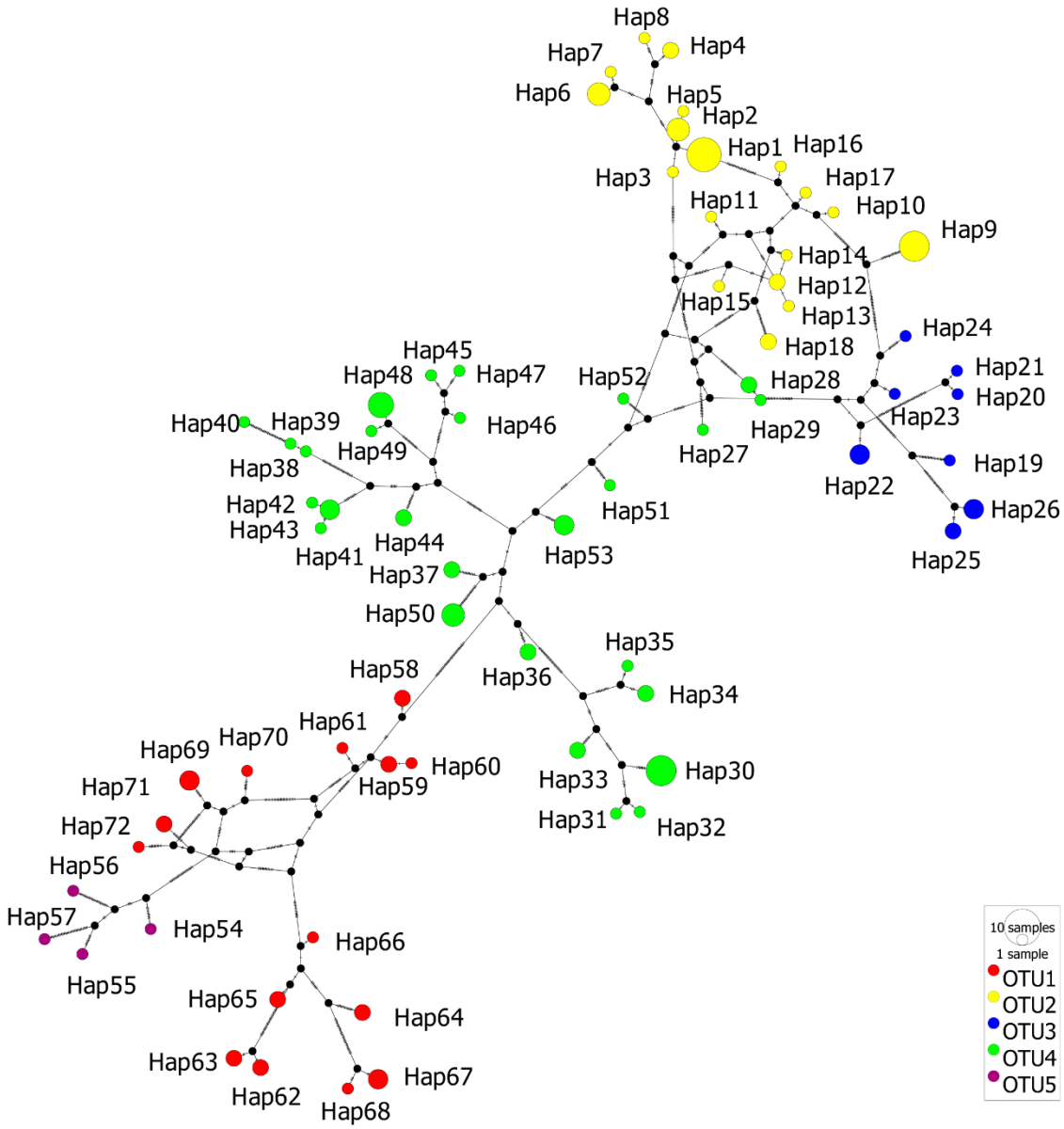

Figure 5. Haplotype network inferred based on the mtDNA (Cytb) using a statistical parsimony method (TCS). Total number of haplotypes = 72. Labels identify the haplotype number. To list of voucher/haplotype see Appendix 2. Colours represent the operational taxonomic units proposed here: red: OTU 1 – *Iphisa elegans*; yellow: OTU 2 – *Iphisa* sp. nov. 2; blue: OTU 3 – *Iphisa* sp. nov. 3; green: OTU 4 – *Iphisa* sp. nov. 1; purple: OTU 5 – *Iphisa soinii*.

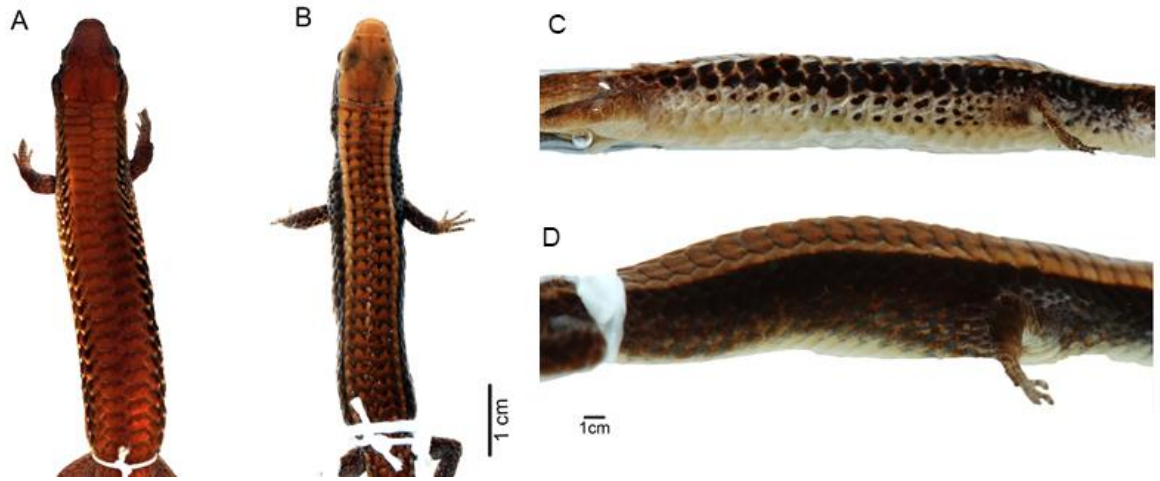

Figure 6. Variation in dorsal and lateral coloration within the genusin Iphisa: in the dorsum and lateral of the body. (A) dark stains with undefined shapes in theon dorsum: MZUSP 102909-OTU 1; (B) dotted dark stains in the dorsum: CORBIDI 0413-OTU 5. (C) well-defined round black stains onin the flanklateral body: CORBIDI 02684-UTO5 (D) gradient of the dark brown gradient on dorsumin lateral dorsum: CORBIDI 04134-UTO 5.;

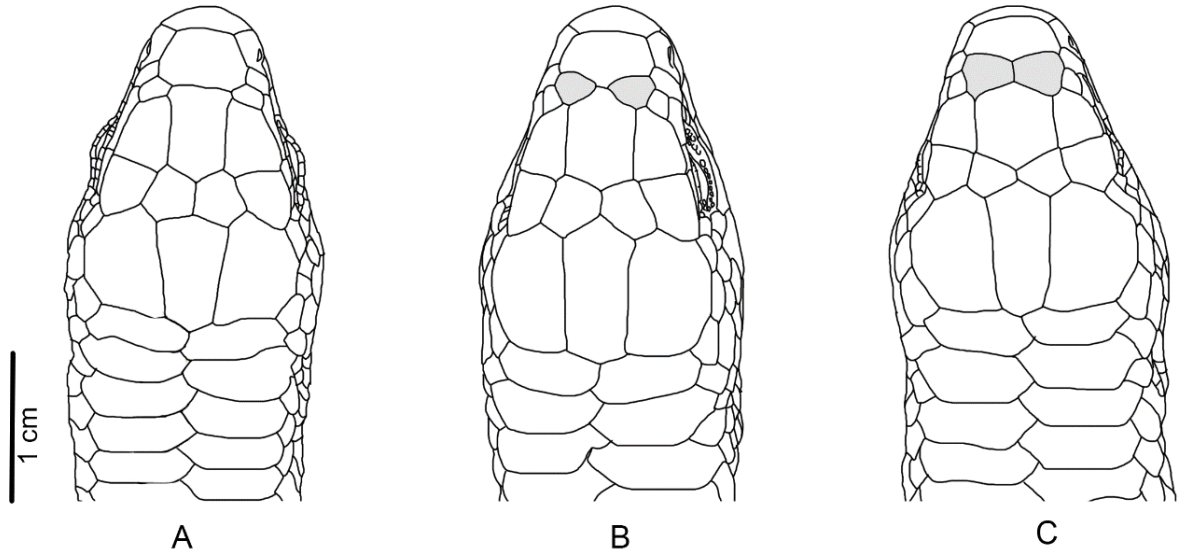

Figure 7. Variation in prefrontal scales (in gray) in *Iphisa*: Absent (A); present with no contact (B); present, in contact (C).

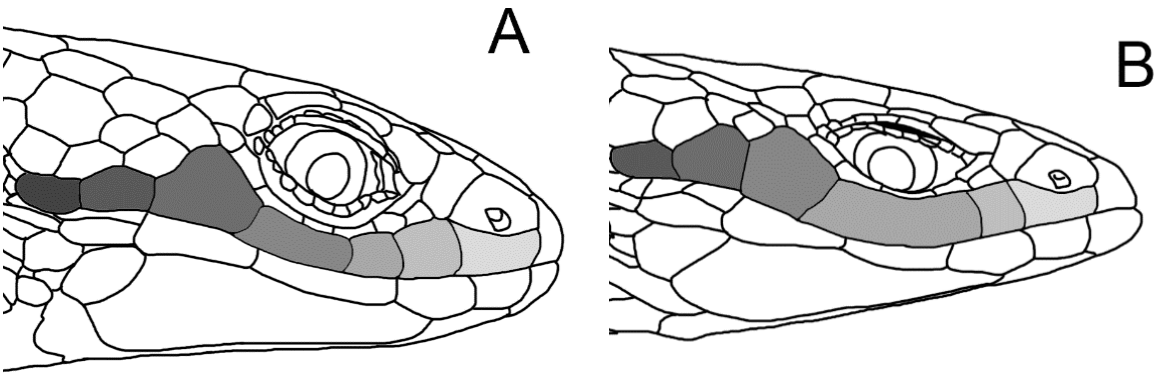

Figure 8. Variations in the number of supralabial scales in *Iphisa*: seven supralabials, characteristic of OTUs 1, 2, 3 and 5 (A); six supralabials, characteristic of OUT 4(B).

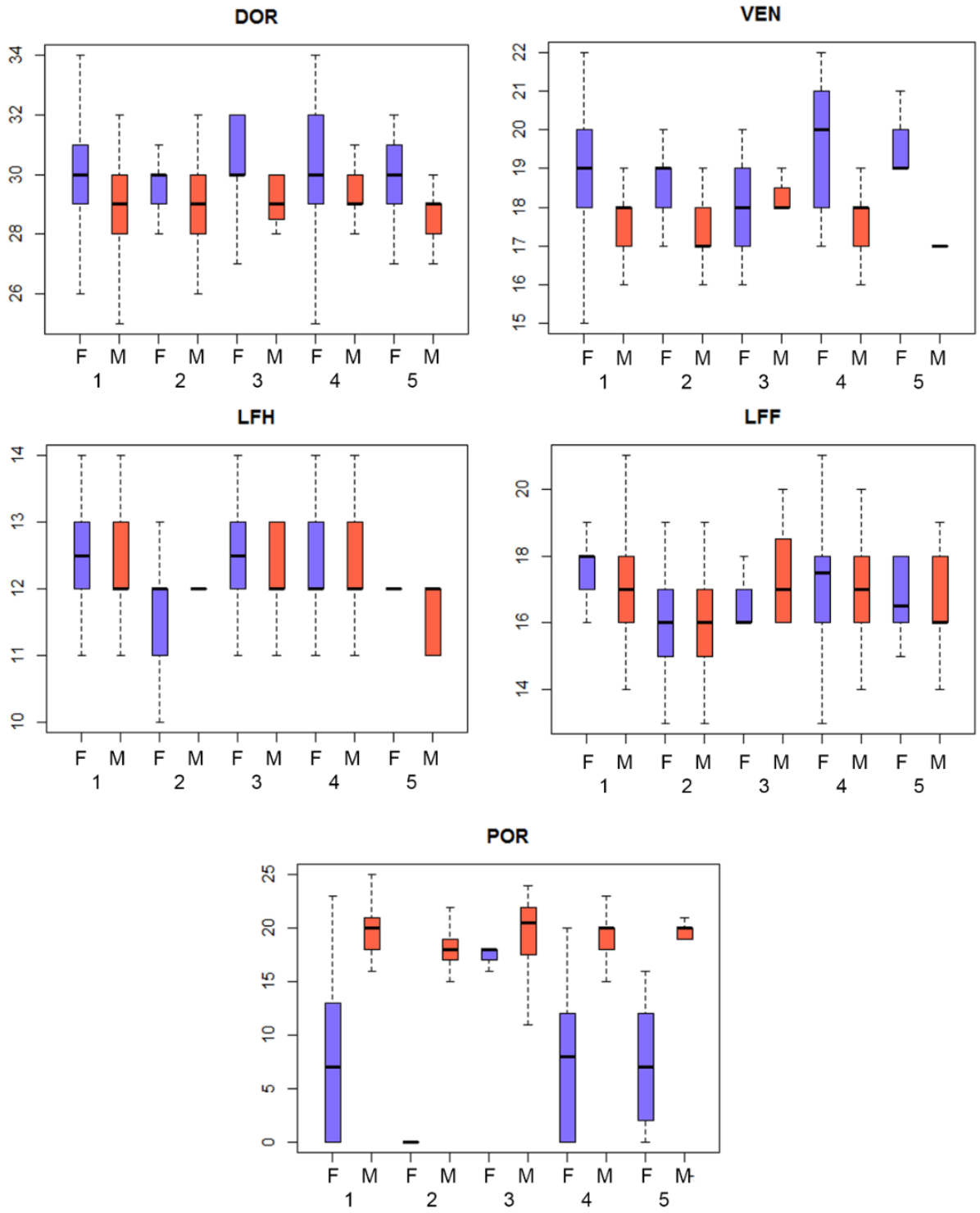

Figure 9. Boxplots with difference between the five taxonomic units of six counts characters. DOR: number of dorsal scales of the right row; VEN: number of ventral scales of the right row; LFH: subdigital lamella of IV finger of the hand; LFF: subdigital lamella of IV finger of toe; POR: femoral pores. Females are represented in blue and males in red.

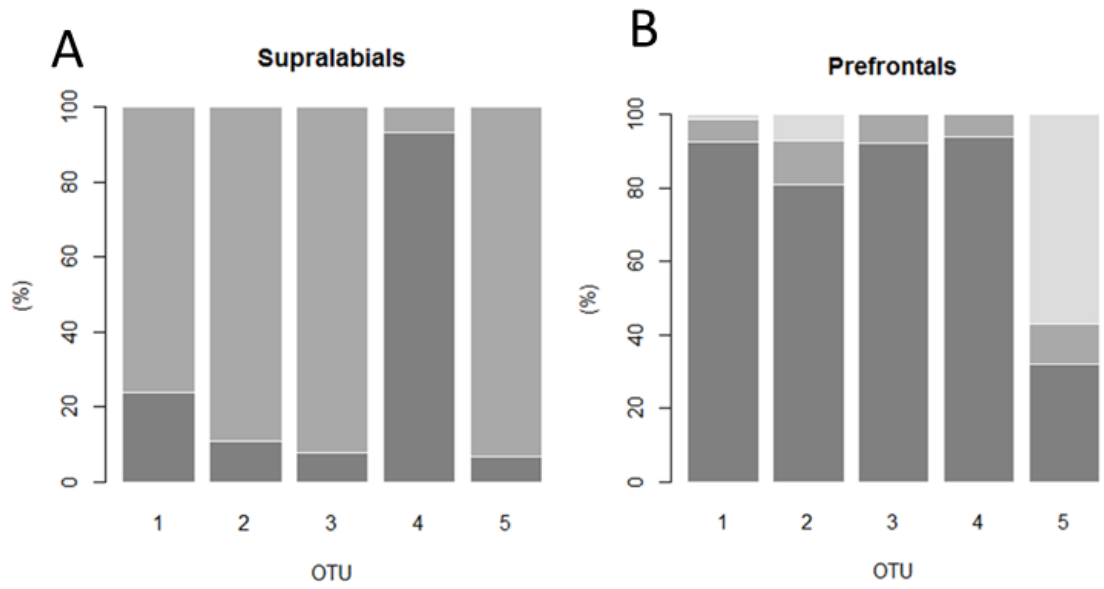

Figure 10. (A) Frequencies of seven (grey) and six (dark grey) supralabials between in the taxonomic units. (B) Frequencies of presence with contact (dark grey), presence with no contact (grey) and absence (light grey) between the prefrontal scales in the taxonomic units. (B) Geographic variation of the prefrontal character.

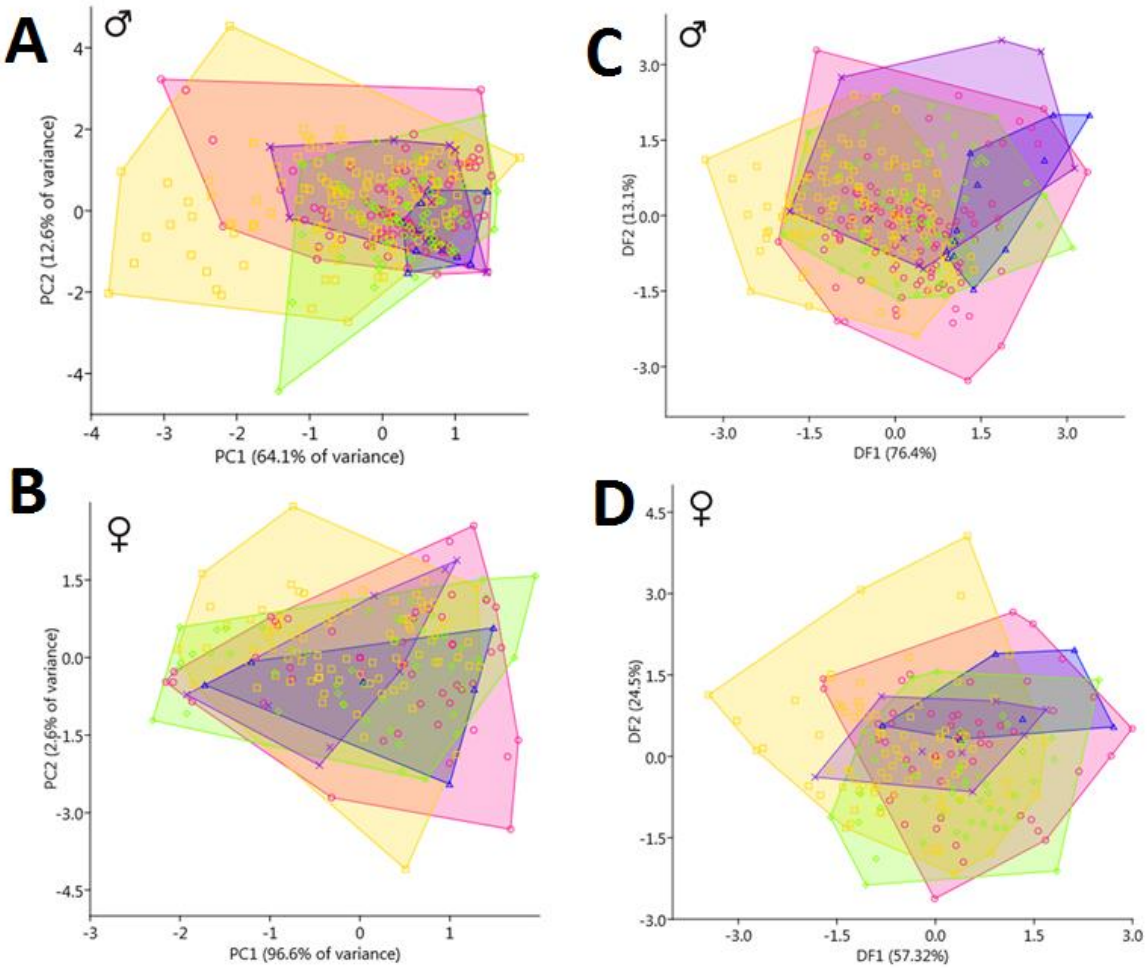

Figure 11. Results of a principal component analysis on the log-transformed morphometric variables (A = males; B = females). Results of discriminant function analysis on the log-transformed morphometric variables (C = males; D = females); red circles: OTU 1; yellow squares: OTU 2; blue triangles: OTU 3; green diamonds: OTU 4; purple crosses: OTU 5.

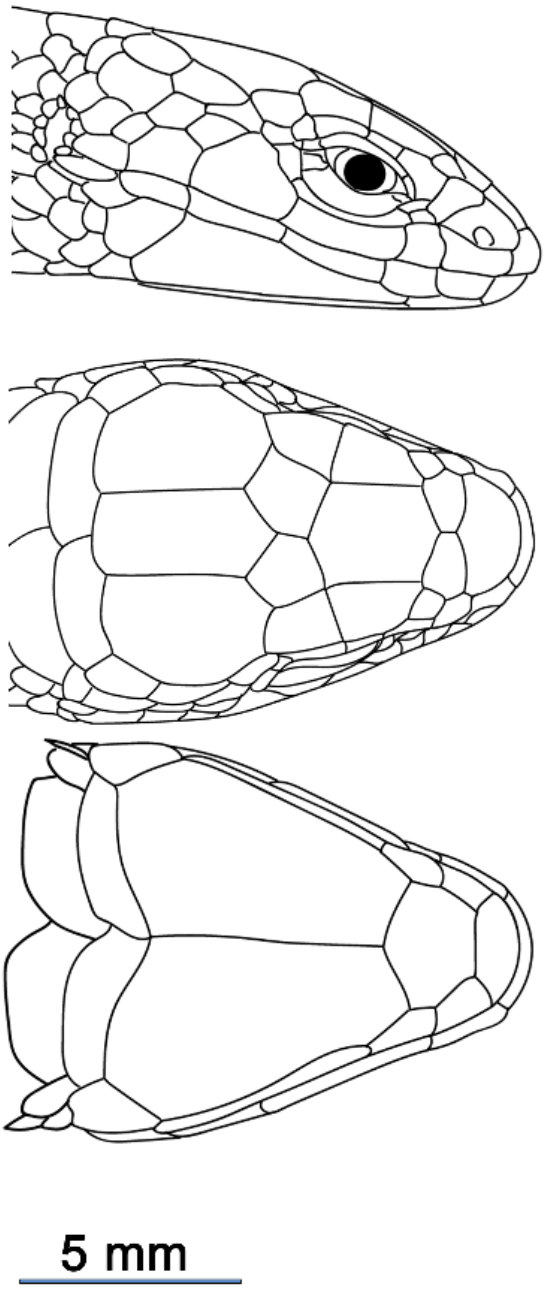

Figure 12. Lateral, dorsal, and ventral views of the head of the holotype of *Iphisa* sp. nov. 1 (SMS 648).

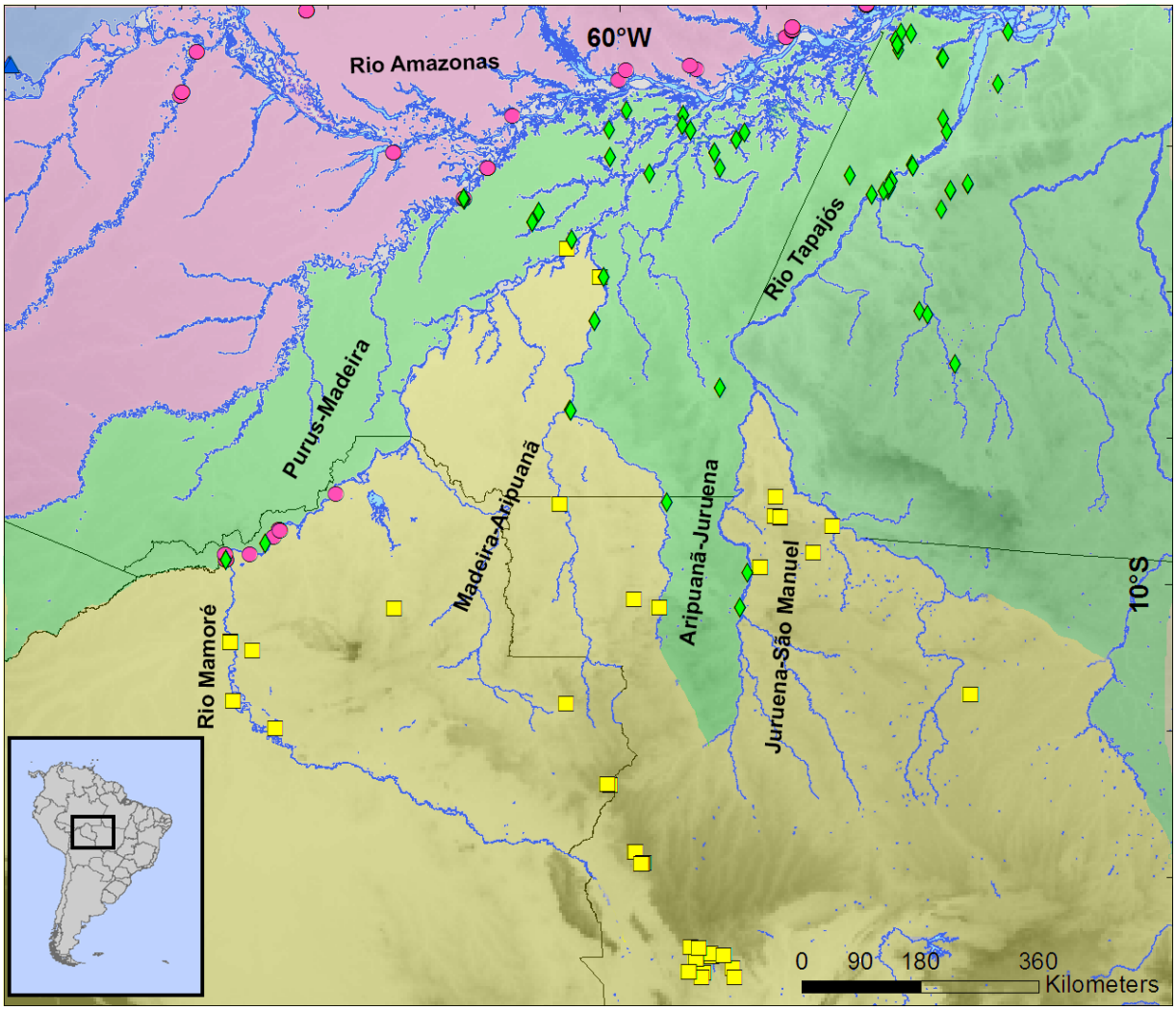

Figure 13. Distribution of Operational Taxonomic Units in Central Amazonia. With details of Amazon Rivers. The colours in the map the same of the records of occurrence of the specimens representing the expanded probably area of occurrence for each OTU: red: OTU 1; yellow: OTU 2; blue: OTU 3; green: OTU 4. Names of Rivers and interfluves in black.

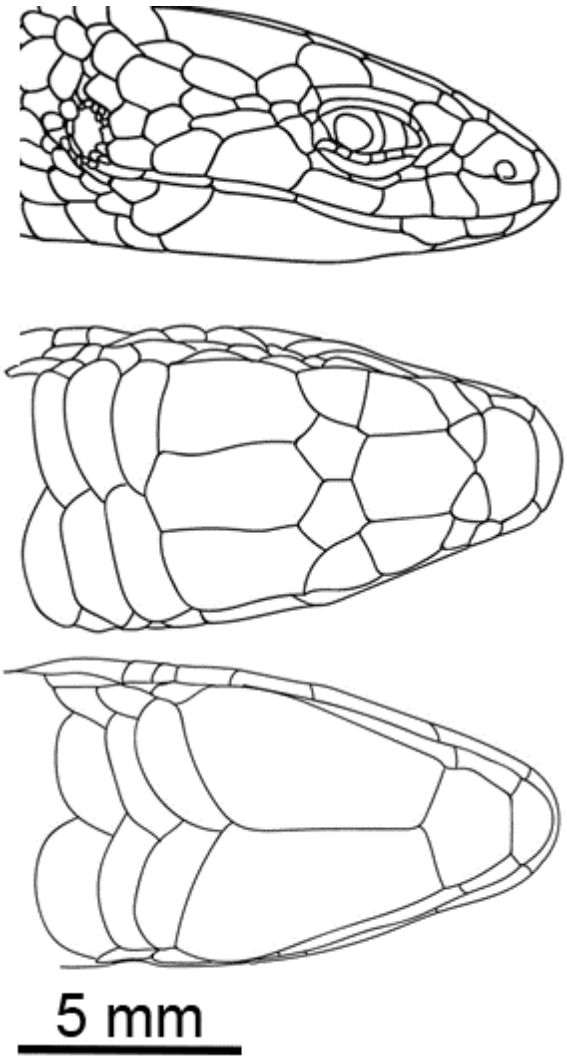

Figure 14. Lateral, dorsal, and ventral views of the head of the holotype of *Iphisa* sp. nov. 2 (UFMT 10126).

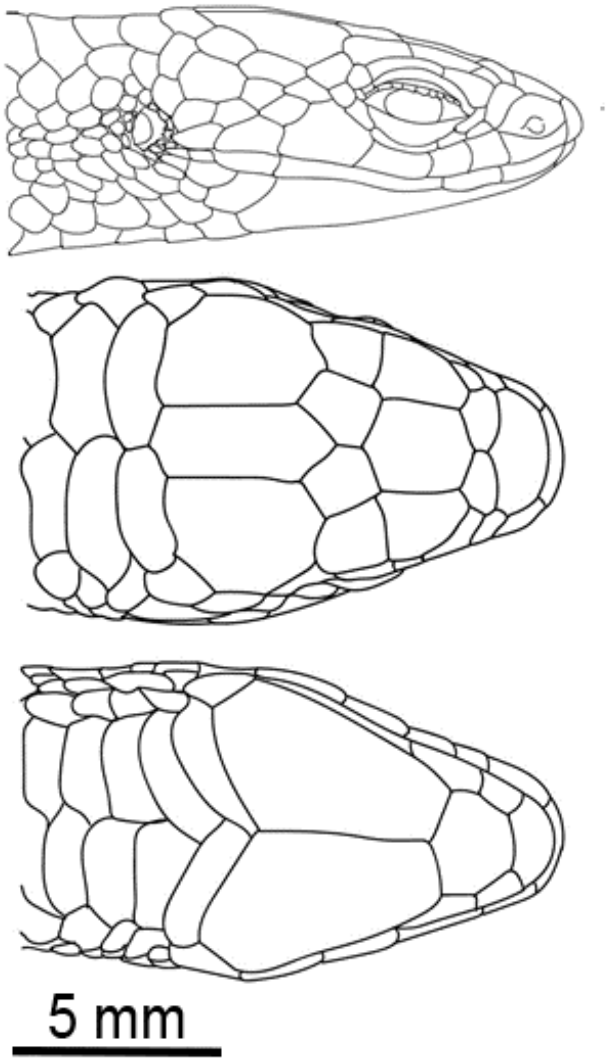

Figure 15. Lateral, dorsal, and ventral views of the head of the holotype of *Iphisa* sp. nov. 3 (MTR 36543).

TABLES

Table 1. Mitochondrial and nuclear genes and primers used in this study, with details of models and alignment lengths.

Gene	Type	Lenght (bp)	Primer	Model	References
16S - RNA ribossomal 16S	mtDNA (ribossomal)	525	CTGTTTACCAAAAACATMRCCTYTAGC	GTR + I + G	Pellegrino et al., 2001
			TAGATAGAAACCGACCTGGATT		
Cytb Citochrome b					
H15149	mtDNA (coding)	641	TGCAGCCCCTCAGAATGATATTTGTCCTCA	GTR + I + G	Kocher et al., 1989
LGL765			GAAAAACCAYCGTTGTWATTCAACT		Bickham et al., 1995
CMOS – oocyte maturation factor Mos	nuDNA (Exon)	416	GCGGTAAAGCAGGTGAAGAAA	HKY + I + G	Saint et al., 1998
			TGAGCATCCAAAGTCTCCAATC		
PRLR prolactin receptor gene	nuDNA (Exon)	270	GACARYGARGACCAGCAACTRATGCC	GTR + I + G	Townsend et al., 2008
			GACYTTGTGRACTTCYACRTAATCCAT		

Table 2. Voucher of the samples used in the haplotype network of the Cytb gene; locality and state; code used in the haplotype network; number of the haplotype.

Voucher	Locality	CODE	Haplotype
UFMT 6052	Araputanga, MT	ARA_MT_51	Hap 1
RGL 1781	UHE Guaporé, MT	GPE_MT_751	Hap 1
UFMT 5296	Vale de São Domingos, UHE Guaporé, MT	GPE_MT_935	Hap 1
UFMT 5291	Vale de São Domingos, UHE Guaporé, MT	GPE_MT_939	Hap 1
UFMT 5289	Vale de São Domingos, UHE Guaporé, MT	GPE_MT_942	Hap 1
RGL1782	Vale de São Domingos, UHE Guaporé, MT	GPE_MT_E1	Hap 1
UFMT 2840	Jauru, MD Jauru River, MT	JRU_MT_276	Hap 1
UNIBAN 1704	Montenegro/Cacaulândia, RO	MOC_RO_422	Hap 1
UFMT 6253	Araputanga, MT	ARA_MT_50	Hap 2
UFMT 2838	Jauru, MD Jauru River, MT	JRU_MT_275	Hap 2
UFMT 2844	Jauru, MD Jauru River, MT	JRU_MT_280	Hap 2
UFMT 10126	Vilhena, RO	VIL_RO_956	Hap 2
UFMT 2843	Jauru, MD Jauru River, MT	JRU_MT_279	Hap 3
UFMT 5959	Nova Bandeirantes, MT	NVB_MT_429	Hap 4
UFMT 6787	Nova Bandeirantes, MT	NVB_MT_431	Hap 4
UFMT 6252	Araputanga, MT	ARA_MT_52	Hap 5
UFMT 7842	Colniza, Estação Ecológica do Roosevelt River, MT	CLZ_MT_152	Hap 6
UFMT 7843	Colniza, Estação Ecológica do Roosevelt River, MT	CLZ_MT_153	Hap 6
UFMT 7857	Colniza, Estação Ecológica do Roosevelt River, MT	CLZ_MT_154	Hap 6
UFMT 7858	Colniza, Estação Ecológica do Roosevelt River, MT	CLZ_MT_155	Hap 6
MTR 10215	São José das Pombas, ME, Aripuanã River, AM	SJP_AM_E6	Hap 6
UFMT 7804	Colniza, Estação Ecológica do Roosevelt River, MT	CLZ_MT_151	Hap 7
MZUSP 81634	Apiacás, MT	API_MT_43	Hap 8
MZUSP 82654	Aripuanã, MT	ARI_MT_54	Hap 9
MZUSP 82655	Aripuanã, MT	ARI_MT_55	Hap 9
MZUSP 82656	Aripuanã, MT	ARI_MT_56	Hap 9
MZUSP 82657	Aripuanã, MT	ARI_MT_57	Hap 9
MZUSP 82659	Aripuanã, MT	ARI_MT_59	Hap 9
MZUSP 82669	Aripuanã, MT	ARI_MT_69	Hap 9
MZUSP 90105	Aripuanã, MT	ARI_MT_78	Hap 9
MTR 10234	São José das Pombas, ME, Aripuanã River, AM	SJP_AM_E7	Hap 10
RCV 2247	Itapinima, AM	ITP_AM_271	Hap 11
MTR 10113	Santa Maria, ME, Aripuanã River, AM	SAN_AM_E3	Hap 12
MTR 10053	Santa Maria, ME, Aripuanã River, AM	SAN_AM_E37	Hap 12
MTR 10056	Porto Walter, AC	SAN_AM_E2	Hap 13
MTR 10114	Santa Maria, ME, Aripuanã River, AM	SAN_AM_E4	Hap 14
MTR 10067	Santa Maria, ME, Aripuanã River, AM	SAN_AM_E38	Hap 15
MTR 10235	São José das Pombas, ME, Aripuanã River, AM	SJP_AM_E8	Hap 17
RCV 2225	Cachoeirinha, Madeira River, AM	CHR_AM_104	Hap 18
VOGT 2204	Cachoeirinha, ME, Madeira River AM	CHR_AM_E9	Hap 18
8134	Curaray	CUR_EQ_E10	Hap 19

LSUMZ 12666	Cuyabeno, Equador	CUY_EQ_187	Hap 20
LSUMZ 12697	Cuyabeno, Equador	CUB_EQ_E11	Hap 21
MTR 36421	São Pedro, Içá River MD, AM	ICA_AM_684	Hap 22
MTR 36543	São Pedro, Içá River MD, AM	ICA_AM_685	Hap 22
MTR 36597	São Pedro, Içá River MD, AM	ICA_AM_686	Hap 22
MTR 36599	São Pedro, Içá River MD, AM	ICA_AM_687	Hap 23
MTR 36600	São Pedro, Içá River MD, AM	ICA_AM_688	Hap 24
MTR 36258	Comunidade Cuiauá, Içá River , ME , AM	ICA_AM_175	Hap 25
MTR 36243	Comunidade Cuiauá, Içá River , ME , AM	ICA_AM_176	Hap 25
MTR 36228	Açaí, Içá River, ME, AM	ICA_AM_1	Hap 26
MTR 36106	Comunidade Cachoeirinha, Içá River, AM	ICA_AM_173	Hap 26
MTR 36788	Comunidade Cachoeirinha, Içá River, AM	ICA_AM_174	Hap 26
MZUSP 100252	São Sebastião, Abacaxis River, ME, AM	ABX_AM_693	Hap 27
MZUSP 100256	Igarapé-açu, Abacaxis River, MD, AM	ABX_AM_603	Hap 28
MZUSP 100257	Igarapé-açu, Abacaxis River, MD, AM	ABX_AM_604	Hap 28
MZUSP 100258	Igarapé-açu, Abacaxis River, MD, AM	ABX_AM_605	Hap 29
MTR 19004	Moiobamba, MD, Purus River, AM	MOI_AM_412	Hap 30
MTR 19094	Moiobamba, MD, Purus River, AM	MOI_AM_414	Hap 30
MTR 19144	Moiobamba, MD, Purus River, AM	MOI_AM_415	Hap 30
MTR 19172	Moiobamba, MD, Purus River, AM	MOI_AM_416	Hap 30
MTR 19177	Moiobamba, MD, Purus River, AM	MOI_AM_417	Hap 30
MTR 19180	Moiobamba, MD, Purus River, AM	MOI_AM_418	Hap 30
MTR 19242	Moiobamba, MD, Purus River	MOI_AM_E15	Hap 30
SMS 678	Fazenda Walmir, ME Madeira River, Autazes, AM	AUT_AM_E20	Hap 31
SMS 694	Fazenda Walmir, ME Madeira River, Autazes, AM	AUT_AM_E21	Hap 32
MZUSP 100244	Porto Velho, UHE Jirau, Caiçara, RO	JIU_AM_508	Hap 33
H649	UHE Jirau, ME, Caiçara, RO	JIU_RO_E30	Hap 33
INPA 20302	Campo Tupana, AM	CTU_AM_119	Hap 34
INPA 20304	Campo Tupana, AM	CTU_AM_120	Hap 34
INPA 20305	Campo Tupana, AM	CTU_AM_121	Hap 35
MPEG 22322	Itaituba, PARNA da Amazônia, PA	TPJ_AM_257	Hap 36
MPEG 22324	Itaituba, PARNA da Amazônia, PA	TPJ_AM_258	Hap 36
MPEG 28243	Juruti, Adutora, PA	JUR_AM_292	Hap 37
MPEG 28244	Juruti, Mutum, PA	JUR_AM_304	Hap 37
INPA 18444	Comunidade Projó, Alto Aripuanã River, MD, AM	CPJ_AM_181	Hap 38
INPA 18445	Comunidade Projó, Alto Aripuanã River, MD, AM	CPJ_AM_178	Hap 39
H 4823	Caiçara, MD, Madeira River, RO	CAI_RO_105	Hap 40
UFMT 6738	Colniza, Parque Estadual Igarapés do Juruena, MT	CLZ_MT_156	Hap 41
977200	Juruena	JUR_MT_E16	Hap 42
UFMT 6010	Cotriguaçu	CTG_MT_E18	Hap 43
977241	Juruena	JUR_MT_E17	Hap 43
976975	Juruena	JUR_MT_E39	Hap 43
MTR 10143	Cachoeira das Pombas, MD, Aripuanã River, AM	CHP_AM_E19	Hap 44
MTR 10210	Cachoeira das Pombas, Aripuanã River , AM	PMB_AM_103	Hap 44
INPA 18432	Comunidade Projó, Alto Aripuanã River, MD, AM	CPJ_AM_177	Hap 45

INPA 18434	Comunidade Projó, Alto Aripuanã River, MD, AM	CPJ_AM_180	Hap 46
INPA 18433	Comunidade Projó, Alto Aripuanã River, MD, AM	CPJ_AM_179	Hap 47
INPA 26263	FLONA do Trairão, PA	TRA_PA_E22	Hap 48
INPA 26264	FLONA do Trairão, PA	TRA_PA_E23	Hap 48
INPA 26265	FLONA do Trairão, PA	TRA_PA_E24	Hap 48
INPA 26283	FLONA do Trairão, PA	TRA_PA_E25	Hap 48
INPA 26285	FLONA do Trairão, PA	TRA_PA_E27	Hap 48
INPA 26284	FLONA do Trairão, PA	TRA_PA_E26	Hap 49
MZUSP 100249	São Sebastião, Abacaxis River, ME, AM	ABX_AM_690	Hap 50
MZUSP 100253	São Sebastião, Abacaxis River, ME, AM	ABX_AM_696	Hap 50
MTR 12948	São Sebastião, Abacaxis River, ME, AM	ABX_AM_697	Hap 50
MTR 12751	São Sebastião, ME, Abacaxis River, AM	ABX_AM_E28	Hap 50
MTR 10002	Lago Cipotuba, AM	LCB_AM_324	Hap 51
MZUSP 100251	Igarapé-açu, Abacaxis River, MD, AM	ABX_AM_692	Hap 52
SMS 604	São Sebastião dos Bargas, Nova Olinda, MD, Madeira River, AM	NVO_AM_182	Hap 53
SMS 648	São Sebastião dos Bargas, Nova Olinda, MD, Madeira River, AM	NVO_AM_183	Hap 53
SMS 669	São Sebastião dos Bargas, Nova Olinda, MD, Madeira River, AM	NVO_AM_184	Hap 53
LSUMZ 13903	Porto Walter, AC	PWT_AC_549	Hap 54
MTR 28447	PARNA Serra do Divisor, AC	SDV_AC_456	Hap 55
MHNC 10115	EEBB Pithecia, River Samiria, Dist. Parinari, Loreto, Peru	PR_PER_193	Hap 56
MHNC 10082	Hamburgo, Samiria River, Dist. Parinari, Loreto, Peru	HB_PER_247	Hap 57
MZUSP 100246	Porto Velho, UHE Jirau, Mutum, RO	JIU_AM_536	Hap 58
H521	UHE Jirau, ME, Caiçara, RO	JIU_RO_E29	Hap 58
MZUSP 100245	Porto Velho, UHE Jirau, Abunã, RO	JIU_AM_502	Hap 59
MZUSP 101617	Porto Velho, UHE Jirau, ME do madeira , RO	JIU_AM_511	Hap 59
MZUSP 100247	Porto Velho, UHE Jirau, Abunã, RO	JIU_AM_503	Hap 60
MZUSP 100568	Porto Velho, UHE Jirau, ME do madeira , RO	JIU_AM_510	Hap 61
MTR 33559	Maraã, River Japurá, AM	JAP_AM_382	Hap 62
PLVP638	Trilha da Praia Alta, PARNA Jaú	JAU_AM_E31	Hap 63
PLVP616	Trilha Caju, PARNA Jaú	JAU_AM_E32	Hap 63
MTR 19084	Moiobamba, MD, Purus River, AM	MOI_AM_410	Hap 64
MTR 19111	Moiobamba, MD, Purus River, AM	MOI_AM_411	Hap 64
MTR 18750	Lago Chaviana, Itapuru, MD, Purus River, AM	LCV_AM_316	Hap 65
MTR 18984	Lago Chaviana, Itapuru, MD, Purus River, AM	LCV_AM_322	Hap 65
MTR 18797	Lago Chaviana, Itapuru, MD, Purus River, AM	LCV_AM_319	Hap 66
MPEG 27402	Serra do Acarai,Oriximiná, PA	ACA_PA_E33	Hap 67
IRSNB 17316	Kaieteur National Park, Guyana	KNP_GY_308	Hap 67
IRSNB 17317	Kaieteur National Park, Guyana	KNP_GY_309	Hap 67
LG 1413	REBIO Trombetas River, PA	TRB_PA_568	Hap 68
MZUSP 88462	Alto do Maracá River, Boca do Igarapé Camaipi , AP	IGC_AP_15	Hap 69
MZUSP 88463	Alto do Maracá River, Boca do Igarapé Camaipi , AP	IGC_AP_16	Hap 69
MZUSP 88464	Igarapé Camaipi, AP	IGC_AP_17	Hap 69
MTR 6324	Igarape Camaipi Maracá River, PA	IGC_PA_E34	Hap 69
MPEG 27334	ESEC Grão-Pará Sul, PA	EGP_PA_E35	Hap 71
MPEG27333	ESEC Grão-Pará Sul, PA	EGP_PA_E36	Hap 71

T**able 3**. Results of the non-parametric *Kruskal–Wallis* test for comparison among geographic groups for seven scale counts, as represented by the average and the standard deviation (SD) values of each count, and the significance level (*p-value*) of the geographic variation. Min and Max values are between parenthesis and the highest average marked in bold as well the significant value in *p-value* column.

		UTO 1	**UTO 2**	**UTO 3**	**UTO 4**	**UTO 5**	***Kruskal-Wallis***
	SEX	F = 57 M = 113	F = 89 M =70	F = 6 M =12	F = 49 M =76	F = 10 M =9	*p - value*
LFH	F	**12.7±1**	11.8±1	**12.5±1**	**12.2±1.1**	**12.2±1.1**	**< 0,05**
		(10-17)	(10-14)	(11-14)	(10-15)	(10-14)	
	M	12.3±1.1	**12.04±1**	12.3±1.1	12.1±1.1	12±1.1	0.2506
		(10-16)	(10-14)	(11-13)	(10-14)	(11-14)	
LFF	F	**17.5±1.5**	16.2±1.5	16.5±1.6	17.1±1.6	16.8±1.6	**< 0,05**
		(15-20)	(13-24)	(16-18)	(13-21)	(15-18)	
	M	17±1.3	**16.3±1.3**	**17.4±1.4**	**17.2±1.4**	**16.4±1.4**	**< 0,05**
		(14-21)	(13-19)	(16-20)	(14-20)	(14-19)	
POR	F	7.4±7	0±0	16.7±7.3	7.2±7.2	7.4±7.2	**< 0,05**
		(0-23)	0	(16-20)	(0-20)	(0-16)	
	M	**19.7±4.3**	**16.2±5**	**18.8±4.1**	**19.5±3.9**	**18.3±3.9**	**< 0,05**
		(16-25)	(12-22)	(7-24)	(15-23)	(10-21)	
DOR	F	**30.2±1.7**	**29.7±1.7**	**30.2±1.8**	**30.5±1.8**	**29.3±1.8**	0.1297
		(26-34)	(25-33)	(27-32)	(25-34)	(27-32)	
	M	28.8±1.4	28.9±1.3	29.1±1.3	29.3±1.4	28.7±1.4	**< 0,05**
		(25-32)	(26-32)	(28-30)	(28-31)	(27-30)	
VEN	F	**19±1.4**	**18.7±1.5**	18±1.6	**19.6±1.6**	**19.1±1.5**	**< 0,05**
		(15-22)	(15-21)	(16-20)	(17-22)	(17-21)	
	M	17.5±1.2	17.3±1.2	**18.1±1.2**	17.9±1.2	17.2±1.2	**< 0,05**
		(16-19)	(16-19)	(17-19)	(16-19)	(16-19)	
RSL	F	6.7±0.5	6.86±0.5	6.8±0.5	**6.1±0.5**	**7±0**	**< 0,05**
		(6-7)	(6-7)	(6-7)	(6-7)	-7	
	M	**6.8±0.5**	**6.9±0.5**	**7±0**	6±0.5	6.8±0.5	**< 0,05**
		(6-7)	(6-7)	-7	(6-7)	(6-7)	
RIL	F	6.7±0.5	**6.04±0.5**	**6±0**	**6.1±0.5**	**6±0**	0.5496
		(5-7)	(5-7)	-6	(6-7)	-6	
	M	**6.8±0.5**	6±0.5	**6±0.3**	**6.1±0.5**	**6.1±0.5**	0.4375
		(5-7)	(5-7)	(5-7)	(6-7)	(6-7)	

Table 4. Variation of categorical characters and relative frequency for all individuals examined in the genus *Iphisa*. Gular (GUL); scales around midbody (SAM); anal plate (AP); right supralabial (RSL); right infralabial (RIL); major supralabials (MSL); scales under eye (SUE); major infralabial (MIL); infralabial in contact with chin (ICH); supraocular (SO); supraciliar (SC); prefrontal (PF) and frontoparietal (FRO). Highest values are marked in bold.

		Frequence (%)				
		OTU				
		1	2	3	4	5
	N	186	249	20	134	33
GUL	7	14.7	5	0	3.8	9.7
	8	**82.9**	**92.6**	**83.3**	**88.7**	**80.6**
	9	2.4	2.5	16.7	7.5	9.7
SAM	**4**	**91.3**	**83.2**	**84.6**	**86.3**	**93.3**
	5	8.7	16.8	15.4	13.7	6.6
AP	**5**	**100**	**100**	**100**	**100**	**100**
RSL	**6**	21.5	10.7	7.7	**93.8**	6.6
	7	**78.5**	**89.3**	**92.3**	6.2	**93.3**
RIL	5	4.3	1.7	7.7	1.5	0
	6	**87.9**	**95**	**84.6**	**93.1**	**96.6**
	7	7.7	3.3	7.7	5.3	3.3
MSL	**4**	28.7	11.5	0	**84.9**	11.1
	5	**71.3**	**88.5**	**100**	15.1	**88.8**
SUE	**3**	25.7	9.6	0	**94.6**	3.8
	3 e 4	**74.3**	**90.4**	**100**	5.4	**96.1**
MIL	**3**	**96.1**	**100**	**100**	**96.2**	**92.6**
	4	3.9	0	0	3.8	7.4
ICH	2 e 3	14	1.9	0	14	0
	2 a 4	**81.8**	**97.2**	**100**	**79.8**	**100**
	2 a 5	4.2	0.9	0	6.2	0
SO	**3**	**100**	**100**	**100**	**99.2**	**100**
	4	0	0	0	0.8	0
SC	3	2.2	0	0	2.3	0
	4	**97.8**	**100**	**100**	**97.7**	**100**
PF	**Contact**	**84**	**81.1**	**92.3**	**93.9**	32.1
	No contact	7	11.9	7.7	6.1	10.7
	Absent	9.1	7	0	0	**57.1**
FRO	**Contact**	**93.8**	**93.9**	**100**	**82.7**	**100**
	No contact	6.2	6.1	0	17.3	0

Table 5. Results of the morphometric variation test for comparison among geographic groups for seven measurements, as represented by the average and the standard deviation (Average±SD) values of each count, and the significance level (*p-value*) of the geographic variation by MANOVA test. Min and Max values are between parenthesis and the highest average marked in bold as well the significant value in *p-value* column.

		UTO 1	**UTO 2**	**UTO 3**	**UTO 4**	**UTO 5**	**Manova**
	SEX	F = 58 M =111	F = 85 M =136	F = 6 M =12	F = 49 M =76	F = 8 M = 9	*p - value*
HL	F	8.5±1.0 (6.4-10.9)	7.8±1 (6.01-10.9)	8.9±1.3 (6.9-11.6)	8.1±1.3 (5.4-11.3)	8.2±0.5 (7.2-8.9.3)	< **0.05**
	M	**9±1.3** (6.8-11.6)	**8.2±1** (5.7-10.3)	**10.5±1.5** (9.2-13.6)	**9.1±1** (7.08-10.7)	**9.9±2.1** (7.1-13.04)	< **0.05**
HW	F	6±1 (4.1-7.3)	5.5±0.7 (4.1-7.5)	6.2±1 (5.2-6.9)	5.5±0.9 (3.6-7.3)	5.4±1.07 (3.3-6.2)	< **0.05**
	M	**6.6±0.9** (4.8-8.3)	**5.9±1** (3.8-8.5)	**7.1±0.5** (6.8-7.4)	**6.5±0.9** (4.5-8.3)	**6±1.2** (3.9-7.3)	< **0.05**
SVL	F	44.1±8.6 (24.9-56.7)	39.6±6.6 (25.3-51.6)	42.7±6.7 (28.1-52.14)	41.2±8.7 (24.7-54.9)	40±7.5 (26.8-47.9)	< **0.05**
	M	**45.1±5.6** (35.06-54.36)	**40.1±6.1** (24.9-51.3)	**48.1±4.3** (43.5-57.1)	**45.4±4.4** (36.4-53.5)	**45.4±4.4** (33.1-56.7)	< **0.05**
TRL	F	**26.4±6.3** (12.3-34.8)	**23.8±4.6** (13.8-33.3)	24.6±4.6 (14.59-33.3)	24.2±6.4 (10.48-37.12)	23.7±6.4 (13-3.32.8)	0.0872
	M	26.3±4.1 (19.01-31.9)	23.1±4.2 (12.9-32.4)	**26.8±2.3** (23.3-30.1)	**26.1±2.7** (20.5-31.4)	**25.7±2.7** (17.8-31.8)	< **0.05**
ED	F	1.7±0.3 (1.1-2.3)	1.6±0.3 (1.1-2.3)	1.5±0.3 (1.4-1.7)	1.6±0.2 (1.1-2.1)	1.7±0.2 (1.5-2.3)	0.4001
	M	**1.8±0.3** (1.2-2.5)	**1.7±0.3** (1.08-2.4)	**1.6±0.3** (1.3-2.09)	**1.8±0.3** (1.2-2.5)	**1.9±0.3** (1.5-2.1)	0.0801
ND	F	2.5±0.3 (2.1-2.9)	2.2±0.3 (1.4-2.8)	2.5±0.4 (2.3-2.8)	2.3±0.4 (1.4-2.9)	2.5±0.4 (2.3-2.7)	< **0.05**
	M	**2.6±0.3** (2.07-3.4)	**2.4±0.4** (1.6-3.2)	**2.8±0.2** (2.7-3.01)	**2.7±0.4** (1.9-3.3)	**2.6±0.4** (2.09-2.9)	< **0.05**
END	F	1.7±0.3 (1.3-2.3)	1.7±0.3 (1.04-2.33)	1.6±0.3 (1.4-1.9)	1.5±0.3 (0.9-2.02)	1.6±0.3 (1.4-2.0)	< **0.05**
	M	**1.9±0.3** (1.2-2.4)	**1.8±0.3** (0.9-2.5)	**1.9±0.1** (1.7-2.05)	**1.8±0.3** (1.1-2.2)	**1.9±0.3** (1.5-2.2)	< **0.05**

Table 6. Results of Principal Component Analysis (PCA) on seven log10 morphometric measurements transformed from *Iphisa.* The measurements with highest correlation with each component highlighted in bold.

	MALES N = 345		FEMALES N = 205	
	PC 1	PC 2	PC 1	PC 2
HL	**0.371**	-0.138	**0.107**	-0.219
HW	**0.436**	-0.136	**0.073**	**0.008**
SVL	**0.437**	-0.219	**0.811**	-0.542
TRL	**0.508**	-0.311	**0.570**	**0.811**
ED	0.211	**0.734**	0.010	**0.013**
END	0.304	**0.234**	0.021	-0.006
DN	0.293	**0.473**	0.014	**0.004**
Eigenvalue	0.02	0.004	89.8	2.46
% variance	64.2	12.6	96.6	2.6

Table 7. Results of discriminant analysis on log10-transformed morphometric data for males and females of *Iphisa.* The measurements with highest correlation with each component highlighted in bold.

	MALES N = 345		FEMALES N = 205	
	DF 1	DF 2	DF 1	DF 2
HL	**0.050**	**0.006**	**0.623**	**0.418**
HW	**0.041**	-0.038	**0.272**	0.329
SVL	**0.044**	-0.003	**2.899**	**0.920**
TRL	**0.042**	**0.005**	**1.318**	**0.688**
ED	0.007	**0.003**	-0.062	0.054
END	0.029	-0.002	0.107	0.117
DN	0.015	-0.015	-0.094	0.139
Eigenvalue	0.36	0.06	0.23	0.10
% variance	76.4	13.18	57.36	24.51

Table 8 Classification matrix based on the results of the discriminant analysis on log10-transformed morphometric data for males and females of *Iphisa* to each group. Percentages of individuals correctly classified in each group highlighted in bold and underlined.

Classification Matrix								
			Predicted group membership					
		OTU	1	2	3	4	5	Total (%)
Original	% Females	1	**8.3**	4.4	5.9	4.4	4.9	27.8
		2	2.9	**22**	2.9	6.3	7.3	41.5
		3	0.5	0.5	**2**	0	0	2.9
		4	2.4	3.4	2.9	**10.2**	4.9	23.9
		5	0	1	1	0.5	**1.5**	3.9
	% Total		14.1	31.2	14.6	21.5	18.5	100
	% Males	1	**13.9**	6.7	4.3	4.9	2.3	32.2
		2	7.2	**22.3**	1.2	6.7	2	39.4
		3	0.6	0	**2.6**	0	0.3	3.5
		4	3.5	4.6	2.6	**7**	4.6	22.3
		5	0.9	0.6	0.3	0	**0.9**	2.6
	% Total		26.1	34.2	11	18.6	10.1	100
Correctly classified: Females (43.9%) and Male (46.6%)								
crossvalidated (jackniffe)	% Females	1	**7.3**	4.9	5.9	4.4	5.4	27.8
		2	3.9	**20**	3.4	6.8	7.3	41.5
		3	1.5	0.5	**1**	0	0	2.9
		4	3.4	3.4	2.9	**8.8**	5.4	23.9
		5	0	1	1.5	0.5	**1**	3.9
	% Total		16.1	29.8	14.6	20.5	19	100
	% Males	1	**13.3**	6.7	4.3	5.2	2.6	32.2
		2	7.5	**21.7**	1.2	6.7	2.3	39.4
		3	1.2	0	**1.4**	0	0.9	3.5
		4	3.8	4.6	2.6	**6.7**	4.6	22.3
		5	0.9	0.6	0.6	0	**0.6**	2.6
	% Total		26.7	33.6	10.1	18.6	11	100
Correctly classified: Females (38%) and Male (43.7%)								

MATERIAL ANALYSED

Specimens examined

BRAZIL: **Acre**: Cruzeiro do Sul: MTR 28447, UFACF 1173, UFACF 924, UFACF 953, UFACF 961, UFACF 977, UFACF 978. Porto Walter: MPEG 20638. **Amapá**: MNHN 1899-74. Alto do Rio Maracá: MZUSP 88462, MZUSP 88463. Igarapé Camaipi: MZUSP 88464. Itapeuara: UHE Santo Antônio do Jari: INPA 30043. Laranjal do Jari: MPEG 29750~52, MPEG 29754, MPEG 29756, MPEG 29760. Mazagão: MPEG 29737~43, MPEG 29746, MPEG 29748. Serra do Navio: MNRJ 19116, MPEG 15081, MPEG 15188, MPEG 19200, MPEG 19207, MPEG 19600, MPEG 19772~74, MPEG 19778, MPEG 19784, MPEG 19792. **Amazonas**: Açaí: MTR 36228. Autazes: UFMG 2134, UFMG 2135. Benjamin Constant: MPEG 15896, MPEG 15918. Beruri: Lago do Aiapuá: INPA 13848~65. Cachoeira das Pombas: MZUSP 100248. Campo Catuquira: INPA 20298, INPA 20313, INPA 20323, INPA 20324, INPA 20326, INPA 20328. Campo Tupana: INPA 20302. Careiro da Várzea: MPEG 18875. Coari: MTR 36958, MTR 37034, MTR 37085. Comunidade Cachoeirinha: MTR 36106, MTR 36788. Comunidade Cuiauá: MTR 36243, MTR 36258. Comunidade Projó: INPA 18432, INPA 18445. Floresta de Canutama: INPA 34981, INPA 34983. Floresta de Terra Firme: INPA 12981, INPA 12979, INPA 12980, INPA 20089. Igarapé-Açú: MZUSP 100251, MZUSP 100256~60. Itacoatiara: MPEG 29363. Juruá: INPA 15897~99, INPA 15944. Jutaí: MPEG 28149. Lago Chaviana: MTR 18750, MTR 18759, MTR 18795, MTR 18797, MTR 18914, MTR 18920, MTR 18984, MPEG 30406. Lago Cipotuba: MZUSP 91387. Lago Vai Quem Quer: MPEG 30406. Manaus: MZUSP 8354. Maraã: MTR 33554, MTR 33559, MTR 33561, MTR 33584, MTR 33589. Maués: MPEG 27667~69. Moiobamba: MTR 19084, MTR 19111, MTR 19004, MTR 19058, MTR 19094, MTR 19144, MTR 19172, MTR 19177, MTR 19180, MTR 19365, MTR 19372. Nova Olinda: SMS 604, SMS 648, SMS 669. Parque Estadual do Sucunduri: INPA 17425. Parque Estadual Matupiri: INPA 32555~61. Parque Nacional Nascente do Lago Jari: INPA 27327, INPA 27329, INPA 27330, INPA 27775, INPA 28789, INPA 34779. RDS Igapó-Açú: INPA 32682~87. Reserva Adolf Duck: INPA 24649. RESEX Canutama: INPA 34998. Resex Baixo Juruá: INPA 16338, INPA 18797~99, INPA 34998. Apuí: Rio Aripuanã: INPA 12171, INPA 12183, INPA 12184. Rio Madeira: INPA 12174, INPA 12175. Rio Negro: MTR 41103, MTR 41472. Santa Maria: MZUSP 91382~86. São João do Lago da Velha: INPA 34807, INPA 34838. São Pedro: MTR 36421, MTR 36543, MTR

36597, MTR 36599, MTR 36600, MTR 36716. São Sebastião: MZUSP 100249, MZUSP 100250, MZUSP 100252~55, MZUSP 100261, MZUSP 100262. Seringalzinho: PARNA do Jaú: INPA 11684, INPA 11685, INPA 11692, INPA 11743, INPA 11745. Tefé: INPA 9414, INPA 9415~29, INPA 10389, INPA 10641. Urucará: MNRJ 17999, MNRJ 18000, MNRJ 19262, MPEG 29364, MPEG 29365, UFMT 10356, UFMT 10420, UFMT 9646, UFMT 9648, UFMT 9758, UFMT 9762, UFMT 9770, UFMT 9806. **Maranhão**: Bom Jardim: MPEG 31249, MPEG 31250. **Mato Grosso**: Apiacás: MZUSP 81634, UFMT 7242, UFMT 9399, UFMT 10166. Araputanga: UFMT 2841, UFMT 6052, UFMT 6252, UFMT 6253, UFMT 6555. Aripuanã: MZUSP 82655~57, MZUSP 82659~76, MZUSP 90104, MZUSP 90105, UFMT 10248. Cláudia: UFMT 10063~68, UFMT 10070~73, UFMT 10086, UFMT 10090. Colniza: UFMT 6738, UFMT 7804, UFMT 7842, UFMT 7843, UFMT 7857, UFMT 7858. Comodoro: MZUSP 103026, UFMT 9457, UFMT 9465, UFMT 9467, UFMT 9469, UFMT 9472, UFMT 9477, UFMT 9481, UFMT 9482, UFMT 9485, UFMT 9546, UFMT 9557, UFMT 9564. Cotriguaçu: UFMT 8373. Indiavaí: INPA 15988. Jauru: UFMT 2838, UFMT 2839, UFMT 2840, UFMT 2842, UFMT 2843, UFMT 2844. Juara: UFMT 5995, UFMT 6760, UFMT 6788. Juruena: MZUSP 82428~31. Lambari D'Oeste: MZUSP 102883~86, UFMT 10897, UFMT 10903, UFMT 10907. Nova Bandeirantes: UFMT 5959, UFMT 5962, UFMT 6762, UFMT 6787, UFMT 6789. Porto Velho: MZUSP 102909. Reserva Cabeçal: UFMT 2626, 2627. Sapezal: MZUSP 103751, MZUSP 101682, MZUSP 101683, UFMT 5920, UFMT 7459, UFMT 7472, UFMT 7482, UFMT 7482, UFMT 7486, UFMT 7488. Vale de São Domingos: INPA 294, PUCRS 14062, PUCRS 14065, PUCRS 14068, RO 859, RO 861~64, RO 871, RO 873, RO 874, RO 875, RO 879, RO 881, UFMT 4131, UFMT 5092, UFMT 5093~98, UFMT 5100, UFMT 5101, UFMT 5104, UFMT 5277~79, UFMT 5280~86, UFMT 5289~93, UFMT 5295, UFMT 5297~302, UFMT 5306, UFMT 5307, UFMT 5309, UFMT 5311~17, UFMT 5320~28, UFMT 5330, UFMT 5332, UFMT 5333, UFMT 5379, UFMT 5382~85, UFMT 5388, UFMT 5390~92, UFMT 5394, UFMT 5397, UFMT 5399, UFMT 5400, UFMT 5404, UFMT 5405, UFMT 5407, UFMT 5408, UFMT 6998, UFMT 6999, UFMT 7000~17, UFMT 7128~44, UFMT 859, UFMT 860, UFMT 863, UFMT 865~70, UFMT 872, UFMT 876, UFMT 877, UFMT 880, UFMT 882, UFMT 884. **Pará**: Alenquer: MPEG 27335. Almeirim: MPEG 23834, MPEG 23837, MPEG 23838, MPEG 23839. Aveiro: MPEG 29935. Belém: BMNH 1946.9.1-1, MPEG 46. Buburé: MZUSP 53706. Cachoeira da montanha: Rio Tapajós: MZUSP 53661, MZUSP 53662. Faro: UFMT 9632, UFMT 9764, UFMT 9809. Flona Trairão: INPA 26263~65,

INPA 26283~85. Flona Oriximiná: MNRJ 15014, MNRJ 15015. Itaituba: MPEG 21968, MPEG 22322, MPEG 22324, MPEG 22325, MPEG 29033, MPEG 29037, MPEG 29070, MPEG 29151, MPEG 29152, MPEG 29477, MPEG 29478, MPEG 30027, MZUSP 102155~57. Juruti: MPEG 20821, MPEG 25256~61, MPEG 26521, MPEG 28243, MPEG 28244, MPEG 28491, MPEG 28507, MPEG 28565. Novo Progresso: CHUNB 40060. Oriximiná: MPEG 21509, MPEG 24568, MPEG 24569, MPEG 24777, MPEG 27403, MPEG 27404, MPEG 29219, MPEG 29255, UFMT 10416, UFMT 10423, UFMT 9830. Parque Nacional da Amazônia: MZUSP 56713. Flona Caxiuanã: MPEG 25848, MPEG 26291, MPEG 28838. Santarém: MPEG 17664. Santarém: Resex Tapajós Arapiuns: MPEG 10529, MPEG 10576, MPEG 10594, MPEG 10673, MPEG 10699, MPEG 10718, MPEG 11008, MPEG 11023, MPEG 11028, MPEG 11040, MPEG 11046, MPEG 11049, MPEG 11059, MPEG 11066, MPEG 11069, MPEG 11076, MPEG 11084, MPEG 11133, MPEG 11186, MPEG 11203, MPEG 11226, MPEG 11269, MPEG 11270. Taboleiro Leonardo: MZUSP 87785. Terra Santa: Terra Santa: Igarapé Xingu: MPEG 29220, MPEG 29289. Uruá: Parque Nacional da Amazônia: MZUSP 52514, MZUSP 53641. Vai-quem-quer: MZUSP 78214, MZUSP 78215. **Rondônia**: Alto Paraíso: MZUSP 61935. Chupinguaia: MZUSP 103008, UFMT 9439, UFMT 9476, UFMT 9478, UFMT 9483, UFMT 9561, UFMT 9570. Comodoro: MZUSP 103027. Costa Marques: INPA 1057. E. E. Antônio Mujica Nava: MZUSP 92191, Espigão D'Oeste: MPEG 21928. Guajarà-Mirim: CHUNB 22654~71, MPEG 18524, MPEG 21547, MPEG 21548. Machadinho d'Oeste: MZUSP 104338~44, MZUSP 104364. Montenegro/Cacaulândia: MZUSP 89339. Nova Colina: MZUSP 62211. Parecis: MZUSP 103032~35. Pimenta Bueno: CHUNB 18021~23. Porto Velho: INPA 18458, H 0521, H 0649, MZUSP ~14, MPEG 22099, MZUSP 103684, MZUSP 103685, MZUSP 100245, MZUSP 100247, MZUSP 103666, MZUSP 103667, MZUSP 103668, MZUSP 100244, MZUSP 104071, MZUSP 100568, MZUSP 101617, MZUSP 101595, MZUSP 101596, MZUSP 101594, MZUSP 101591, MZUSP 101590, MZUSP 101593, MZUSP 101592, MZUSP 102125, MZUSP 103616~21, MZUSP 103810, MZUSP 103811, MZUSP 103812, MZUSP 103928, MZUSP 103929, MZUSP 103930, MZUSP 104008, MZUSP 104069, MZUSP 104070, MZUSP 100246, MPEG 30726, MPEG 30727, MPEG 30728, MPEG 30729, MPEG 30730, INPA 14763, INPA 14765, INPA 33197, INPA 33233, INPA 33388, INPA 33231, INPA 33269, INPA 33271, INPA 33515, INPA 33272, INPA 33359, INPA 33360, INPA 33395, INPA 33505, INPA 33396, INPA 33603, INPA 33232, INPA 33270, INPA 12172, INPA 12173. Santa Cruz da Serra:

MZUSP 64474. Vilhena: CHUNB 11457, CHUNB 11458, CHUNB 11459, UFMT 10126. GUIANA: Chimapoon R. Potasi: BMNH 1905.11.1.12, BMNH 1905.11.1.13. Demera Falls: BMNH 72.10.16.68. Essequibo: BMNH 1970.715, BMNH 1970.716, AMNH 21294. Kaieteur National Park: IRSNB 17069, IRSNB 17316, IRSNB 17317, IRSNB 17319. Potaro: BMNH 1970.717, MZUSP 103479. Sinnamary: Petit Saut: MPEG 15827, MPEG 15843. COLOMBIA: Vaupés: Taraira: ICN 8075, ICN 8076, ICN 8077. Leticia: ICN 8623. ECUADOR: Napo: KU 126790, KU 126791. Puerto Libre: KU 122173. Rampon: USNM 196107. Sucumbios: Santa Cecilia: KU 109712, KU 112199, KU 122172, KU 175339. FRENCH GUIANA: Camp de Saint Eugène: MNHN 1996-4474, MNHN 1997-2226, MNHN 1997-2229, MNHN 1997-2286, MNHN 1997-2287, MNHN 1997-2310. Mitacara: MNHN 1975-2440. Nouragues: MNHN 2002-0619. Pic Matecho 5: MNHN 2000-5168. RN2, à 7 km de St. Georges de l'Oyapock: MNHN 1995-9476. Sant Limonet: MNHN 1994-8757. PERU: **Loreto:** CORBIDI 2684, MNHN 1978-2191, MNHN 1978-2192, MZUSP 56655, MZUSP 56662. Balsapuerto: CORBIDI 13778. Andoas: CORBIDI 4896, CORBIDI 4638, CORBIDI 4772. Condorcanqui: AMNH 56223, KU- UC - MVZ 163082. Jenaro Herrera: CORBIDI 6320, CORBIDI 6132, MHNSM 16718. Requena: MHNSM 16718, CORBIDI 04134, CORBIDI 12233, CORBIDI 12317. **San Martin:** CORBIDI 09940, KU 209523, USNM 193623. **Cusco**: Pagoreni: CORBIDI 11234, MHNSM 29541, USNM 538401. **Huánuco**: Puerto Inca: CORBIDI 13920, CORBIDI 14471, CORBIDI 16704.

3 CONCLUSÃO

Os resultados de nossas análises estatísticas confirmam parcialmente a similaridade morfológica no gênero, considerada extremamente conservada por estudos anteriores, uma vez que essas análises revelaram alto nível de sobreposição quando considerados a maioria dos caracteres merísticos e morfométricos das diferentes unidades taxonômicas. Por outro lado, as análises dos espécimes ao longo de toda a distribuição do gênero, integrando dados de morfologia externa e de hemipênis, revelaram variações específicas na morfometria e na contagem de estruturas que, em concordância com dados de dois genes mitocondriais e dois nucleares, possibilitaram o diagnóstico de cinco grupos independentes. Até o momento, o gênero *Iphisa* inclui apenas uma espécie, *Iphisa elegans*, com duas subespécies, *Iphisa e. elegans* e *Iphisa elegans soinii*. Os resultados aqui obtidos sugerem que o nome *Iphisa elegans* fique restrito às populações a nordeste da distribuição total do gênero, enquanto *Iphisa soinii* seja considerada uma espécie plena, restrita às populações da Amazônia Peruana e Acre. Além disso, três espécies sem nomes disponíveis são diagnosticadas, totalizando cinco espécies distintas dentro da espécie nominal *Iphisa elegans.* Três das cinco espécies apresentam distribuição simpátrica, ocupando as duas margens do rio Madeira e o interflúvio Madeira-Tapajós. Por fim, esses resultados reforçam a necessidade de revisões cuidadosas e extensivas com abordagens sistemáticas cada vez mais integrativas, que vêm se revelando eficientes na resolução de problemas complexos e possibilitando a diagnose de diversidades anteriormente não reconhecíveis.

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ANEXO – INSTRUCTIONS FOR THE AUTHORS – ZOOLOGICAL JOURNAL OF LINNEAN SOCIETY

Manuscript format and structure/style

BASIC FORMATTING GUIDE

Authors should aim to communicate ideas and information clearly and concisely, in language suitable for the moderate specialist. Papers in languages other than English are not accepted unless invited. When a paper has joint authorship, one author must accept responsibility for all correspondence; the full postal address, telephone and fax numbers, and e-mail address of the author who is to check proofs should be provided. Although the Society does not specify the length of manuscripts, it is suggested that authors preparing long texts (20 000 words or more, including references, etc.) should consult the Editor before considering submission.

Please submit your manuscript in an editable format such as .doc, .docx or .rtf, prepared on A4, paginated, double spaced throughout (i.e. including references and quotations), with ample margins. If you submit your manuscript in a non-editable format such as PDF, this will slow the progress of your paper as we will have to contact you to request an editable copy.

Papers should conform to the following general layout:

Article types

- Original Article
- Review
- Invited Review

Title page

This should be uploaded as a separate file, designation 'Title Page'. It should include title, authors, institutions and a short running title. The title should be concise but informative, preferably shorter than 25 words. Catchy titles are encouraged. Where appropriate the title should include mention of family or higher taxon in the form: 'The Evolution of the Brown Rat, *Rattus norvegicus* (Rodentia: Muridae)'. A subtitle may be included. Papers in numbered series are not accepted. Names of new taxa should not be given in titles.

Abstract

Abstracts must be on a separate page and must be concise, clearly written and cover the context of the paper. The abstract is of great importance as it may be reproduced elsewhere and is all that many may see of your work. It should be about 100–200 words long and should summarize the paper in a form that is intelligible in conjunction with the title. It is advisable to avoid descriptions, lists or jargon if possible. It should not include references. The abstract should be followed by up to ten keywords additional to those in the title (alphabetically arranged and separated by hyphens) identifying the subject matter for retrieval systems. Taxonomic authorities should not be included in the abstract.

Subject matter

The paper should be divided into main sections: INTRODUCTION, MATERIAL AND METHODS, RESULTS, DISCUSSION and CONCLUSION, with the hierarchy of headings below these not exceeding two, except in systematic hierarchies. Results are presented in present tense, whereas previous studies that are discussed need to be presented in past tense. Do not merge results and discussions. Please present your work in clear and concise language, keeping the broad readership in mind.

Separate Results and Discussion sections provide a clear distinction between results of the study at hand and discussion of results of other studies, so these separate sections generally should be used.

The Zoological Codes must be strictly followed. Names of genera and species should be printed in italic or underlined to indicate italic; do not underline suprageneric taxon names. Cite

the author of species on first mention. When new taxonomic names are published, these are marked in bold, followed by the author name and sp. nov., gen. nov. or another abbreviation of the appropriate taxonomic level described on the first mention in the text. Authors can choose any name that is appropriate, but when based on Latin or Latinised Greek the names should be correctly formed.

Etymology of the name needs to be provided.

Voucher specimens used for the study need to be clearly stated by collector, number and the collection where the specimen is housed.

Use SI units, and the appropriate symbols (mm, not millimetre; µm, not micron; s, not sec; min for minute; c for circa; Myr for million years, Mya for million years ago; etc.). Use an n-dash (–), not a hyphen (-), for ranges and use the times sign × (not the letter x) for multiplication, dimensions, crosses and hybrids. Use the negative index (m-1, l-1, h-1) except in cases such as 'per plant'). Avoid elaborate tables of original or derived data, long lists of species, etc.; if such data are absolutely essential, consider including them as appendices or as online-only supplementary material. Avoid footnotes and keep cross references by page to an absolute minimum. Please provide a full English translation [in square brackets] for any quoted matter that is not in English.

References

We recommend the use of a tool such as EndNote or Reference Manager for reference management and formatting.

EndNote reference styles can be searched for here:
http://www.endnote.com/support/enstyles.asp

Reference Manager reference styles can be searched for here:
http://www.refman.com/support/rmstyles.asp

(i) In the text, give references in the following forms: 'Stork (1988) said', 'Stork (1988: 331)' where it is desired to refer to a specific page, and '(Rapport, 1983)' where giving reference simply as authority for a statement. Note that names of joint authors are connected by '&' in the text. For papers by three or more authors, use *et al.* throughout.

(ii) The list of references must include all publications cited in the text and only these. Prior to submission, make certain that all references in the text agree with those in the references section, and that spelling is consistent throughout. In the list of references, titles of periodicals must be given in full, not abbreviated. For books, give the title, place of publication, name of publisher (if after 1930), and indication of edition if not the first. In papers with half-tones, plate or figure citations are required only if they fall outside the pagination of the reference cited. References should conform as exactly as possible to one of these four styles, according to the type of publication cited.

- **Kamiński MJ, Kanda K, Lumen R, Smith AD, Iwan D. 2019.** Molecular phylogeny of Pedinini (Coleoptera, Tenebrionidae) and its implications for higher-level classification, *Zoological Journal of the Linnean Society* 185: 77–97.

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(iii) Other citations such as papers 'in press' may appear on the list but not papers 'submitted', 'in review' or 'in preparation'. These may be cited in the text as 'unpubl. data'. A personal communication may be cited in the text but not in the reference list. Please give the initials and surnames for all authors of personal communications and unpublished data.

(iv) In the case of taxonomic reviews, authors are requested to include full references for taxonomic authorities.

(v) Give foreign language references in Roman alphabet (but include accents in languages that use special letters and accents, like in French, German, Spanish, Swedish, Danish, Czech, etc.). If necessary, transliterate in accordance with a recognized scheme (e.g. pinyin). For the Cyrillic alphabet use British Standard BS 2979 (1958). If only a published translation has been consulted, cite the translation, not the original. Add translations not supplied by the author of the reference in square brackets.

Tables

Keep these as simple as possible, with few horizontal and, preferably, no vertical rules. When assembling complex tables and data matrices, bear the dimensions of the printed page (225 × 168 mm) in mind; reducing typesize to accommodate a multiplicity of columns will affect legibility.

Illustrations

These normally include (1) half-tones reproduced from photographs, (2) black and white figures reproduced from drawings and (3) diagrams. Use one consecutive set of Arabic numbers for all illustrations (do not separate 'Plates' and 'Text-figures' - treat all as 'Figures'). Figures should be numbered in the order in which they are cited in the text. Use upper case letters for subdivisions (e.g. Figure 1A-D) of figures; all other lettering should be lower case.

Half-tones reproduced from photographs: increasingly, authors' original images are captured digitally rather than by conventional film photography. In these cases, please use settings on your equipment for the highest possible image quality (minimum 300dpi). Desktop technology now allows authors to prepare plates by scanning photographic originals and then labelling them using graphics programs such as Adobe Illustrator. These are acceptable provided:

- Resolution is a minimum of 300 dpi at the final required image size. The labelling and any line drawings in a composite figure should be added in vector format. If any labelling or

line drawings are embedded in the file then the resolution must be a minimum of 800 dpi. Please note that vector format labelling will give the best results for the online version of your paper.

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Grouping and mounting: when grouping photographs, aim to make the dimensions of the group (including guttering of 2 mm between each picture) as close as possible to the page dimensions of 168 × 225 mm, thereby optimizing use of the available space. Remember that grouping photographs of varied contrast can result in poor reproduction. If supplied as photographic prints, the group should be mounted on thin card. Take care to keep the surface of the prints clean and free of adhesive. Always provide overlays to protect the photographs from damage.

Lettering and numbering: If supplied as photographic prints, letters and numbers should be applied in the form of dry-transfer ('Letraset') letters, numbers, arrows and scale bars, but not measurements (values), to transparent overlays in the required positions, rather than to the photographs themselves; this helps to avoid making pressure marks on the delicate surface of the prints, and facilitates relabelling, should this be required. Alternatively, pencilled instructions can be indicated on duplicates or photocopies marked 'FOR LABELLING ONLY'. Self-adhesive labels should be avoided, but if they are used, they should not be attached directly to either photographs or overlays, but to photocopies, to indicate where they are to be positioned. Labelling will be inserted electronically by the typesetter in due course.

Colour: the journal is published online-only. The publication of colour figures and images is free of charge.

Black and white figures reproduced from drawings: these should be scanned at a minimum resolution of 800 dpi and supplied in TIFF format. Please note that JPEG, Powerpoint and doc files are not suitable for publication. If it is not possible to provide electronic versions, the figures supplied should be in black ink on white card or paper. Lines must be clean and heavy enough to stand reduction; drawings should be no more than twice page size. The

maximum dimensions of published figures are 168 × 225 mm. Scale bars are the most satisfactory way of indicating magnification. Take account of proposed reduction when lettering drawings; if you cannot provide competent lettering, it may be pencilled in on a photocopy.

Diagrams: in most instances the author's electronic versions of diagrams are used and may be re-labelled to conform to journal style. These should be supplied as vector format Encapsulated PostScript (EPS) files. Please note that diagrams or graphs will not reproduce well in the online version of your paper unless they are in vector format due to low maximum screen resolution.

Type legends for Figures in numerical order on a separate sheet. Where a 'key' is required for abbreviations used in more than one Figure, this should be included as a section of the main text.