Universidade Federal do Rio de Janeiro Programa de Pós-Graduação em Biodiversidade e Biologia Evolutiva

SPECIES DELIMITATION, PHYLOGENY, AND REVISION OF *ABANA* DISTANT, 1908 (HEMIPTERA: CICADELLIDAE: PROCONIINI), A HIGHLY POLYMORPHIC GROUP

Jefferson Sauceda Valderrama

Rio de Janeiro Dezembro de 2023 Jefferson Sauceda Valderrama

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Dissertação de Mestrado submetida ao Programa de Pós-graduação em Biodiversidade e Biologia Evolutiva, Instituto de Biologia, Universidade Federal do Rio de Janeiro, como parte dos requisitos necessários à obtenção do título de Mestre em Biodiversidade e Biologia Evolutiva.

Orientadora: Profa. Dra. Daniela Maeda Takiya

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NOTA

Segundo os critérios do Código Internacional de Nomenclatura Zoológica (artigos 8° e 9°) essa dissertação não constitui publicação e, portanto, quaisquer nomes novos propostos ou atos que afetem a nomenclatura não têm validade.

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RESUMO

DELIMITAÇÃO DE ESPÉCIES, FILOGENIA E REVISÃO DE *ABANA* DISTANT, 1908 (HEMIPTERA: CICADELLIDAE: PROCONIINI), UM GRUPO ALTAMENTE POLIMÓRFICO

Jefferson Sauceda Valderrama Orientadora: Daniela Maeda Takiya

Resumo da Dissertação de Mestrado submetida ao Programa de Pós-graduação em Biodiversidade e Biologia Evolutiva, Instituto de Biologia, Universidade Federal do Rio de Janeiro, como parte dos requisitos necessários à obtenção do título de Mestre em Biodiversidade e Biologia Evolutiva.

Abana é um gênero neotropical de Cicadellidae distribuído da Nicarágua à Bolívia, com distribuição principalmente andina. Atualmente possui seis espécies válidas: A. arnetti, A. dives, A. gigas, A. haupti, A. horvathi e A. tissa, porém algumas delas são idênticas em caracteres da genitália masculina e foram consideradas como diferentes devido ao seu padrão de coloração, característica raramente utilizada para separar espécies dentro de Proconiini. Além disso, algumas espécies apresentam grande variação na coloração intraespecífica, o que representa um problema para sua delimitação. Por essa razão, um estudo taxonômico de Abana baseado na delimitação molecular de suas espécies e análises filogenéticas, incluindo caracteres morfológicos e moleculares, é aqui apresentado para melhor definir e compreender os limites e evolução das espécies do gênero. Filogenias de Abana foram hipotetizadas com base em parcimônia, máxima verossimilhança e inferência Bayesiana usando 108 caracteres morfológicos codificados e 2391 pb de cinco marcadores moleculares (12S, 16S, COI, COII e H3). Todas as análises filogenéticas recuperaram Abana como monofilético e o dividiu em dois grandes clados. Adicionalmente, A. horvathi foi recuperada como um complexo de espécies e seu dimorfismo sexual é relatado pela primeira vez. Finalmente, os resultados da revisão, incluindo fotografias dos tipos primários de todas as espécies, reforçam a validade das seis espécies de Abana anteriormente conhecidas, a proposta de seis novas espécies da Colômbia, Panamá e Peru e a remoção de A. sonora (previamente considerada sinônimo de A. horvathi) do gênero. Abana tissa é registrada pela primeira vez na Colômbia. Uma chave para as espécies e novos registros geográficos também são fornecidos.

Palavras-chave: Auchenorrhyncha; Cicadellinae, Membracoidea; morfologia; sistemática

Rio de Janeiro

Dezembro de 2023

ABSTRACT

SPECIES DELIMITATION, PHYLOGENY, AND REVISION OF ABANA DISTANT, 1908 (HEMIPTERA: CICADELLIDAE: PROCONIINI), A HIGHLY POLYMORPHIC GROUP

Jefferson Sauceda Valderrama Orientadora: Daniela Maeda Takiya

Abstract da Dissertação de Mestrado submetida ao Programa de Pós-graduação em Biodiversidade e Biologia Evolutiva, Instituto de Biologia, Universidade Federal do Rio de Janeiro, como parte dos requisitos necessários à obtenção do título de Mestre em Biodiversidade e Biologia Evolutiva.

Abana is a Neotropical genus of Cicadellidae distributed from Nicaragua to Bolivia, with a mainly Andean distribution. Currently, it includes six valid species: A. arnetti, A. dives, A. gigas, A. haupti, A. horvathi, and A. tissa, however, some of them are identical in characters of the male genitalia and were considered as different because of their colouration pattern, feature rarely used to separate species within Proconiini. Additionally, some species show a large variation in intraspecific colouration, which poses a problem for their delimitation. For this reason, a revisionary study of Abana based on molecular species delimitation and phylogenetic analyses, including morphological and molecular characters, is herein presented to better define and understand Abana species boundaries and evolution. Phylogenies of Abana were hypothesized based on parsimony, maximum likelihood, and Bayesian inference reconstruction methods using 108 morphological coded characters and 2391 pb of five molecular markers (12S, 16S, COI, COII and H3). All phylogenetic analyses recovered Abana as monophyletic and divided into two large clades. Additionally, A. horvathi was recovered as a species complex and its sexual dimorphism is reported for the first time. Finally, the results of the revision, including photographs of the primary types of all species, reinforce the validity of the six previously known Abana species, proposal of six new species from Colombia, Panama and Peru, and transfer of A. sonora (previously considered a synonym of A. horvathi) out of the genus. Abana tissa is recorded for the first time in Colombia. A key to species and new geographical records are also provided.

Keywords: Auchenorrhyncha; Cicadellinae, Membracoidea; morphology; systematics

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INTRODUCTION

Hemiptera, one of the five megadiverse orders of insects, constitutes the largest order of non-holometabolous insects, with approximately 107,000 species worldwide (Bartlett et al. 2018). The oldest known fossil of this order is from the Permian (290-250 million years ago), and the remarkable diversity of the group may be linked to the radiation of angiosperm plants during the Mesozoic era (Grimaldi & Engel, 2005). The monophyly of the group is supported by both molecular (Cryan & Urban, 2012) and morphological data (Yoshizawa & Saigusa, 2001), with the following synapomorphies supporting the order: (1) absence of maxillary and labial palps, (2) structure of the sucking apparatus with mandibular and maxillary stylets housed in a long labial rostrum, and (3) forewings with an anterior axillary fold line forming a fork (Yoshizawa & Saigusa, 2001). Hemiptera is currently divided into four suborders: Heteroptera, Coleorrhyncha, Sternorrhyncha, and Auchenorrhyncha (Cryan & Urban, 2012). The latter includes more than 40,000 species of phytophagous insects and is traditionally divided in two infraorders: Fulgoromorpha and Cicadomorpha. Cicadomorpha comprises around 35,000 species and is divided in three superfamilies: Cercopoidea, Cicadoidea, and Membracoidea (Dietrich, 2005), with the latter comprising five families and including the family Cicadellidae.

Cicadellidae constitutes one of the largest insect families, with approximately 22,000 described species worldwide (Wang *et al.*, 2017), comprising nearly 27 subfamilies (Dietrich, 2005). Cicadellinae is the third largest subfamily, with more than 2,200 described species in 319 genera (Bartlett *et al.* 2018). Of these, 62 genera and approximately 425 species belong to the tribe Proconiini, which is distributed on the New World and has greater diversity in the Neotropics (Young, 1968; Cavichioli & Sakakibara, 1989; Godoy, 2005; Rakitov & Godoy, 2005; McKamey, 2007; Wilson *et*

al., 2009; Carvalho *et al.*, 2011). Some species have high economic importance because they are considered agricultural pests (Sorensen & Gill, 1996), causing damage to various crops (Remes Lenicov *et al.*, 1998) or are involved in the transmission and spread of pathogens to both cultivated and wild plants (Nault & Ammar, 1989; Álvarez *et al.*, 2011). Except for a few of these economically important species, data on the biology, ecology, and life history of most Proconiini remains undocumented.

Included in Proconiini, Abana Distant, 1908 (Fig. 1) has a mainly Andean distribution, but occurs from Nicaragua to Bolivia (Metcalf, 1965; Young, 1968; Freytag & Sharkey, 2002; McKamey, 2007). In his catalog of Homoptera, Metcalf (1965) reported eleven valid species of Abana. A few years later, Young (1968) revised the genus, considering only a total of six valid species: Abana arnetti Young, 1968, A. dives Walker, 1851, A. gigas Fowler, 1898, A. haupti Melichar, 1926, A. horvathi Jacobi, 1905, and A. tissa Distant, 1908. However, in this review, Young (1968) indicated that the male genitalia of A. dives, A. haupti, and A. tissa are identical to the genitalia of A. horvathi and do not illustrate the genitalia of type specimens. Certainly, the only reason for Young (1968) to consider these other species as valid was the distinctive colour pattern, a feature rarely used to separate species within Proconiini. Furthermore, Young (1968) reinforced that, in Cicadellinae, adult colouration varies slightly depending on the time elapsed after the last nymph instar molt, which represents a problem because many species of Abana were described from males that have recently molted (tenerals). It is also notable that there is a great variation in intraspecific colouration (D. Takiya, pers. comm.), so it is necessary to investigate the variation in the intra- and interspecific colouration pattern and in the shape of the male genitalia, for a better delimitation among species of Abana.



Figure 1. Live individuals of *Abana*. **a**, *A. dives* from Ecuador, photo by Andreas Kay; **b**. A. gigas from Costa Rica, photo from an iNaturalist observation (https://www.inaturalist.org/observations/153267107); c, Abana horvtahi male from Ecuador, photo by Andreas Kay; d, A. horvathi female from Ecuador, photo by Andreas Kay; e, A. horvathi male from Ecuador, photo by Andreas Kay; f, A. ochracea sp. nov. photo from iNaturalist from Panama. an observation (https://www.inaturalist.org/observations/102504823); g, A. rufifrons sp. nov. from Panama, photo from iNaturalist observation an (https://www.inaturalist.org/observations/116622840); h, A. tissa from Colombia, photo by Camilo Flórez-V.; i, A. tissa from Ecuador, dead specimen with parasitic photo by Andreas Kay. Photos of Andreas Kay available fungi, in https://www.flickr.com/photos/andreaskay.

Ceotto & Mejdalani (2005) published the first known phylogenetic work including *Abana* species, testing the monophyly of a group of Proconiini genera so called "*Abana* group", based on morphological data. This group, in addition to *Abana*, includes the genera *Acrobelus* Stål, *Acrogonia* Stål, *Deselvana* Young, *Omagua* Melichar, *Raphirhinus* de LaPorte, and *Teletusa* Distant, and was characterized by a single homoplastic feature: the straight basal part of the costal margin of the forewing. Results of these analyses recovered the *Abana* group (excluding *Acrogonia*) and *Abana* as monophyletic, with the latter being the sister group of *Omagua* (but with low branch support). However, in this analysis, they included only three of the six *Abana* known

species. In her unpublished doctoral thesis, Takiya (2007) focused on the monophyly and phylogenetic relationships of the subfamily Cicadellinae and its tribes using morphological and molecular data, including a very big sampling effort for the Proconiini tribe. In the analysis of the morphological dataset, Takiya (2007) recovered Abana as monophyletic, but its relationship to other genera in the Abana group (excluding Acrogonia, which was grouped with other genera in the new tribe "Oncometopiini," proposed by the author) was unresolved. However, resulting phylogenetic topologies based on morphological characters in this work were generally poorly supported and unresolved; furthermore, the author included only two of the six valid Abana species in the morphological analysis. On the other hand, analyses of the concatenated molecular dataset (including sequence data of four molecular markers: 16S, COI, COII, and H3), recovered Abana as the sister group of Teletusa, only statistically supported in Bayesian inference analyses. However, only one specimen of Abana identified as A. horvathi was included in the analyses, not providing any information about the monophyly of the genus and relationships within it. Although these phylogenetic approaches have positioned Abana within the Proconiini tribe, so far there have been no attempts to propose a phylogenetic hypothesis for species of the genus. Young (1968) stated that Abana species are closely related morphologically, with very similar male genitalia, so the genus can be in fact be monophyletic, but this monophyly, as well as relationships among species, need to be explored.

There is an evident large gap in the knowledge of *Abana*, both at the taxonomic level and on its evolution and species phylogenetic relationships, but also on their biology, ecology, and distribution (dispersed data, mostly from type localities). To address this lack of knowledge, a revision of the genus is herein conducted, grounded on species delimitation analyses and phylogenetic hypothesis constructed using both morphological and molecular data. It includes redescriptions of the genus and of the external morphology and terminalia of the six *Abana* previously valid species (including their female terminalia when available), and descriptions of six new species. Additionally, a key to species and new geographical records are provided.

MATERIAL AND METHODS

Specimen sampling and taxonomic review

A total of 193 specimens of Abana were studied here. These specimens are deposited in the following collections: Museo de Historia Natural C.J. Marinkelle, Universidad de los Andes - Bogotá, Colombia (ANDES); The Natural History Museum - London, UK (BMNH); Monte L. Bean Life Science Museum, Brigham Young University – Provo, USA (BYU); Colección Entomológica del Programa de Biología, Universidad de Caldas - Manizales, Colombia (CEBUC); Colección Entomológica Universidad de Antioquia - Medellín, Colombia (CEUA); Coleção Prof. José Alfredo Pinheiro Dutra, Departamento de Zoologia, Universidade Federal do Rio de Janeiro - Rio de Janeiro, Brazil (DZRJ); Field Museum of Natural History – Chicago, Illinois (FMNH); Hungarian Natural History Museum - Budapest, Hungary (HNHM); Colecciones Zoológicas, Instituto de Ciencias Naturales de la Universidad Nacional de Colombia -Bogotá, Colombia (ICN); Insect Collection, Illinois Natural History Survey -Champaign, USA (INHS); Museo Entomológico Francisco Luis Gallego, Universidad Nacional de Colombia sede Medellín - Medellín, Colombia (MEFLG); Museo de Historia Natural Noel Kempff Mercado – Santa Cruz de la Sierra, Bolivia (MHNNK); Moravian Museum – Brno, Czech Republic (MMBC); Museo Javeriano de Historia Natural Lorenzo Uribe, Pontificia Universidad Javeriana – Bogotá, Colombia (MPUJ); Museo de Historia Natural de la Universidad Mayor de San Marcos - Lima, Peru (MUSM); Museum and Institute of Zoology, Polish Academy of Sciences - Warsaw, Poland (MZPW); Insect Collection of the North Carolina State University - Raleigh, USA (NCSU); Staatliches Museum für Tierkunde – Dresden, Germany (SMTD); Entomological Collection of the Smithsonian Tropical Research Institute – Panama City, Panama (STRI); University of Kentucky Insect Collection – Lexington, USA (UKIC);

Museo Entomológico Universidad Nacional Agronomía Bogotá – Bogotá, Colombia (UNAB); and National Museum of Natural History – Washington D.C., USA (USNM). For type material examined, label data are specified between quotation marks (""), labels separated by a comma (,) and line breaks are indicated by a backslash (\).

For species identification, male genitalia were prepared following Oman (1949), while female genitalia prepared following Zanol (1988). Studied structures were preserved in glycerin 10%. Structures of the male and female genitalia, as well as dorsal and lateral habitus of the studied species were observed and photographed at different focal planes on a Leica DFC450 digital camera attached to a Leica M205C stereomicroscope and on a Canon EOS Rebel SL1 camera with a Canon EF 100mm f/2.8 Macro USM objective lens. Images were automatically stacked using softwares Leica Application Suite (LAS) v4.6. and Helicon Focus 8.1.1. Stacked images were edited in Adobe Photoshop.

Photographs of type specimens of the following species were studied: *A. arnetti*; *A. dives*; *A. drusilla* Distant, 1908; *A. gigas*; *A. haupti*; *A. horvathi*; *A. pomposula* Jacobi, 1905; *A. puella* Schmidt, 1928; *A. regia* Melichar, 1926; *A. sonora* Melichar, 1926; *A. subfasciata* Melichar, 1926; *A. tissa*. These represent all valid and invalid names proposed in *Abana* following Young (1968).

Morphological terminologies mainly follow Young (1968, 1977), except for head characteristics that follow Hamilton (1981); chaetotaxy that follows Rakitov (1998); and female genitalia that follow Nielson (1965) and Hill (1970).

Sequence data

DNA was extracted from a hind leg or the entire abdomen of each specimen with DNeasy Blood & Tissue kit (Qiagen) with modifications on the manufacturer's protocol (Appendix S1). Fourteen specimens collected between 1988 to 2023, pinned or preserved in ethanol, representing a total of ten *Abana* species had their DNA extracted and PCR and sequencing was attempted. However, we were only able to generate sequences from representatives of four of the six *Abana* species herein considered valid, in addition to five of the six new species herein described (Table 1).

Five molecular markers were sequenced: the nuclear gene histone H3 subunit, and four mitochondrial genes: 12S and 16S rDNA and cytochrome oxidase subunits I (COI) and II (COII). These markers have been historically used to reconstruct phylogenetic relationships within Auchenorrhyncha and Cicadellidae (Sorensen *et al.*, 1995; Dietrich *et al.*, 1997; Cryan, 2005; Takiya, 2007). Protocols for PCR amplifications followed Takiya (2007, Appendix S2). Primer sequences are listed in Appendix S3. Successful amplifications were purified with ExoSAP-IT (Affymetrix) and sent for Sanger sequencing by Macrogen, Inc. (Seoul, South Korea). Consensus sequences were generated by assemblies of complementary electropherograms with Geneious Prime 2023.1. A BLAST (Basic Local Alignment Search Tool) search of the consensus sequences against the GenBank database was made in order to check if there was any contamination. Generated sequences will be deposited in GenBank.

Multiple sequence alignments were done including sequences generated herein in addition to sequences from outgroup taxa and a single *Abana* specimen from Takiya (2007) available from GenBank (Table 1). Sequences of H3, COI, and COII were aligned using ClustalX (Larkin *et al.*, 2007) available in MEGAX (Kumar *et al.*, 2018) with default penalties for gap opening and extension. These protein-coding genes were translated into amino acid sequences to verify that they were edited correctly and were in the correct reading frame. Sequences of 12S and 16S rDNA were aligned at the online platform MAFFT V.7 (http://mafft.cbrc.jp/alignment/server; Katoh & Standley, 2013) using algorithms E-INS-i and Q-INS-i. The preferred alignment was selected visually for

each marker (12S: E-INS, 16S: Q-INS). To concatenate alignments, the software SequenceMatrix v1.6.7 (Vaidya *et al.*, 2011) was used.

Matrices were partitioned by marker and codon position (for COI, COII, and H3) for the ML analyses, except in the species delimitation analyses (COI not partitioned by codon position), and the best-fit partitioning scheme and model was selected according to the Bayesian information criterion (BIC) score in ModelFinder (Kalyaanamoorthy *et al.*, 2017) implemented in IQ-TREE 2.2.0 (Minh *et al.*, 2020) for ML, and Akaike information criterion (AIC) score in jModelTest (Posada 2008) for BI analyses. For the species delimitation tree reconstruction, the best substitution model selected for the COI sequences was GTR+F+I+G. For phylogenetic analyses, the substitution models selected and applied for each partition of the concatenated (molecular) and combined (molecular + morphology) data matrices in the ML analyses were: (1) 12S + 16S: TIM+F+I+G, (2) COI_pos1 + COII_pos1: TIM2+F+G, (3) COI_pos2 + COII_pos2: TVM+F+R2, (4) COI_pos3 + COII_pos3: K3Pu+F+G, (5) HEX_pos1 + HEX_pos2: JC+I, (6) HEX_pos3: GTR+F+I+G, and (7) Morphology: MK+I+G. Finally, for BI analyses models selected were: (1) 12S: HKY+G, (2) 16S: GTR+I+G, (3) COI: GTR+I+G, (4) COII: GTR+G, (5) H3: GTR+I+G, and (6) Morphology: MK+I+G.

Species	DNA	Sex	Locality (Year)	Н3	COI	COII	168	12S
	voucher							
Abana amazonica sp. nov.	ENT6384	Male	Peru: Amazonas (2008)	ENT6384	ENT6384	ENT6384	-	ENT6384
Abana dives	ENT6387	Male	Colombia: Chocó (2022)	ENT6387	ENT6387	ENT6387	ENT6387	ENT6387
Abana colombiana sp.	ENT6386	Male	Colombia: Boyacá (2017)	ENT6386	ENT6386	ENT6386	ENT6386	ENT6386
nov.								
Abana colombiana sp.	ENT6427	Female	Colombia: Boyacá (2016)		ENT6427			
nov.								
Abana gigas	ENT6581	Male	Costa Rica: Limon (1988)	ENT6581	-	-	-	-
Abana horvathi s.s.	ENT6385	Male	Peru: Cusco (2012)	ENT6385	ENT6385	ENT6385	ENT6385	ENT6385
Abana horvathi s.s.	ENT6602	Female	Peru: Cusco (2012)		ENT6602			
Abana sp. (A. horvathi	PR123	Male	Peru: Huánuco (2002)	MH619134		MH619029	MH656483	
complex)								
Abana minuta sp. nov.	ENT6583	Male	Peru: Huánuco (2002)	ENT6583	-	-	ENT6583	ENT6583
Abana ochracea sp. nov.	ENT6428	Female	Panama: Panama (2005)	ENT6428	-	-	ENT6428	ENT6428
Abana rufifrons sp. nov.	ENT6429/	Female/	Panama: Coclé (2005)	ENT6429	ENT6584	-	ENT6429	ENT6584
	ENT6584	Male						
Abana tissa	ENT6388	Male	Colombia: Antioquia (2022)	ENT6388	ENT6388	ENT6388	ENT6388	ENT6388
Abana tissa	ENT6603	Male	Valle del Cauca (2023)		ENT6603			
			Outgroup					
Acrobelus rakitovi				MH619136		MH619031	MH656487	
Acrocampsa integra				MH619137		MH619032	MH656501	
Aulacizes conspersa	ENT5995		Brazil: Paraná (2018)		ENT5995			
Aulacizes quadripunctata				MH619147		MH619041	MH656495	
<i>Deselvana</i> sp.				MH619166		MH619058	MH656500	
Diestostemma huallagana					MN344080			
Diestostemma excisum				AY869756		AY869778	AY869817	
Omagua fitchi				MH619200	MN345562	MH619092	MH656486	
Oncometopia alpha					KF919585			
Oncometopia facialis				MH619202		MH619094	MH656519	
Paraulacizes irrorata					HQ985136			
Peltocheirus sp.				MH619212		MH619104	MH656502	
Proconia marmorata					MN345868			
Pseudometopia amblardii					MK907397			
Raphirhinus phosphoreus				MH619225	MN344187	MH619118	MH656484	

Table 1. Species of *Abana* and outgroups included in the molecular phylogenetic analyses, with respective DNA specimen voucher code(s) and its(their) locality and year of collection. Accession codes are given for sequences obtained from Genbank.

Teletusa limpida	MH619233	MH619126	MH656485
Teletusa sp.	MN345141		

Morphological data

Proposed primary homologies (de Pinna, 1991) were coded in a matrix of morphological characters in Mesquite 3.70 (Maddison & Maddison, 2019), following the structure proposed by Sereno (2007), with inapplicable characters indicated by "-" and missing or unobserved states indicated by "?". These primary homologies were proposed based on observations of specimens and previous phylogenetic works including specimens of *Abana* (Ceotto & Mejdalani, 2005; Takiya, 2007). It was possible to code morphological characters of five valid *Abana* species and six new species described herein based on specimens. Solely the coding of *A. haupti* was made based on photos of the lectotype and original species description. The coding of *Abana* sp. was based on a dorsal habitus image of a male DNA voucher for sequences available in Genbank from Takiya (2007).

Molecular species delimitation

Unilocus species delimitation analyses for *Abana* species were performed using five different methods: Automatic Barcode Gap Discovery (ABGD; Puillandre *et al.*, 2012; implemented in the web server https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html), Assemble Species by Automatic Partitioning (ASAP; Puillandre *et al.*, 2020, implemented in the web server https://bioinfo.mnhn.fr/abi/public/asap/), Bayesian implementation of Poisson tree processes (bPTP; Zhang *et al.*, 2013, implemented in the web server https://species.h-its.org/ptp/), Multi-rate Poisson tree processes (mPTP; Kapli *et al.*, 2017, implemented in the web server https://mptp.h-its.org), and generalized mixed Yule coalescent (GMYC; Fujisawa & Barraclough, 2013, implemented in the web server https://species.h-its.org/gmyc/).

All analyses were conducted on the barcode (COI) sequences data set. For ABGD and ASAP, the COI alignment was used as input file. For bPTP and mPTP, a phylogenetic tree was constructed using the maximum likelihood (ML) criterion in IQ-TREE 2.2.0 (Minh et al., 2020) with support values calculated by 1,000 replicates of Ultrafast Bootstrap (UFBoot; Minh et al., 2013) and 1,000 replicates of Shimodaira-Hasegawa approximate likelihood ratio test (SH-aLRT; Guindon et al., 2010). A total of 18 terminal taxa were used, including nine specimens corresponding to four species of Abana (Table 1) and nine species used as outgroups: eight from the tribe Proconiini s.s. (Diestostemma huallagana, Omagua fitchi, Paraulacizes irrorata, Proconia marmorata, Pasudometopia amblardii, Raphirrhinus phosphoreus, and Teletusa sp.) and one from the Oncometopiini sensu Takiya (2007) (Oncometopia alpha) used for rooting the tree. Representatives of other Abana species were not included due to the impossibility to obtain COI sequences. The convergence of bPTP analysis was visually checked in the trace plot. Maximum likelihood and Bayesian solutions for bPTP delimitation were considered. For GMYC, an ultrametric tree for the COI sequences was obtained using BEAST v2.7.4 (Bouckaert et al., 2014), with a total of 10 million generations, with sampling every 1,000 generations. Parameter convergence was accessed through Tracer v.1.7 (Rambaut et al., 2018), seeking to achieve effective sample size values of at least 200, once the 25% burn-in was removed. This ultrametric tree was submitted to single and multiple threshold analyses, checking the significance of the delimitation model with respect to the null hypothesis of a single species.

Phylogenetic analyses

Phylogenetic analyses were conducted based on three different data matrices: (1) morphological data with 23 terminal taxa analysed with parsimony (MP); (2) concatenated

molecular data with 20 terminal taxa analysed with ML and Bayesian inference (BI); and (3) combined molecular and morphological data with 25 terminal taxa analysed with ML and BI. The combined matrix included 13 species of *Abana* (Table 1) and 12 species used as outgroups: 11 from the tribe Proconiini *s.s.* (*Acrobelus rakitovi, Acrocampsa integra, Aulacizes quadripunctata, Deselvana excavata, Deselvana sp., Diestostemma excisum, Diestostemma ptolyca, Omagua fitchi, Peltocheirus sp., Raphirrhinus phosphoreus, and Teletusa limpida*), and Oncometopia facialis (Oncometopiini sensu Takiya, 2007) used for rooting the trees. These outgroups were chosen based on a phylogenetic tree result of a combined analyses (morphological + molecular) containing all genera within Proconiini (Takiya, 2007).

Parsimony (MP) analysis was conducted in TNT 1.5 (Goloboff & Catalano, 2016) using Traditional search algorithms with 10,000 replicates to find most parsimonious trees. All characters were treated with equal weights and unordered. Clade support was assessed by non-parametric bootstrap with 10,000 pseudoreplicates (Felsenstein, 1985). Consistency (CI) and retention (RI) indexes for trees and characters were calculated over the consensus trees in Winclada (Nixon, 2002).

Maximum likelihood (ML) analyses were calculated in IQ-TREE (Minh *et al.*, 2020) with support values calculated by 1,000 replicates of UFBoot (Minh *et al.*, 2013) and 1,000 replicates of SH-aLRT (Guindon *et al.*, 2010).

BI analyses were run with MrBayes 3.2.2 (Ronquist *et al.*, 2012). For the concatenated and combined matrices, two independent runs of four Markov chains Monte Carlo (MCMC) for 1 million generations (sample frequency = 500) were conducted. For both analyses, the first 25% trees were discarded as burn-in, parameter mixing, and convergence among runs

was checked with Tracer v1.7.2 (Rambaut *et al.*, 2018) based on ESS values >200. Bayesian Posterior Probability (PP) of clades were presented as percentages.

As recommended, support values considered reliable herein were SH-aLRT ≥ 80 , UFboot ≥ 95 , and PP ≥ 95 (Guindon *et al.*, 2010; Ronquist *et al.*, 2012; Minh *et al.*, 2013). Resulting trees were viewed on FigTree v1.4 (Rambaut, 2012) and vector images exported and edited in Adobe Illustrator.

RESULTS

Molecular species delimitation

Results of molecular delimitation analyses of the DNA barcode region (Fig. 2) for the ABGD method delimited five entities (candidate species) of *Abana*, the same results were found by the GMYC single and multiple threshold analyses, and in both, the model was significantly better than the null hypothesis in the likelihood ratio test (single: LR = 7.454932, LRT results = 0.02405371, threshold time = -0.01816564; multiple: LR = 8.231807, LRT results = 0.0163112, threshold time = -0.07347779). The ASAP model delimited six candidate species of Abana in all results. For the bPTP model, results were different for the maximum likelihood and Bayesian inference partitions, delimiting six and five candidate species respectively, however, for both partitions, only the group Abana tissa "blue morph" + A. tissa "brown morph" and the singleton A. horvathi from Amazonas, Peru, showed support values above 0.95, which suggests that we should be cautious in interpreting the other clusters as independent species. Finally, the mPTP model was extremely conservative and delimited all specimens included in the analysis as belonging to a single species. Here, we used the majority consensus for all results obtained, considering six Abana candidate species: A. tissa ("blue morph" + "brown morph"), A. dives, A. rufifrons sp. nov., and that the nominal species A. horvathi constitutes a species complex (hereinafter referred to as A. horvathi s.l.). Most methods suggest that A. horvathi s.l. include a complex of at least three distinct species (Fig. 2, highlighted in blue, cyan, and dark green). These species are treated as A. horvathi s.s. (male and female specimens from Cusco, Peru) and two new species described below (A. amazonica sp. nov. from Amazonas, Peru, and A. colombiana sp. nov. from Colombia).

Based on these analyses we were also able to associate male and female specimens with very distinct colour pattern in *A. horvathi s.s.* (Figs. 14a-b, 15a-b) and *A. colombiana* **sp. nov.** (Figs. 10a-b, 11a-e), corroborating the sexual dimorphism present in the complex, in accordance with what was observed in the morphological study (Figs. 1c-e, 10a-b, 11a-e, 14a-b, 15a-b, 25e-l, o-p).



Figure 2. Maximum Likelihood tree of *Abana* (-lnL= 3462.784) showing results of species delimitation methods based on the cytochrome c oxidase subunit I (COI) gene. Each vertical bar represents different delimitation schemes obtained with ABGD, ASAP, bPTP, mPTP and GMYC methods. Values below branches are likelihood SH-aLRT / ultrafast bootstrap support values. SH-aLRT < 80 and UFboot < 95 values are not shown.

Data matrices for phylogenetic analyses

A total of 108 morphological characters (Appendix S4) from head, thorax, abdomen, and male and female terminalia were coded for 13 *Abana* terminal taxa (two different individuals were coded for *Abana horvathi s.s.*) and 11 outgroup species (Appendix S5).

Final individual marker alignments were as follows: 12S rDNA (373 bp) for ten specimens representing eight *Abana* species, 16S rDNA (480 bp) for nine specimens representing seven *Abana* species, COI (621 bp) for nine specimens representing six *Abana* species, COI (590 bp) for six specimens representing five *Abana* species, and histone H3 (327 bp) for 11 specimens representing nine *Abana* species. The concatenated molecular matrix included a total of 13 *Abana* terminal species and 12 outgroup taxa.

Phylogeny

Both maximum likelihood (-lnL = 10935.244) and Bayesian Inference analyses of the combined data matrix (Fig. 3) recovered *Abana* as monophyletic with high support values (SH-aLRT = 99.9, UFboot = 100, and PP = 100). This result was also obtained in the ML and BI analyses of the molecular matrix and in the MP morphological analysis (Figs. S1 and S2). In both ML and IB results of the concatenated and combined datasets, *Teletusa limpida* was recovered as sister to *Abana*, with medium to high support (PP = 81 in the combined matrix result, Fig. 3; SH-aLRT = 97.9 and PP = 99 in the concatenated matrix, Fig. S2). However, the morphological parsimony tree, recovered *Omagua fitchi* as the sister to *Abana* with low support (parsimony bootstrap = 71).



Figure 3. Maximum likelihood tree of *Abana* based on combined morphological (108 characters) and molecular data (2391 bp of 12S, 16S, COI, COII, and H3) (-lnL = 10935.244). Thickened branches are those also recovered in the BI analysis. Values above branches are likelihood SH-aLRT / ultrafast bootstrap support and below are Bayesian posterior probabilities (in percentages). Support values SH-aLRT < 80, UFboot < 95, and PP < 80 are not shown. Blue rectangle indicates *Abana*.
Abana haupti was recovered as the sister group of a clade containing all the other species of Abana (Fig. 3), however, this relationship was not recovered neither in BI nor in morphological MP analyses (Figs. S1 and S2). The sister clade of A. haupti had no statistical support and was divided into two major clades (Fig. 3). The first clade contained A. confusa sp. nov., A. minuta sp. nov., and species within the A. horvathi species complex (Abana horvathi s.l.). The A. horvathi species complex was recovered with high support values (SHaLRT = 99.9, PP = 99) and, in addition to A. horvathi s.s., A. amazonica sp. nov., and A. *colombiana* **sp. nov.**, sequences from *Abana* sp., represented by a male DNA voucher from Peru (Huánuco) from Takiya (2007) were also analysed together, placing this specimen as the sister group to A. colombiana sp. nov. This male DNA voucher is very similar to males of other species in the A. horvathi species complex, being impossible to distinguish it from other species based only on dorsal habitus. The clade A. minuta sp. nov. + A. horvathi s.l. was also recovered in the concatenated analyses of the molecular matrix (Fig. S2) with strong support values for almost all relationships. The second clade within Abana except of A. haupti (Fig. 3) was recovered with high support values (SH-aLRT =99.8 and PP =100), and comprised A. arnetti, A. dives, A. gigas, A. ochracea sp. nov., A. rufifrons sp. nov. and A. tissa, however, the main relationships within this clade were unstable and incongruent between ML and BI analyses of the combined matrix, with the exception of the clade formed by A. tissa + A. gigas. This second major clade was also recovered in the concatenated analyses of the molecular matrix (Fig. S2) with strong support values (SH-aLRT=98.6, UFBoot=99, and PP=100), but with different internal relationships among species.

The morphological MP results (Fig. S1) also recovered these two major clades within *Abana*, nonetheless, none of them were supported and species relationships within them were

completely different compared to the combined (molecular + morphological) and concatenated (molecular) results.

Taxonomic revision

Abana Distant, 1908

(Figs. 5-27)

Abana Distant, 1908b: 72 [n. gen.]. Type species: Aulacizes dives Walker 1851b: 791.Young, 1968: 148 [Species list; Species synonymies]; Oman, Knight & Nielson 1990a: 184[Listed]. Ceotto & Mejdalani, 2005 [Phylogeny].

Mesobana Melichar, 19 27a: 322 [n. subgen. of Abana]. Type species: Amblydisca pomposula Jacobi 1905c: 167. Young, 1968: 148 [Synonym of Abana]; Oman, Knight & Nielson 1990a: 229 [Listed].

Diagnosis. Large sharpshooters (14-21 mm). Head well produced (Figs. 8a-d, 23a-b); clypeus (Figs. 8b, d, 23b) protuberant, its contour almost at right angle to profile of face. Pronotum (Figs. 8a, c, 23a) width exceeding transocular width of head; in dorsal view with lateral margins convergent anteriorly. Forewing (Figs. 8a-d, 23a-b) with clavus and most of corium coriaceous, conspicuously punctate. Aedeagus (Fig. 8h) shaft with a basal dorsal spiniform process and a preapical dorsal spiniform process (Fig. 8h); shaft apex with lateral margins projected dorsally, forming a pair of square-shaped lateral projections (Figs. 8h, 23f), each with anterior portion extending anteriorly, forming an anterodorsal projection. Paraphyses (Figs. 8h-j, 23f-h) paired, each elongate and slender, extending between shaft lateral projections and exceeding shaft apex. Dorsal connective strongly (Fig. 23f) or

somewhat (Fig. 8h) sclerotized; in caudal view, somewhat U-shaped, but interrupted medially; with a submedian acute process extending anteriorly (Fig. 23f), sometimes very little and inconspicuous (Fig. 8h).

Species included. Abana amazonica sp. nov., Abana arnetti Young, 1968, Abana colombiana sp. nov., Abana confusa sp. nov., Abana dives Walker, 1851, Abana gigas Fowler, 1898, Abana haupti Melichar, 1926, Abana horvathi Jacobi, 1905, Abana minuta sp. nov., Abana ochracea sp. nov., Abana rufifrons sp. nov., and Abana tissa Distant, 1908.

Total length (mm): males (n = 25) 14.5-19.7 mm, females (n = 15) 18.5-20.5 mm.

Description. Crown (Figs. 8a, c, 10a, d) produced anteriorly; with (Figs. 11d, 19a, 20a, 21a, c) or without (Figs. 8a, c, 10a, d) pubescence; anterior margin subtriangular to triangular (Figs. 8a, c, 10a, d) or rounded (Figs. 5a, c, 6a, 13a); disk with (Figs. 8a, c, 10a, d) or without (Figs. 5a, c, 6a) a distinct depression, without a longitudinal carina laterad of each ocellus (Figs. 8a, c, 10a, d); posterior margin with a M-shaped elevation (Figs. 8a, c, 10a, d), sometimes inconspicuous (Fig. 11a, d) or absent (Fig. 5a, c). Head, in lateral view, with anterior portion of crown not inflated (Figs. 8b, d, 10b, e) forming an acute angle with frons, or inflated (Figs. 26b, 27b, 28b) forming an obtuse angle with frons. Ocelli located on or slightly behind imaginary line between anterior eye angles, each ocellus equidistant between midline of crown and adjacent anterior eye angle (Fig. 8a, c) or closer to the latter (Fig. 26a). Antennal ledges (Figs. 8b, d, 10b, e) longitudinally sulcate and carinate dorsally; anterior edges steeply declivous. Face (Figs. 8b, d, 10b, e) pubescent, with setae more densely distributed towards ventral region, on lorum, clypeus, and rostrum. Frons (Figs. 8b, d, 10b, e) evenly convex or at least flattened medially; muscle impressions distinct. Clypeus (Figs. 8b, d, 10b, e) protuberant, its contour almost at right angle to profile of face; without a median carina. Pronotum (Figs. 8a, c, 10a, d) width exceeding transocular width of head; lateral

margins convergent anteriorly; surface punctate and rugose; with (Figs. 11d, 19a, 20a, 21a, c) or without (Figs. 8a, c, 10a, d) pubescence; posterior margin concave, forming two lobes; in lateral view clearly declivous anteriorly; dorsopleural carina present and complete, arched slightly upwards at midlength. Scutellum (Figs. 8a, c, 10a, d) transversely striate at posterior half, posterior to scutellar suture. Forewing (Figs. 8a-d, 10a-b, d-e) with veins distinct and elevated; clavus and corium strongly coriaceous, both conspicuously punctate, with punctures distributed throughout the tegmen (Figs. 26a-b, 27a-b, 28a-b) or grouped bordering the veins (Figs. 8a-d, 10a-b, d-e); with four apical cells, base of fourth usually slightly more distal than base of third; without an anteapical plexus of veins, but with anteapical supernumerary crossveins to costal margin; claval veins parallel, without crossveins. Hind wing (Figs. 8a-d, 10a-b, d-e) at rest extending nearly as far as apex of forewing; vein R2+3 obsolete (Figs. 9c, 10a, 21c). Profemur with setal row IC multiseriate, setae subequal in aspect and indistinct from AV; setal row AM reduced to AM1. Hind leg with femoral setal formula 2:0:0, 2:1:0, or 2:2:0; tibia with AD row of cuculate setae without intercalaries; AD and PD setae similar in size, but not in number (PD more setose than AD, but not reaching double the amount of setae); PD row with setae irregularly spaced; AV and PV rows of setae unmodified; first tarsomere shorter than combined length of second and third.

Colouration. The colour pattern is very variable inter- and intraspecifically (in some species), even showing sexual dimorphism in species of the *A. horvathi* species complex. In general, species of *Abana* have completely dark heads (Figs. 11a-e, 13a-b, 19a-b) or with the anterior portion showing colourations ranging from light yellow to ochraceous-yellow and reds (Figs. 5a-d, 8a-d, 15a-d, 17a-b, 26a-b). Thorax colouration is generally dark, varying from reddish-brown (Fig. 26a-b) to dark brown (Figs. 17a-b, 19a-b) in dorsal view, and

showing (Figs. 8b, d, 26b) or not (Figs. 11b, e, 13b, 17b) some ivory or yellow areas of different sizes. Pronotum may have a pair of maculae varying in size and position, ranging from light ivory (Fig. 26a) to orangish yellow (Figs. 8a, c, 10a, d), or almost completely yellow (Fig.15a, c). Forewings also have general dark colouration, varying from reddish brown (Figs. 25a-d, 27a-b) to dark brown (Figs. 5a-d, 11a-e, 17a-d, 19a-b) and black (Figs. 8a-b, 26a-b), and sometimes with light ivory or yellow stripes or maculae varying in size, number, and position (varying inter- and intraspecifically, Figs. 13a-b, 7a-b, 14a-b, 19a-b, 20a-b, 21a-d, 24a-d, 27a-b, 28g-r). Abdomen general colouration dark, varying from dark brown to black, with some ivory or yellow areas of different sizes (Fig. 8b, d), or it can be completely dark (Fig. 10 b, d) or yellow (Fig. 26b).

Male terminalia. Pygofer (Fig. 8e) in lateral view angularly produced; abruptly narrowed on dorsal margin near midlength, forming a deep concavity until apex; ventral margin with a distinct median concavity (Fig. 5e) or regularly convex (Fig. 8e); preapical region convex (Fig. 8e) or with a small concavity (Fig. 11f, 24c); microsetae sparse and uniformly distributed; without processes. Subgenital plates (Fig. 8f) triangular in ventral view; separate along their entire length; in lateral view, extending (Fig. 8e) or not (Figs. 5e, 23c) to apex of pygofer; each plate with numerous dispersed microsetae. Connective (Fig. 8g) Y-shaped; stem much longer than arms, gradually broadened apically, not keeled; arms almost parallel (Fig. 5g) to parallel (Fig. 7e), converging anteriorly (Fig. 8g) or slightly divergent (Fig. 13e); base of arms with (Figs. 5g, 23e) or without (Fig. 8g) a dorsal rim, when present, U shaped (Fig. 23e) or V shaped (Fig. 5g). Style apodeme (Fig. 23e) variable in length and thickness; apophysis extending posteriorly to before (Fig. 23e), as far (Fig. 5g), or slightly beyond (Figs. 17e, 19e) connective apex; preapical (Fig. 8g) and inner lobe (Fig. 8g) present; inner lobe shape varying from rounded (Fig. 8g), subtriangular (Fig. 23e, 26e),

or subquadrate (Fig. 24e); angle formed between preapical lobe and apical portion varying from acute (Figs. 23e, 26e) to almost right (Fig. 8g); apical portion variable in size and length; apex acute. Aedeagus (Fig. 8h-j) symmetrical; preatrium inconspicuous; shaft with a basal dorsal spiniform process and a preapical dorsal spiniform process extending dorsally not reaching (Fig. 5h), reaching (Fig. 8g), or extending slightly beyond dorsal margin of lateral projections (Fig. 24f); apex (Fig. 8h-j) with lateral margins projected dorsally, forming a pair of square-shaped lateral projections, each with anterior portion extending anteriorly, forming an anterodorsal projection variable in length and thickness. Paraphyses (Fig. 8h-j) paired, elongate and slender; basally separated and connected to base of aedeagus by membrane; extending between lateral projections and exceeding shaft apex. Dorsal connective strongly (Fig. 23f) or somewhat (Fig. 8h) sclerotized; in caudal view, somewhat U-shaped, but interrupted medially; with a submedian acute process extending anteriorly (Fig. 23f), sometimes very little and inconspicuous (Fig. 8h).

Female terminalia. Abdominal sternite VII (Fig. 9e), in ventral view, approximately 1.5 times wider than long; strongly produced posteriorly, triangular in form; lateral margins sinuous; ventral surface with microsetae distributed at median third and towards lateral margins; posterior margin median third with a pair of dentiform (Fig. 9e) or digitiform (Fig. 25e) posterior projections; area in between projections concave (Fig. 25e), straight (Fig. 27c), or projected posteriorly as a bifurcate process (Fig. 9e). Sternite VIII completely membranous. Pygofer (Fig. 9f), in lateral view, produced posteriorly; apex almost truncate, with a median concavity; surface with longer microsetae along central, ventral, and posterior regions, and shorter microsetae uniformly distributed all over surface. First valvifer (Fig. 9g), in lateral view, subtriangular. First valvula (Fig. 9g-h) with dorsal sculptured area strigate on almost all dorsal surface, strigae arranged horizontally at basal third and becoming oblique

towards apex; ventral sculptured area strigate, but faintly marked at basal two-thirds; apex rounded. Second valvifer (Fig. 9i), in lateral view, longer than wide. Second valvula (Fig. 9ij), in lateral view, distinctly expanded beyond basal curvature, gradually becoming narrower towards apex; dorsal margin with separate teeth varying in number between 78 and 89, each subtriangular and wide at base, becoming small and subquadrate towards apex; preapical prominence distinct; apex narrowly rounded and slightly projected posteriorly, forming a little apical lobe. Third valvula (Figs. 6i, 9k, 12i, 27i), in lateral view, with basal half narrow and apical half distinctly expanded; apex rounded (Figs. 6i, 27i), subtriangular (Fig. 9k), or triangular (Fig. 12i).

Distribution. Bolivia, Colombia, Costa Rica, Ecuador, Nicaragua (doubtful), Panama and Peru.

Remarks. *Abana* is herein recovered as monophyletic (Fig. 3). However, its relationships with other genera within Proconiini remain unresolved. Results obtained from the combined matrix (Fig. 3) agree with results obtained from the molecular matrix (Fig. S2), recovering *Abana* as a sister group of the genus *Teletusa*, however, in morphological analyses it was recovered as a sister group of *Omagua* (Fig. S1). Specimens of *Abana* are more similar to *Omagua* in external morphology and male genitalia, sharing characteristics such as: (1) transition from crown to face, in lateral view, forming an acute angle, sometimes obtuse in *Abana* (approximately right in *Teletusa*), (2) clypeus profile angulate (rounded in *Teletusa*), (3) lateral margins of pronotum converging anteriorly (approximately parallel in *Teletusa*), (4) forewings with deep punctures (not sculptured in *Teletusa*), (5) apex of forewing truncate (convex in *Teletusa*), (6) base of dorsal margin of pygofer with a deep round emargination (concave in *Teletusa*), (7) inner lobe of style present (absent in *Teletusa*), (8) paraphyses paired, symmetrical and elongate (reduced to a single small sclerite in *Teletusa*), and (9)

aedeagal shaft apex in ventral view, without lateral lobes (present in *Teletusa*). These two genera also share the characteristic lateral margins of the aedeagal shaft apex projected dorsally forming paired lateral projections, a unique character within Proconiini, however, they differ in the form of these lateral projections, being square in *Abana* and subtriangular in Omagua. Furthermore, Abana and Teletusa shared a few characteristics that distinguish them from *Omagua*, such as: (1) frons unsculptured (striated in *Omagua*), (2) metatibia with AD and PD setal rows similar in aspect (AD more robust in *Omagua*), (3) setal row PD extended from base of the metatibia (restricted to apical half in *Omagua*), (4) pygofer disk with both fine and robust macrosetae (only robust in *Omagua*), and (5) dorsal connective, in lateral view, with a submedian acute anterior process (absent in *Omagua*). Nonetheless, Abana have some characters that clearly distinguish it from *Omagua* and *Teletusa*, including: (1) superior portion of frons with a round scar, remnant of nymphal process (absent in *Omagua* and *Teletusa*), (2) dorsomedian area of frons evenly convex or flat (distinctly depressed in Omagua and Teletusa), (3) pronotum width larger than transocular width (shorter in *Omagua* and *Teletusa*), (4) basal portion of costal margin of forewing in lateral view distinctly curved (approximately straight in *Omagua* and *Teletusa*), (5) profemur setal row IC multiseriate (uniseriate in *Omagua* and *Teletusa*), and (6) aedeagus with basal and preapical dorsal spiniform processes, processes that are unique within Proconiini.

After the revision of the type material of all valid and invalid species proposed by Young (1968), almost all the synonyms proposed by the author are maintained here. The only exception was the species *Abana sonora* Melichar, 1926, which Young (1968) treated as a junior synonym of *A. horvathi*, and is herein placed as *incertae sedis* in Cicadellini. The female lectotype of *A. sonora* (Fig. 4) definitely does not belong to *Abana*, being similar in external morphology to some species of the genus *Zaruma* Melichar, 19265, however,

because the specimen is a female, a more precise placement within Cicadellini cannot be provided.



Figure 4. *Abana sonora* Melichar, 1926, female lectotype (MMBC). **a**, dorsal habitus; **b**, lateral habitu; **c**, specimen labels. Scale bar 1.0 mm.

Key to Abana species

9e,	12c,	16c,	18c,	21e), in	ventral	view,	with	area	in	between	posterior	projecti	ons p	projecto	ed
pos	sterio	rly as	s a bi	furcate	process										7

2. (1) Male forewing (Figs. 13a-b, 7a-b, 14a-b) with one or two transversal light strip	es. Style
(Fig. 13e, 7e, 14e) with inner lobe rounded	3
2' Male forewings (Figs. 23a-b, 24a-b, 26a-b) completely black, without transver	sal light
stripes. Style with inner lobe subtriangular (Figs. 23e, 26e) or subquadrate (Fig. 24e)
	lex 5

5. (2') Anterior portion of crown, in lateral view, inflated (Figs. 26b, 27b, 28b) or not (Figs. 23b, 28e, h, k, n, q). Pronotum (Figs. 23a, 26a, 28a, d, g, j, m, p) with two anterolateral

11. (10) Body colouration (Figs. 11a-e, 12a-b) mostly castaneous-brown, brochosome cover may add purple or blue tinge. Head and thorax (Figs. 11a-e, 12a-b) completely castaneous, sometimes with few small and inconspicuous yellow areas on pleurites. Forewings castaneous to dark brown, including venation. Fore- and middle legs (Fig. 11e) with femora, tibiae, and tarsi yellow, with dark brown areas at basal and apical portions, or legs completely dark brown (Figs. 11b, 12b). Pygofer (Fig. 11f) with small concavity ventrally at preapical region. Style (Fig. 11h) reaching connective apex; apical portion almost as long as wide. *A. gigas* Fowler, 1898

11' Body colouration (Figs. 19a-b, 21a-d, 22a-b) mostly dark brown, brochosome cover may add blue tinge (Figs. 20a-b, 21c-d). Head and thorax completely castaneous, sometimes with

Abana arnetti Young, 1968

(Figs. 5-6)

Abana arnetti Young, 1968: 150 [n. sp.]. Type(s): USNM.



Figure 5. *Abana arnetti* Young, 1968. **a**, male lectotype (USNM), dorsal habitus; **b**, same male, lateral habitus; **c**-**j**, male from Gatún, Panama (NCSU); **c**, dorsal habitus; **d**, lateral habitus; **e**, genital capsule, lateral view; **f**, subgenital plates, ventral view; **g**, connective and styles, dorsal view; **h**, aedeagus, anal tube, and paraphyses, lateral view; **i**, aedeagus, anal tube, and paraphyses, posterior view. Scale bars **a**-**d**: 1.0mm, **e**-**j**: 0.5mm.



Figure 6. *Abana arnetti* Young, 1968, female from Gatun, Panama (NCSU). **a**, dorsal habitus; **b**, lateral habitus; **c**, sternite VII, ventral view; **d**, pygofer, lateral view; **e**, first valvifer and first valvula, lateral view; **f**, detail of first valvula apex, lateral view; **g**, second valvifer and second valvula, lateral view; **h**, detail of second valvula, lateral view; **i**, third valvula, lateral view. Scale bars **a-b**: 1.0mm, **c-i**: 0.5mm.

Diagnosis. Body colouration (Fig. 5a-d, 6a-b) mostly dark yellow and brown; anterior portion of crown (Fig. 5a, c) and dorsal portion of frons (Fig. 5b, d) with light colouration, continuously darker ventrally; pronotum (Figs. 5a, c, 6a) castaneous, darker near anterior

margin; forewing (Fig. 5a-d, 6a-d) colouration not sexually dimorphic. Crown anterior margin (Fig. 5a, c) rounded; anterior portion (Fig. 5b, d), in lateral view, straight, not inflated; disk without a distinct depression; M-shaped elevation bordering posterior margin absent. Connective (Fig. 5g) arms almost parallel; base of arms with a V-shaped dorsal rim. Style (Fig. 5g) with apodeme wide and long, 0.8 times as long as apophysis lenght; inner lobe rounded; apical portion almost as wide as long; extending as far as connective apex. Aedeagal shaft (Fig. 5h-j) with anterodorsal projections wide and short. Dorsal connective (Fig. 5h-j) sclerotized; submedian acute process conspicuous.

Total length: males (n = 2) 18.6 mm, females (n = 1) 20.4 mm (excluding ovipositor), 21.2 mm (including ovipositor).

Description. Crown (Figs. 5a, c, 6a) without pubescence; anterior margin rounded; in lateral view, anterior portion (Fig. 5b, d, 6b), straight, not inflated, forming an acute angle with frons; disk without a distinct depression; posterior margin M-shaped elevation absent. Ocelli located on imaginary line between anterior eye angles; each slightly closer to adjacent anterior eye angle than to midline. Frons flattened medially. Pronotum (Figs. 5a, c, 6a) surface without pubescence. Forewing (Figs. 5a-d, 6a-b) with punctures grouped bordering veins; base of fourth apical cell aligned or slightly more distal than base of third. Hind legs with femoral setal formula 2:0:0 or 2:1:0. Other characters as in generic description.

Colouration. Body colouration (Figs. 5a-d, 6a-b) mostly brown; brochosome cover may give a blue to purple tinge to most of wing. Crown (Figs. 5a, c, 6a) dark yellow, except for two triangular brown maculae on posterior portion extending from antennal ledges to midline of crown on posterior margin. Frons (Figs. 5b, d, 6b) with upper two-thirds dark yellow, continuing yellow area of crown; ventral third brown, as well as clypeus. Gena (Figs. 5b, d, 6b) anterodorsal portion brown, continuing brown area of crown to frons and clypeus; posteroventral portion dark yellow. Pronotum (Figs. 5a, c, 6a) castaneous, except for broad brown anterior marginal stripe; thorax (Figs. 5b, d, 6b), in lateral view, mostly dark yellow, with some brown areas of variable sizes on all pleural sclerites. Forewing (Figs. 5a-d, 6a-b) dark brown, lighter basally. Legs (Figs. 5b, d, 6b) almost completely brown; coxae of all legs, each with a dark yellow macula. Abdomen brown, with dark yellow areas, mostly at lateral margins.

Male terminalia. Pygofer (Fig. 5e) ventral margin, in lateral view, with distinct median concavity, preapical region convex. Subgenital plates (Fig. 5e), in lateral view, ending clearly before pygofer apex. Connective (Fig. 5g) with arms almost parallel; base of arms with a V-shaped dorsal rim. Style (Fig. 5g) with apodeme wide and long, 0.8 times as long as apophysis lenght; inner lobe rounded; angle formed between preapical lobe and apical portion almost right; apical portion subquadrate, almost as wide as long; extending as far as connective apex. Aedeagal shaft (Fig. 5h-j), in lateral view, with preapical dorsal spiniform process almost attaining (lectotype) or not dorsal margin of lateral projections; anterodorsal projections broad and short. Dorsal connective (Fig. 5h-j) sclerotized; submedian acute process conspicuous. Other characters as in generic description.

Female terminalia. Abdominal sternite VII (Fig. 6c), in ventral view, with a pair of lateral dentiform projections on median third of posterior margin; area in between lateral projections projected posteriorly as a bifurcate process. Second valvula (Fig. 6g), in lateral view, with 82 separated teeth on dorsal margin. Third valvula (Fig. 9k) apex rounded. Other characters as in generic description.

Distribution. Panama (Colón and Panamá Oeste provinces). Before this work, this species was known for Barro Colorado Island (Panamá Oeste Province) and Gatún (Colón Province) in Panama (Young, 1968), here, its distribution is expanded to Gamboa in Colón.

Material examined. Holotype (based on photographs of habitus and male genitalia): PANAMA: Panamá Oeste: 1 Male, Barro Colorado Island, C.Z., 1944-xi-22-24, at light, R. H. Arnett, Jr. (USNM). Other specimens: PANAMA: Colón: 1 Male, Gatun C. Z., Tres Rios plantation, 1930-iii, T. O. Zschokke (NCSU). 1 Female, same data (NCSU). 1 specimen without abdomen, Gamboa, Canal area, Pipeline Road, 3km NW Gamboa, 1995-iv-09, C. Stockwell (BYU).

Remarks. This species was recovered as the sister group of *Abana ochracea* **sp. nov.** in the combined ML phylogeny (Fig. 3), however, this relationship was not supported in the BI analysis of the same dataset. A. arnetti differs from A. ochracea sp. nov. in the following characters: (1) anterior margin of crown (Fig. 5a, c) rounded (subtriangular to triangular in A. ochracea sp. nov., Fig. 18a, c), (2) crown disk (Fig. 5a, c) without a depression (present in A. ochracea sp. nov., Fig. 18a, c), (3) pygofer (Fig. 5e) with a preapical concavity on ventral margin (absent in A. ochracea sp. nov., Fig. 18e), (4) base of connective arms (Fig. 5g) with a dorsal V-shaped rim (rim absent in A. ochracea sp. nov., Fig. 18g), (5) style (Fig. 5g) with apical portion as long as wide (twice longer than wide in A. ochracea sp. nov., Fig. 18g), (6) apodeme of style (Fig. 5g) wide and long (narrow and short in A. ochracea sp. nov., Fig. 18g), and (7) dorsal connective (Fig. 5h-j) sclerotized with a conspicuous submedian acute anterior process (inconspicuous in A. ochracea sp. nov., Fig. 18h). The general colouration pattern (Figs. 5a-d, 18a-d) of the two species is somewhat similar, however, A. *arnetti* can be clearly distinguished by its general dull yellow and more brown colouration, and by the colouration of pronotum (Fig. 5a, c), being completely brown (ochraceous yellow in A. ochracea sp. nov., Fig. 18a, c). No molecular information was obtained for this species.

Abana confusa sp. nov.

(Fig. 7)



Figure 7. *Abana confusa* **sp. nov.**, male holotype (NCSU). **A**, dorsal habitus; **b**, lateral habitus; **c**, genital capsule, lateral view; **d**, subgenital plate, ventral view; **e**, connective and styles, dorsal view; **f**, aedeagus, anal tube, and paraphyses, lateral view; **g**, aedeagus, anal tube and paraphyses, ventral view; **h**, aedeagus, anal tube, and paraphyses, posterior view. Scale bars **a-b**: 1.0mm, **c-h**: 0.5mm.

Diagnosis. Body colouration (Fig. 7a-b) mostly orange and black; anterior portion of crown (Fig. 7a) and dorsal portion of frons (Fig. 7b) orange, crown with contrasting dark maculae posteriorly and frons with contrasting dark maculae inferiorly; pronotum (Fig. 7a) dark brown to black, with two anterolateral orange maculae; male forewing (Fig. 7a-b) dark

brown, with two broad orange transverse transcommisural stripes: one at basal half and another preapical, aligned to clavus apex. Crown anterior margin (Fig. 7a) subtriangular, apex truncate; anterior portion (Fig. 7b), in lateral view, straight, not inflated; disk with a distinct depression; M-shaped elevation bordering posterior margin present and conspicuous. Connective (Fig. 7e) arms parallel; base of arms with a U-shaped dorsal rim. Style (Fig. 7e) with apodeme wide and long, 0.8 times as long as apophysis lenght; inner lobe rounded; apical portion almost as long as wide; not extending to connective apex. Aedeagal shaft (Fig. 7f-h) with anterodorsal projections slender and long. Dorsal connective (Fig. 7f-h) sclerotized; submedian acute process conspicuous.

Total length: males (n = 1) 16.9 mm.

Description. Crown (Fig. 7a) without pubescence; anterior margin subtriangular, apex truncate; in lateral view, anterior portion (Fig. 7b), straight, not inflated, forming an acute angle with frons; disk with a distinct depression; posterior margin M-shaped elevation present and conspicuous. Ocelli located on imaginary line between anterior eye angles; each slightly closer to adjacent anterior eye angle than to midline. Frons evenly convex medially. Pronotum (Fig. 7a) surface without pubescence. Forewing (Fig. 7a-b) with punctures distributed throughout tegmen; base of fourth apical cell slightly more distal than base of third. Hind legs with femoral setal formula 2:0:0. Other characters as in generic description.

Colouration. Body colouration (Fig. 7a-b) mostly orange and black. Crown orange, except for a black macula on posterior portion between antennal ledges, almost interrupted medially dividing into two subquadrate areas. Frons (Fig. 7b) with upper two-thirds also orange, ventral third black, as well as, clypeus and gena, continuing black area of crown. Pronotum (Fig. 7a) dark brown to black, with two anterolateral orange maculae continuing laterally to proepimeron. Scutellum (Fig. 7a) black. Thorax (Fig. 7b), in lateral view, with

pleurites mostly orange, with small black areas; anepisternum (Fig. 7b) black. Forewing (Fig. 7a-b) dark brown, lighter at apex, with two broad orange transverse transcommissural stripes: one at basal half, broader at clavus, reaching costal margin and another broader at corium, reaching costal margin, aligned to clavus apex. Legs (Fig. 7b) almost completely orange, with some brown to black small areas mostly at apex of tibiae and tarsomeres of all legs. Abdomen colouration unknown.

Male terminalia. Pygofer (Fig. 7c) ventral margin, in lateral view, regularly convex until apex. Subgenital plates (Fig. 7c), in lateral view, ending clearly before pygofer apex. Connective (Fig. 7e) with arms converging anteriorly; base of arms with a U-shaped dorsal rim. Style (Fig. 7e) with apodeme wide and long, 0.8 times as long as apophysis lenght; inner lobe rounded; angle formed between preapical lobe and apical portion acute; apical portion subquadrate, almost as long as wide; not extending to connective apex. Aedeagal shaft (Fig. 7f), in lateral view, with preapical dorsal spiniform process extending to dorsal margin of lateral projections; anterodorsal projections (Fig. 7f-h) slender and long. Dorsal connective (Fig. 7f-h) sclerotized; submedian acute process conspicuous. Other characters as in generic description.

Female. Unknown

Distribution. Peru (Huánuco Region).

Material examined. Holotype: PERU: Huánuco: 1 Male, Monson Valley Tingo Maria, 1954-vi-29 (NCSU).

Etymology. The specific epithet '*confusa*' comes from the Latin and means "confusing". This name is given because the holotype is a male with striped colouration similarly to that shown in females of the *A. horvathi* complex, which can cause confusion during identification.

Remarks. This species was recovered as the sister group of *A. minuta* **sp. nov.** + *A. horvathi* species group (*A. amazonica* **sp. nov.**, *A. colombiana* **sp. nov.**, and *A. horvathi s.s.*) with low statistical support (Fig. 3), and shares with these species similar external morphology and male genitalia. However, *A. confusa* **sp. nov.** can be distinguished from these four species by the male colour pattern of the forewings (Fig. 7a-b), with two broad transverse stripes, resembling the colour pattern of some females of *A. colombiana* **sp. nov.** and *A. horvathi s.s.* species (Figs. 11a-b, 28g-k). Males of *A. haupti* also display two light transverse stripes on forewings (Fig. 13a-b) nonetheless, *A. confusa* **sp. nov.** can be distinguished from the latter mostly by the morphology of the head and body colouration (see remarks in *A. haupti* above). No molecular information was obtained for this species.

Abana dives Walker, 1851

(Figs. 8-10)

Aulacizes dives Walker 1851: 791 [n. sp.]. Type(s): BMNH. Young 1965: 174 [Holotype clarified]; Metcalf 1965: 644 [Catalogued]; Young 1968: 150 [Out of subgenus]
Abana drusilla Distant, 1908: 73 [n. sp.]. Type(s): BMNH. Young 1965: 174 [Lectotype designated]; Metcalf 1965: 645 [Catalogued]; Young 1968: 150 [n. syn. of Abana dives].



Figure 8. *Abana dives* Distant, 1908. **a**, male from Risaralda, Colombia (MPUJ_ENT 0059640), dorsal habitus; **b**, same male, lateral habitus; **c**, male from Valle del Cauca, Colombia (NCSU), dorsal habitus; **d**, same male, lateral habitus; **e**, genital capsule, lateral view; **f**, subgenital plates, ventral view; **g**, connective and styles, dorsal view; **h**, aedeagus, anal tube and paraphyses, lateral view; **i**, aedeagus, anal tube and paraphyses, ventral view; **j**, aedeagus, anal tube and paraphyses, posterior view. Scale bars **a-d**: 1.0mm, **e-j**: 0.5mm.



Figure 9. *Abana dives* Distant, 1908. **a**, female from Risaralda, Colombia (MPUJ_ENT 0059471), dorsal habitus; **b**, same female, lateral habitus; **c**, female from Valle del Cauca, Colombia (ICN 101510), dorsal habitus; **d**, same female, lateral habitus; **e**, sternite VII, ventral view; **f**, pygofer, lateral view; **g**, first valvifer and first valvula, lateral view; **h**, detail of first valvula apex, lateral view; **i**, second valvifer and second valvula, lateral view; **j**, detail of second valvula, lateral view; **k**, third valvula, lateral view. Scale bars **a**-**d**: 1.0mm, **e**-**k**: 0.5mm.



Figure 10. Dorsal and lateral habitus and labels of type specimens of *Abana dives* Distant, 1908 and synonyms. **a-c**, *A. dives*, male holotype (BMNH); **d-f**, *A. drusilla*, female lectotype (BMNH). Scale bars: 1.0mm.

Diagnosis. Body colouration (Figs. 8a-d, 9a-d, 10a-b, d-e) mostly light yellow and dark brown or black; anterior portion of crown (Fig. 8a, c) and dorsal portion of frons (Fig. 8b, d) yellow, with contrasting dark maculae posteriorly; pronotum (Figs. 8a, c, 9a, c, 10a, d) varying from light brown to dark brown; disk with or without two circular maculae of variable sizes, sometimes merged anteriorly, generally orange-yellow and conspicuous; forewing (Fig. 8a-d, 9a-d) colouration not sexually dimorphic. Crown anterior margin (Fig. 8a, c) subtriangular to triangular; anterior portion (Fig. 8b, d), in lateral view, straight, not inflated; disk with a distinct depression; M-shaped elevation bordering posterior margin present and conspicuous. Connective (Fig. 8g) arms converging anteriorly; base of arms without a dorsal rim. Style (Fig. 8g) with apodeme narrow and shorter than basal width of apophysis, one fifth as long as the entire style; inner lobe rounded; apical portion twice as long as wide; extending as far as or almost to connective apex. Aedeagal shaft (Fig. 8h-j) with anterodorsal projections wide and short. Dorsal connective (Fig. 8h-j) somewhat sclerotized; submedian acute process small and inconspicuous.

Total length: males (n = 5) 19.7 mm, females (n = 2) 21 mm (excluding ovipositor), 23.1 mm (including ovipositor).

Description. Crown (Figs. 8a, c, 9a, c, 10a, d) without pubescence; anterior margin subtriangular to triangular; in lateral view, anterior portion (Fig. 8b, d, 9b, d), straight, not inflated, forming an acute angle with frons; disk with a distinct depression; posterior margin M-shaped elevation present and conspicuous. Ocelli located on imaginary line between anterior eye angles (holotype) or slightly behind it, equidistant between midline of crown and the adjacent anterior eye angle. Frons evenly convex or flattened medially. Pronotum (Figs. 8a, c, 9a, c, 10a, d) surface with or without (holotype) pubescence. Forewing (Figs. 8a-d, 9a-d, 10a-b, d-e) with punctures grouped bordering veins; base of the fourth apical cell slightly more distal than base of the third. Hind legs with femoral setal formula 2:0:0 or 2:1:0. Other characters as in generic description.

Colouration. Body colouration (Figs. 8a-d, 9a-d, 10a-b, d-e) mostly light yellow and dark, varying from light brown in teneral specimens to dark brown and black; brocosome cover may give them a blue to purple tinge on dark parts of the head, thorax, and wings. Crown (Figs. 8a, c, 9a, c, 10a, d) varying from ivory (holotype) to yellow, except for two triangular to subtriangular dark areas on posterior portion, extending from antennal ledges to midline of crown on posterior margin. Frons (Figs. 8b, d, 9b, d, 10b, e) with upper two-thirds also varying from ivory (holotype) to yellow; ventral third dark, as well as clypeus. Gena

(Figs. 8b, d, 9b, d, 10b, e) with brown macula over anterodorsal portion, continuing brown area of crown to frons and clypeus; posteroventral portion ivory (holotype) to yellow. Pronotum (Figs. 8a, c, 9a, c, 10a, d) varying from light brown to castaneous and dark brown (holotype); anterior portion with a dark marginal stripe, varying from dark brown (holotype) to black, sometimes not very distinctive or absent; disk completely dark, without maculae (Figs. 8c-d, 9c-d, 10d-e) or with two circular maculae (holotype, Figs. 8a-b, 9a-b, 10a-b) of variable sizes, sometimes merged anteriorly, generally orange-yellow and conspicuous but showing castaneous and inconspicuous colourations in some cases. Thorax (Figs. 8b, d, 9b, d, 10b, e), in lateral view, with yellow areas of variable sizes on all pleural sclerites. Forewings (Figs. 8a-d, 9a-d, 10a-b, d-e) castaneous (holotype) to dark brown, vein colouration lighter in some cases. Legs (Figs. 8b, d, 9b, d, 10a-b, d-e) varying from castaneous to dark brown (holotype). Coxae of all legs with ivory or yellow areas. Femora of all legs completely brown (holotype) or ivory to yellow, except at basal and apical portions. Abdomen (Figs. 8b, d, 9b, d, 10e) dark brown or black, with yellow areas mostly at posterolateral margin of pleurites, continuing to posterior margins of sternites.

Male terminalia. Pygofer (Fig. 8e) ventral margin, in lateral view, regularly convex until apex. Subgenital plates (Fig. 8e-f), in lateral view, almost reaching apex of pygofer. Connective (Fig. 8g) with arms converging anteriorly; base of the arms without a dorsal rim. Style (Fig. 8g) with apodeme narrow and shorter than basal width of apophysis, 0.3 times as long as apophysis lenght; apical portion twice as long as wide; extending as far as or almost to connective apex. Aedeagal shaft (Fig. 8h-j), in lateral view, with preapical dorsal spiniform process not extending to dorsal margin of lateral projections; anterodorsal projections broad and short. Dorsal connective (Fig. 8h-j) somewhat sclerotized; submedian acute process small and inconspicuous. Other characters as in generic description.

Female terminalia. Abdominal sternite VII (Fig. 9e), in ventral view, with a pair of lateral dentiform projections on median third of posterior margin; area in between lateral projections projected posteriorly as a bifurcate process. Second valvula (Fig. 9i), in lateral view, with 85 separated teeth on dorsal margin. Third valvula (Fig. 9k) apex subtriangular. Other characters as in generic description.

Distribution. Colombia (Antioquia [**new record**], Chocó [**new record**], Risalda [**new record**], and Valle del Cauca departments) and Ecuador (Esmeraldas Province [**new record**]). Before this work, *A. dives* was known from Colombia in Valle del Cauca and Cali (Distant, 1908) and from Ecuador in Cachabé, Paramba (Distant, 1908; Melichar, 1926), and Chimbo (Melichar, 1926). Here, we expand considerably the distribution of this species in Colombia, with new records for the departments of Antioquia, Chocó, and Risaralda, and we also expand the distribution of this species in Ecuador, recording it from Esmeraldas Province for the first time.

Material examined. Holotype (based on photographs of habitus): 1 Male, "HOLOTYPE \ *Aulacizes*\ *dives*\ Walker\ D.A. Young, 63", "Type", "LECTO-\TYPE", "NHMUK 013588909" (BMNH). Lectotype (based on photographs of habitus): ECUADOR: 1 Female, "Ecuador.\ Rosenberg.\ 99-104.", "Cachabé,\ low c. I. 97.\ (Rosenberg).", "LECTOTYPE\ *Abana\ drusilla* Dist.\ D.A. Young, 63", "*Abana\ drusilla* Dist.", "Type", "LECTO-\TYPE", "NHMUK 013588910" (BMNH). Other specimens: COLOMBIA: Antioquia [new record]: 1 Male, Alejandría, Encarnación, 1650 m.a.s.l., 1980-xii, Maleza, A. Madrigal (MEFLG: 7867-4). 2 Males, Frontino, 1317 m.a.s.l., 1989vii, Bosque, G. Morales & C. Mantilla (MEFLG: 7868-2, 7868-3). 1 Female, same data, except: Murrí, 1982-v, E. Acevedo (MEFLG: 7867-5/13597). 1 Female, Medellín, 1538 m.a.s.l, 1983-viii, Pastizal, O. Osorio (MEFLG: 7868-1). 1 Female, Mutatá, Vereda San José de León, Finca la Soledad 2, 7°30'6.423673"N, 76°30'47.083511"W, 437m.a.s.l, 2021-ii-05/2021-ii-09, Bosque, Manual, D. Uchima, A. Mejía & J. C. Calderón (CEUA: 124358). 1 Female, same data, except: 7.49502N, -76.5117W, 477 m.a.s.l, 2022-vii-03/2022-vii-08, Borde de bosque, Red entomológica, J. Sauceda-V., I. Ceballos-C., A. Mejía & J. C. Calderón (CEUA: 124359). 1 Female, same data, except: 7.50116N, -76.50207W, 501 m.a.s.l, Bosque (CEUA: 124360). 2 Males, same data, except: 7.50183N, -76.51296W, 434 m.a.s.l, (CEUA: 124361, 124362). 1 Female, same data, except: (CEUA: 124363). 3 Males, same data, except: 7.49502N, -76.5117W, 477 m.a.s.l, Borde de bosque (CEUA: 124368, 124369, 124370). 1 Female, same data, except: (CEUA: 124371). 1 Male, same data, except: camino entre P1 y P2, 7.49223N, -76.50401W, 477-773 m.a.s.l., Bosque (CEUA: 124373). 2 Females, Mutatá, Villa Arteaga, 66m.a.s.l, 1947-viii, F. L. Gallego (MEFLG: 7867-1, 7867-2). 1 Male, Turbo, 2 m.a.s.l, 1948-i, F. L. Gallego (MEFLG: 7867-3). Chocó [new record]: 1 Male, Bahía Solano, Cerca de la cascada del aeropuerto, 6.20292N, -77.3947W, 21 m.a.s.l, 2019-vii-06, Manual, I. Ceballos-C. (CEUA: 66360). 1 Female, same data except: Cascada del aeropuerto, 2022-i-15, Bosque, I. Ceballos-C. (CEUA: 124375). 1 Male, same data except: DNA voucher Entomologia DZRJ ENT6387 (CEUA: 124376). 1 Male, San José del Palmar, Vereda Damasco, escuela Santa Lucía, 800 m.a.s.l., 2007-iv-14, Sandra Correa (CEBUC). 1 Female, same data. 1 Male, same data, except: 850m.a.s.l, 2007-iv-13, Liliana Cardona (CEBUC). Risaralda [new record]: 1 Male, Mistrató, Puerto de Oro, 988 m.a.s.l, 1991-ix, Fernando Fernández (ICN: 041331). 1 Male, Pueblo Rico, Área Amurrupá, aproximadamente 1.1km WSW de Santa Cecilia, 402m.a.s.l, 2018-ii-19-23, Bosque húmedo tropical, Red entomológica, N Cossio | C Pineda (MPUJ_ENT: 0058709). 2 Females, same data, except: (MPUJ_ENT: 0058710, 0058711). 1 Female, same data, except: J Torres (MPUJ_ENT: 0059471). 1 Male, same data, except: (MPUJ_ENT: 0059509). 2 Females, same data, except:

Colecta manual, V Casallas | S Mayorga (MPUJ_ENT: 0059638, 0059639). 1 Male, same data, except: (MPUJ ENT: 0059640). 1 Female, same data, except: J. Bolívar (MPUJ ENT: 0060423). 1 Male, same data, except: (MPUJ ENT: 0060424). 1 Male, same data, except: Mateo Ramírez (MPUJ_ENT: 0060445). 1 Female, same data, except: A. Ariza (MPUJ_ENT: 0061038). 1 Female, same data, except: W. Moya (MPUJ_ENT: 0061221). 1 Male, same data, except: C. Ramírez (MPUJ ENT: 0061224). 1 Female, Pueblo Rico, Santa Cecilia, 1991-x-10, F. Cubillos (ICN: 041332). Valle del Cauca: 1 Female, Medio Calima, Bajo Chidral, 250 m.a.s.l, 1991-ii-15, R. Aldana (ICN: 101509). 1 Female, same data, except: DNA voucher Entomologia DZRJ ENT6585 (ICN: 101510). 1 Male, Restrepo, Rio Azul R. loravo, 500 m.a.s.l, 1984-ii-07, P. Saray (ICN: 041333). 1 Female, 5km W. of Cisneros, 1969-ii-28, R.E. Woodruff (UKIC). 1 Female, Bajo Anchicaya, 400 m.a.s.l., 1984-iii-23, M. Suarez T. (NCSU). 1 Female, same data. 1 Male, same data. 1 Female, Rio Dagua (USNM). 1 Female, same data, except, W.F.H. Rosenberg (USNM). 1 Female, Valle Pichinde, 1969viii-25, D.H. Messersmith (USNM). ECUADOR: 2 Females, Cachabé, Rosenberg (USNM). Esmeraldas province [new record]: 1 Female, Bulún (USNM). 1 Male, Esmeraldas, San Lorenzo (9km.S), 1979-iii-25, Ultraviolet light, Jos. J. Anderson (USNM).

Remarks. This species was recovered as the sister group of the clade (*A. tissa* + *A. gigas*) in the ML combined tree (Fig. 3), however, it was poorly supported and not congruent to the BI analysis. Morphologically, this species is somewhat similar to *A. ochracea* **sp. nov.**, mostly in the characters of the male genitalia, with both species having a connective (Figs. 8g, 18g) without a dorsal rim, style (Figs. 8g, 18g) with apodeme narrow and short and dorsal connective (Figs. 8h-j, 18h-j) somewhat sclerotized, with submedian acute process inconspicuous, but it can be clearly distinguished from *A. ochracea* **sp. nov.** by the colouration pattern (Figs. 8a-d, 18a-d), being the yellow parts of the body light yellow in *A*.

dives (ochraceous yellow in *A. ochracea* **sp. nov.**) and the dark parts mostly dark brown or black (brown in A. *ochracea*). The pronotum colouration (Fig. 8a, c, 9a, c, 10a, d) may also be a diagnostic character, with the dark disk showing two variable sized circular maculae, sometimes merged anteriorly, generally orange-yellow and conspicuous but showing castaneous and inconspicuous colourations in some cases. However, some specimens may not show these maculae, having the pronotum completely dark, a character shared with its sister group (*A. tissa* + *A. gigas*). Nonetheless, *A. dives* can be distinguished from these other two species by it general body colouration pattern (Fig. 8a-d), especially the yellow colouration of crown and frons (being completely dark in *A. gigas* and *A. tissa*, Figs. 12a-d, 23a-d).

Based on the study of photographs of the male holotype of *A. dives* (without abdomen) and female lectotype of *A. drusilla* from Ecuador (Fig. 10a-b, d-e), we agree with Young (1968) that these two are conspecific. The external morphology is identical, and they only differ in the presence of a contrasting lighter macula on the pronotum, which is consistent with variation found herein in Colombian specimens.

Abana gigas Fowler, 1898

(Figs. 11-12)

Amblydisca gigas Fowler 1898a: 212 [n. sp.]. Type(s): BMNH. Young 1965: 177 [Lectotype designated]; Metcalf 1965: 645 [Catalogued]; Young 1968: 150 [Out of subgenus].



Figure 11. *Abana gigas* Fowler, 1898. **a**, male lectotype (BMNH), dorsal habitus; **b**, same male, lateral habitus; **c**, same male labels; **d**, male from Limon, Costa Rica (USNM), dorsal habitus; **e**, same male, lateral habitus; **f**, genital capsule, lateral view; **g**, subgenital plates, ventral view; **h**, connective and styles, dorsal view; **i**, aedeagus, anal tube and paraphyses, lateral view; **j**, aedeagus, anal tube and paraphyses, ventral view; **k**, aedeagus, anal tube and paraphyses, posterior view. Scale bars **a-e**: 1mm, **f-k**: 0.5mm.



Figure 12. *Abana gigas* Fowler, 1898, female from Costa Rica (NCSU). **a**, dorsal habitus; **b**, lateral habitus; **c**, sternite VII, ventral view; **d**, pygofer, lateral view; **e**, first valvifer and first valvula, lateral view; **f**, detail of first valvula apex, lateral view; **g**, second valvifer and second valvula, lateral view; **h**, detail of second valvula, lateral view; **i**, third valvula, lateral view. Scale bars **a-b**: 1mm, **c-i**: 0.5mm.

Diagnosis. Body colouration (Figs. 11a-e, 12a-b) mostly castaneous-brown, brochosome coverage may add a purple or blue tinge; head (Fig. 11a-e) and pronotum (Figs. 11a, d, 12a) completely dark, without markings; forewing (Fig. 11a-e, 12a-b) colouration not

sexually dimorphic. Crown anterior margin (Fig. 11a, d) subtriangular to triangular; anterior portion (Fig. 11b, e), in lateral view, straight, not inflated; disk with a distinct depression; M-shaped elevation bordering posterior margin inconspicuous. Connective (Fig. 11h) arms almost converging anteriorly; base of arms with a V-shaped dorsal rim. Style (Fig. 11h) with apodeme wide and long, 0.8 times as long as apophysis lenght; inner lobe rounded; apical portion rectangular, 1.5 times as long as wide; extending as far as connective apex. Aedeagal shaft (Fig. 11i-k) with anterodorsal projections wide and short. Dorsal connective (Fig. 11i-k) sclerotized; submedian acute process conspicuous.

Total length: males (n = 2) 18.3 mm, females (n = 1) 20.5 mm.

Description. Crown (Figs. 11a, d, 12a) pubescent; M-shaped elevation bordering posterior margin inconspicuous. Ocelli closer to adjacent anterior eye angle than to midline of crown. Hind legs with femoral setal formula 2:1:0 or 2:2:0. Other characters as in *A. dives* description.

Colouration. Body (Figs. 11a-e, 12a-b) colouration mostly castaneous, brochosome cover may give them a purple and blue tinge. Head and thorax (Figs. 11a-e, 12a-b) almost completely to completely (lectotype) castaneous, with sometimes little and inconspicuous yellow areas on pleurites of thorax. Pronotum (Figs. 11a, d, 12a) completely brown. Forewings (Figs. 11a-e, 12a-b) castaneous (lectotype) to dark brown. Fore- and middle legs (Figs. 11b, e, 12b) with femora, tibiae, and tarsi yellow, with dark brown areas at basal and apical portions. Hind leg (Figs. 11b, e, 12b) castaneous to dark brown, with or without apical yellow area on femur. Abdomen (Figs. 11b, e, 12b) almost completely dark, with very narrow yellow areas along posterolateral margins of pleurites and on posterior margins of sternites.

Male terminalia. Pygofer (Fig. 11f) ventral margin, in lateral view, with a distinct median concavity, preapical region also with a small concavity. Base of connective arms

(Fig. 11h) with a V-shaped dorsal rim. Style (Fig. 11h) with apodeme wide and long, 0.8 times as long as apophysis; apical portion rectangular, 1.5 times as long as wide; extending as far as connective apex. Aedeagal shaft (Fig. 11i), in lateral view, with preapical dorsal spiniform process not extending to dorsal margin of lateral projections. Dorsal connective (Fig. 11i-k) sclerotized; submedian acute process conspicuous. Other characters as in *A. dives* description.

Female terminalia. Second valvula (Fig. 12g), in lateral view, with 78 separated teeth on dorsal margin. Third valvula (Fig. 12i) apex triangular. Other characters as in *A. dives* description.

Distribution. Costa Rica (Guanacaste [new record], Heredia [new record], and Limón [new record] provinces) and Panama (Bocas del Toro Province [new record]). Before this work, A. gigas was recorded from Costa Rica (Fowler, 1898; Distant, 1908; Melichar, 1926; Metcalf, 1965; Young, 1968) and Panama (Metcalf, 1965) without specific locality records within these countries. Here, we give specific locality records for the first time in Guanacaste, Heredia, and Limón provinces in Costa Rica, and for the province of Bocas del Toro in Panama. The known distribution of this species also includes records for Ecuador and Nicaragua, both are considered doubtful herein. The first one was given by Young (1968), however, the author does not provide information on the specimen from which he obtained this information, nor where it is deposited, and after the present review and the absence of any specimen of this species in Ecuador or in any other South American country, we strongly believe that the record made by Young (1968) is due to a misidentification, and that the species is not distributed in South America. Finally, about the Nicaragua record, it was reported by Freytag & Sharkey (2002), nonetheless, in that work, the authors cite Young (1968) as the source of the information, however, that record does not exists in Young's
work. Because of this, the lack of traceability of the information and absence of other records for Nicaragua, we consider this record to be doubtful as well. It is true that, given the known distribution of this species, the probability of potential presence of it in Nicaragua can be high, however, there is no evidence confirming this hypothesis.

Material examined. Lectotype (based on photographs of habitus): COSTA RICA: 1 Female, "Costa Rica.\ Salle.", "B.C.A. Homopt.II.\ Amblydisca\ gigas,\ Fowl." "Amblydisca\ gigas. Fowler\ TYPE", "LECTOTYPE\ Amblydisca\ gigas\ Fowler\ D. A. Young, 63", "TYPE", "LECTO-\TYPE", "NHMUK 013588911" (BMNH). Other specimens: COSTA RICA: 1 Male, C.R. No 506, C.H. Ballou (NCSU). 1 Female, same data. Guanacaste [new record]: 1 Male, Carillo, Schild & Burgdorf (USNM). 1 Female, same data. Heredia [new record]: 1 Male, Heredia, Finca La Selva, 1976-vii-21-30, J.C. Solomon (USNM). 1 Female, same data. 2 Male, same data, except: 1995-i-12, S.M. Clark (BYU). 1 Female, same data. 1 Female, same data, except: near Pto. Viejo, 1973-iii-17-19, D.C. Rentz (USNM). 1 Male, same data. 1 Male, same data, except: 10°25"N, 84°00"W, 179ft, 2004-ii-25, C.R. Bartlett, J. Cryan, J. Urban, DNA voucher Entomologia DZRJ 6697 (DZRJ). Limón [new record]: 1 Female, Cairo, 1932-v-23, C.H. Ballou (USNM). 3 Males, Rio Dantas W of Guapiles, 1988-xii-26, A.S. Menke, DNA voucher Entomologia DZRJ ENT6581 (USNM). 4 Females, same data. 1 Female, Parismina, M. Valerio (USNM). **PANAMA** (based on photographs of habitus): Bocas del Toro: 1 Male, Bocas del Toro, Corriente Grande, 9°17'30"N, 82°32'41"W, 100 m.a.s.l., 1980-i-26, H.P. Stockwell (STRI). 2 Males, same data, except: 1980-xi-14, H. Wolda (STRI). 1 Female, same data. 1 Male, same data, except: 1979-xii-16, H. Wolda (STRI). 1 Female, same data, except: Buena Vista, 8°50'N, 82°15'W, 1977-i-09, R. Dressler (STRI).

Remarks. This species was recovered as the sister group of *A. tissa* (Fig. 3) with good statistical support. These two species share a general dark body colouration (Figs. 11a-e, 19ab) and pubescent crown (Figs. 11a, d, 19a, 20a) and differ from other *Abana* species in the colouration of the head, being almost completely dark to completely dark. *A. gigas* can be easily distinguished from *A. tissa* in the following combination of characters: (1) body colouration (Fig. 11a-e) mostly castaneous-brown (dark brown in *A. tissa*, Fig. 19a-b), brocosome coverage (Fig. 11d-e) may afford a purple tinge on head and thorax (only blue in some specimens of *A. tissa*, Fig. 20a-b), (2) fore- and middle legs (Fig. 11b, e) with femora, tibiae, and tarsi yellow, with dark brown areas at basal and apical portions (legs completely brown in *A. tissa*, Fig. 19b, 20b), and (3) male pygofer (Fig. 11f) with a small preapical ventral concavity (preapical region convex in *A. tissa*, Fig. 19c).

Abana haupti Melichar, 1926

(Fig. 13)

Abana haupti Melichar, 1926: 324 [n. sp.]. Type(s): MMBC. Young & Lauterer 1966: 264 [Lectotype designated]; Metcalf 1965: 645 [Catalogued]; Young 1968: 150 [Out of subgenus].



Figure 13. *Abana haupti* Melichar, 1926, male lectotype (MMBC). **a**, dorsal habitus; **b**, lateral habitus; **c**, genital capsule, lateral view; **d**, subgenital plate, ventral view; **e**, connective and styles, dorsal view; **f**, aedeagus, anal tube and paraphyses, lateral view; **g**, aedeagus, anal tube and paraphyses, ventral view; **h**, aedeagus, anal tube and paraphyses, posterior view. Scale bars **a-b**: 1.0mm, **c**: 0.5mm, **d-e**, **g-h**: 0.3mm, **f**: 0.2mm.

Diagnosis. Body colouration (Fig. 13a-b) mostly ivory- and castaneous. Head (Fig. 13a-b) and pronotum (Fig. 13a) completely castaneous, pronotum darker near posterior margin; male forewing (Fig. 13a-b) castaneous, with two ivory transcommissural transverse stripes: one narrower at basal half and another preapical, aligned to clavus apex. Crown anterior margin (Fig. 13a) rounded; anterior portion (Fig. 13b), in lateral view, straight, not inflated; disk with a distinct depression; M-shaped elevation bordering posterior margin

present and conspicuous. Connective (Fig. 13e) with arms slightly divergent; base of arms with a V-shaped dorsal rim. Style (Fig. 13e) with apodeme wide and long, 0.9 times as long as apophysis lenght; inner lobe rounded; apical portion almost as long as wide; not extending to connective apex. Aedeagal shaft (Fig. 13f-h) with anterodorsal projections slender and long. Dorsal connective (Fig. 13f-h) sclerotized; submedian acute process conspicuous.

Total length: males (n = 1) 16.9 mm.

Description. Crown anterior margin (Fig. 13a) rounded. Ocelli located on imaginary line between anterior eye angles; each slightly closer to adjacent anterior eye angle than to midline. Pronotum (Fig. 13a) surface without pubescence. Forewing (Fig. 13a-b) with punctures distributed throughout the tegmen; base of the third and fourth apical cells at the same level. Other characters as in *A. dives* description.

Colouration. Body colouration (Fig. 13a-b) mostly castaneous, including entire head and legs. Thorax (Fig. 13a-b) almost completely castaneous, except for posterior portion of the pronotum and the entire scutellum, which are dark brown, the latter with two black lateral maculae on anterior portion, before scutellar suture, not reaching lateral margin. Forewing (Fig. 13a-b) also castaneous, dark brown basally and smoky light brown apically, and with two ivory transcommissural transverse stripes: one at basal half, not reaching costal margin, broad at corium but narrowing at clavus and another preapical, restricted to corium, broader, reaching costal margin, and aligned to clavus apex.

Male terminalia. Pygofer (Fig. 13c) ventral margin, in lateral view, regularly convex until apex. Subgenital plates (Fig. 13c), in lateral view, almost reaching pygofer apex. Connective (Fig. 13e) with arms slightly divergent; base of arms with a V-shaped dorsal rim. Style (Fig. 13e) with apodeme wide and long, 0.9 times as long as apophysis length; inner lobe rounded; angle formed between preapical lobe and apical portion acute; apical portion almost as long as wide; not extending to connective apex. Aedeagal shaft (Fig. 13f), in lateral view, with preapical dorsal spiniform process extending to dorsal margin of lateral projections; anterodorsal projections (Fig. 13f-h) slender and long. Dorsal connective (Fig. 13f-h) sclerotized; submedian acute process conspicuous. Other characters as in generic description.

Female. Unknown

Distribution. Peru (Junín Region).

Material examined. Lectotype (based on photographs of habitus): PERU: Junín: 1 male, Chanchamayo (MMBC).

Remarks. This species was recovered as the sister group of the remainder *Abana* species in the combined phylogenetic result (Fig. 3), nevertheless, its position was unstable and unsupported in all analyses (Figs. 3, S1 and S2), possibly because of the lack of sequence data. It is known only from the male lectotype. The external morphology of this species is similar to that of *A. confusa* **sp. nov.** and to some females of *A. colombiana* **sp. nov.** and *A. horvathi s.s.*, mostly for the presence of two transverse light stripes on forewings (Figs. 13a-b, 25a-b, 28g-k), however, *A. haupti* can be clearly distinguished by its rounded anterior margin of crown (Fig. 13a), and by head and thorax completely castaneous (Fig. 13a-b). No molecular information was obtained for this species.

Abana minuta sp. nov.

(Fig. 14)



Figure 14. *Abana minuta* **sp. nov.**, male holotype (DZRJ). **a**, dorsal habitus; **b**, lateral habitus; **c**, genital capsule, lateral view; **d**, subgenital plate, ventral view; **e**, connective and styles, dorsal view; **f**, aedeagus, anal tube, and paraphyses, lateral view; **g**, aedeagus, anal tube, and paraphyses, ventral view; **h**, aedeagus, anal tube, and paraphyses, posterior view. Scale bars **a-b**: 1.0mm, **c-h**: 0.5mm.

Diagnosis. Body colouration (Fig. 14a-b) mostly yellow and purplish-castaneous; anterior portion of crown (Fig. 14a) and frons (Fig. 14b) yellow, crown with contrasting dark maculae posteriorly; pronotum (Fig. 14a) castaneous; anterior margin with a black marginal stripe, anterolateral yellow paired maculae present; male forewing (Fig. 14a-b) purplish-

castaneous, with one broad preapical ivory transcommisural stripe aligned to clavus apex. Crown anterior margin (Fig. 14a) subtriangular ending truncate; anterior portion (Fig. 14b), in lateral view, straight, not inflated; disk with a distinct depression; M-shaped elevation bordering posterior margin present and conspicuous. Connective (Fig. 14e) arms converging anteriorly; base of arms with a U-shaped dorsal rim. Style (Fig. 14e) with apodeme wide and long, as long as apophysis length; inner lobe rounded; apical portion almost as long as wide; not extending to connective apex. Aedeagal shaft (Fig. 14f-h) with anterodorsal projections slender and long. Dorsal connective (Fig. 14f-h) sclerotized; submedian acute process conspicuous.

Total length: males (n = 1) 14.5 mm (To the tip of the wings), 15.1 mm (To the tip of the abdomen).

Description. Frons evenly convex medially. Forewing (Fig. 14a-b) with base of third and fourth apical cells aligned. Other characters as in *A. confusa* **sp. nov.** description.

Colouration. Body colouration (Fig. 14a-b) mostly yellow, except in dorsal view. Crown (Fig. 14a) ivory, except for two triangular black areas on posterior portion, extending from antennal ledges to midline of crown on posterior margin. Frons (Fig. 14b) completely ivory, continuing to anterodorsal portion of gena (Fig. 14b), posteroventral portion of gena (Fig. 14b) black, continuing black area of crown to clypeus. Clypeus (Fig. 14b) dark. Pronotum (Fig. 14a) castaneous, with two anterolateral ivory maculae continuing laterally to proepimeron; anterior portion margined with black. Scutellum (Fig. 14a) dark brown with two black lateral maculae on anterior portion, before scutellar suture, not reaching lateral margin. Thorax (Fig. 14b), in lateral view, varying from ivory to yellow, with a small dark brown central macula on upper part of anepisternum. Forewing (Fig. 14a-b) purplishcastaneous, with one anteapical non-transcommissural broad ivory stripe, restricted to corium, reaching costal margin, aligned to clavus apex; apex fuscous becoming yellow. Legs (Fig. 14b) almost completely yellow, with some small brown areas mostly at apex of hind femora and tarsomeres of all legs. Abdomen (Fig. 14b) completely yellow.

Male terminalia. Subgenital plates (Fig. 14c), in lateral view, almost reaching the pygofer apex but ending before. Style (Fig. 14e) with apodeme wide and long, as long as the apophysis length. Aedeagal shaft (Fig. 14f), in lateral view, with preapical dorsal spiniform process extending dorsally slightly beyond dorsal margin of lateral projections. Other characters as in *A. confusa* **sp. nov.** description.

Female. Unknown.

Distribution. Peru (Huánuco Region).

Material examined. Holotype: PERU: Huánuco: 1 Male, 9km S Tingo María, Pte. Cuevas, 9°21'27"S, 75°59'32"W, 620m.a.s.l, 2002-x-24, Manual, C.H. Dietrich, DNA voucher Entomologia DZRJ ENT6583 (DZRJ).

Etymology. The specific epithet '*minuta*' comes from the latin "mĭnūtus" which means "small". This name is given due to the small size of this species compared with the size of the other species of *Abana* genus.

Remarks. This species was recovered as the sister group of the *A. horvathi* species complex. *Abana minuta* **sp. nov.** is also only known from the male holotype, but shares a very similar colour pattern of the wings with some female specimens of *A. horvathi s.s.* (Fig. 27a-b), however, it can be distinguished from species of its sister clade by the following characters: (1) small size, less than 16 cm, (2) frons (Fig. 14b) completely ivory (distintly dark colouration on ventral third in *A. horvathi s.l.*), (3) an episternum (Fig. 14b) with a small dark brown central macula on upper part (almost completely to completely dark in *A*.

horvathi s.l.), and (4) abdomen (Fig. 14b) completely yellow (mostly dark with some yellow areas in *A. horvathi s.l.*)

Abana ochracea sp. nov.

(Figs. 15-16)



Figure 15. *Abana ochracea* **sp. nov. a**, male holotype (USNM), dorsal habitus; **b**, same male, lateral habitus; **c**, male paratype (USNM), dorsal habitus; **d**, same male, lateral habitus; **e**, genital capsule, lateral view; **f**, subgenital plates, ventral view; **g**, connective and styles, dorsal view; **h**, aedeagus, anal tube, and paraphyses, lateral view; **i**, aedeagus, anal tube, and paraphyses, posterior view. Scale bars **a-d**: 1.0mm, **e-j**: 0.5mm.



Figure 16. *Abana ochracea* **sp. nov.**, female paratype (USNM). **a**, dorsal habitus; **b**, lateral habitus; **c**, sternite VII, ventral view; **d**, pygofer, lateral view; **e**, first valvifer and first valvula, lateral view; **f**, detail of first valvula apex, lateral view; **g**, second valvifer and second valvula, lateral view; **h**, detail of second valvula, lateral view; **i**, third valvula, lateral view. Scale bars **a-b**: 1.0mm, **c-i**: 0.5mm.

Diagnosis. Body colouration (Figs. 15a-d, 16a-b) mostly ochraceous yellow and brown; anterior portion of crown (Figs. 15a, c, 16a) and dorsal portion of frons (Figs. 15b, d,

16b) ochraceous yellow, crown with contrasting brown maculae posteriorly and frons with contrasting brown maculae inferiorly; pronotum (Figs. 15a, c, 16a) ochraceous yellow, except for a broad anterior castaneous marginal stripe; forewing (Fig. 15a-d, 16a-b) colouration not sexually dimorphic. Crown anterior margin (Fig. 15a, c) subtriangular to triangular; anterior portion (Fig. 15b, d), in lateral view, straight, not inflated; disk with a distinct depression; M-shaped elevation bordering posterior margin inconspicuous. Connective (Fig. 15g) arms converging anteriorly; base of arms without a dorsal rim. Style (Fig. 15g) with apodeme narrow and short, less than basal width of apophysis, 0.4 times as long as apophysis length; inner lobe rounded; apical portion twice as long as wide; not extending to connective (Fig. 15h-j) somewhat sclerotized; submedian acute process small and inconspicuous.

Total length: males (n = 2) 19.6 mm, females (n = 1) 20 mm.

Description. Crown (Figs. 15a, c, 16a) M-shaped elevation bordering posterior margin inconspicuous. Ocelli located on imaginary line between anterior eye angles, each closer to adjacent eye angle than to crown midline. Frons flattened medially. Forewing (Figs. 15a-d, 16a-b) with base of fourth apical cell aligned with or slightly more distal than base of third. Other characters as in *A. dives* description.

Colouration. Body colouration (Figs. 15a-d, 16a-b) mostly ochraceous yellow and brown. Crown (Figs. 15a, c, 16a) ochraceous yellow, except for a castaneous to brown area on posterior margin, which can be complete between antennal ledges or divided into two triangular areas, extending from antennal ledges to midline of crown on posterior margin. Frons (Figs. 15b, d, 16b) with upper two-thirds ochraceous yellow, continuing yellow area of crown, ventral third brown, as well as clypeus. Gena (Figs. 15b, d, 16b) anterodorsal portion brown, continuing brown area of crown to frons and clypeus; posteroventral portion yellow. Pronotum (Figs. 15a, c, 16a) ochraceous yellow, except for an anterior broad castaneous to brown marginal stripe. Scutellum (Figs. 15a, c, 16a) castaneous to dark brown. Thorax (Figs. 15b, d, 16b), in lateral view, mostly ochraceous brown, with some yellow to ochraceous yellow areas of variable sizes on all pleural sclerites. Forewing completely dark brown (Figs. 15a-b, 16a-b), with a basal small macula or with macula extending to the middle of the wing, castaneous (Fig. 15c-d), if the latter, with some small yellow maculae of variable sizes on median area; brochosome cover may give a purple tinge on dark parts of wing. Legs (Figs. 15b, d, 16b) castaneous to yellowish brown, except for coxae, which are ochraceous brown. Abdomen (Fig. 15c-d) ochraceous brown, with some yellow areas on posterolateral margins of pleurites and on posterior margins of sternites.

Male terminalia. Pygofer (Fig. 15e), in lateral view, with a distinct median concavity on ventral margin; preapical region also with a small concavity ventrally. Subgenital plates (Fig. 15e), in lateral view, almost extending to pygofer apex but ending before. Style (Fig. 15g) with apodeme narrow and short, less than basal width of apophysis, approximately 0.4 times as long as apophysis length; not extending to connective apex. Other characters as in *A. dives* description.

Female terminalia. Second valvula (Fig. 16g), in lateral view, with 81 separate teeth on dorsal margin. Third valvula (Fig. 16i) apex subtriangular. Other characters as in *A. dives* description.

Distribution. Panama (Coclé, Colón, Panamá, and Panamá Oeste provinces).

Material examined. Holotype: PANAMA: Panamá: 1 Male, Melo Pello, Los Altos de Cerro Azul Área de Conservación Cerro Jefe summit, 09.23691N, 79.40472W, 942m.a.s.l., 2005-viii-24, Sweeping, J.N. Zahniser (USNM). Paratypes: PANAMA: Colón:

1 Male, Gamboa, C.Z. RioAguaSalud, 1967-vii, W.W. Wirth (USNM). 1 Female, PanMan, 3.11, AugustBusck (USNM). 2 Males, same data, except: PanFeo, 24.11 (USNM). Panamá: 1 Female, same data as holotype, except DNA voucher Entomologia DZRJ ENT6428 (USNM).1 Male, same data except: elfin rainforest, 09.237°N, 079.405°W, 1006 m.a.s.l., S.H. McKamey (USNM). 1 Female, same data. 1 Male, same data, except: DNA voucher Entomologia DZRJ ENT6582 (USNM). Panamá Oeste: 1 Male, Cerro Campana, 08°40'N, 79°56'W, 820 m.a.s.l., 1976-vii-16, Wayne E. Clark (USNM). 1 Male, Barro Colorado Is, C. Z. Aus. '39, J. Zetek (USNM). Other specimens (based on photographs of habitus): PANAMA: Coclé: 1 Male, Cerro el Gaital, 1300 m.a.s.l., 1982-viii-10, R.L. Dressler (STRI). Colón: 1 Female, PortoBello, 1911-iii-12, AugustBusck (STRI). Panamá: 1 Male, Escobal Road Atl. Canal Zone, 1973-ix-20, D. Engleman (STRI). 1 Male, Canal Zone, Panama Summit, 1947-i, NLH Krauss (STRI). Panamá Oeste: 1 Male, Barro Colorado, 1979-i-07, Estribi (STRI). 2 Males, Cerro Campana, 08°40'N, 79°56'W, 800 m.a.s.l., 1974-v-25, Engleman (STRI). 1 Male, same data, except: 1970-v-30, H.P. Stockwell (STRI). 1 undetermined, same data, except: Distr. Chame, 1975-viii-23, H.D. Engleman (STRI). 1 Male, same data, except: 1975-i-11, H. Wolda (STRI). 1 Male, same data, except: 850 m.a.s.l., 1974-vi-28, Stockwell (STRI). 1 Female, same data, except: 1970-v-30 (STRI).

Etymology. The specific epithet '*ochracea*' comes from the latin "ochraceus", referring to the predominantly ochre colouration of this species.

Remarks. This species was recovered as the sister group of *A arnetti* (Fig. 3, see discussion on *A. arnetti* remarks above).

Abana rufifrons sp. nov.

(Figs. 17-18)



Figure 17. *Abana rufifrons* **sp. nov.**, male holotype (USNM). **a**, dorsal habitus; **b**, lateral habitus; **c**, genital capsule, lateral view; **d**, subgenital plate, ventral view; **e**, connective and styles, dorsal view; **f**, aedeagus, anal tube and paraphyses, lateral view; **g**, aedeagus, anal tube and paraphyses, ventral view; **h**, aedeagus, anal tube and paraphyses, posterior view. Scale bars **a-b**: 1.0mm, **c-h**: 0.5mm.



Figure 18. *Abana rufifrons* **sp. nov.**, female paratype (USNM). **a**, dorsal habitus; **b**, lateral habitus; **c**, sternite VII, ventral view; **d**, pygofer, lateral view; **e**, first valvifer and first valvula, lateral view; **f**, detail of first valvula apex, lateral view; **g**, second valvifer and second valvula, lateral view; **h**, detail of second valvula, lateral view; **i**, third valvula, lateral view. Scale bars **a-b**: 1.0mm, **c-i**: 0.5mm.

Diagnosis. Body colouration (Figs. 17a-b, 18a-b) mostly brown to dark brown; anterior portion of crown (Figs. 17a, 18a) and dorsal portion of frons (Figs. 17b, 18b) rufous; crown

with contrasting dark maculae posteriorly and frons with contrasting dark maculae posteriorly inferiorly; pronotum (Figs. 17a, 18a) brown to dark brown, except for an anterior broad darker marginal stripe; forewing (Fig. 17a-b, 18a-b) colouration not sexually dimorphic. Crown anterior margin (Fig. 17a) subtriangular to triangular; anterior portion (Fig. 17b), in lateral view, straight, not inflated; disk with a distinct depression; M-shaped elevation bordering posterior margin inconspicuous. Connective (Fig. 17e) arms almost parallel; base of arms with a V-shaped dorsal rim. Style (Fig. 17e) with apodeme wide and long, as long as apophysis length; inner lobe rounded; apical portion approximately 1.4 times longer than wide; extending beyond connective apex. Aedeagal shaft (Fig. 17f-h) with preapical dorsal spiniform process sometimes with a basal small posterior dentiform process; anterodorsal projections wide and short. Dorsal connective (Fig. 17h-j) sclerotized; submedian acute process conspicuous.

Total length: males (n = 1) 19.3 mm, females (n = 1) 20.5 mm.

Description. Crown (Figs. 17a, 18a) M-shaped elevation bordering posterior margin inconspicuous. Ocelli closer to adjacent eye angle than to crown midline. Frons evenly convex medially. Pronotum (Figs. 17a, 18a) surface without pubescence. Hind legs with femoral setal formula 2:0:0. Other characters as in *A. dives* description.

Colouration. Body colouration (Figs. 17a-b, 18a-b) mostly brown to dark brown. Crown (Figs. 17a, 18a) rufous, except for two triangular black areas on posterior portion, extending from antennal ledges to midline of crown on posterior margin. Frons (Figs. 17b, 18b) with upper two-thirds rufous, continuing rufous area of crown; ventral third brown, as well as clypeus. Gena (Figs. 17b, 18b) black on dorsal half and dark brown on ventral half, continuing dark area of crown to frons and clypeus. Thorax (Figs. 17a-b, 18a-b) almost completely to completely castaneous, may have some small and inconspicuous yellow areas on pleurites. Pronotum (Figs. 17a, 18a) brown to dark brown, except for a broad anterior darker marginal stripe. Forewing (Figs. 17a-b, 18a-b) castaneous to dark brown. Fore- and middle legs (Figs. 17a-b, 18b) with femora, tibiae, and tarsi yellow, with dark brown areas at basal and apical portions. Hind leg (Figs. 17a-b, 18b) dark brown, with an apical yellow area on femur. Abdomen completely dark.

Male terminalia. Pygofer (Fig. 17c), in lateral view, with a distinct median concavity on ventral margin; preapical region convex ventrally. Subgenital plates (Fig. 17c), in lateral view, almost extending to pygofer apex, but ending before. Connective (Fig. 17e) with arms almost parallel; base of arms with a V-shaped dorsal rim. Style (Fig. 17e) with apodeme wide and long, as long as apophysis length; angle formed between preapical lobe and apical portion acute; apical portion approximately 1.4 times longer than wide; extending beyond connective apex. Aedeagal shaft (Fig. 17f), in lateral view, with preapical dorsal spiniform process almost attaining dorsal margin of lateral projections, base of this process with a small and posterior dentiform process sometimes present. Dorsal connective (Fig. 17f-h) sclerotized; submedian acute process conspicuous. Other characters as in *A. dives* description.

Female terminalia. Second valvula (Fig. 18g), in lateral view, with 89 separate teeth on dorsal margin. Third valvula (Fig. 18i) apex subtriangular. Other characters as in *A. dives* description.

Distribution. Panama (Bocas del Toro and Coclé provinces).

Material examined. Holotype: PANAMA: Coclé: 1 Male, N of El Copé, 08.66819N, 80.59268W, 790 m.a.s.l, 2005-viii-17, Mercury vapor light, J.N. Zahniser (USNM). Paratypes: PANAMA: Bocas del Toro: 1 Male, 16 rd km N Lago Fortuna, "Willie Mazu" tourista spot, 08.793°N, 082.193°W, 507 m.a.s.l., 2005-viii-19-20, S.H. McKamey (USNM). 1 Male, same data. Coclé: 1 Male, same data as holotype. 1 Female, same data, except: DNA

voucher Entomologia DZRJ ENT6429 (USNM). 3 Males, same data, except: 08.688N, 080.593W, 2005-viii-18, S.H. McKamey (USNM). 2 Females, same data. 1 Male, same data, except: DNA voucher Entomologia DZRJ ENT6584 (USNM). **Other specimens** (based on photographs of habitus): **PANAMA**: **Bocas del Toro:** 1 Male, Changuinola-1, 1980-i-16-17, M. Estrebi (STRI). **Coclé:** 1 Female, El Copé, 1980-xi-03, J. Jaen (STRI).

Etymology. The specific epithet '*rufifrons*' comes from the latin rūfus ("red") + frōns ("forehead, front"), referring to the rufous colour present on the anterior part of the head of this species.

Remarks. This species was recovered as the sister group of the clade (*A. ochracea* **sp. nov.** + *A. arnetti*) + (*A. dives* + (*A. tissa* + *A. gigas*)), but without statistical support. *Abana rufifrons* **sp. nov.** is similar to *A. tissa* mainly due to the general brown to dark brown colouration of the body (Figs. 17a-b, 19a-b) and to *A. gigas* also due to the brown colouration of the body and yellow colouration of fore- and middle legs (Figs.10d, 17b), however, the former can be clearly distinguished from both species by the rufous colouration of anterior region of head (Fig. 17a-b) and dark stripe along anterior margin of pronotum (Fig. 17a).

Abana tissa Distant, 1908

(Figs. 19-22)

Abana tissa Distant, 1908: 73 [n. sp.]. Type(s): BMNH. Young 1965: 196 [Lectotype designated]; Metcalf 1965: 645 [Catalogued]; Young 1968: 150 [Out of subgenus].



Figure 19. *Abana tissa* Distant, 1908, "brown morphotype". **a**, male from Antioquia, Colombia (CEUA 124372), dorsal habitus; **b**, same male, lateral habitus; **c**, genital capsule, lateral view; **d**, subgenital plates, ventral view; **e**, connective and styles, dorsal view; **f**, aedeagus, anal tube, and paraphyses, lateral view; **g**, aedeagus, anal tube, and paraphyses, ventral view; **h**, aedeagus, anal tube, and paraphyses, posterior view. Scale bars **a-b**: 1.0mm, **c-h**: 0.5mm.



Figure 20. *Abana tissa* Distant, 1908, "blue morphotype". **a**, male from Antioquia, Colombia (CEUA 124372), dorsal habitus; **b**, same male, lateral habitus; **c**, male from Valle del Cauca, Colombia (CEUA), dorsal habitus; **d**, same male, lateral habitus; **e**, genital capsule, lateral view; **f**, subgenital plates, ventral view; **g**, connective and styles, dorsal view; **h**, aedeagus, anal tube, and paraphyses, lateral view; **i**, aedeagus, anal tube, and paraphyses, posterior view. Scale bars **a-d**: 1.0mm, **e-j**: 0.5mm.



Figure 21. *Abana tissa* Distant, 1908. **a**, "brown morphotype", female from Córdoba, Colombia (MEFLG 7921), dorsal habitus; **b**, same female, lateral habitus; **c**, "blue morphotype", female from Valle del Cauca, Colombia (CEUA 66361), dorsal habitus; **d**, same female, lateral habitus; **e**, sternite VII, ventral view; **f**, pygofer, lateral view; **g**, first valvifer and first valvula, lateral view; **h**, detail of first valvula apex, lateral view; **i**, second valvifer and second valvula, lateral view; **j**, detail of second valvula, lateral view; **k**, third valvula, lateral view. Scale bars **a-d**: 1.0mm, **e-k**: 0.5mm.



Figure 22. *Abana tissa* Distant, 1908, male lectotype (BMNH). **a**, dorsal habitus; **b**, lateral habitus; **c**, specimen labels. Scale bar 1.0 mm.

Diagnosis. Body colouration (Figs. 19a-b, 21a-d) mostly dark brown and yellow; brochosome coverage may give a blue tinge on head, thorax, and forewings in some cases (Figs. 20a-b, 21c-d); head (Figs. 19a-b, 21a-d) almost completely to completely dark brown, sometimes with gena completely yellow (Fig. 20b); pronotum (Figs. 19a, 20a) completely dark brown; male forewing (Fig. 19a-b) dark brown; venation at basal half of corium (Figs. 19a-b, 21a-d, 22a) with three distinct yellow to orange regions, sometimes merged anteriorly. Crown anterior margin (Fig. 19a, 20a) subtriangular to triangular; anterior portion (Fig. 19b, 20b), in lateral view, straight, not inflated; disk with a distinct depression; M-shaped elevation bordering posterior margin inconspicuous. Connective (Fig. 19e) arms converging anteriorly; base of the arms with (Fig. 19e) or without (Fig. 20e) a V-shaped dorsal rim. Style (Fig. 19e) with apodeme broad and long (Fig. 19e) approximately 0.8 times as long as the apophysis lenght, or narrow and slightly extended anteriorly beyond connective base (Fig. 20e), approximately 0.3 times as long as the apophysis length; inner lobe rounded; apical portion approximately four times as long as wide; extending beyond connective apex. Aedeagal shaft (Fig. 19f-h) with anterodorsal projections wide and short. Dorsal connective sclerotized (Fig. 19f-h) or somewhat sclerotized (Fig. 20f-h), submedian acute process conspicuous (Fig. 19f) or inconspicuous (Fig. 20f).

Total length: males (n = 5) 18.5 mm, females (n = 3) 19.3 mm.

Description. Crown (Figs. 19a, 20a, 21a, d, 22a) pubescent; M-shaped elevation bordering posterior margin inconspicuous. Ocelli, each closer to adjacent eye angle than to crown midline. Frons evenly convex medially. Pronotum (Figs. 19a, 20a, 21a, d, 22a) surface with pubescence. Forewing (Figs. 19a, 20a, 21a, d, 22a) with base of fourth apical cell aligned with or slightly more distal than base of third. Hind leg with femoral setal formula 2:0:0. Other characters as in *A. dives* description.

Colouration. Body colouration (Figs. 19a-b, 21a-d, 22a-b) mostly dark brown, brochosome coverage may give a blue tinge on head, thorax, and forewings (Figs. 20a-b, 21c-d). Head (Figs. 19a-b, 22a-b) completely dark or with gena (Figs. 20a-b, 21a-d) yellow. Thorax (Figs. 19a-b, 22a-b) completely dark brown, with some small and inconspicuous yellow areas on pleurites, or pleurites (Figs. 20a-b, 21a-d) almost completely yellow. Forewing (Figs. 19a-b, 21a-d, 22a) castaneous to dark brown, with venation on basal half of corium with three distinct yellow to orange regions, sometimes merged anteriorly. Legs (Figs. 19b, 20b, 21b, d, 22b) brown to dark brown. Abdomen completely dark (Fig. 19b, 22a-b) or with some yellow areas on posterolateral margins of tergites and posterior margins of sternites (Figs. 20a-b, 21a-d).

Male terminalia. Pygofer (Fig. 19c), in lateral view, with a distinct median concavity on ventral margin; preapical region convex ventrally. Subgenital plates (Fig. 19c), in lateral view, not reaching apex of pygofer, ending clearly before. Base of connective arms with (Fig. 19e) or without (Fig. 20e) a dorsal rim, when present, V-shaped. Style (Fig. 19e) with apodeme broad and long (Fig. 19e), approximately 0.8 times as long as apophysis, or narrow and short (Fig. 20e), approximately 0.3 times as long as apophysis length; angle formed between preapical lobe and apical portion acute; apical portion approximately four times as long as wide; extending beyond connective apex. Aedeagal shaft (Fig. 19f), in lateral view, with preapical dorsal spiniform process not extending to dorsal margin of lateral projections. Dorsal connective sclerotized (Fig. 19f-h) or somewhat sclerotized (Fig. 20f-h); submedian acute process conspicuous (Fig. 19f) or inconspicuous (Fig. 20f). Other characters as in *A. dives* description.

Female terminalia. Second valvula (Fig. 21i), in lateral view, with 85 separate teeth on dorsal margin. Third valvula (Fig. 21k) apex rounded. Other characters as in *A. dives* description.

Distribution. Colombia [**new record**] (Antioquia, Córdoba, and Valle del Cauca departments) and Ecuador. Before this work *A. tissa* was only known for Ecuador in Cachabé (Distant, 1908). Here, we expand its distribution to Colombia, recorded from different localities in departments of Antioquia, Córdoba, and Valle del Cauca.

Material examined. Lectotype (based on photographs of habitus): 1 Male, "Ecuador.\ Rosenberg.\ 99-104.", "Cachabé,\ low c., XII. 96.\ (Rosenberg).", "LECTOTYPE\ *Abana*\ *tissa*\ Distant\ D. A. Young, 63.", "*Abana*\ *tissa*\ Dist", "Type", "LECTO-\TYPE", "NHMUK 013588912" (BMNH). Other specimens: COLOMBIA [new record]: Antioquia: 1 Male, Mutatá, Vereda San José de León, Finca la Soledad 2, camino entre P1 y P2, 7.49223, -76.50401, 477-773 m.a.s.l., 2022-vii-03-08, Bosque, Red entomológica, J. Sauceda-V., I. Ceballos-C., A. Mejía & J. C. Calderón (CEUA: 124364). 3 Females, same data, except: (CEUA: 124365, 124366, 124367). 1 Male, same data, except: (CEUA: 124374). 1 Male, same data, except: DNA voucher Entomologia DZRJ ENT6388 (CEUA: 124372). Córdoba: 1 Female, Montería, 18 m.a.s.l., 1970-viii, Betancur (MEFLG: 7921).
Valle del Cauca: 1 Female, Buenaventura, Vereda Córdoba, Reserva Forestal Nacional Protectora San Cipriano y Escalerete, 3°49'52"N, 76°53'25"W, 110 m.a.s.l., 2019-xi-29, Bosque, Manual, J. Sauceda-V. (CEUA: 66361). 1 Male, same data, except: 3.8311111N, -76.8902778W, 110 m.a.s.l., 2023-i-03-07, Bosque, Manual, J. Sauceda-V. (CEUA). 2
Females, same data. 1 Male, same data, except: DNA voucher Entomologia DZRJ ENT6603 (CEUA). 1 Female, Calima, 1485 m.a.s.l., 1961-i, Bosque, F. L. Gallego (MEFLG: 7922).
ECUADOR: 1 Male, Cachabé, Rosenberg (USNM). 1 Undetermined, same data.

Remarks. This species was recovered as the sister group of A gigas (Fig. 3, see discussion on A. gigas remarks above). Among specimens from Colombia, two morphotypes were initially detected for this species, the first one coinciding with the colour pattern of the type specimen (referred herein as "brown morphotype", Figs. 19a-b, 21a-b, 22a-b) and the second one with colour pattern very different from the type specimen (referred herein as "blue morphotype", Figs. 20a-b, 21c-d), also including some distinguishing characters of the male genitalia, such as absence of a dorsal rim at base of connective arms (present in the brown morphotype); style with apodeme narrow and short (broad and long in the brown morphotype); and dorsal connective somewhat sclerotized, with the submedian acute process inconspicuous (very sclerotized and conspicuous in the brown morphotype). The latter was found in localities of the Department of Valle del Cauca, where no specimens of the brown morphotype were found, however, this locality is within the apparent distributional range of the brown morphotype, which seems to extend from the foothills of the western face of the Andes mountain range in the province of Esmeraldas in Ecuador to the foothill forests at the northernmost end of the Western Mountain Range of the Andes in Colombia. Both morphotypes were studied in the molecular species delimitation analyses and were recovered as the same species in five of the six methods results (Fig. 2). Due to these results and the lack of clear evidence of a disjunct distribution between both morphotypes, they are considered here as the same species.

Abana horvathi species complex

(Figs. 22-27)

Diagnosis. Body colouration (Fig. 23a-b, 24a-b, 26a-b) mostly ivory-yellow and dark brown to black; anterior portion of crown (Fig. 23a, 24a, 26a) and dorsal portion of frons (Fig. 23b, 24b, 26b) yellow, crown with contrasting dark maculae posteriorly and frons with contrasting dark maculae inferiorly; pronotum (Fig. 23a, 24a, 26a, 28a, d, g, j, m, p) reddish brown, anterior portion with black marginal stripe complete or medially interrupted, with anterolateral yellow paired maculae, sometimes very little and inconspicuous dorsally, or very extended transversally, merging and forming a transversal stripe; male forewing (Fig. 23a-b, 24a-b, 26a-b) black; female forewing (Figs. 27a-b, 28g-r) with one or two ivory transverse stripes: one at basal half (variable width and length or absent) and another aligned with clavus apex (also variable in width and length or may be absent), sometimes well extended and merged, covering almost completely (Fig. 28m-n) to completely (Fig. 28p-q) the wing area. Crown anterior margin (Figs. 23a, 24a, 26a, 28g, j, m, p) subtriangular, sometimes apex truncate; anterior portion (Fig. 23b, 24b, 26b, Fig. 28d, g, j, m, p), in lateral view, straight, not inflated; disk with a distinct depression; M-shaped elevation bordering posterior margin present and conspicuous. Connective (Fig. 23e, 24e, 26e) arms converging anteriorly; base of arms with a U- or V-shaped dorsal rim. Style (Fig. 23e, 24e, 26e) with apodeme wide and long, almost as long as apophysis length; inner lobe subtriangular or subquadrate; apical portion as long as wide; not extending to connective apex. Aedeagal shaft (Fig. 23f-h, 24f-h, 26f-h) with anterodorsal projections slender and long. Dorsal connective (Fig. 23f-h, 24f-h, 26f-h) sclerotized; submedian acute process conspicuous.

Species included. *Abana amazonica* sp. nov., *Abana colombiana* sp. nov., and *Abana horvathi* Jacobi, 1905.

Dstribution. Bolivia, Colombia, Ecuador, and Peru.

Remarks. Five specimens identified as A. horvathi were delimited based on their COI sequences. This nominal species was recovered as a species complex, dividing it into three different species (Fig. 2). One of them was identified here as A. horvathi, due to the similar morphology of the sequenced specimen with the lectotype of A. horvathi (Figs. 26a-b, 28ab), and to their collection localities being very close to each other, both within the Cusco department in Peru. The other two species were described here as new species, A. amazonica sp. nov. and A. colombiana sp. nov. The COI analyses was also useful to associate male and female specimens and corroborate the sexual dimorphism present within this species complex, with most males showing completely dark forewings and females showing a lighter forewing colouration with transversal light stripes variable in size and number (Figs. 25a-d, 27a-b, 28g-r). The distinct colour pattern among females apparently carry important taxonomic information when separating species within A. horvathi s.l., however, due to the little variability found in males and the lack of appropriate specimens for molecular study that would allow us to associate males with females for most of these female morphotypes (with the exception of those treated in the molecular species delimitation analyses), this work continues to treat most of the female different morphotypes as the same species within A. horvathi s.s. It is clear that the real species richness within A. horvathi s.l is still to be discovered and requires greater efforts and sampling to allow it to be effectively delimited.

Sequences from a DNA voucher from Peru (Huánuco) identified as *A. horvathi* in the work of Takiya (2007) were included in the phylogenetic analyses herein presented, placing this specimen as the sister group to *A. colombiana* **sp. nov.** For this specimen from Huánuco, only a dorsal photo was available for morphological study, being impossible to distinguish it from other species of *A. horvathi s.l.* based only on dorsal habitus, nonetheless, we had access to other male specimens from near collection localities within the Huánuco department and the morphological study of these specimens show us that they shared similar external morphology with *A. horvathi s.s.* specimens (as expected for males within this species complex), nonetheless, they clearly differ in the form of the anterior portion of crown in lateral view, being straight in the first ones and inflated in the latter. We strongly believe that the inflated anterior portion of the crown can be, in fact, an autapomorphy of the *A. horvathi s.s.* species within *A. horvathi s.l.*, because of this, the specimen of Huánuco is here considered a different species (referred as *Abana* sp.) that need to be study in deep.

The current morphological concept of *A. horvathi* established by Young (1968) is based on illustrations of the male pygofer and aedeagus from a specimen from Cuzco (Peru), which he stated that was identical to the male genitalia of the holotype (Fig. 28a-b) and of the male lectotype of the considered synonym *A. pomposula* (Fig. 28d-e). Both types are from Marcapata (Peru) and have the distinct male colouration of this species complex, crown yellow with posterior portion with contrasting black macula(e), pronotum mostly castaneous, and completely black forewings. They seem to vary only in the shape of the crown posterior macula(e), in *A. horvathi* lectotype it is a complete black stripe, while in *A. pomposula* lectotype, there are two triangular black maculae (incomplete medially). The utility of the

few male colour pattern characters used to delimit species within the A. horvathi complex is difficult to assess, as *Abana* in general are not well represented in collections and there are few individuals available for study, most of them very old for sequence data analyses. Furthermore, the aedeagus pictured in Young (1968) showed the distinct characteristic of slender and long anterodorsal projections of the lateral apical projections of aedeagus shaft apex, which is useful to distinguish most other *Abana* species from the *A. horvathi* complex, however it cannot be used to distinguish species within the complex, nor from other related species, A. minuta sp. nov., A. haupti, and A. confusa sp. nov. It is impossible to distinguish all these species based solely on aedeagus characteristics. To make matters more confusing, Young (1968) understanding that the species was probably sexually dimorphic in colouration, he synonymized four other species (one of them removed from Abana herein) under A. horvathi which were described based on female specimens that show very distinct colour pattern from the male colouration and high colour polymorphism among them (Fig. 28g-r). Thus, the current morphological concept of A. horvathi includes a high amount colour polymorphism, while male genitalia characters vary little, but in structures such as connective and style, that are not usually the primary source of cicadelline species diagnostic characteristics. Again, how useful this variation is currently unknown given the paucity of specimens.





Figure 23. *Abana amazonica* **sp. nov.**, male holotype (MUSM). **a**, dorsal habitus; **b**, lateral habitus; **c**, genital capsule, lateral view; **d**, subgenital plate, ventral view; **e**, connective and styles, dorsal view; **f**, aedeagus, anal tube, and paraphyses, lateral view; **g**, aedeagus, anal tube, and paraphyses, ventral view; **h**, aedeagus, anal tube, and paraphyses, posterior view. Scale bars **a-b**: 1.0mm, **c-h**: 0.5mm.

Diagnosis. Body colouration (Fig. 23a-b) mostly ivory-yellow and dark brown to black; anterior portion of crown (Fig. 23a) and dorsal portion of frons (Fig. 23b) yellow, crown with contrasting dark maculae posteriorly and frons with contrasting dark maculae inferiorly; pronotum (Fig. 23a) reddish brown; anterior portion with a marginal black stripe

interrupted medially, with anterolateral yellow paired maculae; male forewing (Fig. 23a-b) completely black. Crown anterior margin (Fig. 23a) subtriangular, apex truncate; anterior portion (Fig. 23b), in lateral view, straight, not inflated; disk with a distinct depression; M-shaped elevation bordering posterior margin present and conspicuous. Connective (Fig. 23e) arms converging anteriorly; base of arms with a U-shaped dorsal rim. Style (Fig. 23e) with apodeme wide and long, almost as long as apophysis lenght; inner lobe subtriangular; apical portion as long as wide; not extending to connective apex. Aedeagal shaft (Fig. 23f-h) with anterodorsal projections slender and long. Dorsal connective (Fig. 23f-h) sclerotized; submedian acute process conspicuous.

Total length: males (n = 1) 18.7 mm.

Description. Crown (Fig. 23a) without pubescence; anterior margin subtriangular, apex truncate; in lateral view, anterior portion (Fig. 23b), straight, not inflated, forming an acute angle with frons; disk with a distinct depression; with conspicuous M-shaped elevation on posterior margin. Ocelli located on imaginary line between anterior eye angles; each slightly closer to adjacent anterior eye angle than to midline. Frons convex medially. Pronotum (Fig. 23a) surface without pubescence. Forewing (Fig. 23a-b) with punctures distributed throughout tegmen; base of fourth apical cell slightly more distal than base of third. Hind leg with femoral setal formula 2:1:0. Other characters as in generic description.

Male colouration. Body colouration mostly black (Figs. 23a-b). Crown (Fig. 23a) ivory, except for a black area on posterior portion (Fig. 23a), between antennal ledges, complete, and with anterolateral sides extending anteriorly. Frons (Figs. 23b) with upper two-thirds varying from ivory to yellow; ventral third dark, as well as clypeus. Gena (Figs. 23b) with anterodorsal portion ivory to yellow; posteroventral portion black, continuing black area of crown to clypeus. Pronotum (Fig. 23a) reddish-brown, with two anterolateral ivory

maculae continuing laterally to proepimeron; anterior portion with a black broad stripe, medially interrupted. Scutellum (Fig. 23a) completely black or becoming brown at posterior portion, posterior to scutellar suture. Thorax (Fig. 23b), in lateral view, with pleurites mostly ivory to yellow, with some brown areas; anepisternum black. Forewing (Fig. 23a-b) mostly black, but turning brown at apex. Legs (Fig. 23a) almost completely yellow, with some small brown areas mostly at apices of tibiae and tarsomeres of all legs. Abdomen (Fig. 23b) black, with yellow areas along posterolateral margins of tergites and posterior margins of sternites.

Male terminalia. Pygofer (Fig. 23c) ventral margin, in lateral view, regularly convex medially; preapical region with a small ventral concavity. Subgenital plates (Fig. 23c), in lateral view, not extending to pygofer apex, ending clearly before. Connective (Fig. 23e) with arms converging anteriorly; base of arms with a U-shaped dorsal rim. Style (Fig. 23e) with apodeme wide and long, almost as long as apophysis lenght; inner lobe subtriangular; angle formed between preapical lobe and apical portion acute; apical portion as long as wide; not extending to connective apex. Aedeagal shaft (Fig. 23f), in lateral view, with preapical dorsal spiniform process extending to dorsal margin of lateral projections; anterodorsal projections (Fig. 23f-h) slender and long. Dorsal connective (Fig. 23f-h) sclerotized; submedian acute process conspicuous. Other characters as in generic description.

Female. Unknown.

Distribution. Peru (San Martín Region).

Material examined. Holotype: PERU: San Martín: 1 Male, Amazonas, Aguas Verdes, Bagua/Tarapoto Rd (5N) AT km 403, 5°41'23"S, 77°38'13"W, 1125 m.a.s.l., 2008ix-26/2008-x-03, Malaise, M.E. Irwin & G. Antón Amaya, DNA voucher Entomologia DZRJ ENT6384 (MUSM). **Etymology.** The specific epithet '*amazonica*' refers to the ecosystem of the type locality where the species was found, which corresponds to the Peruvian Amazon Forest.

Remarks. Phylogenetic analyses recovered this species in the A. horvathi species complex as the sister group of the clade A. colombiana sp. nov. + Abana sp. with high support values (Fig. 3). The general external morphology and characters of the male genitalia of this species are very similar to the species recovered in its sister clade, however, A. amazonica sp. nov. can be clearly distinguished from A. colombiana sp. nov. by the following characters: (1) hind leg with femoral setal formula 2:1:0 (2:0:0 in A. colombiana sp. nov., although this characters may vary intraspecifically), (2) anterolateral ivory maculae of pronotum well extended transversally in dorsal view (very short and inconspicuous dorsally in A. colombiana sp. nov.), (3) base of connective arms with a U-shaped dorsal rim (Vshaped in A. colombiana sp. nov.), and (4) inner lobe of style subtriangular (subquadrate in A. colombiana sp. nov.). This species, at present, cannot be distinguished of A. horvathi s.s. based on male external morphology or genital characters. However, we decided to describe this species based on present molecular delimitation, its distribution in the peruvian Amazon piedmont far from A. horvathi s.s. localities, and there is a possibility that once females of this species are discovered, morphological diagnostic characters will be found.

(Figs. 23-24)



Figure 24. *Abana colombiana* **sp. nov.**, male holotype (ICN: 101511). **a**, dorsal habitus; **b**, lateral habitus; **c**, genital capsule, lateral view; **d**, subgenital plate, ventral view; **e**, connective and styles, dorsal view; **f**, aedeagus, anal tube and paraphyses, lateral view; **g**, aedeagus, anal tube and paraphyses, ventral view; **h**, aedeagus, anal tube and paraphyses, posterior view. Scale bars **a-b**: 1.0mm, **c-h**: 0.5mm.



Figure 25. *Abana colombiana* **sp. nov. a**, female paratype from Santa Maria, Boyacá, Colombia (MPUJ_ENT: 0043234), dorsal habitus; **b**, same female, lateral habitus; **c**, female paratype from Villavicencio, Meta, Colombia (FMNH), dorsal habitus; **d**, same female, lateral habitus; **e**, sternite VII, ventral view; **f**, pygofer, lateral view; **g**, first valvifer and first valvula, lateral view; **h**, detail of first valvula apex, lateral view; **i**, second valvifer and second valvula, lateral view; **j**, detail of second valvula, lateral view; **k**, third valvula, lateral view. Scale bars **a-d**: 1.0mm, **e-k**: 0.5mm.

Diagnosis. Body colouration (Fig. 24a-b) mostly ivory-yellow and dark brown to black; anterior portion of crown (Fig. 24a) and dorsal portion of frons (Fig. 24b) yellow, crown with contrasting dark maculae posteriorly and frons with contrasting dark maculae inferiorly; pronotum (Fig. 24a) reddish brown; anterior margin with a black area along, complete; anterolateral light paired maculae present but very little and inconspicuous

dorsally; male forewing (Fig. 24a-b) completely black; female forewing (Fig. 25a-d) reddish brown on anterior half, becoming black towards apex, with one or two narrow transverse ivory stripe(s) (Fig. 24a-b): one transcommissural at basal half and another (may be absent) not transcommissural aligned with clavus apex (Fig. 25c-d). Crown anterior margin (Fig. 24a) subtriangular, apex sometimes truncate; anterior portion (Fig. 24b), in lateral view, straight, not inflated; disk with a distinct depression; M-shaped elevation bordering posterior margin present and conspicuous. Connective (Fig. 24e) arms converging anteriorly; base of arms with a deep V-shaped dorsal rim. Style (Fig. 24e) with apodeme wide and long, 0.9 times as long as apophysis lenght; inner lobe subquadrate; apical portion as long as wide; not extending to connective apex. Aedeagal shaft (Fig. 24f-h) with anterodorsal projections slender and long. Dorsal connective (Fig. 24f-h) sclerotized; submedian acute process conspicuous.

Total length: males (n = 3) 18 mm, females (n = 2) 18.5 mm.

Description. Anterior margin of crown (Figs. 24a, 25a) subtriangular, apex sometimes truncate. Hind leg with femoral setal formula 2:0:0. Other characters as in *A. amazonica* **sp. nov.** description.

Male colouration. Pronotum (Fig. 24a) black anterior stripe complete; anterolateral ivory maculae (Fig. 24a-b) very small and inconspicuous dorsally, continuing laterally to proepimeron. Legs (Fig. 24b) almost completely yellow, with some small brown to black areas mostly at apex of tibiae and tarsomeres of all legs. Other characters as in description of *A. amazonica* male colouration.

Female colouration. Forewing (Fig. 25a-d) reddish brown on anterior half, becoming black towards apex; with one or two transverse narrow ivory stripes (Fig. 25a-b): one on anterior half wing, transcommissural, not reaching costal margin; and another (may be
absent) restricted to corium, reaching costal margin, aligned to clavus apex (Fig. 25c-d). Other characters as in male colouration above.

Male terminalia. Base of connective arms (Fig. 24e) with a V-shaped dorsal rim. Style (Fig. 24e) with apodeme wide and long, 0.9 times as long as apophysis length; inner lobe subquadrate; apical portion not extending to connective apex. Aedeagal shaft (Fig. 24f), in lateral view, with preapical dorsal spiniform process extending dorsally slightly beyond dorsal margin of lateral projections. Other characters as in *A. amazonica* **sp. nov.** description.

Female terminalia. Abdominal sternite VII (Fig. 25c), in ventral view, posterior margin with a pair of digitiform projections on median third, area in between projections concave, not projected posteriorly. Second valvula (Fig. 25g), in lateral view, with 78 separate teeth on dorsal margin. Third valvula (Fig. 24i) apex subtriangular. Other characters as in generic description.

Distribution. Colombia (Boyacá, Cundinamarca, Meta, and Putumayo departments).

Material examined. Holotype: COLOMBIA: Boyacá: 1 Male, Santa María, Vereda Cachipay, 4.87852, -73.24464, 811 m.a.s.l., 2017-xi-09, Manual, G. Andrade-C., DNA voucher Entomologia DZRJ ENT6386 (ICN: 101511). Paratypes: COLOMBIA: Boyacá: 1 Female, same data as holotype, except: Quebrada La Argentina, aprox. 0.5km SSW de Santa María, 850 m.a.s.l., 2016-iii-07-11, Quebrada, Colecta nocturna, J. Rodríguez, DNA voucher Entomologia DZRJ ENT6427 (MPUJ_ENT: 0043234). 1 Female, same data, except: C. Nariño & N. Sarmiento (MPUJ_ENT: 0037000). 1 Male, same data, except: colecta manual, E. Uribe (MPUJ_ENT: 0041748). 1 Male, same data, except: sendero Hyca Quye, aproximadamente 5.5km NW de Santa María, 900 m.a.s.l., 2016-viii-15-19, Red entomológica, C. Rodríguez (MPUJ_ENT: 0048023). 1 Male, same data, except: sector La Almenara, aproximadamente 1.7km NNE de Santa María, 1123 m.a.s.l., 2017-ii-13-17, Colecta manual, J. Benavides, J. D. Bolivar & N. Cossio (MPUJ_ENT: 0052477). **Cundinamarca:** 1 Male, Chaguani, Centro, 4°57'N, 74°36'W, 1100 m.a.s.l., 2012-ix-11, Y. Angel (UNAB). **Meta:** 1 Male, Meta, 1932, B. Guevara (USNM). 1 Female, Villavicencio, 1938-vii-17 (FMNH). 1 Male, same data, except: Bosque Bavaria, 2005-v-14, Pitfall, Grupo 1 (ICN: 101506). 1 Male, same data, except: Humedal la Madrid, 4°4'35"N, 73°39'W, 480 m.a.s.l., 2015-viii-24, Red entomológica, C. Hernández, DNA voucher Entomologia DZRJ ENT6600 (UNAB). 1 Male, Susumuco, 17-vi (NCSU). **Nariño:** 1 Male, Pasto, B. Guevara (USNM). **Putumayo:** 1 Male, Mocoa, Vereda Pueblo Viejo, Finca Villa Loca, 1°11'28.1"N, 76°38'48.3"W, 700 m.a.s.l., 2015-iii-22, Manual, S. García, DNA voucher Entomologia DZRJ ENT6601 (UNAB: 029). **Other specimens: COLOMBIA: Boyacá:** 1 Male, Santa María, 2015-v-07-09, D. Lozano (ANDES-E).

Etymology. The specific epithet '*colombiana*' refers to the country where the types of this species were found, in Colombia.

Remarks. A male and female specimen (Figs. 24a-b, 25a-b) of *A. colombiana* **sp. nov.** were associated as conspecific in the species delimitation analyses (Fig. 2). These results suggest that the species is sexually dimorphic in colour pattern. Phylogenetic analysis recovered this species as the sister group of *Abana* sp., a male peruvian specimen with sequences generated by Takiya (2007), but this specimen voucher was not studied herein.

Abana horvathi Jacobi, 1905

(Figs. 25-27)

Amblydisca horvathi Jacobi 1905: 166 [n. sp.]. Type(s): SMTD. Young & Lauterer 1964: 294 [Lectotype designated]; Metcalf 1965: 645 [Catalogued]; Young 1968: 150 [Illustration: Figure 139];

Amblydisca pomposula Jacobi 1905: 167 [n. sp.]. Type(s): SMTD. Young & Lauterer 1964: 295 [Lectotype designated]. Metcalf 1965: 646 [Catalogued]; Young 1968a: 150 [syn. of *Abana horvathi*].

Abana regia Melichar, 1926: 324 [n. sp.]. Type(s): MMBC. Metcalf 1965: 646 [Catalogued]; Young 1968: 150 [syn. of *Abana horvathi*].

Abana subfasciata Melichar, 1926: 325 [n. sp.]. Type(s): HNHM. Metcalf 1965: 646 [Catalogued]; Young & Soos 1964: 467 [Lectotype designated]; Young 1968: 150 [syn. of *Abana horvathi*].

Abana subfasciata albidipennis Melichar, 1926: 325 [n. subsp.]. Type(s): HNHM. Young & Soos 1964: 467 [Lectotype designated]. Metcalf 1965: 646 [Catalogued]; Young 1968: 150 [syn. of *Abana horvathi*].

Abana puella Schmidt 1928: 51 [n. sp.] Type(s): MZPW. Metcalf 1965: 644 [Catalogued]; Young & Nast 1963: 269 [Lectotype designated]; Young 1968: 150 [syn. of *Abana horvathi*]



Figure 26. *Abana horvathi* Jacobi, 1905, male from Cusco, Peru (DZRJ). **a**, dorsal habitus; **b**, lateral habitus; **c**, genital capsule, lateral view; **d**, subgenital plate, ventral view; **e**, connective and styles, dorsal view; **f**, aedeagus, anal tube, and paraphyses, lateral view; **g**, aedeagus, anal tube, and paraphyses, ventral view; **h**, aedeagus, anal tube, and paraphyses, posterior view. Scale bars **a-b**: 1.0mm, **c-h**: 0.5mm.



Figure 27. *Abana horvathi* Jacobi, 1905, female from Cusco, Peru (DZRJ). **a**, dorsal habitus; **b**, lateral habitus; **c**, sternite VII, ventral view; **d**, pygofer, lateral view; **e**, first valvifer and first valvula, lateral view; **f**, detail of first valvula apex, lateral view; **g**, second valvifer and second valvula, lateral view; **h**, detail of second valvula, lateral view; **i**, third valvula, lateral view. Scale bars **a-b**: 1.0mm, **c-i**: 0.5mm.



Figure 28. Dorsal and lateral habitus and labels of type specimens of *Abana horvathi* and synonyms. **a-c**, *A. horvathi*, male lectotype (SMTD); **d-f**, *A. pomposula*, male lectotype (SMTD); **g-i**, *A. puella*, female lectotype (MZPW); **j-l**, *A. regia*, female syntype (MMBC); **m-o**, *A. subfasciata*, female lectotype (HNHM); **p-r**, *A. subfasciata var. albidipennis*, female lectotype (HNHM). Scale bars: 1.0mm.

Diagnosis. Body colouration (Fig. 26a-b) mostly ivory-yellow and dark brown to black; anterior portion of crown (Fig. 26a) and dorsal portion of frons (Fig. 26b) yellow, crown with contrasting dark maculae posteriorly and frons with contrasting dark maculae inferiorly; pronotum (Fig. 26a) reddish brown, anterior portion with black marginal stripe complete or medially interrupted, with anterolateral yellow paired maculae; male forewing (Fig. 26a-b) black; female forewing (Figs. 27a-b, 28g-r) with one or two ivory transverse stripes: one transcommissural at basal half (may be absent or with variable width) and another not transcommissural aligned with clavus apex. Crown anterior margin (Figs. 26a, 27a, 28g,

j, m, p) subtriangular, sometimes ending truncate; anterior portion (Fig. 26b), in lateral view, inflated (Figs. 26b, 27b, 28a), forming an obtuse angle in the transition to frons; disk with a distinct depression; M-shaped elevation bordering posterior margin present and conspicuous. Connective (Fig. 26e) arms converging anteriorly; base of arms with a U-shaped dorsal rim. Style (Fig. 26e) with apodeme wide and long, almost as long as apophysis lenght; inner lobe subtriangular; apical portion as long as wide; not extending to connective apex. Aedeagal shaft (Fig. 26f-h) with anterodorsal projections slender and long. Dorsal connective (Fig. 26f-h) sclerotized; submedian acute process conspicuous.

Total length: males (n = 1) 17.01 mm, females (n = 4) 18.5 mm.

Description. Anterior margin of crown (Figs. 26a, 27a, 28a, d, g, j, m, p) subtriangular, apex sometimes truncate; anterior portion of crown, in lateral view, straight, not inflated (Fig. 28e, h, k, n, q), forming an acute angle with frons, or inflated (lectotype, Figs. 26b, 27b, 28b), forming an obtuse angle with frons. Forewing (Figs. 26a-b, 27a-b, 28a, g-r) with base of fourth apical cell aligned or slightly more distal (lectotype) than base of third. Hind leg with femoral setal formula 2:0:0 or 2:1:0. Other characters as in *A. amazonica* **sp. nov.** description.

Male colouration (based on *A. horvathi* male lectotype and similar male at hand). Crown (Figs. 26a, 28a, d) black stripe on posterior portion, interrupted medially, forming two triangular areas. Pronotum (Fig. 26a, 28a, d) anterior portion with a black broad marginal complete stripe. Other characters as in description of *A. amazonica* **sp. nov.** male colouration.

Female colouration (based on associated female to similar male above). Body (Fig. 27a-b) colouration mostly ivory and castaneous. Scutellum (Fig. 27a) dark brown with two black lateral maculae on the anterior portion, before scutellar suture, reaching lateral margins. Forewing (Fig. 27a-b) castaneous, becoming black at clavus apex and translucent yellow at

wing apex; with one broad posterior ivory transverse stripe, restricted to corium, reaching costal margin, aligned to clavus apex. Other characters as in male colouration.

Colouration found in other females. Anterolateral yellow ivory maculae of pronotum (Fig. 28m-r) well extended transversally, sometimes merged, forming a transversal stripe. Scutellum (Fig. 28j) completely black at anterior portion and dark brown posterior to scutellar suture. May have two transverse stripes. Anterior forewing stripe (Fig. 28g-l) broad, transcommissural, reaching costal margin, broadening (Fig. 28g-h) or narrowing (Fig. 28j-k) at clavus. Posterior stripe (Fig. 28j) sometimes extending beyond brachial cell, almost reaching claval suture. Other specimens had anterior and posterior stripes very broad (Fig. 28m-q), merged at submedian posterior portion towards costal margin, and forming a big macula covering almost (Fig. 28m-n) or entirely (Fig. 28p-q) the wing.

Male terminalia. Characters of the male terminalia (Fig. 26c-h) as in *A. amazonica* sp. nov. description.

Female terminalia. Abdominal sternite VII (Fig. 27c), in ventral view, posterior margin with area in between projections almost straight. Second valvula (Fig. 27g), in lateral view, with 88 separate teeth on dorsal margin. Third valvula (Fig. 27i) apex rounded. Other characters as *A. colombiana* **sp. nov.** description.

Distribution. Bolivia (Cochabamba [**new record**] and Santa Cruz [**new record**] departments), Ecuador (Morona-Santiago [**new record**] and Pastaza provinces), and Peru (Cusco, Huánuco [**new record**], Madre de Dios [**new record**], and Junín regions). Before this work, *A. horvathi* was known from Bolivia in Coroico, Nor Yungas province, and Mapiri, Larecaja province, both in La Paz department (Melichar, 1926); from Colombia without specific locality data (Young, 1968); from Ecuador in Canelos and Rio Villano, Pastaza Province (Schmidt, 1928); and from Peru in Marcapata in Cusco Region (Jacobi, 1905;

Melichar, 1926), Chanchamayo province in Junín Region (Schmidt, 1928) and "Juanfué" and "Cumbasé" localities (Melichar, 1926). Here, we extend the distribution of this species in Bolivia to Cercado and Ichilo provinces (Cochabamba and Santa Cruz departments respectively); in Ecuador to Orellana and Morona Santiago provinces; and in Peru to Huánuco and Madre de Dios departments. Record of this species by Young (1968) to Colombia are probably based on the similar species *A. colombiana* **sp. nov.** described herein, as no specimens of *A. horvathi s.s.* was studied from that country.

Material examined. Lectotype (based on photographs of habitus): 1 Male, "Peru S\ Marcapata\ Garlepp c.", "Coll. A. Jacobi\ 1913-9", "A. Jacobi\ Typus", "LECTOTYPE\ Amblydisca horvathi Jacobi Young+Lauterer", "a. horvathi Jac.", "Staatl. Museum fü Tierkunde, Dresden" (SMTD). Other type material (based on photographs of habitus): 1 Female, "Peru\ Marcapata", "Abana\ sonora Mel", "sonora M. \ DET. L. MELICHAR", "TYPUS" [paralectotype], "hung" (MMBC). 1 Female, "Bolivia", "LECTOTYPE\ Abana\ subfasciata Mel. \ Young & Soós '63", "Abana \ subfasciata Mel", "subfasciata M. \ DET. L. MELICHAR", "TYPUS" (HNHM). 1 Female, "Bolivia", "LECTOTYPE\ Abana subfas-\ ciata var. albid-\ipennis Mel. \ Young & Soós '63", "v. albidipennis\ M.\ DET. L. MELICHAR", "TYPUS" (HNHM). 1 Female, "Ecuador Canelos", "Abana puella Schmidt Edm. Schmidt\ determ. 1928", "puella\ Schmidt\ 1928", "Typus", "Lecto-\typus" (MZPW). 1 Male, "Peru S\ Marcapata\ Garlepp c.", "Coll. A. Jacobi\ 1913-9", "LECTOTYPE\ Amblydisca pomposula Jacobi Young+Lauterer", "Staatl. Museum für Tierkunde, Dresden" (SMTD). 1 Female, "Sud-America\ Cumbase", "regia Mel\ det. Melichar", "Coll. Breddin", "Syn-\ typus", "Collectio\ Dr. L. Melichar\ Moravské museum Brno", "Invent. c. \ 3025 /Ent. \ Mor. Museum, Brno" (MMBC). Other specimens: BOLIVIA: Cochabamba [new record]: 1 Female, Cristal Mayu, 1949-x-03, L. E. Pena (NCSU). 1 undetermined,

Osunto, 1921-22, G. Mc Creigh (USNM). Santa Cruz [new record]: 1 Male, Ichilo province, Santa Cruz, Campamento Macuñucu GP-PNA - Río Saguayo-Rio Yapage, 1997ix-06, J. C. Salvatierra (MHNNK, based on photographs of habitus). ECUADOR: 1 Female, Eastern Ecuador, F.W. Gading (USNM). Orellana [new record]: 1 Female, Reserva Étnica Waorani, Transect Ent, 1km S. Onkone Gare Camp, lot#95, 00°39'10"S, 76°26'00"W, 220 m.a.s.l., 1995-ii-08, Terre firme forest, Fogging, T. L. Erwin, DNA voucher: Takiya, Rakitov & Dietrich PR106 (INHS). 1 Female, same data, except: Tiputini Biodiversity Station, nr. Yasuni National Park, lot#204, 00°37'55"S, 76°08'39"W, 200-250 m.a.s.l., 1999-ii-07 (USNM). Morona-Santiago [new record]: 1 Male, Macas, Oriente Ecuador, 1921-vii, J.B. Rorer (USNM). 2 Females, same data.. 1 Male, Ecuador (USNM). PERU: 1 Female, N. E. Peru, 1935-xi-24 (NCSU). 1 Male, Peru (DZRJ). 1 Male, Yahuarmayo, 2010-ii-12, C.H.T. Townsend (USNM). Junín: 1 Female, Chanchamayo (NCSU). Cusco: 4 Males, Cusco, 3 rd km E Quincemil, 13°13'03"S, 70°43'40"W, 633 m.a.s.l., 2012-viii-20/2012-ix-01, Sweep, A.P.M Santos & D. M. Takiya (MUSM). 1 Male, same data, except: 8 km W Quincemil, Pte. Manire, 13°17'56"S, 70°47'49"W, 773 m.a.s.l., 2012-viii-31, DNA voucher Entomologia DZRJ ENT6385 (DZRJ). 1 Female, same data, except: Central Hidroeléctrica de Quincemil, 13°17'03"S, 70°46'53"W, 757 m.a.s.l., 2012-viii-26-28, Varredura, DNA voucher Entomologia DZRJ ENT6602 (DZRJ). 1 undetermiend, same data, except: 19 rd km W Quincemil, Río Araza tributary, 13°20'10"S, 70°50'57"W, 874 m.a.s.l., 2012-viii-23-31, Malaise, R.R. Cavichioli, J.A. Rafael, A.P.M. Santos & D. M. Takiya (DZRJ). 1 Male, Cusco (DZRJ). 1 undetermined, Cusco, Hacienda María, 900 m.a.s.l., 1952-xii, F. L. Woytknowski (NCSU). Huánuco [new record]: 1 Male, Tingo Maria, 1962-vii-09, W.T. Van Velzen (USNM). 1 Male, same data, except: 1944-ix-17, E.J. Hambleton (USNM). 1 Male, same data, except: 9km S Tingo Maria, Pte. Cuevas, 9°21'27" S, 75°59'32" W, 620 m.a.s.l., 2002x-04, G. Solis, DNA voucher: Takiya, Rakitov & Dietrich PR123 (INHS). **Madre de Dios** [**new record**]: 1 Female, Tambopata Res. Zone Tambopata Research Cntr on Rio Tambopata, 13°08.305'S, 69°36.502"W, 622 ft, 2004-x-03-07, C.R. Bartlett (DZRJ).

Remarks. Phylogenetic combined analyses (Fig. 3) recovered *A. horvathi s.s.* as sister to all remaining included species of the complex. The concept of *A. horvathi* herein was restricted to males with body colouration (Fig. 26a-b) mostly ivory-yellow and dark brown to black, anterior portion of crown (Fig. 26a) and dorsal portion of frons (Fig. 26b) yellow, crown with contrasting dark maculae posteriorly and frons with contrasting dark maculae inferiorly, pronotum (Fig. 26a) reddish brown, anterior portion with black marginal stripe complete or medially interrupted, with anterolateral yellow paired maculae, and forewing (Fig. 26a-b) black; and females with similar colouration pattern except for the forewing (Figs. 27a-b, 28g-r), being castaneous with one or two ivory transverse stripes: one transcommissural at basal half (may be absent or with variable width) and another not transcommissural aligned with clavus apex, sometimes merged and fully extended, covering almost completely to completely the wing area. It also can be distinguished from other *A. horvathi s.l.* treated herein by the anterior part of the crown, in lateral view, that is inflated.

After the study of the external morphology of the type material of this species synonyms, it is clear that females exhibit a high polymorphism within *A. horvathi s.s.* as defined here, and results obtained in the species delimitation analyses suggest that the female colouration pattern carry important taxonomic information to distinguish species, with different female morphotypes delimited as different species (Figs. 25a-d, 27a-b). Thus, it is very likely that the species *A. horvathi s.s.* as presented here continues to be itself a group of several species, with the different morphotypes of females detected (Figs. 28g-r) representing different species. However, this issue could not be addressed in depth in the present work

due to the impossibility of obtaining genetic sequences for the majority of these different female morphotypes.

DISCUSSION

This is the first taxonomic work on *Abana* to be published after the revision of Young (1968), published a little more than half a century ago. Although Young (1968) provided informative illustrations and key to all species for most Proconiini genera, in *Abana*, the author refrained from providing a key to species and more illustrations of the male genitalia for the following reasons: (1) species are closely related morphologically, the male genitalia being very similar in the species of which males were available for study; (2) several species are known from only one sex, and (3) series are very short in most collections, and until better series are available it seems inadvisable to try to construct a key to species.

Although, we agree that the available material is still scarce, herein we described six new *Abana* species, elevating the number of species to 12. The present study also provides redescriptions and photographs of diagnostic characters for the six previously described *Abana* species and an identification key that will help future taxonomic work and identification of *Abana* species. The internal female terminalia of five of the six previously valid species of *Abana* (*A. arnetti*, *A. dives*, *A. gigas*, *A. horvathi*, and *A. tissa*) were also herein described and illustrated in detail for the first time, being firstly done for the genus. Some female genitalia structures, especially the sternite VII, apparently provide important phylogenetic utility that can be assessed in more detail in the future.

Before this study, only two previous works provided information about phylogenetic relationships concerning to *Abana* genus. The first one was published by Ceotto & Mejdalani (2005), testing the monophyly of a group of Proconiini genera so called "*Abana* group", based on morphological data and including three of the six *Abana* valid species, recovering the genus *Abana* as monophyletic and as the sister group of *Omagua* with low branch support.

The second work corresponds to the unpublished doctoral thesis of Takiya (2007), in which the author attempts to test the monophyly and phylogenetic relationships of Cicadellinae subfamily and its tribes using morphological and molecular data, however, this study only includes two of the six previously known Abana species for the morphological analyses and one for the molecular analyses. The parsimony strict consensus tree of the morphological phylogenetic analysis of Takiya (2007) recovers Abana as monophyletic, but in a polytomy with the other genera of the Abana group; and for the analyses of the concatenated molecular dataset (including four molecular markers: 16S, COI, COII and H3), the only species tested, Abana sp. (identified as A. horvathi in the study), was recovered as the sister group of *Teletusa* in both the BI and MP trees, only statistically supported in the BI analyses. The present work corroborates previous works, recovering the Abana genus as a monophyletic group with strong to medium support in all analyses (Figs. 3, S1, S2), but is the first study that included all *Abana* species to hypothesize phylogenetic relationships. Results of the combined dataset (morphology + molecular, Fig. 3) and of the molecular concatenated dataset (Fig. S2) agree with results of the molecular analysis of Takiya (2007), with *Teletusa* recovered as the sister group of *Abana* with medium to high support values. Nonetheless, the morphological MP results recovered the same relationship of Ceotto & Mejdalani (2005), being *Omagua* the sister group of *Abana* (Fig. S1), however, this relationship was also not supported statistically. *Teletusa* is a monotypic genus, with highly modified morphology, as T. limpida is known to mimic megachilid bees (Mejdalani et al. 2002), so it is not surprising that morphological phylogenetic analyses are inconsistent in placing this species and may give incongruent results to molecular analysis. To resolve the placement of *Abana* within the tribe Proconiini, a broader taxon sampling, including a greater number of species within the most closely related genera, and gene sampling, is probably necessary.

Besides the uncertain position of the species A. haupti, all the phylogenetical analyses presented here recovered two major clades within *Abana* with high to middle support values in the combined and concatenated (molecular) results, but not supported in the MP morphological results (Figs. 3, S1, S2). The first major clade contains the species related to the A. horvathi species complex, in agreement with results of species delimitation analysis (Fig. 2). Specimens within this clade share a similar general colour pattern, especially in head and thorax (Figs. 7a-b, 14a-b, 24a-b, 25a-d, 26a-b, 27a-b), with gena being anteriorly light and posteriorly dark, pronotum reddish brown with two anterolateral light maculae in almost all species, and forewing sometimes showing one or two transversal light stripes on anterior and/or posterior portions. Additionally, all species share male and female terminalia characters, such as: style (Fig. 26e) with angle formed between preapical lobe and apical portion acute; anterodorsal projections of the aedeagal shaft (Fig. 26f-h) slender and long; and female abdominal sternite VII (Fig. 27c), in ventral view, with a pair of digitiform projections at median third of posterior margin. Finally, a sexual colour dimorphism was corroborated in the A. horvathi complex and is reported for the first time here and, more importantly, the morphological study of these females showed that their colouration patterns carry important taxonomic information to separate different species (Figs. 25a-d, 27a-b). Thus, it is very likely that the species A. horvathi s.s. as presented here continues to be a group of several species. This issue could not be addressed in depth in the present work due to the impossibility of obtaining genetic sequences for the majority of these different female morphotypes. All species within this clade are distributed in South America, between Colombia and Bolivia, in piedmont forests along the Andes Mountain range. Specimens from Cusco (Peru) were herein identified as A. horvathi s.s. due to the similar morphology with the lectotype of the species (See A. horvathi species complex remarks above). Additionally, sequences from a DNA voucher from Peru (Huánuco) identified as *A. horvathi* in the work of Takiya (2007) were included in the phylogenetic analyses herein presented, placing this specimen as the sister group to *A. colombiana* **sp. nov.**, considering this Huánuco specimen as another different species within *A. horvathi s.l.* (See *A. horvathi* species complex remarks above).

The second major clade within *Abana* was recovered containing species *A. arnetti*, *A.* dives, A. gigas, A. ochracea sp. nov., A. rufifrons sp. nov., and A. tissa (Figs. 3, S2), and also containing A. haupti in the MP morphological analyses results (Fig. S1). These species (excluding A. haupti) share male and female terminalia characters that clearly separate them from species of the abovementioned clade, such as: style (Fig. 8g) with angle formed between preapical lobe and apical portion almost right (except in A. tissa); anterodorsal projections of the aedeagal shaft (Fig. 8h-j) broad and short; and female abdominal sternite VII (Fig. 9e), in ventral view, with a pair of dentiform projections at median third of posterior margin, with the area in between projections projected posteriorly as a bifurcate process. Nonetheless, relationships among species within this clade were unstable, varying in all analyses (Figs. 3, S1, S2). Species of this clade are distributed in the northern part of South America and in the southernmost part of Central America, between Costa Rica and Ecuador, and exhibit its higher diversity in Central America. Interestingly, species from Central America and South America were recovered in two separate clades in the concatenated molecular analyses herein presented (Fig. S2), however, this relationship was not recovered in other analyses.

With respect to the uncertain position of *A. haupti*, we consider that this species belongs to the clade including *A. horvathi s.l.* because it shares important characteristics with the species of that group, specially the forewing (Fig. 7a-b) showing two transversal light stripes, style (Fig. 7e) with angle formed between preapical lobe and apical portion acute; and

anterodorsal projections of the aedeagal shaft (Fig. 7f-h) slender and long. This relationship was found only in the BI analyses results (not shown here) of the combined morphological + molecular dataset, however, it was not supported.

With this work, the knowledge about the evolution and distribution of *Abana* genus increases significantly, however, the general knowledge about the biology, ecology and life history of its species continues to be scarce. All specimens studied here are apparently associated with well-preserved forest habitats and may be an interesting model to be used in ecology and conservation studies. This work lays an important base for future studies that seek to clarify or contribute to the knowledge of *Abana* and its species, especially within the *A. horvathi* species complex.

CONCLUSION

The present study complements taxonomic data for the leafhopper genus *Abana*, adding complementary descriptions, information about male and female morphologies, making available images of species and DNA sequence data, and significantly expands the geographical knowledge about the distribution of species. In addition, with the descriptions of six new species, we increased the number of *Abana* species from six to 12 known species. However, deeper studies within some species of the genus, specially within the *A. horvathi* species complex, are necessary to better assess and quantify the real diversity found within *Abana*. The results provided herein show that is necessary to study poorly known taxonomic groups to better quantify the biodiversity, especially of abundant and diverse insect groups, such as neotropical leafhoppers.

SUPPLEMENTARY INFORMATION

Appendix S1. Protocol for DNA extraction with DNeasy Blood & Tissue Kit (modified from Qiagen, 2006)

- 1. Extract the hind leg and associated muscle, or the entire abdomen for old museum specimens, and place it in a 1.5 or 2.0 ml microcentrifuge tube.
- 2. Add 180 μ L of Buffer ATL.
- Add 20 μL of Proteinase K. Mix thoroughly by vortexing and incubate at 55° for 48 hours.
- Vortex for 15 seconds. Add 200 μL of Buffer AL and 200 μL of ethanol (96-100%) and vortex again.
- Pipet the solution from step 4 including any precipitate into a mini spin column (DNeasy Mini spin column provided with the kit) placed in a 2 mL collection tube.
- 6. Centrifuge at 8,000 rpm for 60 s and discard flow-through and collection tube.
- 7. Place the column in a new 2 mL collection tube and add 500 μ L of Buffer AW1.
- 8. Repeat step 6.
- 9. Place the column in a new 2 mL collection tube and add 500 μ L of Buffer AW2.
- 10. Centrifuge at 14,000 rpm for 5 min and discard flow-through and collection tube.
- 11. Place the column in a clean 1.5 or 2.0 mL microcentrifuge tube and add 50 μ L of Buffer AE directly onto the membrane.
- 12. Incubate at 70° for 5 min.
- 13. Centrifuge at 8,000 rpm for 1 min.
- 14. Keep the solution in the microcentrifuge tube in a freezer.
- 15. Repeat steps 11 to 14 in a new microcentrifuge tube to enhance the total amount of DNA obtained.

Appendix S2. PCR protocol

PCR reaction (total volume of 25 μ L):

- 5 µL of 10X Green Taq Buffer (PROMEGA)
- 13 µL of DEPC H2O
- 3.5 µL of MgCl2 25mM (PROMEGA)
- 0.5 µL of dNTP 2,5mM (Invitrogen)
- 1.0 µL of forward primer 10mM
- 1.0 µL of reverse primer 10mM
- 0.1 µL of Taq DNA polymerase (PROMEGA)
- 1.0 µl of DNA template.

Thermocycler program from Takiya (2007):

- 1. Initial denaturing at 94° C for 3 min;
- 35 cycles of denaturing at 94° C for 1 min, annealing at 50° C for 1 min and extension at 72° C for 2 min;
- 3. Final extension period of 72° C for 7 min.
- 4. Cool down at 4° C on hold.

Appendix S3. Sequences of primers used for amplification and sequencing of molecular markers used for reconstructing the phylogeny of *Abana*.

Molecular marker	Primer	Sequence (5'-3')	Reference					
Cytochrome oxidase I	LCO (F)	GGTCAACAAATCATAAAGATATTGG	Folmer et al. 1994					
	HCO (R)	TAAACTTCAGGGTGACCAAAAAATCA	Folmer et al. 1994					
	C1-N-2191 (R)	CCCGGTAAAATTAAAATATAAACTTC	Simon et al. 1994					
	Ron (F)	GGATCACCTGATATAGCATTCCC	Monteiro & Pierce 2001					
Cytochrome oxidase II	3037 (F)	TAGTATGGCAGATTAGTGCAATGAA	Takiya et al. 2006					
	C2 (R)	CCRCAAATTTCWGARCATTGACCA	Takiya et al. 2006					
12S rDNA	SR-J-14233 (F)	AAGAGCGACGGGGGGGATGTGT	Simon et al. 1994					
	SR-N-14588 (R)	ARACTAGGATTAGATACCCTAYTAT	Simon et al. 1994					
16S rDNA	16S+ (F)	CCGGTYTGAACTCARATCA	Takiya et al. 2006					
	16S- (R)	CRMCTGTTTAWCAAAAACAT	Takiya et al. 2006					
Histone H3	HF (F)	ATGGCTCGTACCAAGCAGACGGC	Ogden & Whiting 2003					
	HR (R)	ATATCCTTGGGCATGATGGTGAC	Ogden & Whiting 2003					

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek AR. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* **3**(5): 294-9.

Monteiro A, Pierce NE. 2001. Phylogeny of Bicyclus (Lepidoptera: Nymphalidae) inferred from COI, COII, and EF-1a gene sequences. *Molecular phylogenetics and evolution* **18**(2): 264-281.

Ogden TH, Whiting MF. 2003. The problem with "the Paleoptera problem:" sense and sensitivity. *Cladistics* 19(5): 432-442.

Simon C, Frati F, Beckenbach A, Crespi B, Liu H, Flook P. 1994. Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. *Annals of the entomological Society of America* **87**(6): 651-701.

Takiya DM, Tran PL, Dietrich CH, Moran NA. 2006. Co-cladogenesis spanning three phyla: leafhoppers (Insecta: Hemiptera: Cicadellidae) and their dual bacterial symbionts. *Molecular ecology* **15**(13): 4175-4191.

Appendix S4. List of morphological characters coded for the phylogenetic analysis of *Abana*.

Head

1. Crown, length in relation to interocular width (CI: 25; RI: 40; Ceotto & Mejdalani, 2005):

- (0) larger
- (1) equal or shorter

2. Crown, anterior margin, aspect (CI: 42; RI: 0; adapted from Ceotto & Mejdalani, 2005):

- (0) subtriangular to triangular
- (1) rounded
- (2) converging anteriorly but ending truncate
- (3) quadrate
- **3.** Crown, disk, surface concavity (CI: 40; RI: 62):
 - (0) not distinctly depressed
 - (1) distinctly depressed
 - (2) foveate

4. Crown, pubescence (CI: 20; RI: 50; adapted from Ceotto & Mejdalani, 2005, Takiya, 2007):

(0) absent

(1) present

5. Crown, ocelli, position in relation to imaginary line between anterior eye angles (CI: 50; RI: 0):

(0) at line

(1) slightly behind

- 6. Crown, ocellus, distance to midline and anterior eye angles (CI: 33; RI: 75):
 - (0) equidistant
 - (1) closer to adjacent anterior eye angle

7. Crown, short longitudinal carinae laterad of ocelli (CI: 33; RI: 0; adapted from Takiya, 2007):

- (0) absent
- (1) present
- 8. Crown, posterior half, dark area (CI: 50; RI: 88):
 - (0) absent
 - (1) present
- 9. Crown, posterior half, dark area, aspect (CI: 50; RI: 50):
 - (0) complete, forming a line between antennal ledges
 - (1) interrupted medially, forming two triangular to subtriangular areas
- **10.** Crown, posterior margin, M-shaped elevation (CI: 50; RI: 75):
 - (0) absent
 - (1) present
- 11. Crown, posterior margin, M-shaped elevation, aspect (CI: 25; RI: 25):
 - (0) inconspicuous
 - (1) conspicuous

12. Crown, lateral view, plane in relation to the plane of the body (CI: 33; RI: 20; adapted from Ceotto & Mejdalani, 2005, Takiya, 2007):

- (0) approximately horizontal, parallel to dorsum
- (1) declivent anteriorly
- (2) acclivent anteriorly

13. Transition from crown to face in lateral view, angle, type (CI: 50; RI: 0; Ceotto & Mejdalani, 2005, Takiya, 2007):

- (0) acute
- (1) approximately right to slightly obtuse
- 14. Antennal ledges, anterior end, aspect (CI: 20; RI: 50; Takiya, 2007):
 - (0) round or truncate
 - (1) with concavity
- **15.** Frons, texture (CI: 50; RI: 75; Takiya, 2007):
 - (0) unsculptured
 - (1) striated, granulose, or rugose
- 16. Frons, superior portion (CI: 66; RI: 87; Takiya, 2007):
 - (0) without scar or process

- (1) with round scar remnant of nymphal process
- (2) with elongate cylindrical process directed dorsally
- **17.** Frons, superior portion, colouration (CI: 25; RI: 33):
 - (0) dark brown to black
 - (1) red
 - (2) pale-yellow to ochraceous-yellow
- **18.** Frons, dorsomedian area (CI: 25; RI: 50; Takiya, 2007):
 - (0) evenly convex or flat
 - (1) with distinct median depression
- **19.** Frons, ventral third, colouration in relation to superior portion (CI: 12; RI: 12):
 - (0) concolorous
 - (1) with contrasting darker colour
- 20. Clypeus, profile, aspect (CI: 33; RI: 71; adapted from Ceotto & Mejdalani, 2005,

Takiya, 2007):

- (0) rounded, continuing the profile of frons
- (1) angulate
- 21. Gena, dark area continuous to dark area of crown (CI: 50; RI: 88):
 - (0) absent
 - (1) present
- 22. Gena, dark area continuous to dark area of crown, extension (CI: 100; RI: 100):
 - (0) over whole gena
 - (1) over anterodorsal portion
 - (2) restricted to posteroventral portion

Thorax

23. Pronotum, width in relation to transocular width (CI: 40; RI: 57; Ceotto & Mejdalani, 2005, Takiya, 2007):

- (0) shorter
- (1) subequal to
- (2) larger than

24. Pronotum, lateral margins, orientation in relation to the other (CI: 50; RI: 0; Ceotto & Mejdalani, 2005, Takiya, 2007):

- (0) approximately parallel
- (1) convergent anteriorly
- 2 divergent anteriorly
- 25. Pronotum, anterior fourth along anterior margin, contrasting dark area (CI: 50; RI:
- 87):
- (0) absent
- (1) present
- 26. Pronotum, anterior fourth along anterior margin, dark area, aspect (CI: 100; RI: 100):
 - (0) complete
 - (1) interrupted medially, forming two maculae
- 27. Pronotum, anterolateral light paired maculae (CI: 100; RI: 100):
 - (0) absent
 - (1) present

28. Pronotum, anterolateral light paired maculae, extension in relation to a longitudinal imaginary line with inner angle of eye (CI: -; RI: -):

- (0) not extending to
- (1) extending to or beyond
- **29.** Pronotum, disk, paired yellow rounded maculae (CI: -; RI: -):
 - (0) absent
 - (1) present
- **30.** Pronotum, midlength, surface aspect (CI: 50; RI: 50; Takiya, 2007):
 - (0) flattened or convex
 - (1) with lateral depressions
- **31.** Pronotum, lateral view, dorsal profile, aspect (CI: 33; RI: 0; Takiya, 2007):
 - (0) evenly convex
 - (1) anterior portion at lower plane than posterior portion

32. Pronotum, lateral view, dorsopleural carinae, shape (CI: 100; RI: 100; Ceotto & Mejdalani, 2005):

- (0) distinctly curved
- (1) approximately straight
- **33.** Pronotum, dorsopleural carina, anterior end alignment (CI: 25; RI: 0; Takiya, 2007):

- (0) with posterior corner of eyes
- (1) below posterior corner of eyes
- **34.** Mesoscutellum, surface texture (CI: 33; RI: 33; Ceotto & Mejdalani, 2005):
 - (0) striate
 - (1) shagreen
- **35.** Pleural sclerites, general colouration (CI: 20; RI: 50):
 - (0) mostly light
 - (1) mostly dark to completely dark
- 36. Anepisternum, colouration of superior margin in relation to posterior margin (CI: 33;

RI: 50):

- (0) concolorous
- (1) contrastingly lighter
- **37.** Anepisternum, dorsomedian region, dark spot (CI: -; RI: -):
 - (0) absent
 - (1) present
- **38.** Katepisternum, lateral view, enlargement (CI: 50; RI: 50; Takiya, 2007):
 - (0) not enlarged
 - (1) enlarged and usually inflated

Wings

39. Forewing, lateral view, basal portion of costal margin, shape (CI: 25; RI: 50; Ceotto & Mejdalani, 2005):

- (0) distinctly curved
- (1) approximately straight

40. Forewing, appendix, sclerotization in relation to corium (CI: 50; RI: 50; adapted from Takiya, 2007):

- (0) as sclerotized as corium
- (1) distinctly membranous
- **41.** Forewing, sculpturing (CI: 33; RI: 33; Ceotto & Mejdalani, 2005, Takiya, 2007):
 - (0) not sculptured
 - (1) with deep punctures
- **42.** Forewing, punctures, distribution (CI: 50; RI: 71; Takiya, 2007):

- (0) punctures throughout
- (1) punctures restricted to clavus
- (2) punctures mostly restricted to venation
- **43.** Forewing, chaetotaxy (CI: 16; RI: 44; Takiya, 2007):
 - (0) not distinctly pubescent
 - (1) pubescent
- 44. Forewing, chaetotaxy, pubescence, distribution (CI: 33; RI: 33; Takiya, 2007):
 - (0) distributed throughout
 - (1) mostly restricted to venation
- **45.** Forewing, venation, type (CI: 33; RI: 0; Takiya, 2007):
 - (0) not reticulate
 - (1) reticulate
- **46.** Forewing, supranumerary apical costal crossveins (CI: 33; RI: 0; Takiya, 2007):
 - (0) absent
 - (1) more than 2 present
- 47. Forewing, segment of M between connections with r-m1 and m-cu2, angle (CI: 25;
- RI: 50; Takiya, 2007):
 - (0) forming acute angle with R4+5
 - (1) parallel with R4+5, not forming an angle
- **48.** Forewing, crossvein m-cu2, position (CI: 40; RI: 0; Takiya, 2007):
 - (0) distad of r-m1
 - (1) aligned with r-m1
 - (2) basad of r-m1

49. Forewing, appendix, inner margin, largest width in relation to apical margin width

- (CI: 16; RI: 0; Takiya, 2007):
 - (0) as wide as of apical margin
 - (1) two times broader than that of apical margin
- **50.** Forewing, apex, aspect (CI: 66; RI: 83; Takiya, 2007):
 - (0) convex
 - (1) truncate
 - (2) concave

51. Forewing, female, median region of clavus, transverse light stripe (CI: 25; RI: 40):

(0) absent

(1) present

52. Forewing, female, median region of clavus, transverse light stripe, extension in relation to costal margin (CI: 50; RI: 0):

(0) not reaching

(1) reaching

53. Forewing, female, median region of clavus, transverse light stripe, extension in relation to anal margin (CI: -; RI: -):

(0) not reaching

(1) reaching

54. Forewing, female, median region of clavus, transverse light stripe, length in relation to width (CI: 50; RI: 50):

(0) narrow, 0.5 times as long as wide

(1) almost to or longer than wide

55. Forewing, female, median region of clavus, transverse light stripe, width at clavus in relation to width at corium (CI: -; RI: -):

(0) subequal

(1) wider

(2) narrower

56. Forewing, anterior half of corium, venation, colouration (CI: -; RI: -):

(0) concolorous

(1) with distinct yellow to orange regions

57. Forewing, female, corium region aligned to clavus apex, transverse light stripe (CI: 33; RI: 66):

(0) absent

(1) present

58. Forewing, female, corium region aligned to clavus apex, transverse light stripe, extension in relation to claval suture (CI: 100; RI: 100):

(0) not extending to

(1) extending to

(2) extending beyond, reaching anal margin

59. Forewing, female, corium region aligned to clavus apex, transverse light stripe, length in relation to median anteapical cell length (CI: 50; RI: 0):

- (0) narrow, less than half length
- (1) almost half length
- (2) broad, more than half length
- **60.** Hindwing, vein R2+3 (CI: 50; RI: 0; Takiya, 2007):
 - (0) complete
 - (1) incomplete

Legs

- 61. Profemur, setal row IC, chaetotaxy (CI: 33; RI: 71; Takiya, 2007):
 - (0) uniseriate
 - (1) multiseriate
- 62. Profemur, setal row AV, chaetotaxy (CI: 100; RI: 100; Takiya, 2007):
 - (0) uniseriate
 - (1) multiseriate
- 63. Protibia, PD edge, aspect (CI: 50; RI: 33; Ceotto & Mejdalani, 2005):
 - (0) not expanded
 - (1) inferior portion flattened and expanded
 - (2) completely flattened and expanded
- 64. Metafemur, penultimate setae of apical setal formula (CI: 33; RI: 0):
 - (0) present, single (2:1:X)
 - (1) present, double (2:2:X)
 - (2) absent
- **65.** Metatibia, setal row AD, setae, aspect (CI: 33; RI: 0; Takiya, 2007):
 - (0) similar to PD setae
 - (1) more robust than PD setae
- 66. Metatibia, setal row PD, extension on tibia (CI: 50; RI: 0; Takiya, 2007):
 - (0) extends from base
 - (1) restricted to apical half

67. Metatibia, setal row PD, setae, length in relation to distance between setae (CI: 33; RI: 50; Takiya, 2007):

- (0) subequal to or longer than
- (1) shorter than half distance between setae

68. Metatarsomere I, ventral view, plantar chaetotaxy (CI: 50; RI: 0; Ceotto & Mejdalani, 2005):

- (0) two uniseriate rows
- (1) uni- or biseriate basally, multiseriated apically
- (2) scattered
- (3) single row
- 69. Abdomen, pleurites and sternites, colouration (CI: 33; RI: 20):
 - (0) completely dark
 - (1) completely light

(2) with contrasting light and dark maculae

Male terminalia

70. Pygofer, ventral margin, median region, shape (CI: 25; RI: 50):

- (0) convex
- (1) with a clear concavity
- 71. Pygofer, disk, macrosetae, aspect (CI: 50; RI: 33; Takiya, 2007):
 - (0) robust
 - (1) elongate and fine
 - (2) both fine and robust

72. Pygofer, base of dorsal margin, aspect (CI: 100; RI: 100; Ceotto & Mejdalani, 2005,

Takiya, 2007):

- (0) continuously straight or concave
- (1) with deep round emargination
- 73. Pygofer, ventral margin, preapical region, aspect (CI: 25; RI: 40):
 - (0) convex
 - (1) with a small concavity
- 74. Subgenital plates, lateral view, length in relation to pygofer length (CI: 25; RI: 40):(0) subequal, reaching pygofer apex

- (1) distinctly longer
- (2) shorter, ending before pygofer apex
- 75. Subgenital plate, dorsal surface, aspect (CI: 50; RI: 0; Takiya, 2007):
 - (0) slightly concave
 - (1) with dentiform process associated to style apex
- 76. Subgenital plates, dentiform process, distance in relation to style apex (CI: 50; RI: 0):
 - (0) short, closely associated
 - (1) distant, not closely associated
- 77. Connective, anterior arms, direction (CI: 33; RI: 0; Takiya, 2007):
 - (0) strongly divergent
 - (1) converging anteriorly or when parallel, distance between arms is smaller than arm

width

- 78. Connective, longitudinal dorsal keel (CI: 100; RI: 100; adapted from Takiya, 2007):(0) absent
 - (1) present

79. Connective, apex or subapical region, articulation (CI: 100; RI: 100; adapted from Takiya, 2007):

- (0) articulated with aedeagus
- (1) fused with aedeagus
- (2) articulated with additional sclerite (paraphyses)
- **80.** Connective, base of anterior arms, dorsal rim (CI: 33; RI: 0):
 - (0) absent
 - (1) present
- 81. Connective, base of anterior arms, dorsal rim, shape (CI: 25; RI: 57):
 - (0) broad U
 - (1) V-shaped
- 82. Style, dorsal view, apex, shape (CI: 50; RI: 66; Ceotto & Mejdalani, 2005):
 - (0) foot-shaped, directed externally
 - (1) variable
- **83.** Style, apex, extension in relation to connective apex (CI: 25; RI: 50):
 - (0) not extending to

- (1) extending to
- (2) extending beyond
- 84. Style, apical portion, length (CI: 25; RI: 45):
 - (0) as long as wide or a little bit wider
 - (1) 1.4 to 2.0 times as long as wide
 - (2) more than 2.0 times as long as wide
- 85. Style, apodeme, length in relation to apophysis length (CI: 50; RI: 80):
 - (0) long, subequal to or at least longer than half length
 - (1) shorter than half length
- **86.** Style, inner lobe (CI: 25; RI: 40):
 - (0) absent
 - (1) present
- 87. Style, inner lobe, shape (CI: 50; RI: 50):
 - (0) subtriangular
 - (1) rounded
 - (2) subquadrate
- **88.** Style, preapical lobe, angle formed with apical portion (CI: 25; RI: 40):
 - (0) acute
 - (1) almost right
 - (2) obtuse
- **89.** Paraphyses, aspect (CI: 50; RI: 0; adapted from Takiya, 2007):
 - (0) paired symmetrical processes
 - (1) single process or small sclerite
 - (2) single or paired asymmetrical processes
 - (3) trifurcate
 - (4) single process modified into sheath surrounding shaft
- 90. Paraphyses, length of rami, lateral view (CI: 100; RI: 100; Ceotto & Mejdalani, 2005):
 - (0) short
 - (1) long
- 91. Dorsal connective, aspect (CI: -; RI: -; Takiya, 2007):
 - (0) U-shaped sclerite

- (1) H-shaped sclerite
- 92. Dorsal connective U-shaped, median interruption (CI: 100; RI: 100):
 - (0) absent
 - (1) present
- **93.** Dorsal connective, lateral view, submedian acute anterior process (CI: 33; RI: 66):
 - (0) absent
 - (1) present
- 94. Dorsal connective, lateral view, submedian acute anterior process, aspect (CI: 50; RI:

0):

- (0) conspicuous, well extended anteriorly
- (1) little and inconspicuous
- 95. Aedeagus, lateral view, base, dorsal spiniform process (CI: 100; RI: 100):
 - (0) absent
 - (1) present
- **96.** Aedeagus, lateral view, shaft, preapical dorsal spiniform process (CI: 100; RI: 100; Ceotto & Mejdalani, 2005):
 - (0) absent
 - (1) present

97. Aedeagus, lateral view, shaft, preapical dorsal spiniform process, extension in relation to dorsal margin of shaft (CI: 50; RI: 0):

- (0) ending before
- (1) ending at
- (2) extending slightly beyond

98. Aedeagus, shaft apex, lateral margins, aspect (CI: 100; RI: 100; adapted from Ceotto & Mejdalani, 2005):

- (0) projected dorsally, forming a pair of lateral projections
- (1) without lateral projections

99. Aedeagus, shaft apex, lateral view, lateral projections, shape (CI: -; RI: -; Ceotto & Mejdalani, 2005):

- (0) square-shaped
- (1) subtriangular

100. Aedeagus, shaft apex, lateral view, lateral projections, anterior portion, anterodorsal projection (CI: -; RI: -):

(0) absent

(1) present

101. Aedeagus, shaft apex, lateral view, lateral projections, anterior portion, anterodorsal projection, aspect (CI: 100; RI: 100):

(0) broad and short

(1) slender and long

102. Aedeagus, apex, ventral view, lateral lobes (CI: 50; RI: 50; Ceotto & Mejdalani, 2005):

- (0) present
- (1) absent

103. Aedeagus, atrium, ventral margin, projection as ventral process(es) (CI: 100; RI: 100; Takiya, 2007):

- (0) absent
- (1) present

Female terminalia

104. Sternite VII, posterior margin, shape (CI: 50; RI: 85; Ceotto & Mejdalani, 2005):

(0) trilobate

(1) not trilobate

- 105. Sternite VII, posterior margin, lateral lobe projected posteriorly (CI: 100; RI: 100):(0) absent
 - (1) present
- **106.** Sternite VII, posterior margin, median third, paired lateral projections (CI: 50; RI: 85):
 - (0) absent
 - (1) present

107. Sternite VII, posterior margin, median third, paired lateral projections, shape (CI: 100; RI: 100):

- (0) dentiform
- (1) digitiform

(2) subtriangular

108. Sternite VII, posterior margin, median third, in between lateral projections, aspect (CI: 100; RI: 100):

- (0) rectilinear
- (1) concave
- (2) projected as a bifurcate process

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
Abana amazonica sp. nov.	1	0	1	0	0	1	0	1	0	1	1	0	0	1	0	1	2	0	1	1	1	2
Abana arnetii	1	1	0	0	0	1	0	1	1	1	0	0	0	0	0	1	2	0	1	1	1	1
Abana dives	1	0	1	0	0&1	0	0	1	0&1	1	1	0&1	0	1	0	1	2	0	1	1	1	1
Abana colombiana sp. nov.	1	0	1	0	0&1	1	0	1	0&1	1	1	0&2	0	1	0	1	2	0	1	1	1	2
Abana gigas	1	0	1	1	0&1	1	0	0	-	1	0	0	0	1	0	1	0	0	0	1	0	-
Abana haupti	1	1	1	0	0	1	0	0	-	1	1	0	0	?	0	1	0	0	0	1	0	-
Abana horvathi s.s.	1	0&2	1	0	0&1	1	0	1	1	1	1	2	0	1	0	1	2	0	1	1	1	2
Abana confusa sp. nov.	1	0	1	0	0	1	0	1	0	1	1	0	0	1	0	1	2	0	1	1	1	0
Abana minuta sp. nov.	1	2	1	0	0	1	0	1	1	1	1	0	0	1	0	1	2	0	0	1	1	2
Abana ochracea sp. nov.	1	0	1	0	0	1	0	1	0&1	1	0	0	0	0	0	1	2	0	1	1	1	1
Abana rufifrons sp. nov.	1	0	1	0	0	1	0	1	1	1	1	0	0	0&1	0	1	1	0	1	1	1	0
Abana sp.	1	0	1	0	0	1	0	1	0	1	1	0	0	?	0	1	2	0	1	1	1	?
Abana tissa	1	0	1	1	0	1	0	0	-	1	0	1	0	1	0	1	0	0	0	1	0	-
Acrobelus rakitovi	0	0	2	1	1	0	0	0	-	0	-	0	0	0	0	0	0	0	0	0	0	-
Acrocampsa integra	0	0	2	1	0	0	1	0	-	0	-	0	0	0	0	0	2	1	1	1	0	-
Aulacizes quadripunctata	1	1	1	0	0	0	1	0	-	0	-	1	0	0	1	0	1	1	1	1	0	-
Deselvana sp.	0	0	2	1	0	1	0	0	-	1	0	0	0	0	0	0	0	1	1	0	0	-
Deselvana excavata	0	0	2	0&1	0	0	0	0	-	1	1	0	0	1	0	0	0	1	1	0	0	-
Diestostemma ptolyca	0	1	0	0	1	1	0	0	-	0	-	0	0	0	1	1	2	0	0	0	0	-
Omagua fitchi	1	0	2	0	0	1	0	0	-	1	1	1	0	1	1	0	2	1	0	1	0	-
Oncometopia facialis	1	0	0	1	0	0	0	0	-	0	-	1	-	1	1	0	0	0	1	0	0	-
Peltocheirus sp.	1	3	2	1	0	0	0	0	-	1	1	1	1	0	1	0	0	1	0	0	0	-
Raphirhinus phosphoreus	0	0	2	1	0	0	1	0	-	1	1	2	0	1	0	2	2	0	1	0	0	-
Teletusa limpida	1	3	1	1	0	0	0	0	-	1	1	0	1	0	0	0	0	1	0	0	0	-

Appendix S5. Morphological data matrix used for the phylogeny of *Abana*.
	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44
Abana amazonica sp. nov.	2	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	-
Abana arnetii	2	1	1	0	0	-	0	0	0	0	0	0	0	1	0	1	0	0	1	2	1	1
Abana dives	2	1	0&1	0	0	-	0&1	0	0	0	0	0	0	1	0	1	0	0	1	2	1	1
Abana colombiana sp. nov.	2	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	-
Abana gigas	2	1	0	-	0	-	0	0	0	0	0	0	1	0	0	1	0	0	1	2	1	1
Abana haupti	2	1	0	-	0	-	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	-
Abana horvathi s.s.	2	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	-
Abana confusa sp. nov.	2	1	1	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	-
Abana minuta sp. nov.	2	1	1	0	1	1	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	-
Abana ochracea sp. nov.	2	1	1	0	0	-	0	0	0	0	0	0	0	1	0	1	0	0	1	2	0&1	1
Abana rufifrons sp. nov.	2	1	1	0	0	-	0	0	0	0	0	0	1	0	0	1	0	0	1	2	0	-
Abana sp.	2	1	1	0	1	1	0	0	0	0	0	0	?	?	?	1	0	0	1	0	0	-
Abana tissa	2	1	0	-	0	-	0	0	0	0	0	0	0&1	0&1	0	1	0	0	1	2	1	1
Acrobelus rakitovi	1	1	0	-	0	-	0	0	0	0	0	0	1	1	0	1	0	1	0	-	1	0
Acrocampsa integra	0	0	0	-	0	-	0	1	1	0	1	0	0	0	0	1	0	1	1	0	1	0
Aulacizes quadripunctata	1	1	0	-	0	-	0	1	0	1	0	0	1	0	0	1	1	0	1	2	0	-
<i>Deselvana</i> sp.	2	1	0	-	0	-	0	0	0	0	1	0	0	1	0	1	1	0	0	-	1	0
Deselvana excavata	2	1	0	-	0	-	0	0	0	0	0	0	1	0	0	1	1	0	0	-	0	-
Diestostemma ptolyca	1	1	0	-	0	-	0	0	1	1	0	1	0	0	0	0	0	0	1	0	0	-
Omagua fitchi	0	1	0	-	0	-	0	0	0	0	1	0	0	0	0	1	1	0	1	1	0	-
Oncometopia facialis	0	2	0	-	0	-	0	0	0	1	0	1	0	0	0	0	1	0	1	2	1	1
Peltocheirus sp.	0	0	0	-	0	-	0	1	1	1	0	0	1	0	0	0	0	1	1	0	1	0
Raphirhinus phosphoreus	0&1	1	0	-	0	-	0	0	0	0	0	1	1	0	0	1	1	0	1	0	0	-
Teletusa limpida	0	0	0	-	0	-	0	0	0	0	1	1	1	0	0	1	1	-	0	-	1	1

	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66
Abana amazonica sp. nov.	0	1	1	0	0	1	?	?	?	?	?	0	?	?	?	1	1	-	0	0	0	0
Abana arnetii	0	1	0&1	0	1	1	0	-	-	-	-	0	0	-	-	1	1	-	0	0&2	0	0
Abana dives	0	1	0	0	0	1	0	-	-	-	-	0	0	-	-	1	1	-	0	0&2	0	0
Abana colombiana sp. nov.	0	1	1	0	0	1	1	0	1	0	0	0	1	0	0	1	1	-	0	2	0	0
Abana gigas	0	1	0&1	0	0	1	0	-	-	-	-	0	0	-	-	1	1	-	0	0&1	0	0
Abana haupti	0	1	1	0	1	1	1	0	1	1	2	0	1	1	2	?	?	?	?	?	?	?
Abana horvathi s.s.	0	1	0	0	0	1	0&1	0	0	0	-	0	1	0	1	1	1	-	0	0&2	0	0
Abana confusa sp. nov.	0	1	1	0	1	1	1	1	1	1	1	0	1	2	2	1	1	-	0	2	0	0
Abana minuta sp. nov.	0	1	0	0	1	1	0	-	-	-	-	0	1	1	2	1	1	-	0	2	0	0
Abana ochracea sp. nov.	0	1	0	0	0	1	0	-	-	-	-	0	0	-	-	1	1	-	0	0&2	0	0
Abana rufifrons sp. nov.	0	1	0	0	0	1	0	-	-	-	-	0	0	-	-	1	1	-	0	0&2	0	0
Abana sp.	0	1	1	0	0	1	?	?	?	?	?	0	?	?	?	1	1	-	0	0&2	0	0
Abana tissa	0	1	0	0	0	1	0	-	-	-	-	1	0	-	-	1	1	-	0	2	0	0
Acrobelus rakitovi	0	0	-	?	1	0	0	-	-	-	-	0	0	-	-	1	0	1	0	0&2	0	0
Acrocampsa integra	0	1	1	0	0	1	0	-	-	-	-	0	0	-	-	0	0	0	1	2	0	0
Aulacizes quadripunctata	0	0	1	0	0	0	0	-	-	-	-	0	0	-	-	1	0	0	0	2	0	0
Deselvana sp.	1	1	1	0	0	1	1	1	1	1	0	0	1	1	1	1	1	-	0	2	0	0
Deselvana excavata	1	1	1	2	0	0	1	0	1	0	0	0	1	1	0	1	1	-	1	2	0	0
Diestostemma ptolyca	1	1	-	-	1	0	0	-	-	-	-	0	0	-	-	1	0	0	0	0	0	0
Omagua fitchi	0	1	1	2	0	1	0	-	-	-	-	0	0	-	-	1	0	1	0	2	1	1
Oncometopia facialis	0	0	0	1	0	0	0	-	-	-	-	0	0	-	-	1	0	0	0	0&2	1	0
Peltocheirus sp.	0	1	1	0	0	2	0	-	-	-	-	0	0	-	-	0	1	-	2	2	0	0
Raphirhinus phosphoreus	0	1	1	2	0	0	1	0	1	0	0	0	0	-	-	1	0	1	1	2	1	1
Teletusa limpida	0	1	1	1	0	0	0	-	-	-	-	0	0	-	-	1	0	1	1	2	0	0

	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88
Abana amazonica sp. nov.	0	1	2	0	2	1	1	2	1	0	1	0	2	1	0	1	0	0	0	1	0	0
Abana arnetii	0	1	2	1	2	1	0	2	1	0	1	0	2	1	1	1	1	0	0	1	1	1
Abana dives	0	1	2	0	2	1	0	0	1	0	1	0	2	0	-	1	1	1	0&1	1	1	1
Abana colombiana sp. nov.	0	1	2	0	2	1	1	2	1	0	1	0	2	1	1	1	0	0	0	1	2	0
Abana gigas	0	1	0	1	2	1	1	0	1	0	1	0	2	1	1	1	1	1	0	1	1	1
Abana haupti	?	?	?	0	2	1	0	0	1	0	1	0	2	1	1	1	0	1	0	1	1	0
Abana horvathi s.s.	0	1	2	0	2	1	1	2	1	0	1	0	2	1	0	1	0	0	0	1	0	0
Abana confusa sp. nov.	0	1	?	0	2	1	0	0	1	0	1	0	2	1	0	1	0	0	0	1	1	0
Abana minuta sp. nov.	0	1	1	0	2	1	0	2	1	0	1	0	2	1	0	1	0	0	0	1	1	0
Abana ochracea sp. nov.	0	1	2	1	2	1	1	0	1	0	1	0	2	0	-	1	0	1	0&1	1	1	1
Abana rufifrons sp. nov.	0	1	0	1	2	1	0	0	1	0	1	0	2	1	1	1	2	1	0	1	1	1
Abana sp.	0	1	?	0	2	1	?	0	1	?	1	0	2	?	?	1	?	?	?	?	?	?
Abana tissa	0	1	0&2	1	2	1	0	2	1	1	1	0	2	0&1	1	1	2	2	0&1	1	1	0
Acrobelus rakitovi	0	1	0	0	2	0	0	1	0	-	0	0	2	1	1	1	2	2	0	0	-	2
Acrocampsa integra	0	0	2	0	1&2	0	0	2	1	?	1	0	2	1	1	1	1	1	1	1	1	0
Aulacizes quadripunctata	0&1	1	2	0	1	0	0	1	1	0	1	0	0	1	1	1	2	1	1	1	0	1
<i>Deselvana</i> sp.	1	1	2	0	1	1	0	0	1	1	1	0	2	1	1	0	1	2	1	1	0	1
Deselvana excavata	1	1	2	0	2	1	0	0	1	0	1	0	2	1	0	0	1	1	0	0	-	1
Diestostemma ptolyca	0	1	1	0	1	0	0	2	1	0	1	1	0	1	1	1	2	2	1	0	-	2
Omagua fitchi	1	0	1	1	0	1	0	0	1	0	1	0	2	1	0	1	2	0	0	1	1	2
Oncometopia facialis	0	2	1	0	2	0	0	0	0	-	0	1	0	0	-	1	2	1	1	0	-	1
Peltocheirus sp.	1	1	2	0	1	0	1	1	1	0	1	0	1	1	1	1	2	-	1	0	-	-
Raphirhinus phosphoreus	1	0	2	0	2	1	0	2	1	0	1	0	2	1	0	0	1	0	0	1	0	2
Teletusa limpida	0	1	2	1	2	0	0	0	1	0	0	0	2	1	0	0	2	0	0	0	-	1

	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108
Abana amazonica sp. nov.	0	1	0	1	1	0	1	1	1	0	0	1	1	1	0	?	?	?	?	?
Abana arnetii	0	1	0	1	1	0	1	1	0&1	0	0	1	0	1	0	1	0	1	0	2
Abana dives	0	1	0	1	1	1	1	1	2	0	0	1	0	1	0	1	0	1	0	2
Abana colombiana sp. nov.	0	1	0	1	1	0	1	1	2	0	0	1	1	1	0	1	0	1	1	1
Abana gigas	0	1	0	1	1	0	1	1	0	0	0	1	0	1	0	1	0	1	0	2
Abana haupti	0	1	0	?	1	0	1	1	1	0	0	1	1	1	0	?	?	?	?	?
Abana horvathi s.s.	0	1	0	1	1	0	1	1	1	0	0	1	1	1	0	1	0	1	1	0
Abana confusa sp. nov.	0	1	0	1	1	0	1	1	1	0	0	1	1	1	0	?	?	?	?	?
Abana minuta sp. nov.	0	1	0	1	1	0	1	1	2	0	0	1	1	1	0	?	?	?	?	?
Abana ochracea sp. nov.	0	1	0	1	1	1	1	1	1	0	0	1	0	1	0	1	0	1	0	2
Abana rufifrons sp. nov.	0	1	0	1	1	0	1	1	1	0	0	1	0	1	0	1	0	1	0	2
Abana sp.	0	1	0	?	1	?	1	1	?	0	0	1	1	1	0	?	?	?	?	?
Abana tissa	0	1	0	1	1	0&1	1	1	1	0	0	1	0	1	0	1	0	1	0	2
Acrobelus rakitovi	0	0	1	-	0	-	0	0	-	1	-	-	-	1	0	0	1	0	-	-
Acrocampsa integra	1	0	0	?	?	?	0	0	-	1	-	-	-	1	0	?	?	?	?	?
Aulacizes quadripunctata	-	-	0	0	0	-	0	0	-	1	-	-	-	1	1	0	1	0	-	-
Deselvana sp.	0	1	0	1	1	0	0	0	-	1	-	-	-	1	0	0	1	0	-	-
Deselvana excavata	0	0	0	1	0	-	0	0	-	1	-	-	-	0	0	0	1	0	-	-
Diestostemma ptolyca	-	-	0	0	0	-	0	0	-	1	-	-	-	-	1	0	1	0	-	-
Omagua fitchi	0	1	0	1	0	-	0	0	-	0	1	0	-	1	0	1	0	1	2	0
Oncometopia facialis	-	-	-	-	0	-	0	0	-	1	-	-	-	1	1	1	1	1	2	0
Peltocheirus sp.	-	-	0	0	0	-	0	0	-	1	-	-	-	1	0	0	1	0	-	-
Raphirhinus phosphoreus	0	0	0	1	1	0	0	0	-	1	-	-	-	0	0	0	1	0	-	-
Teletusa limpida	1	-	0	1	1	0	0	0	-	1	-	-	-	0	0	0	1	0	-	-



Figure S1. Strict consensus tree obtained from three most parsimonious trees (L=326, CI=41, RI=57) resulted from parsimony analyses of morphological characters of *Abana*. Bootstrap support values are given below branches. Blue rectangle indicates *Abana* genus.



Figure S2. Maximum likelihood tree of *Abana* based on 2391 bp of 12S, 16S, COI, COII, and H3 (-lnL = 9381.526). Thickened branches are those also recovered in the Bayesian inference analysis. Values above branches are likelihood SH-aLRT / ultrafast bootstrap support values and below are Bayesian posterior probabilities (in percentages). Support values SH-aLRT < 80, UFboot < 95, and PP < 80 are not shown. Blue rectangle indicates *Abana*.

REFERENCES

- Álvarez DG, Pérez AH, Díaz JS, Maestre MH, Beltrán JH. 2011. Transmisión del Virus el Mosaico Suave del Ñame a *Dioscorea rotundata* (Dioscoreaceae) por *Oncometopia* sp. (Cicadellidae). *Revista Colombiana de Entomología* **37**(1): 77-79.
- Bartlett CR, Deitz LL, Dmitriev DA, Sanborn AF, Soulier-Perkins A, Wallace MS. 2018.
 The diversity of the true hoppers (Hemiptera: Auchenorrhyncha). In: Foottit RG, Adler
 PH, (eds) Insect Biodiversity II: Science and Society: Wiley-Blackwell, Chichester;
 501–590. <u>https://doi.org/10.1002/9781118945582.ch19</u>
- Bouckaert R, Heled J, Kühnert D, Vaughan T, Wu C-H, Xie D, Suchard MA, Rambaut A, Drummond AJ. 2014. BEAST 2: a software platform for Bayesian evolutionary analysis. *PLoS Computational Biology* **10**: 1–6.
- Carvalho RA, Mejdalani G, Takiya DM. 2011. Phylogenetic placement and taxonomy of the Neotropical sharpshooter genus *Desamera* Young, with description of its sister group, *Ciccamera* gen. nov. (Hemiptera: Cicadellidae: Cicadellinae). *Systematics and biodiversity* 9(1): 59–75.
- Cavichioli RR, Sakakibara AM. 1989. Novo gênero e espécie de Proconiini (Homoptera, Cicadellidae). *Revista Brasileira de Zoologia* **6**(1): 171–174. https://doi.org/10.1590/S0101- 81751989000100018
- Ceotto PC, Mejdalani G. 2005. Phylogenetic analysis of the *Abana* group of genera (Hemiptera: Cicadellidae: Cicadellinae: Proconiini). *Systematic Entomology* **30**(3): 480-496.

- Cryan JR. 2005. Molecular phylogeny of Cicadomorpha (Insecta: Hemiptera: Cicadoidea, Cercopoidea and Membracoidea): adding evidence to the controversy. *Systematic Entomology* **30**(4): 563-574.
- Cryan JR, Urban JM. 2012. Higher-level phylogeny of the insect order Hemiptera: is Auchenorrhyncha really paraphyletic?. *Systematic entomology* **37**(1), 7-21.
- De Pinna MC. 1991. Concepts and tests of homology in the cladistic paradigm. *Cladistics* **7**(4): 367-394.
- Dietrich CH. 2005. Keys to the families of Cicadomorpha and subfamilies and tribes of Cicadellidae (Hemiptera: Auchenorrhyncha), *Florida Entomologist* **88**(4): 502–517.
- Dietrich CH, Whitcomb RF, Black WC. 1997. Phylogeny of the North American grassland leafhopper genus *Flexamia* (Homoptera: Cicadellidae) based on mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* **8**: 139–149.
- Distant WL. 1908. VIII. —Rhynchotal notes—XLIV. (concluded from vol. i. p. 531). *Annals* and Magazine of Natural History, Series 8 2: 57-84. doi: 10.1080/00222930808692453
- Felsenstein J. 1985. Confidence limits on phylogenetics: an approach using the bootstrap. *Evolution* **39:** 783-791.
- Fowler WW. 1898. Order Rhynchota. Suborder Hemiptera-Homoptera. Biologia Centrali-Americana **2**: 201–216.
- Freytag PH, Sharkey MJ. 2002. A preliminary list of the leafhoppers (Homoptera: Cicadellidae) of Colombia. *Biota Colombiana* **3**(2): 235–283.
- Fujisawa T, Barraclough TG. 2013. Delimiting species using single-locus data and the generalized mixed Yule coalescent approach: a revised method and evaluation on simulated data sets. *Systematic Biology* 62: 702–724.

- Godoy C. 2005. A new genus of brachypterous leafhoppers (Hemiptera: Cicadellidae: Cicadellinae: Proconiini) from Costa Rica. *Proceedings of the Entomological Society of Washington* **107**(21): 259–266.
- Goloboff PA, Catalano SA. 2016. TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics* **32**(3): 221-238.
- Grimaldi D, Engel SM. 2005. Evolution of the Insects. Cambridge University Press, New York, United States, 770 pp.
- Guindon S, Dufayard JF, Lefort V, Anisimova M, Hordijk W, Gascuel O. 2010. New Algorithms and Methods to Estimate Maximum-Likelihood Phylogenies: Assessing the Performance of PhyML 3.0. *Systematic Biology* **59**: 307–321.
- Hamilton KGA. 1981. Morphology and evolution of the rhynchotan head (Insecta: Hemiptera, Homoptera). *Canadian Entomologist* **113**: 953–974.
- Hill BG. 1970. Comparative morphological study of selected higher categories of leafhoppers (Homoptera: Cicadellidae). Dissertation (PhD), North Carolina State University (NCSU), Raleigh, University Microfilms, Ann Arbor, 187 pp.
- Jacobi A. 1905. Vorbericht über eine Homopterenfauna der Anden, nebst Diagnosen neuer Arten. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin* **6:** 163-188.
- Kalyaanamoorthy S, Minh BQ, Wong TK, Von Haeseler A, Jermiin LS. 2017. ModelFinder:
 fast model selection for accurate phylogenetic estimates. *Nature methods* 14(6): 587–589.
- Kapli P, Lutteropp S, Zhang J, Kobert K, Pavlidis P, Stamatakis A, Flouri T. 2017. Multirate Poisson tree processes for single-locus species delimitation under maximum likelihood and Markov chain Monte Carlo. *Bioinformatics* **33**(11): 1630-1638.

- Katoh K, Standley DM. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* **30**(4): 772–780.
- Kumar S, Stecher G, Li M, Knyaz C, Tamura K. 2018. MEGA X: molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution* **35**(6): 1547-1549.
- Larkin MA, Blackshields G, Brown NP, Chenna R, McGettigan PA, McWilliam H, Higgins DG. 2007. Clustal W and Clustal X version 2.0. *Bioinformatics* **23**(21): 2947-2948.
- Maddison WP, Maddison DR. 2019. Mesquite: a modular system for evolutionary analysis. Version 3.61. Available at: <u>http://www.mesquiteproject.org</u>
- McKamey SH. 2007. Taxonomic catalogue of the leafhoppers (Membracoidea). Part 1. Cicadellinae. *Memoirs of the American entomológical Institute* **78:** 1-394.
- Mejdalani G, Takiya DM, Felix M, Ceotto PC, Yanega D. 2002. *Teletusa limpida* (Signoret):
 a Neotropical proconiine leafhopper that mimics megachilid bees (Hymenoptera: Apoidea), with notes on Batesian mimicry in the subfamily Cicadellinae (Hemiptera: Cicadellidae). *Denisia, Linz* 4: 215-224.
- Melichar L. 1926. Monographie der Cicadellinen. III. Annales Historico-Naturales Musei Nationalis Hungarici 23: 273–1394.
- Metcalf ZP. 1965. Cicadelloidea, Part 1, Tettigellidae. General Catalogue of the Homoptera.
 United States Department of Agriculture, Agricultural Research Service, Washington,
 D.C. 6(1): [i-ii], 1-730.
- Minh BQ, Nguyen MAT, von Haeseler A. 2013. Ultrafast Approximation for Phylogenetic Bootstrap. *Molecular Biology and Evolution* **30**(5): 1188–1195.

- Minh, BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, von Haeseler A, Lanfear R. 2020. IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. *Molecular Biology and Evolution* 37:1530-1534. https://doi.org/10.1093/molbev/msaa015
- Nault L, Ammar E. 1989. Leafhoppers and planthoppers transmission of plant viruses. Annual Review of Entomology **34:** 503-529.
- Nielson MW. 1965. A revision of the genus *Cuerna* (Homoptera, Cicadellidae). *Technical Bulletin of the United States Department of Agriculture* **1318:** 1–48.
- Nixon KC. 1999. Winclada v.0.9.99 v. beta. University of Ithaca, New York, USA.
- Oman PW. 1949. The Nearctic leafhoppers (Homoptera: Cicadellidae). A generic classification and check list. *Memoirs of the Entomological Society of Washington* **3**: 1–253.
- Posada D. 2008. jModelTest: Phylogenetic Model Averaging. *Molecular Biology and Evolution* **25:** 1253-1256.
- Puillandre N, Lambert A, Brouillet S, Achaz G. 2012. ABGD, Automatic Barcode Gap Discovery for primary species delimitation. *Molecular Ecology* 21: 1864–1877.
- Puillandre N, Brouillet S, Achaz G. 2020. ASAP: assemble species by automatic partitioning. *Molecular Ecology Resources* 21(2): 609-620.
- Rakitov RQ. 1998. On differentiation of cicadellid leg chaetotaxy (Homoptera: Auchenorrhyncha: Membracoidea). *Russian Entomology Journal* (for 1997) 6(3–4): 7–27.
- Rakitov RA, Godoy C. 2005. New egg-powdering sharpshooters (Hemiptera: Cicadellidae: Proconiini) from Costa Rica. *Annals of the Entomological Society of America* 98(4): 444–457. https://doi.org/10.1603/0013-8746(2005)098[0444:NESHCP]2.0.CO;2

- Rambaut A. 2012. FigTree v1. 4.0. University of Oxford, Oxford, UK. Available at: http://tree.bio.ed.ac.uk/software/figtree.
- Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA. 2018. Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* **67**(5): 901–904.
- Remes-Lenicov AMM, Virla EG, Manca ME. 1998. Difusión de *Tapajosa rubromarginata* (Homoptera: Cicadellidae) sobre cultivos cerealeros de la Argentina. *Revista de la Sociedad Entomológica Argentina* **57**(1-4): 18
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539– 542.
- Schmidt E. 1928. Die Cicadellinen des Stettiner Museums. II. Stettiner entomologische Zeitung 89: 31-62.
- Sereno PC. 2007. Logical basis for morphological characters in phylogenetics. *Cladistics* **23**(6): 565–587. https://doi.org/10.1111/j.1096-0031.2007.00161.x
- Sorensen JT, Campbell BC, Gill RJ, Steffen-Campbell JD. 1995. Non-monophyly of Auchenorrhyncha (Homoptera), based upon 18S rDNA phylogeny: eco-evolutionary and cladistic implications within pre-Heteropterodea Hemiptera (*s.l.*) and a proposal for new monophyletic suborders. *Pan-Pacific Entomologist* **71**: 31–60.
- Sorensen JT, Gill RJ. 1996. A range extension of *Homalodisca coagulata* (Say) (Hemiptera: Clypeorrhyncha: Cicadellidae) to southern California. *Pan-Pacific Entomologist* **72**(3), 160-161.

- Takiya DM. 2007. Systematic studies on the leafhopper subfamily Cicadellinae (Hemiptera: Cicadellidae). Dissertation (PhD in Entomology), Graduate College, University of Illinois, Urbana Champaign: xvii+166pp.
- Vaidya G, Lohman DJ, Meier R. 2011. SequenceMatrix: concatenation software for the fast assembly of multi-gene datasets with character set and codon information. *Cladistics* 27: 171–180.
- Walker FA. 1851. List of the specimens of homopterous insects in the collection of the British Museum. Part III. London: Edward Newman, Vol. 3, 637–907.
- Wang Y, Dietrich CH, Zhang Y. 2017. Phylogeny and historical biogeography of leafhopper subfamily Evacanthinae (Hemiptera: Cicadellidae) based on morphological and molecular data. *Scientific Reports* 7: 45387.
- Wilson MR, Turner JA, McKamey SH. 2009. Sharpshooter Leafhoppers of the World (Hemiptera: Cicadellidae subfamily Cicadellinae). Amgueddfa Cymru - National Museum Wales. Available online at <u>http://naturalhistory.museumwales.ac.uk/Sharpshooters</u>. [Accessed: 31 Oct 2023].
- Yoshizawa K, Saigusa T. 2001. Phylogenetic analysis of paraneopteran orders (Insecta: Neoptera) based on forewing base structure, with comments on monophyly of Auchenorrhyncha (Hemiptera). *Systematic Entomology* **26:** 1–13.
- Young DA. 1965. Cicadelline types in the British Museum (Natural History) (Homoptera: Cicadellidae). Bulletin of the British Museum (Natural History) Entomology 17(4): 163-199.
- Young DA. 1968. Taxonomic study of the Cicadellinae (Homoptera: Cicadellidae), Part 1, Proconiini. *Bulletin of the United States National Museum* **261:** 1–287. https://doi. org/10.5962/bhl.part.20869

- Young DA. 1977. Taxonomic study of the Cicadellinae (Homoptera: Cicadellidae). Part 2, New World Cicadellini and the genus Cicadella. *Bulletin of the North Carolina Agricultural Experiment Station* **239:** 1–1135.
- Young DA, Lauterer P. 1964. Cicadelline lectotypes from the A. Jacobi collection (Homoptera, Cicadellidae). *Reichenbachia* **2:** 293-296.
- Young DA, Lauterer P. 1966. Types of Cicadellinae (Homoptera, Cicadellidae) in the Moravian Museum. *Casopis Moravskeho Musea v Brne* **51**: 261-270.
- Young DA, Nast J. 1963. Cicadelline types of species described by Edmund Schmidt (Homoptera, Cicadellidae). *Annales Zoologici (Warsaw)* **21:** 265-271.
- Young DA, Soos A. 1964. Types of Cicadellinae (Homoptera, Cicadellidae) in the Hungarian Natural History Museum. *Annales Historico-Naturales Musei Nationalis Hungarici* 56: 465-467.
- Zanol KMR. 1988. Morfologia de *Neophlepsius gracilis* (Osborn, 1923). *Revista Brasileira de Entomologia* **32**(1): 69–93.
- Zhang J, Kapli P, Pavlidis P, Stamatakis A. 2013. A general species delimitation method with applications to phylogenetic placements. *Bioinformatics* **29**(22): 2869-2876.