



PROGRAMA DE PÓS-GRADUAÇÃO EM ZOOLOGIA  
UNIVERSIDADE FEDERAL DO PARÁ  
MUSEU PARAENSE EMÍLIO GOELDI



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**REVISÃO TAXONÔMICA E ANÁLISE FILOGENÉTICA DO GÊNERO  
*PROTOPOLYBIA* DUCKE, 1905 COM O USO DE CARACTERES  
MORFOLÓGICOS E MOLECULARES  
(HYMENOPTERA, VESPIDAE, POLISTINAE)**

Belém, 2018

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Tese apresentada ao Programa de Pós-Graduação em Zoologia, do convênio da Universidade Federal do Pará e Museu Paraense Emílio Goeldi, como requisito parcial para obtenção do grau de doutor em Zoologia.

Área de concentração: Evolução

Linha de Pesquisa: Taxonomia e Sistemática

**Orientador: Prof. Dr. Orlando Tobias Silveira**

Belém, 2018

**Dados Internacionais de Catalogação na Publicação (CIP) de acordo com ISBD  
Sistema de Bibliotecas da Universidade Federal do Pará  
Gerada automaticamente pelo módulo Ficat, mediante os dados fornecidos pelo(a) autor(a)**

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S237r Santos Junior, José Nazareno Araújo dos.  
Revisão taxonômica e análise filogenética do gênero  
Protopolybia Ducke, 1905 utilizando caracteres morfológicos e  
moleculares (Hymenoptera, Vespidae, Polistinae) / José Nazareno  
Araújo dos Santos Junior. — 2019.  
99 f. : il. color.

Orientador(a): Prof. Dr. Orlando Tobias Silveira  
Tese (Doutorado) - Universidade Federal do Pará, Instituto de  
Ciências Biológicas, Programa de Pós-Graduação em  
Biodiversidade e Biotecnologia, Belém, 2019.

1. Vespas sociais. 2. Taxonomia. 3. Filogenia. 4.  
Polistinae. I. Título.

CDD 591.012

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FOLHA DE APROVAÇÃO

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## **AGRADECIMENTOS**

Ao Programa de Pós-Graduação em Zoologia da UFPA/MPEG pela formação proporcionada ao longo dos últimos quatro anos.

Ao Museu Paraense Emílio Goeldi, na pessoa do Dr. Orlando Tobias Silveira pela infraestrutura fornecida ao longo do desenvolvimento deste projeto.

Ao Dr. Orlando Tobias Silveira pelas orientações e ensinamentos ao longo dos últimos quatro anos de doutorado.

Ao Conselho Nacional de Desenvolvimento Científico e Tecnológico pela concessão da Bolsa de estudos.

Ao Dr. James M. Carpenter (AMNH), pelo empréstimo de material biológico bem como os conselhos ao longo do trabalho, os quais me ajudaram a enriquecer os resultados do trabalho.

Ao Dr. Gavin Broad, Jaswinder Boparai e Natalie Dale-Skale (MN-Londres), por todo suporte durante minha visita ao Museu.

Ao Dr. John Rawlins (CM, Pittsburg) e Dr. John Wenzel (CM, Pittsburg), Dr. Dominique Zimmerman (NMW), Hannes Baur (NHMB) pelo envio de material para comparação com exemplares.

Aos curadores das coleções científicas nacionais INPA, MPEG, MZUSP, UFRJ/MN-RJ, FIOCRUZ-RJ, UFPR e UFMA.

Ao Dr. Alexandre Padovan Aleixo (MPEG) por fornecer o espaço necessário no laboratório de biologia molecular do MPEG para realização das análises moleculares.

Aos Alunos do laboratório de Biologia molecular do Museu Paraense Emílio Goeldi pela forma sempre solicita em que se dispuseram a me ajudar durante o processo de extração e amplificação das sequencias de DNA.

Ao Dr. William L. Overal (MPEG), pelas sugestões agregadas aos manuscritos publicados bem como sua colaboração na revisão final dos manuscritos antes da submissão.

Aos meus pais, minha namorada e meus irmãos, sem os quais certamente eu não concluiria essa longa jornada!

## SUMÁRIO

**ABSTRACT**

**RESUMO**

|                                                                                                                                                                                                 |    |
|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----|
| <b>INTRODUÇÃO GERAL</b> .....                                                                                                                                                                   | 1  |
| Referências Bibliográficas.....                                                                                                                                                                 | 4  |
| Capítulo 1 - A new species of the genus <i>Protopolybia</i> Ducke, 1905 (Hymenoptera, Vespidae, Polistinae), with taxonomic contributions to the <i>exigua</i> species-group .....              | 8  |
| Capítulo 2 - Taxonomic revision of the <i>Protopolybia sedula</i> species-group (Hymenoptera, Vespidae, Polistinae), with a new identification key to species .....                             | 17 |
| Capítulo 3 - Taxonomic revision of the <i>Protopolybia picteti-emortualis</i> species-group (Richards, 1978) (Hymenoptera: Vespidae, Polistinae), with the description of two new species ..... | 32 |
| Capítulo 4 - Taxonomic revision of the <i>P. chartergoides</i> species-group of the genus <i>Protopolybia</i> Ducke, 1905 (Hymenoptera: Vespidae, Polistinae) .....                             | 56 |
| Capítulo 5 - Análise filogenética do gênero <i>Protopolybia</i> Ducke, 1905 usando caracteres morfológicos e moleculares (Vespidae, Polistinae, Epiponini) .....                                | 69 |
| <b>CONCLUSÕES GERAIS</b> .....                                                                                                                                                                  | 84 |
| <b>ANEXOS</b> .....                                                                                                                                                                             | 85 |

## RESUMO

Polistinae é uma das mais diversas subfamílias de Vespidae com cerca de 950 espécies, 25 gêneros e quatro tribos. Seus representantes são reconhecidos por apresentarem garras tarsais simples e ausência de paratégula. Ducke (1905) descreveu dois novos gêneros para Polistinae: *Protopolybia* e *Pseudochartergus*. Bequaert (1938) revisou *Pseudochartergus* reconhecendo somente duas espécies. Bequaert (1944a) realizou a primeira revisão de *Protopolybia*, na qual descreveu quatro espécies novas, considerou *P. minutissima* e *P. sedula* como formas de uma única espécie e definiu *P. bella* como espécie tipo do gênero. Richards (1978) fez a segunda revisão de *Protopolybia* e o gênero passou a compreender 23 espécies e duas subespécies. Por considerar inconsistentes os caracteres diagnósticos de *Pseudochartergus* e *Protopolybia*, Carpenter e Wenzel (1989) propuseram sua sinonímia, reconhecendo como caráter diagnóstico a presença de um processo posterior medial no metanoto. Carpenter (2011) propôs a sinonímia de quatro espécies do gênero. Santos-Junior et al. (2015) revisaram o grupo de *Protopolybia exigua* e usando caracteres morfológicos propuseram a primeira filogenia para *Protopolybia sensu* Carpenter & Wenzel (1989). Contudo, ainda existe um razoável número de espécies cuja identificação é imprecisa. Assim, esse projeto buscou ampliar o conhecimento sobre a taxonomia e o relacionamento filogenético das espécies de *Protopolybia* através de uma revisão e elaboração de uma filogenia usando caracteres morfológicos e moleculares. Para análise molecular foram isolados os fragmentos do genoma nuclear e mitocondrial - *citocromo subunidade I* (COI), 28s, 12s e 16s, contudo apenas o primeiro e último foram utilizados. Como resultados têm-se notas adicionais para o grupo de *Protopolybia exigua*, assim como a descrição de uma nova espécie. Para o grupo de espécies *P. sedula*, todas as espécies são redescritas, uma nova chave de identificação é apresentada e as genitálias de *P. weyrauchi* e *P. sedula* são descritas. No grupo de espécies de *P. picteti-emortualis*, duas novas espécies são descritas. No grupo de espécies de *P. chartergoides*, propõe-se a sinonimização de uma subespécie, e redescrive-se as quatro espécies válidas, bem como a genitália masculina de *P. chartergoides*, *P. fuscatus* e *P. pallidibalteatus*. Quanto à filogenia de *Protopolybia*, a hipótese de monofilia do grupo de espécies de *P. chartergoides* é corroborada. A sua posição relativa dentro de *Protopolybia* é resolvida, com indicação de uma relação mais estreita com o grupo de *P. sedula*. Por outro lado, na presente análise o grupo de *P. exigua* resulta parafilético.

**Palavras-chave:** Vespas sociais, taxonomia, filogenia, Polistinae

### ***ABSTRACT***

Polistinae is one of the most diverse subfamilies of Vespidae with about 950 species, 25 genera and four tribes. Their representatives are recognized for presenting simple tarsal claws and lacking parategula. Ducke (1905) described two new genera for Polistinae: *Protopolybia* and *Pseudochartergus*. Bequaert (1938) reviewed *Pseudochartergus* recognizing only two species. Bequaert (1944a) made the first revision of *Protopolybia*, in which he described four new species, and considered *P. minutissima* and *P. sedula* as forms of a single species and assigned *P. bella* as type species of the genus. Richards (1978) performed the second revision of *Protopolybia* recognizing 23 species and two subspecies. Carpenter and Wenzel (1989), considering inconsistent the diagnostic characters separating *Pseudochartergus* and *Protopolybia*, proposed their synonymy, based on the synapomorphic medial posterior process on the metanotum. Carpenter (2011) proposed the synonymy of four species of the genus. Santos-Junior et al. (2015) reviewed the *Protopolybia exigua* species-group and using morphological characters proposed the first phylogeny for *Protopolybia* sensu Carpenter & Wenzel (1989). However, there is still a reasonable number of species whose identification is inaccurate. Thus, this project aims to extend the knowledge of the taxonomy and of phylogenetic relationships of the species of *Protopolybia* using morphological characters complemented with molecular data. For molecular analysis, fragments were isolated of the nuclear and mitochondrial genome - cytochrome subunit I (COI), 28s, 12s and 16s. Such an effort resulted on additional notes for the *Protopolybia exigua* species-group, with description of a new species. For the *P. sedula* species-group, all species are redescribed, a new identification key is presented and the genitalia of *P. weyrauchi* and *P. sedula* are described. In the *P. picteti-emortualis* species-group, two new species are described. In the group of species of *P. chartergoides*, it is proposed the synonymization of a subspecies, and the four valid species are redescribed, as well as the male genitalia of *P. chartergoides*, *P. fuscatus* and *P. pallidibalteatus*. As for the phylogeny of *Protopolybia*, the monophyly hypothesis of the group of *P. chartergoides* species is corroborated. Its relative position within *Protopolybia* is resolved, indicating a closer relationship with the group of *P. sedula*. On the other hand, in the present analysis the *P. exigua* group is paraphyletic.



***Keywords:*** Social wasps, taxonomy, phylogeny, Polistinae

## INTRODUÇÃO GERAL

Hymenoptera é uma ordem megadiversa de insetos que compreende aproximadamente 115 mil espécies com distribuição cosmopolita (Sharkey 2007). A biologia do grupo desperta o interesse e a admiração do homem, por seus representantes exibirem uma grande diversidade de hábitos e complexidade de comportamentos que culminam na organização social de vespas, abelhas e formigas (Triplehorn & Johnson 2005).

Os himenópteros foram tradicionalmente subdivididos nas subordens Symphyta (parafilética) e Apocrita. Por sua vez, as espécies de Apocrita eram dispostas em dois grupos: Parasitica constituído por espécies parasitóides de outros insetos e Aculeata por espécies capazes de ferocar. Entretanto, estas características não permitiam uma separação clara entre os dois grupos, dada a existência do hábito fitófago entre alguns Parasitica e do parasitoidismo em muitos Aculeata (Ronquist et al. 1999; Carpenter & Marques 2001).

A realização de análises filogenéticas proporcionou uma nova visão das relações de parentesco entre alguns grupos de Hymenoptera, passando-se a desconsiderar a separação de Apocrita nos dois grupos (Triplehorn & Johnson 2005). Trabalhos recentes têm considerado a subdivisão de Aculeata (=Vespomorfa), em quatro grupos (Aculeata parasitas, vespas predadoras, abelhas e formigas) (Sharkey 2007). Atualmente, Apocrita é amplamente aceite como monofilético, fundamentalmente em razão de suas espécies possuírem o mesossoma separado do metassoma por uma constrição (Triplehorn & Johnson 2005).

Representante de Apocrita, Vespidae é um grupo monofilético composto por seis subfamílias viventes (Euparagiinae, Masarinae, Eumeninae, Stenogastrinae, Polistinae, Vespinae) e uma extinta (Priorvespinae), cujos representantes apresentam antenas geniculadas frequentemente curvadas nos machos, asas anteriores com célula discal alongada, pronoto alcançando a tégula, asas posteriores com três células fechadas, primeiro tergo metassomal fundido ao externo e oviposição no interior de uma célula vazia (Carpenter 1982, 1991).

Polistinae é uma das mais diversas subfamílias de Vespidae, com cerca de 950 espécies, 25 gêneros e quatro tribos. No Brasil, ocorrem 21 gêneros e cerca de 300 espécies pertencentes às tribos Polistini, Mischocyttarini e Epiponini. Seus representantes são facilmente reconhecidos por

apresentarem garras tarsais simples, entradas espiraculares secundárias no mesossoma e ausência de paratégula (Carpenter & Marques, 2001).

Em seu trabalho sobre os vespídeos sociais da América do Sul, Ducke (1905) descreveu dois novos gêneros para Polistinae: *Protopolybia* incluindo *Polybia bella* Von Ihering, 1903; *Polistes minutissima* Spinola, 1851; *Polybia holoxantha* Ducke, 1904 e *Chartergus nitidus* Ducke, 1904; e *Pseudochartergus* para a espécie tipo *Charterginus cinctellus* (Fox, 1898) mais *C. fuscatus* (Fox, 1898). Ducke (1910) reconheceu 11 espécies para *Protopolybia*.

Bequaert (1938) revisou *Pseudochartergus* reconhecendo somente duas espécies. No mesmo trabalho ele também questionou a validade dos dois gêneros, por considerar como insignificantes suas diferenças morfológicas e biológicas, propondo *Protopolybia* como subgênero de *Pseudochartergus*.

Bequaert (1944a) realizou a primeira revisão de *Protopolybia*, na qual descreveu quatro espécies novas, considerou *Protopolybia minutissima* e *P. sedula* como formas de uma única espécie e, definiu *P. bella* como espécie-tipo de *Protopolybia*. Bequaert (1944b) apresentou uma chave de identificação que permite uma fácil diferenciação entre *Protopolybia* e *Pseudochartergus*.

Richards (1978), em sua revisão de vespas sociais das Américas, elevou ao nível de espécie muitas das variedades propostas por Bequaert (1944a). A partir de então, *Protopolybia* passou a compreender 23 espécies e duas subespécies.

Por considerar duvidosos os caracteres diagnósticos de *Pseudochartergus* e *Protopolybia* Carpenter e Wenzel (1989) propuseram sua sinonímia, reconhecendo como principal caráter morfológico diagnóstico a presença de um processo posterior medial no metanoto. Entretanto, não fizeram qualquer comentário a respeito do posicionamento filogenético das espécies de *Pseudochartergus* dentro de *Protopolybia* ampliado.

Carpenter (2011) propôs a sinonímia de quatro espécies de *Protopolybia*. Santos-Junior *et al.* (2015) revisou o grupo de *Protopolybia exigua* e utilizando caracteres morfológicos propôs a primeira filogenia para *Protopolybia sensu* (Carpenter e Wenzel, 1989).

Atualmente, o gênero *Protopolybia* compreende 39 espécies de vespas sociais com ocorrência da Guatemala até a Argentina. No Brasil, são reconhecidas dezesseis espécies, sendo somente uma endêmica (Carpenter & Marques, 2001; Silveira, 2004). No que se refere ao estado

atual do conhecimento das relações de parentesco entre as espécies de *Protopolybia*, o gênero foi dividido em quatro grupos (*exigua*, *picteti-emortualis*, *sedula* e *chartergoides*), cujas relações, contudo, são imprecisas (Santos-Junior *et al.*, 2015).

*Protopolybia* apresenta poliginia e fundação de colônias por enxameamento, que é feito por um grupo de fêmeas estéreis juntamente com poucas fêmeas inseminadas (Jeanne, 1991). Os ninhos apresentam razoável variedade estrutural, sendo comumente constituídos de uma câmara ligada ao substrato por numerosos pedúnculos (Richards, 1978; Wenzel, 1998).

Nos últimos anos, problemas de identidade têm sido verificados relacionados aos conceitos específicos de espécies do gênero *Protopolybia*, em particular, as do grupo de *P. picteti* (Richards, 1978), visto que há um razoável número de espécies cuja identificação é imprecisa, tratando-se, eventualmente, de táxons novos.

Quanto às relações evolutivas entre espécies dos diferentes gêneros de Polistinae, várias hipóteses filogenéticas têm sido propostas utilizando dados morfológicos: Andena *et al.* (2007a) para *Pseudopolybia* de Saussure; Andena *et al.* (2007b) para *Angiopolybia* Araújo; Pickett e Wenzel (2007) para *Apoica* Lepeletier; Silveira (2008) para *Mischocyttarus* de Saussure; Andena *et al.* (2009a) para *Synoeca* de Saussure; Andena *et al.* (2009b) para *Epipona* Latreille; Santos-Junior *et al.* (2015), para *Protopolybia* Ducke. De outro modo, poucas filogenias para gêneros de Polistinae têm sido propostas utilizando caracteres moleculares (Pickett e Wenzel 2004; Pickett *et al.* 2006; Menezes *et al.*, 2015).

Dentre os gêneros de Polistinae, *Protopolybia* apresenta várias espécies com pouca diferenciação morfológica, fazendo com que a diagnose seja baseada em padrões de cor e, quando possível, na morfologia externa da genitália do macho, a qual é bastante diversificada, porém somente poucas espécies têm descrição de tal estrutura. Nesse sentido, os dados moleculares são uma importante ferramenta para a compreensão das relações filogenéticas e definição de linhagens evolutivas no gênero *Protopolybia*.

A presente tese teve como objetivo geral ampliar o conhecimento taxonômico e do relacionamento filogenético das espécies de *Protopolybia* Ducke, 1905. Nesse sentido, foi realizada a revisão taxonômica do gênero *Protopolybia* Ducke, 1905 com ênfase nas espécies dos grupos de *P. chartergoides*, *P. picteti-emortualis* e *P. sedula* com base em caracteres da morfologia externa, descrevendo espécies novas e redescrivendo as espécies já conhecidas para o gênero,

propondo também uma hipótese filogenética para *Protopolybia* utilizando dados morfológicos e moleculares.

Desta feita, a fim de tornar a apresentação dos dados mais organizada, a tese foi estruturada a dividindo em cinco capítulos, a saber: 1) A new species of the genus *Protopolybia* Ducke, 1905 (Hymenoptera, Vespidae, Polistinae), with taxonomic contributions to the exigua species-group; 2) Taxonomic revision of the *Protopolybia sedula* species-group (Hymenoptera, Vespidae, Polistinae), with a new identification key to species; 3) Taxonomic revision of the *Protopolybia picteti-emortualis* species-group (Richards, 1978) (Hymenoptera: Vespidae, Polistinae), with the description of two new species; 4) Taxonomic revision of the *P. chartergoides* species-group of the genus *Protopolybia* Ducke, 1905 (Hymenoptera: Vespidae, Polistinae) e 5) Análise filogenética do gênero *Protopolybia* Ducke, 1905 usando caracteres morfológicos e moleculares (Vespidae, Polistinae, Epiponini). Ressalta-se que os dois primeiros capítulos já foram publicados nos anos de 2017 e 2018, respectivamente.

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# Capítulo 1

**A new species of the genus *Protopolybia* Ducke, 1905 (Hymenoptera, Vespidae, Polistinae), with taxonomic contributions to the exigua species-group**

O capítulo 1 desta tese foi elaborado e formatado conforme as normas da publicação científica *Zootaxa*, as quais se encontram em anexo.

## A new species of the genus *Protopolybia* Ducke, 1905 (Hymenoptera, Vespidae, Polistinae), with taxonomic contributions to the *exigua* species-group

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### ABSTRACT

A new species of Neotropical social wasp, *Protopolybia lidiae* Santos & Silveira, **sp. nov.** (Brazil: Pará) is described and illustrated. The hitherto unknown male of *P. minutissima* (Spinola, 1851) and the nest of *P. clypeata* Santos, Silveira & Carpenter, 2015, are described. Additional information on nest variation and new collection records are presented for other species of the *exigua* species-group.

**Key words:** social wasps, Epiponini, Neotropical region, nest, collection records

### Introduction

*Protopolybia* Ducke 1905, presently comprises 35 species of Neotropical social wasps, of minute to small size, whose range extends from Panama to Argentina. This genus has recently been divided into four species-groups: the *P. chartergoides* species-group, *P. sedula* species-group, *P. picteti* + *P. emortualis* species-group and *P. exigua* species-group (Santos-Junior et al. 2015). First recognized by Richards (1978), the *P. exigua* species-group is currently composed of 13 species, which are characterized by a characteristic shape of the propodeal dorsum, which is gently convex around a narrow median furrow, a very narrow clypeus ca. twice as high as wide, and average anterior wing length of ca. 4.3 mm. The propodeal shape is further altered in some species such as *P. bituberculata* Silveira & Carpenter 1995, *P. chanchamayensis* Bequaert, 1944, and *P. similis* Santos-Junior et al. 2015, which have a more bulging propodeal surface around the furrow (Richards 1978; Silveira & Carpenter 1995; Santos-Junior et al. 2015). The nests of these species are considerably variable with respect to characters such as the presence of an envelope, internal structure and/or external form (Bequaert 1994; Richards 1978; Carpenter & Wenzel 1989; Wenzel 1991, 1998). Despite recent efforts to elucidate the taxonomy and phylogenetic relationships in the genus, more work is still needed to fill information gaps in several of the species groups, e.g. form of larval stages, male genitalia, and nests, as well as finding better resolved and supported phylogenetic hypotheses. Furthermore, some of the species groups still seem to have a significant portion of species yet to be described. In this paper, we describe a new species and offer additional information for other members of the *P. exigua* species-group.

### Material and methods

Specimens of the new species were compared to type material of *Protopolybia diligens* (Smith 1857), *P. rugulosa* Ducke 1907, *P. similis* Santos-Junior et al. 2015, and *P. collombiana* Santos-Junior et al. 2015. Type specimens are deposited in the collections of the American Museum of Natural History, New York (AMNH), Natural History Museum, London (NHM), Museu Paraense Emílio Goeli, Belém (MPEG), Universidade Estadual Paulista Julio de Mesquita Filho, São José do Rio Preto (UNESP-IBILCE), and Rio Claro, São Paulo (UNESP).

The terminology and abbreviations of the names of structures are based on Silveira (2006) and Santos-Junior et al. (2015). The terminology for male genitalia is based on Carpenter & Mateus (2004).

Specimens were examined under a stereomicroscope equipped with an ocular micrometer. Morphological structures were photographed using a Leica DFC420 digital camera coupled to the stereomicroscope. The images were processed using LAS 3.6 software and edited using Helicon Focus 6.0 and Photoshop CS3. Male

genitalia were dissected and immersed in 10% KOH solution for 6 hours at room temperature, then washed in running water, and stored in glycerin in Eppendorf tubes. Drawings of male genitalia were made using a stereomicroscope equipped with a camera lucida. Measurements of the 14 body structures were taken as proposed by Santos-Junior et al. (2015). The architectural characteristics of the nest were described according to Wenzel (1991, 1998). The nests were measured with a stainless steel ruler and are expressed in length-to-width ratios.

The abbreviation “T” refers to metasomal terga. Proportions of body measurements are defined as in Santos-Junior et al. (2015). New distribution records are marked with an asterisk (\*).

***Protopolybia lidiae* Santos & Silveira, sp. nov.**

(Figs 1–4)

**Diagnosis.** Clypeus very high and narrow ( $HC_{lp}/MiWC_{lp}= 1.13$ ), with ventral margin narrowly subtruncate and produced ventrally (Fig. 1); occipital carina not reaching mandible insertion, extending approximately for three fourths of height of gena (Fig. 2), ground color black with few marks, yellow (Fig. 4).

**Description.** FEMALE. Length of fore wing 4.40 mm; clypeus narrow ( $HC_{lp}= 0.53$ ;  $MxWC_{lp}= 0.58$ ;  $TeW= 0.44$ ;  $MiWC_{lp}= 0.47$ mm), ventral margin narrowly subtruncate and produced ventrally (Fig. 1); tentorial pit closer to antennal socket than to eye margin; interantennal area narrow, approximately equal to diameter of antennal socket; mandible relatively short, with length  $0.66 \times$  times distance between eye at vertex; occipital carina little developed, extending for approximately three fourths of height of gena (Fig. 2); pronotal carina obtuse, preceded by short linear prominence; mesoscutum as long as wide; mesepisternal groove absent; scrobal groove abbreviated; scutellum with median line; metanotum triangular and short, with length  $0.72 \times$  width of central disk; metanotal lobe with apex narrowly rounded (Fig. 3); propodeum gently convex around narrow median groove; T1 posteriorly triangular, with petiole  $1.38 \times$  longer than wide; T1 notably narrower than T2.

Frons, mesoscutum and mesopleuron finely reticulated; scutellum and metanotum with weak punctures anteriorly; metasomal segments reticulated; ventral margin of clypeus with elongate golden bristles; eye glabrous; body almost completely covered with short bristles, except propodeum and anterior portion of T1 with long and sparse bristles.

Black, with few yellow spots (Fig. 4); antennomeres black dorsally and brown ventrally; mandible brown; clypeus with yellow V-shaped mark, inner and outer orbit with mark that not touching vertex and occiput, interantennal area with two small spots, pronotum with marks on pronotal carina and anterior prominence of fovea, mesopleural mark, two metapleural marks, scutellum partially, dorsal paired spots on propodeum, posterior bands on T1–T2 (Figs 3, 4), yellow; metanotum with two small yellow spots or black; vertex and mesoscutum black; T3–T5 black. Coxae, femora, tibiae and tarsi black; wings hyaline, venation brown.

MALE. Unknown.

NEST. Unknown.

**Type material.** *Holotype*, f#, BRAZIL, Pará, Altamira, Serra do Pardo,  $05^{\circ}52'N$   $52^{\circ}48'W$ , 28.iv.2012 (S.S. Silva) (MPEG); *paratypes*: 33 f# (same data as holotype). **Other material.** BRAZIL: Pará, Novo Progresso, Área 2 Fazenda, 1 f#, 20.xi.2005 (J. Dias), 1 f#, 22.xi.2005, 1 f#, 26.xi.2005 (MPEG).

**Distribution.** Brazil (Pará).

**Remarks.** *Protopolybia lidiae* sp. nov. belongs to the *P. exigua* species-group (Santos-Junior et al. 2015), with morphology and color pattern resembling those of *P. similis*, *P. diligens* and *P. minutissima*. However, *P. lidiae* differs from *P. similis* in the shape of its propodeum (gently convex around a narrow median groove) and its occipital carina, which does not reach the mandible insertion (Figs 2, 5). *Protopolybia lidiae* can also be confused with a variant of *P. diligens*, and although its clypeus is equally narrow (Figs 1, 6), the apex is different, being produced ventrally. Moreover, the metanotal process is wider with the apex more acute (Figs 3, 7), and it has no basal band on T2. The similarity between *P. lidiae* and *P. minutissima* is mainly in their color pattern and narrowing of the clypeus; however, *P. lidiae* is clearly differentiated by the shape of its occipital carina, which does not reach the mandible insertion, but extends to about  $\frac{3}{4}$  of the height of the gena (Figs 2, 8).

**Etymology.** The specific name is in honor grandmother of first author (J.N. Santos), called Lídia.

***Protopolybia minutissima* (Spinola, 1851)**

**Material examined.** ECUADOR: Sucumbios, 6f#, Limoncocha, 06.vii.1971 (M. Naumann); BRAZIL: Amazonas, 1m#, 13f#, Presidente Figueiredo, vii.2013 (A. Somavilla) (INPA), Acre, 1f#, Rio Branco, 04.x.1998 (S. Mateus) (UNESP-IBILCE).

**Distribution.** Surinam; French Guiana; Ecuador (Napó), Peru (Junín), Brazil (Amazonas, Mato Grosso, Pará, Rondônia, Acre), Mexico.

**Remarks.** The last revision of the group included only new collection records and annotations about its distribution. According to Santos-Junior et al. (2015), *P. minutissima* is similar to *P. similis*, particularly with regard to the width of the clypeus and shape of the occipital carina, which extends to the insertion of the mandible. The male and its genitalia are here described, and the cited revision provides additional traits for the identification of *P. minutissima*.

MALE (hitherto unknown). Length of fore wing 4.2 mm; eyes wide, strongly produced inwards; clypeus very narrow, with elongate silvery bristles (Fig. 9); ventral margin narrowly curved; tentorial pit closer to eye margin than to antennal socket; gena very narrow (Fig. 10); mandibles black; color like female. Parameral spine without elongate bristles; basal and apical angles of paramere widened (Fig. 11); digitus narrow with apical margin approximately rounded and with sparse bristles; basal process not acuminate (Fig. 14); cuspis with few and sparse bristles; ventral process of aedeagus not laterally projecting (Figs 12, 13), strongly sclerotized and weakly serrated; preapical region of aedeagus not angular in lateral view.

Regarding the apex of the aedeagus, its shape is sharply expanded laterally, forming two lobes in common with other species of the *P. exigua* species-group, such as *P. bituberculata*, *P. diligens* and *P. clypeata* (Santos-Junior et al. 2015). Furthermore, a dorsal view of the aedeagus also revealed a median emargination, a trait that seems to be a synapomorphy of the genus, although this is less developed in *P. holoxantha* (Ducke 1904) and *P. bituberculata*.

***Protopolybia diligens* (Smith, 1857)**

**Material examined.** BOLIVIA: Sara, 1f# (Steinbach); ECUADOR: Santiago-Zamora, Cumbaratza, S.E. Loja, 1f#, 31.iii.1965 (L.E. Pena); Pastaza, Jibaria Shurupe, 1 f#, 7.xi.1987 (M. Huybenz) (AMNH); BRAZIL: Maranhão, 113f#, 25.iv.2015, Ninho B1 (Borges, R.C.), 166f#, Ninho B2 (MPEG); Mato Grosso, 3f#, Utariti, Rio Papagaio, vii-viii.1961 (K. Lenko) (MZUSP).

**Distribution.** Colombia, Peru, Brazil (Amazonas, Maranhão, Pará, \*Mato Grosso); \*Bolivia, \*Ecuador.

**Remarks.** Richards (1978) described the shape of the nests of *P. exigua* as circular, with a diameter of about 3.5 and 1.2 cm high, presenting one or two combs. Like *P. exigua*, *P. diligens* also has a round nest, measuring 0.9–3.5 in height and 4.3–5.85 cm in length, with the number of combs varying from one to three (Figs 15, 16). In addition, three *P. diligens* nests shaped differently from the one described above were collected in São José de Ribamar, Maranhão, Brazil. Two of them are remarkably narrower and longer, reminiscent of the nests of *P. bituberculata*; both have a single comb, but they differ in size, one measuring 12.0 × 2.5 cm and the other 9.9 × 2.9 cm (Figs 17, 18).

***Protopolybia clypeata* Santos, Silveira & Carpenter, 2015**

**Nest.** Presents the two distinctive traits of the nest of this genus, the comb attached to the substrate by a central peduncle and several lateral auxiliary peduncles, and in this case, in addition, it has an envelope with one or more lateral exit holes. The nest, which is composed of paper carton and secretion, consists of a single comb, approximately hexagonal in shape ([http://research.amnh.org/pbi-hym/locality/specimenimages/specimen/AMNH\\_HYM%2000000116-1.jpg](http://research.amnh.org/pbi-hym/locality/specimenimages/specimen/AMNH_HYM%2000000116-1.jpg); [http://research.amnh.org/pbi-hym/locality/specimenimages/specimen/AMNH\\_HYM%2000000292-1.jpg](http://research.amnh.org/pbi-hym/locality/specimenimages/specimen/AMNH_HYM%2000000292-1.jpg)), measuring 5.08 × 3.81 × 3.81, slender like that of *P. bituberculata*, and entirely cream colored (Figs. 19 and 20). Four nests collected by J.M. Carpenter and A. Davidson in Peru are nests of *P. clypeata*. Two are completely finished (collection codes: 990318–3, 000310–3; <http://research.amnh.org/iz/hymenoptera/collection/display.php?sid=401247>;

<http://research.amnh.org/iz/hymenoptera/collection/display.php?sid=401246>), one is missing its envelope (collection code: 000310–2; <http://research.amnh.org/iz/hymenoptera/collection/display.php?sid=395360>), and the fourth is in an incipient stage of construction (collection code: 990317–2; <http://research.amnh.org/iz/hymenoptera/collection/display.php?sid=401251>). The first, second and fourth nests were mistakenly identified as *Protopolybia rugulosa* Ducke = *Protopolybia minutissima* (Spinola) (Carpenter 2012), and the third was not identified.

**Material examined.** ECUADOR: Napo, 8km E. Mishualli, 1f#, 28.xii.1987 (M. Huybensz) (AMNH).

**Distribution.** Colombia, Peru, Brazil (Acre), \*Ecuador.

### *Protopolybia collombiana* Santos, Silveira & Carpenter, 2015

**Material examined.** BRAZIL: Acre, Cruz do Sul, 2f#, 23.iii.1982 (Tech, G.M.) (UNESP).

**Distribution.** Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia, \*Brazil.

**Remarks.** The nest of *P. collombiana* consists of a single comb, with an approximately rhomboid-hexagonal shape, averaging 50 mm in length and 35 mm in width. The envelope consists of a single sheet of brown or beige plant fibers with color (Bequaert 1944). Rau (1933) presents almost the same description for *P. collombiana* (as *P. sedula*) from Barro Colorado Island, Panama. However, a nest of *P. collombiana* collected at Tena, Ecuador presents a distinctly green color with some narrow whitish markings (collection code: 901217–18; [http://research.amnh.org/pbi-hym/locality/specimenimages/specimen\\_thumbnails/AMNH\\_HYM%2000000572-0.jpg](http://research.amnh.org/pbi-hym/locality/specimenimages/specimen_thumbnails/AMNH_HYM%2000000572-0.jpg)). This is the first description of this variation in the envelope of the nest.

### *Protopolybia similis* Santos, Silveira & Carpenter, 2015

**Material examined.** BRAZIL: Pará, Juruti, Trevo do Mutum, 1f#, 02°36'S56°18'W, 28.xi.2008 (S.S. Silva & J. Dias) (MPEG).

**Distribution.** Peru, \*Brazil (Pará).

## Discussion

*Protopolybia lidiae* sp. nov. is described from the Brazilian Amazon, thus increasing the number of species in the *P. exigua* group to 14, and making this the most diverse group of *Protopolybia*. In the identification key proposed by Santos-Junior et al. (2015), *P. lidiae* stands next to *P. rubrithorax* Bequaert and *P. diligens* in terms of “occipital carina not reaching mandible insertion; T1 without paired lateral wing-like pointed processes; pronotal prominence well separated from fovea and pronotal carina; color of mesoscutum variable;” and is distinguishable from these species by the very high and narrow clypeus and by the ventral margin, which is narrowly subtruncate and produced ventrally.

The nest of *P. collombiana* described here, unlike those of other species of the *P. exigua* species-group, has a greenish colored envelope, a characteristic shared with species belonging to the genus *Brachygastra* Perty, 1833. This greenish color comes from the vegetal material containing chlorophyll which the insect uses. Over time, the chlorophyll fades, giving place to the cream color found in the envelope of the aforementioned nest.

With regard to the variation in the shape of the nests of *P. diligens*, two points should be mentioned: 1) Nests of the same species with a different number of combs, color and shape were observed on the same substrate in Belém. 2) The nests collected in São José de Ribamar presented only one pattern, an elongate shape similar to that of the palm leaves used as substrate.

## Acknowledgements

We are very grateful to all the institutions, facilitators of loans and the two anonymous reviewers for their corrections and suggestions. The first author is grateful to R.C. Borges for offering some nests for this study, to CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico, grant 140080/2015-5) for financial support and, to the subject editor A. Lelej for this help in editing and publishing this paper.

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## Figure legends

**FIGURES 1–4.** *Protopolybia lidiae*, sp. nov. 1. Head, frontal view; 2. Head, lateral view; 3. Scutellum, metanotum and propodeum, dorsal view; 4. Holotype specimen, lateral view. *clp*, clypeus; *mp*, metanotal process; *gm*, genal margin.

**FIGURES 5–8.** 5. *Protopolybia similis*, head, lateral view; 6. *P. diligens*, head on frontal view; 7. *P. diligens*, scutellum, metanotum and propodeum on dorsal view; 8. *P. minutissima*, head on lateral view. *gm*, genal margin; *clp*, clypeus; *mp*, metanotal process.

**FIGURES 9–14.** *Protopolybia minutissima*, m#. 9. Head, frontal view; 10. Lateral view; 11. Paramere of male genitalia; 12. Aedeagus, ventral view; 13. Aedeagus, lateral view; 14. Volsella, lateral view. Scale for 11–14 = 0.2 mm.

**FIGURES 15–20.** Nests. 15, 16. *Protopolybia diligens* oval shape, lateral view; 17, 18. *P. diligens* elongate shape, lateral view; 19. *P. clypeata* frontal view, 20. *P. clypeata*, lateral view (Font: AMNH collection - <http://research.amnh.org/iz/hymenoptera/collection/display.php?sid=401247>).

Plate 1



Plate 2



Plate 3

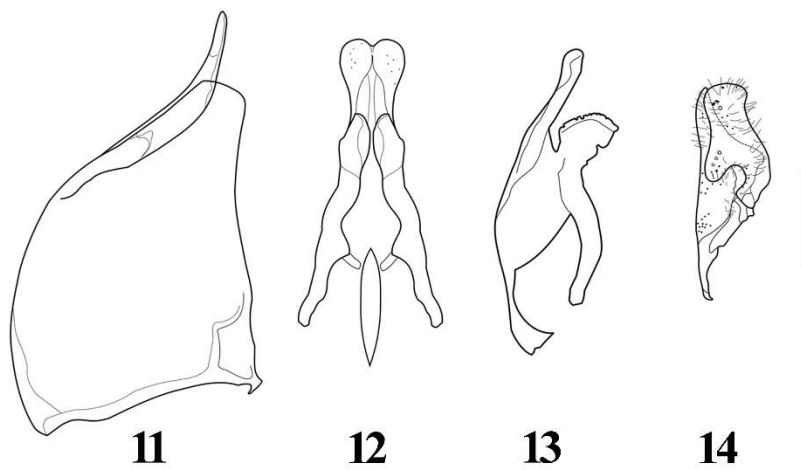
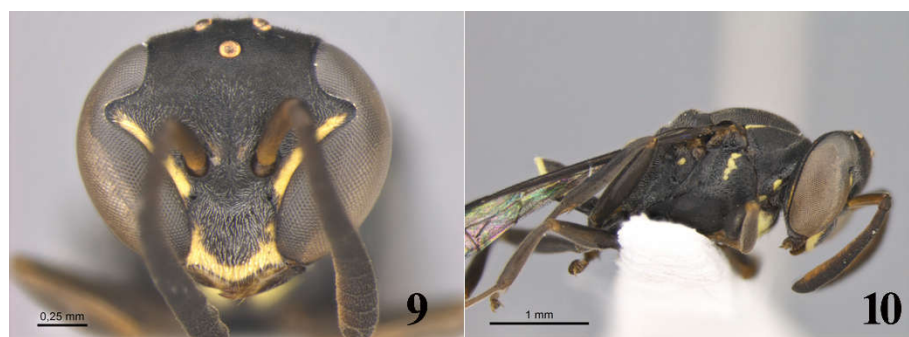




Plate 4



Full title of manuscript: **A new species of the genus *Protopolybia* Ducke, 1905 (Hymenoptera, Vespidae, Polistinae), with taxonomic contributions to the *exigua* species-group**

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Family name of first author: **SANTOS**

File name of manuscript: **Santos\_et\_al\_Protopolybia**

Number of plates: [located on ftp server /1\_ZhangZ/Lelej/Santos\_et\_al\_Protopolybia/] **Four**

Number of references cited in this ms: **17**

Number of new taxa described in this article: **One**

Did you use m# and f# symbols (♂♀): **Yes**

High taxon: Hymenoptera: Vespoidea: **Vespidae**

Author names for running title (use &): **SANTOS ET AL.**

Preferred short running title: **A NEW SPECIES OF THE GENUS *PROTOPOLYBIA***

Accepted by A. Lelej: May 5, 2017; published in July 3, 2017

# Capítulo 2

## **Taxonomic revision of the *Protopolybia sedula* species-group (Hymenoptera, Vespidae, Polistinae), with an new identification key to species**

O capítulo 2 desta tese foi elaborado e formatado conforme as normas da publicação científica *Zootaxa*, as quais se encontram em anexo.

## Taxonomic revision of the *Protopolybia sedula* species-group (Hymenoptera, Vespidae, Polistinae), with an new identification key to species

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### ABSTRACT

A taxonomic review of the *P. sedula* species-group is presented. New diagnostic characters are described and all species redescribed. The male genitalia of *P. sedula* (de Saussure) and *P. weyrauchi* Bequaert are described and drawn. New collection records and a new identification key for the species-group are given.

**Key words:** Social wasps, Neotropical, diversity, new key, Epiponini.

### Introduction

The genus *Protopolybia* Ducke, 1905, is a group of social wasps of the subfamily Polistinae, tribe Epiponini. Currently, the genus comprises 36 described species whose Neotropical distribution ranges from Mexico to Argentina (Silveira & Carpenter 1995; Santos-Junior et al. 2015, 2017). In a phylogeny of the genus, the latter authors divided it into four groups, which include the *P. sedula* species group comprising *Protopolybia sedula* (de Saussure), *P. acutiscutis* (Cameron), *P. amarella* Bequaert and *P. weyrauchi* Bequaert.

The *P. sedula* species group is characterized by its occipital carina that fades away very close to the mandible and its nest with incorporation of nearby vegetation. Additionally, there is a nest feature unique to this species group: combs in separate blocks or in a continuous descending spiral (Wenzel 1991, 1998; Santos-Junior et al. 2015).

With regard to the taxonomic history of this species group, Bequaert (1944a) described two species (*P. amarella* and *P. weyrauchi*), and also the nest of the latter species. In addition, *P. sedula* and *P. acutiscutis* were considered variants of *P. minutissima* (Spinola) and *P. pumila* (de Saussure) respectively. In the second revision of the genus *Protopolybia*, Richards (1978) raised the variants described by Bequaert species level, synonymizing *P. pumila* with *P. sedula*, and noting the existence of two forms: typical *sedula* and a dark morph.

Despite the small number of species described relative to the other groups of the genus, little information is available, and information about the male and the behavior of some of the species, such as *P. amarella* and *P. acutiscutis*, remains unknown. This paper aims to make a taxonomic revision of the *P. sedula* species group, presenting new collection records, describing male genitalia and giving a new identification key.

### Material and methods

Acronyms of collections which provided specimens for this study are cited according to Evenhuis (2007), followed by the name of their respective curators: Natural History Museum (British Museum), London, England (BMNH), Dr. G. Broad; Muséum National d'Histoire Naturelle, Paris, France (MNHN), Dr. C. Villemant; American Museum of Natural History, New York, USA (AMNH), Dr. J.M. Carpenter; Universidad Nacional de Colombia, Bogotá, Colombia (ICN), Dr. F. Fernandez; Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil (INPA), Dr. A.L. Henriques; Museu Paraense Emílio Goeldi, Belém, Pará, Brazil (MPEG), Dr. O.T. Silveira; Universidade Federal do Maranhão, São Luís, Maranhão, Brazil (UFMA), Dr. G.G. Azevedo; Universidade do Rio Janeiro, Museu Nacional, Rio de Janeiro, Rio de Janeiro, Brazil (UFRJ-MN), Dr. F. Vivallo; Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP), Dr. C.R. Ferreira Brandão; Universidade Estadual Paulista “Júlio de Mesquita Filho”, Rio Claro, São Paulo, Brazil (UNESP), Dr. E. Giannotti; Universidade Estadual Paulista “Júlio de Mesquita Filho”, São

José do Rio Preto, São Paulo, Brazil (UNESP-IBILCE), Dr. F.B. Noll; Universidade Federal do Paraná, Museu de Entomologia Pe. Jesus Santiago Moure, Curitiba, Paraná, Brazil (UFPR), Dr. G.A.R. Melo.

#### *Morphological studies, measurements and terminology*

Specimens were examined under a LEICA MZ16 stereomicroscope equipped with an ocular micrometer and a camera lucida. Morphological structures were photographed with a LEICA DFC 420 digital camera coupled to the stereomicroscope. The images were processed using LAS V3.6 software and edited using the Helicon Focus 6.0.18 program and Photoshop CS5. The genitalia of males were extracted and immersed in 10% KOH solution for six hours, washed in running water, and subsequently stored in glycerin in Eppendorf tubes. Drawings of male genitalia were made using an optical microscope equipped with a camera lucida.

Measurements of the body structures were made using a stereomicroscope equipped with an ocular micrometer, using the following abbreviations proposed in part by Silveira (2006) and Santos-Junior et al. (2015). Measurements of the female clypeus are presented on a relative scale given in “units of the minimum clypeus width” (MiWClp).

The terminologies used by Silveira and Carpenter (1995), Carpenter and Marques (2001), and Silveira (2004) were adopted to describe the external morphology of the specimens. The terminologies of Carpenter and Mateus (2004) and Andena et al. (2007) were adopted to describe the morphology of the male genitalia. The abbreviation T refers to numbered metasomal terga. New records in the distributions are asterisked (\*).

#### **Genus *Protopolybia* Ducke, 1905**

*Protopolybia* Ducke, 1905: 7, 9, 17. Type species: *Polybia bella* R. von Ihering, 1903 by subsequent designation (Bequaert 1944a).

*Pseudochartergerus* Ducke 1905: 8, 9, 15. Type species *Charterginus cinctellus* Fox, 1898 (= *Nectarina chartergoides* Gribodo, 1892) by subsequent designation (Bequaert 1938). Junior subjective synonym of *Protopolybia* Ducke, 1905 according to Carpenter and Wenzel (1990: 185)

*Protopolybia* Ducke: Bequaert 1938: 103.

*Pseudochartergerus* Ducke: Bequaert 1938: 103.

*Protopolybia* Ducke: Bequaert 1944a: 97, 98, 99 (part).

*Protopolybia* Ducke: Bequaert 1944b: 252, 265 (part).

*Pseudochartergerus* Ducke: Bequaert 1944b: 252, 264 (part).

*Protopolybia* Ducke: Richards 1978: 8, 136.

*Pseudochartergerus* Ducke: Richards 1978: 8, 154.

#### **Taxonomy of *Protopolybia sedula* species-group**

The group of species herein referred to as *Protopolybia sedula* comprise four species. Detailed descriptions of *Protopolybia acutiscutis*, *P. amarella*, *P. sedula* and *P. weyrauchi* have been given in previous works (Bequaert 1944a, b; Richards 1978), But they are redescribed here, in view of the new traits described by Santos-Junior et al. (2015). Additional information is presented for species in general, whenever available, including new collection records, descriptions of the male genitalia. Information about species distribution, other than from the material examined here, was taken from Richards (1978), Richards (Unpublished manuscript), Sarmiento (1994) and West-Eberhard et al. (1995).

#### ***Protopolybia acutiscutis* (Cameron, 1906)**

(Figs. 1, 2, 3, 21, 25)

*Polybia acutiscutis* Cameron, 1906: 385. (holotype: f#, Honduras (BMNH), examined).

*Polybia acutiscutis* Cameron 1907: 183; Ducke 1910: 539;

*Protopolybia pumila* var. *acutiscutis*: Bequaert 1944a: 123, 125; 1949: 131.

*Protopolybia acutiscutis*: Richards 1978: 140, 150; Carpenter & Wenzel 1990: 182, 184; Almeida & Castro 1991: 47; Sarmiento 1994: 359; West-Eberhard et al. 1995: 586; Rasmussen & Asenjo 2009: 49; Santos et al 2015: 43.

**Diagnosis.** Pronotal fovea distinct, but shallow; metanotal lobe with apex slightly rounded (Fig. 1); wing-like processes on petiole of T1 reduced and not very sharp (Fig. 3); color black richly marked with yellow spots; front with a extensive Y-shaped mark (Fig. 2).

**Redescription.** FEMALE. Length of fore wing 4.86 mm; clypeus relatively wide, approximately as long as wide (HClp=0.73; MxWClp=0.78; TeW= 0.56; MiWClp= 0.69 mm), with ventral margin pointed; tentorial pit closer to antennal socket than to eye margin; interantennal area relatively wide, approximately two times diameter of antennal socket; mandibles relatively short with length  $0.9 \times$  distance between eyes at vertex; occipital carina distinct, fading very close to insertion of mandible; humerus normal, pronotal carina blunt, non-lamellate, distinctly extending downwards at side; pronotal fovea distinct, pronotal prominence extending above and close to pronotal carina, nearly collinear with fovea; length of mesoscutum  $1.15 \times$  its width; mesepisternal groove absent; scutellum with short but well-marked median line; metanotum triangular, length of median axis  $0.82 \times$  width of central disk; propodeum with wide and shallow cavity; first metasomal segment with petiole very short, distal margin wider and nearly straight, cup-like; T1 notably narrower than T2.

Front, mesoscutum, scutellum and metanotum with moderate micropunctuation and shallow mesopunctuation (Fig. 25); ventral region of mesopleuron with distinct punctures; clypeus with short golden bristles, on apical margin, which has elongated bristles; eyes with minute and sparse bristles; body almost completely covered by short bristles; propodeum with long and sparse bristles.

Coloration: species black, richly marked with yellow spots; antennae ventrally testaceous or brown, dorsally black; mandibles, clypeus almost entirely, inner and outer orbit with wide bands that extend to the vertex and occiput, front with a extensive Y-shaped mark (Fig. 2), two wide marks on vertex, extensive mark on the pronotal carina and fovea, two stripes on mesoscutum, tegulae partially, large spot on mesepisternum extending to area below scrobe, one spot on metapleuron, scutellum and metanotum partially, propodeum with paired dorsal marks, distal band on T1, basal band and distal band on T2, T3 to T5 with distal band, yellow. Coxae yellow, femora black to brown, tibiae brown to black; tarsi brown; wings hyaline, venation brown.

**Material examined.** BELIZE: 5387, 1f#, (P. Cameron), 4f#, Blancaneaux, Goldman-Salvin collection (BMNH); BOLIVIA: La Paz, Chulumani, 1f#, 26.iii.1979, 1f#, 25.iii.1979, 1f#, 3.iv.1979 (M. Cooper) (BMNH); BRAZIL: Mato Grosso, 2f#, Barra dos Bugres, R. E. Serra das Araras, Arm. Susp. 1.6m, 24.i.1986 (M. Zanuto), 1f#, Serra Roncador, R.S. Base Camp, 13.vii.1968 (without collector) (BMNH); Maranhão, 1f#, Aldeia Araçu, Igarapé Gurupi-Una, 50km E de Canindé, ii.1966, (Malkin) (MZUSP); 1f#, Santo Amaro, Urbano Santos, SMVESP42, 03°14'S, 43°25'W, 16.v.2004 (Azevedo, G.G. & Amorim, L.R.) (UFMA); Pará, 25f#, Belterra, 12.xii.1999 (G.C. Venturieri); 2f#, Capitão Poço, 01.iii.1978 (P. Tadeu); 3f#, Bragança, 01.ii.1978 (W. França); 2f#, Conceição do Araguaia, 17–21.xi.1979; 1m# Benevides, viii.1911 (Ducke); 1f#, Serra Norte, Serraria, 28.i.1985; 1f#, N1 Serraria, 18.i.1985 (M. Zanuto) (MPEG); 2f#, Cachimbo, x.1955 (Pe. Pereira) (MZUSP); Amazonas, 1f#, Teffé, 02.x.1904 (Ducke) (MPEG), 1f#, vi.2011 (Somavilla) (INPA); Maturaca, Alto Rio Cauaburi, 12–17.xii.1962 (J. Bechyné); COLOMBIA: Magdalena, 13f#, Pueblo Bello, 45km W. Valledupar, Sierra Nevada de S. Marta, 15.vii.1968 (B. Malkin) (AMNH); 5f#, San Lorenzo, 27.ii.1972, 1200m (without collector), 1f# S. Pedro de La Sierra, 1300m, 12.ii.1974 (M. Cooper), 1f#, Nariño, Barbacoas, 21.iii.1974, 1f#, Putumayo, Mocoa, 4.vii.1978, 1f#, N. de Sant Maracaibo basin, Tibu, 15–16.vi.1976; 1f#, Caquetá, Yuruyaco, Florencia, 26.i.1979 (M. Cooper) (BMNH); 1f#, Valle, Via Cali-Anchicayá, 705m, Vda El Engaño, 23.iii.1995 (C. Sarmiento) (ICN); ECUADOR: Napo, 1f#, Anangu, 25–30.xi.1987 (Huybensz, M.) (AMNH), 1f#, Napo, Limoncocha, 20.vi.1977 (C.W. Rettemeyer & R. Chadab) (BMNH); GUATEMALA: Moca, 2f#, Such., 3000ft, 25.vi.1947 (Donor, F.J. & P. Vaurie); 1f#, 500ft, 30.viii.1947 (AMNH); GUYANA: Mabaruna, 1f#, vii.1929 (L.D. Cleare) (BMNH); PANAMA: Canal Zone, 2f#, Barro Colorado, 11.ii.1976 (R. Chadab) (BMNH); PERU: Madre de Dios, 1f#, 156km from Puerto Maldonado, 10–30.ix.1962 (L.E. Pena) (AMNH), 3f#, Valle Chanchamayo, 800m, 1939 (W. Weyrauch) (BMNH).

**Distribution.** Belize, Bolivia: La Paz; Brazil: \*Amazonas, Maranhão, Mato Grosso, Pará, \*Rondonia; Colombia: Antioquia, \*Caquetá, Cauca, Magdalena, Meta, Nariño, Putumayo; Costa Rica, Ecuador: Napo; Guatemala, Honduras, Panama, Peru: Junin, Loreto; Venezuela: Caracas, D. F., Mérida;

***Protopolybia amarella* Bequaert, 1944**

(Figs. 4, 5, 6, 22, 26)

*Protopolybia amarella* Bequaert, 1944a: 101, 113. (holotype: f#, Guyana, Source of R. Essequibo (MCZ, Cambridge), examined); 1944b: 266, 267; Richards 1978: 139, 149; Sarmiento 1994: 359; Rasmussen & Asenjo 2009: 49.

*Protopolybia mellea* Ducke: Overal 1978: 11 (nomen nudum).

**Diagnosis.** Pronotal carina blunt, non-lamellate, distinctly extending downwards at side, humerus normal, pronotal carina blunt; pronotal fovea distinct and deep, metanotal lobe with apex pointed (Fig. 4); wing-like processes on petiole of T1 reduced and not very sharp; species yellow, with light ferruginous and very few black markings, commonly on the mesoscutum (Fig. 6).

**Redescription.** FEMALE. Length of fore wing 4.87 mm; clypeus relatively wide, approximately as long as wide (HClp=0.75; MxWClp=0.88; TeW= 0.59; MiWClp= 0.78 mm), with ventral margin pointed; tentorial pit closer to antennal socket than to eye margin; interantennal area relatively wide, approximately 2 × diameter of antennal socket; mandibles relatively short with length 0.8 × distance between eyes at vertex; occipital carina distinct, fading very close to insertion of mandible; humerus normal, pronotal carina blunt, non-lamellate, distinctly extending downwards at side; pronotal fovea distinct, pronotal prominence extending above and close to pronotal carina, nearly collinear with fovea; length of mesoscutum 1.02 × its width; mesepisternal groove absent; scutellum with short but well-marked median line; metanotum triangular, length of median axis approximately 0.82 × width of central disk, metanotal lobe with apex pointed; propodeum with wide and shallow cavity; T1 with petiole very short, wing-like processes reduced and not very sharp, distal margin wider and nearly straight, cup-like; T1 notably narrower than T2.

Front, mesoscutum, scutellum and metanotum with moderate micropunctuation and shallow mesopunctuation (Fig. 26); ventral region of mesopleuron with distinct punctures; clypeus with short golden bristles, except ventral margin, which has elongated bristles; eyes with minute and sparse bristles; body almost completely covered by short bristles; propodeum with long and sparse bristles.

Coloration: species entirely yellow, except on mesoscutum which has small and sparse black marks (Fig. 5); wings hyaline, venation testaceous.

**Material examined.** BRAZIL: Acre, 1f#, Rio Branco, Reserva Catuaba, 12.viii.1993 (M.L. Oliveira) (MZUSP), 1f#, Cruzeiro do Sul, 23.ii.1968 (without collector) (BMNH); Pará, 1f#, Gorotire, 51W8S, 18.viii.1978 (D.A. Posey); 1f#, Serra Norte, Est. Fofoca, 23.viii.1984 (M.F. Torres); 1f#, Est. Manganês, 19–22.viii.1984 (MPEG); Amazonas, 1f#, Ipixuna, vi.2011 (A. Somavilla) (INPA); Rondônia, 1f#, V. Rondonia, Aeroporto, 18.vi.1978 (without collector) (BMNH); BRITISH GUIANA: 1f#, New River, Boundary Mark12.v..1938 (C.A. Hundson); COLOMBIA: 1f#, Putumayo, Mocoa, 600m, 6.xi.1974 (M. Cooper), 1f#, 31.v.–7.vi.1976 (BMNH); PERU: Pachitea, 1f#, 9239 (without date and collector) (MPEG), 1f#, Tingo Maria, 1.viii.1971 (BMNH).

**Distribution.** Brazil: Acre, \*Amazonas, \*Pará; Bolivia: Pando; Colombia: Amazonas; Guyana, Peru: Huánuco, Loreto, R. Pachitea.

### *Protopolybia sedula* (de Saussure, 1854)

(Figs 7, 8, 9, 13, 14, 15, 16, 23, 27)

*Polybia sedula* de Saussure, 1854: 169, 170. (syntype: f#, Brazil, BA (MNHN), examined); Dalla Torre 1904: 78; Carpenter 1999: 18.

*Polybia pumila* de Saussure, 1863: 239 (holotype: f#, Brasilia, Freiress, 235 (SMF), examined); Dalla Torre 1894: 165; Fox 1898: 449 (in part); Dalla Torre 1904: 78; Carpenter and Van der Vecht 1991: 215; Carpenter 1999: 18.

*Polybia minutissima sedula*: R. von Ihering 1904: 179, 247, pl. 6 fig. 9 (nest; Brazil; Peru; Suriname).

*Protopolybia pumila*: Ducke 1905: 18; Bequaert 1944a: 101, 123; 1944b: 266, 270; 1949: 131; Machado & Rodrigues 1975: 95–102; Machado: 1977: 771–784; Richards 1978: 150; Overal 1978: 11.

*Protopolybia punctulata* Ducke, 1907: 166, 167. (syntype: f#, Barbacena, 20.x.1905 (Ducke), examined); Richards 1978: 142; Nascimento 1979: 11; Obrecht & Huber 1993: 178; Carpenter 1999: 1, 18.

*Protopolybia sedula*: Ducke 1907: 166 (key), 167; 1907 (1908): 94; 1908: 85; 1910: 470, 474; 1914: 309–311; 1918: 324; Bertoni 1918: 204; Fonseca 1926: 171 (nest); Overal 1978: 11 (list); Richards 1978: 144; Carpenter &

Wenzel 1990 (1989): 180, 183; Machado 1982: 189–192; Almeida & Castro 1991: 47; Sarmiento 1994: 359; Silveira & Carpenter 1996 (1995): 49; Garcete-Barrett 1999: 32; Rasmussen & Asenjo: 2009; Santos et al. 2015: 43. *Protopolybia minutissima* var. *sedula*: Martorell & Salas 1939: 251; Bequaert 1944a: 106, 109; 1944b: 267; 1949 (1948): 131.

*Protopolybia sedula* morph *sedula*: Richards 1978: 140, 150.

**Diagnosis.** Front with two spots yellow; pronotal carina weakly lamellate, extending downwards less at side and humerus normal; petiole of T1 narrow, without wing-like processes; species black moderately marked with yellow spots (Fig. 7).

**Redescription.** FEMALE. Length of fore wing 4.75 mm; clypeus relatively wide, approximately as long as wide (HClp=0.63; MxWClp=0.70; TeW= 0.52; MiWClp= 0.63 mm), with ventral margin pointed; tentorial pit closer to antennal socket than to eye margin; interantennal area relatively wide, approximately two times diameter of antennal socket; mandibles relatively short with length  $0.78 \times$  distance between eyes at vertex; occipital carina distinct, fading very close to insertion of mandible; humerus normal, pronotal carina weakly lamellate, extending downwards less at sides; pronotal fovea distinct, pronotal prominence extending above and close to pronotal carina, nearly collinear with fovea; length of mesoscutum  $1.05 \times$  its width; mesepisternal groove absent; scutellum with short but well-marked median line; metanotum triangular, length of median axis  $0.82 \times$  width of central disk; propodeum with a wide and shallow cavity; T1 with petiole short, distal margin wider and nearly straight, cup-like; T1 notably narrower than T2.

Front, mesoscutum, scutellum and metanotum with moderate micropunctuation and shallow mesopunctuation (Fig. 27); ventral region of mesopleuron with distinct punctures; clypeus with short golden bristles, except on ventral margin, which has elongated bristles; eyes with minute and sparse bristles; body almost completely with short bristles; propodeum with long and sparse bristles.

Coloration: species black, richly marked with yellow to whitish spots; antennae ventrally testaceous, dorsally brown; mandibles, clypeus almost entirely, inner and outer orbit with wide bands that extend to vertex and occiput, front with two marks (Fig. 8), two oblique marks on vertex (Fig. 9), narrow mark on pronotal carina and on fovea; two stripes on mesoscutum, tegulae with a small mark (Fig. 9), mesepisternum with two spots, one spot on metapleuron, two on scutellum and metanotum, propodeum with paired dorsal marks, distal narrow band on T1, basal lateral spots, and narrow distal band on T2, T3 to T5 with narrow distal band, yellow. Coxae, femora, tibiae black to brown; tarsi testaceous; wings hyaline, venation brown.

**Genitalia.** Basal and apical angles of paramere widened (Fig. 13); digitus narrow with apical margin rounded, and with short and few bristles (Fig. 16); basal process pointed; cuspis with short and sparse bristles; ventral process of aedeagus approximately angular, not laterally produced in dorsal view, very sclerotized and laterally serrated (Fig. 14 and 15); pre-apical region of aedeagus not angular.

**Material examined.** ARGENTINA: Misiones, 1f#, Dos de Mayo, xii.1973 (Fritz); Alto Paraná, 1f#, Bemberg, 15–17.iii.1934 (BMNH); BOLIVIA: Rurrenabaque, 7f#, 2m#, Rio Beni, 1921–22 (W.M. Mann) (AMNH); 7f#, 25.iv.1979 (M. Cooper); 4f#, x.1921 (W.M. Mant) (BMNH), Alto Beni, 4f#, S. Rio Inicua, i.1976 (Peña); La Paz, 1f#, Plazuela to Inquisivi, 1400–2200m, xii.1984 (L.E. Peña) (AMNH); BRAZIL: Amapá, 2f#, Serra do Navio, x.1959 (Bicelli) (MZUSP); Acre, 3f#, Rio Branco, 25.x–8.xi.1991 (F. Ramos, A. Henriques, I. Gorayeb, N. Bittencourt) (MPEG); Amazonas, 1f#, Itacoatiara, AM–010 km215, Faz. Aruanã, 0302S5850W, 24.iv.1994 (F.J. Peralta); 1f#, Parna do Jaú, 19.iii a 5.iv.2003 (M.L. Oliveira, J.A. Cunha) (INPA); Pará, 3f#, Conceição do Araguaia, 17–21.ix.1979 (W.L. Overal) (MPEG); Mato Grosso, 3f#, Xavantina, 21.vii.1968 (Rodrigues, V.M.); 3f#,  $12^{\circ}50'S51^{\circ}47'W$ , 14.iii.1968 (O.W. Richards); 14f#, 09.x.1968; 8f#, 27.ix.1968; 1f#, 15.ii.1968 (UFRJ-MN); 1f#, Utiariti, Rio Papagaio, x.1966; 4f#, xi.1966 (Lenko & Pereira); Goiás, 2f#, Dianópolis, 11–14.i.1962 (J. Bechyne); 1f#, Alvorada do Norte, Faz. Mattos, 10.vii.1991 (S.T.P. Amarante & C.F. Martins) (MZUSP); Espirito Santo, 1f#, Santa Teresa, ii.1964 (C.T. Elias); 2f#, Victoria [=Vitória] 29.i.1928 (J.F. Zikán) (UFRJ-MN); 2f#, Colonia Mutum, v.1912 (E. Garbe); 3f#, (Garbe) (MZUSP); 31.i.1928; Minas Gerais, 1f#, Caxambu; 4f#, Serra da Caraça, 1380m, xi.[1]961 (Kloss, Lenko, Martins & Silva); 1f#, Rondonópolis, 14.xii.1950; 1f#, 27.xi.1950; 1f#, 30.xi.1950; 7f#, Passos, ix.1963 (C.T. Elias) (MZUSP); 1f#, Belo Horizonte, 05.v.2000; 1f#, 08.v.2000; 1f#, 31.v.2000 (Zanette, L.R.S.) (MPEG); Rio de Janeiro, 2f#, Itatiaia, Faz. Penedo, 15.ii.1942 (Vygod) (UFRJ-MN); N. Friburgo (date and collector not specified) (MPEG); Paraná, 1f#, São João Petrópolis, 6–12.vi.1967 (C. & C.T.

Elias); 1f#, Parque estadual de campinhos, Tunas do Paraná, 24.i.2004 (Gonçalves & Aguiar) (UFPR); Rondônia, 1f#, Vilhena, 17.xii.1986 (C. Elias) (UFPR); 1f#, Porto Velho, 08.vii.2010 (Noll, F.B.) (UNESP-IBILCE); São Paulo, 9f#, São Paulo, 01.ii.1944 (Z. Prado); 1f#, Piquette (MZUSP); 3f#, Rio Claro, 21.xi.1970; 2f#, 07.x.1970, 1f#, 13.i.1971 (Machado, V.L.); 1f#, 14.iii.1969 (Rodrigues, V.M.) (UNESP); 1f#, Ribeirão Preto, Campus USP, 24.viii.1999 (Zanella); 1f#, Franca, i.1911 (E. Garbe); 1f#, Itu, 09.ii.1961; 1f#, Salesópolis, Est. Biol. Beraceia 8–9.x.1988; 1f#, Campos da Serra, Cabeceiras do Rio M<sup>o</sup> Boy Guassu, 25.xi.1940 (F. Lane); 1female, Jaboticabal, Monte Alto, vii.1914 (R.v. Ihering) (MZUSP); 3f#, Ribeirão Preto, 27.viii.1979 (S. Pompolo); 1f#, Colônia 2RP; 2f#, 2m#, 12.i.1979; 1f#, Itatiaya [=Itatiaia], 700m, 13.xi.1931 (W. Zikán); 1f#, Est. Biológica, 13.xi.1931 (M. Zikán); 1f#, Trav. Lopes Et. Oiticica, Eug. Lafevre, 01.xi.1937 (UFRJ-MN); 1f#, Santo Amaro, 11.xi.1921 (AMNH); Santa Catarina, 1f#, São Bento do Sul, 26°19'S49°18'W, 15.x.2001 (Penteado Dias & Equipe) (MZUSP); COLOMBIA: Caqueta, 1f#, Yuruyaco, Florencia, 26.i.1979; 1f#, N. de Sant, Maracaibo Basin, Tibu, 15–16.vi.1976 (M. Cooper) (BMNH); ECUADOR: Sucumbios, 9f#, Limoncocha, 0°24'S76°36'W, nest#16135, 28.vi.1971 (M. Nauman); Oriente, 1f#, Rio Cholayacu, 2.iii.1969 (L. Pena); Napo, 3f#, Anangu, 25–30.xi.1987 (Huybensz, M.); FRENCH GUIANA: 2f#, La Mana, 1854 (Melinon) (MZUSP); GUYANA: Bartica, Kartabo, 1f#, 25.iv.1924 (MZUSP?); Warratuk, 1f#, 31.viii.1937 (Richards & Smart) (BMNH); Mazaruni, 1f#, 31.viii.1937 (Richards Coll.) (BMNH); PARAGUAY: 1f#, Puerto Bertoni (Bertoni) (MZUSP); PARAGUAY: Bertoni (date and collector not specified) (MPEG); PERU: Loreto, 3f#, Divisoria, 1500m, ii.1947 (W. Weyrauch); 1f#, Oxapampa, 1600m, 1940 (Weyrauch); Madre de Dios, 2f#, Loromayo, 10.ix.1962 (L.E. Pena); 1f#, 156km from Puerto Maldonado, 10–30.ix.1962 (AMNH); Valle Chanchamayo, 1f#, 5.iii.1949 (T. Schunke) (BMNH); 3f#, 1.031; 1f#, Pachitea; 1f#, ix. 1895; 1f#, 1. 031; (MZUSP); 6f#, Oxapampa, 1600m, 1940 (Weyrauch) (UFRJ-MN); SURINAM: 2f# (MZUSP); VENEZUELA: 1f#, 24.vi.1926 (H.E. Box).

**Distribution.** Argentina: Misiones; Bolivia: Beni, \*La Paz; Brazil: \*Amapá, \*Acre, \*Amazonas, Bahia, \*D. F., Espírito Santo, Goiás, Maranhão, Mato Grosso, Minas Gerais, Pará, Rio de Janeiro, \*Rondônia, Santa Catarina, São Paulo; Colombia: \*Amazonas, \*Caqueta, Magdalena, \*Putumayo; Ecuador: Napo; French Guiana; Guyana; Paraguay; Peru: Huánuco, Junín, Loreto, Cerro de Pasco; Surinam, Venezuela.

**Remarks.** *P. sedula* is widely distributed throughout most of South America, except for Chile. In this paper, we present new collection records of this species in the Amazon. Note that Richards (1978) considered the same species (black and *sedula*) as “*morphs*,” based mainly on their color pattern and punctures. In some individuals, we also observed the existence of much less obvious wing-like processes, as in *P. amarella* and *P. acutiscutis*. Nevertheless, other traits indicate that only one species can be recognized. Thus, we propose that such observations should be treated only as variation among individuals, as in *P. minutissima*.

### ***Protopolybia weyrauchi* Bequaert, 1944**

(Figs. 10, 11, 12, 17, 18, 19, 20, 24, 28)

*Protopolybia weyrauchi* Weyrauch, 1943: 73 (nomen nudum).

*Protopolybia weyrauchi* Bequaert, 1944a: 126 (holotype: f#, Peru, San Ramon, Valle Chanchamayo 800m, 01.ii.1940 (W. Weyrauch), examined; paratype: 2m#, 45f# (same data as holotype) (AMNH), examined).

*Protopolybia weyrauchi*: Richards, 1978: 140, 149; Rasmussen & Asenjo, 2009: 50; Rasmussen & Lamas 2011: 57.

**Diagnosis.** Cuticle dull to shiny; mesoscutum and scutellum with strong and dense micropunctuation and shallow mesopunctuation; color brown, richly marked with yellow to whitish spots (Fig. 10), metanotum triangular, metanotal process elongate (Fig. 11); pronotal fovea distinct, preceded by anterior prominence relatively distant from the pronotal carina.

**Redescription.** FEMALE. Length of fore wing 5.10 mm; clypeus relatively wide, approximately as long as wide (HC1p=0.65; MxWC1p= 0.70; TeW= 0.48; MiWC1p= 0.63 mm), with ventral margin pointed; tentorial pit closer to antennal socket than to eye margin; interantennal area relatively wide, approximately two times diameter of antennal socket; mandibles relatively short with length 0.71 × distance between eyes at vertex; occipital carina distinct, fading very close to insertion of mandible; humerus normal, pronotal carina blunt, non-lamellate, distinctly extending downwards at side; pronotal fovea distinct, preceded by anterior prominence relatively distant from the pronotal carina; length of mesoscutum approximately 1.02 × its width;



mesepisternal groove absent; scutellum with short but well-marked median line; metanotum triangular, length of median axis approximately  $0.93 \times$  width of central disk, metanotal process elongate; propodeum with a wide and shallow cavity; first metasomal segment with petiole short, almost as long as wide; T1 notably narrower than T2.

Front, mesoscutum, scutellum and metanotum with strong and dense micropunctuation and shallow mesopunctuation (Fig. 28); ventral region of mesopleuron and T2 to T5 with distinct punctures; clypeus with short golden bristles, except ventral margin, which has elongated bristles; eyes with minute and sparse bristles; body almost completely with short bristles; propodeum with long bristles.

Coloration: species brown, richly marked with yellow to whitish spots; antennae ventrally testaceous, dorsally brown to black; mandibles, clypeus, inner and outer orbit and front testaceous with yellowish spots, extensive mark on the pronotal carina and fovea, two stripes on the mesoscutum, tegulae partially (Fig. 12), large spot on the mesepisternum extending to scrobe, extensive mark on metapleuron, scutellum and metanotum partially, propodeum with paired dorsal marks, T1 with distal band, T2 with basal piriform mark, and distal band yellow on T2, T3 to T5. Coxae yellow, femora and tibiae brown to black; tarsi brown; wings hyaline, venation brown.

MALE. Length of fore wing 5.5 mm; eyes wide, strongly produced inwards; clypeus narrow, longer than wide, with elongated gold bristles, ventral margin little produced and pointed; tentorial pit closer to eye margin than to antennal socket; gena very narrow; color pattern as female. *Genitalia*. Basal angle of paramere widened, apical angle narrower (Fig. 17); digitus narrow with apical margin approximately curved, and with short bristles (Fig. 20); basal process narrow, but not distinctly pointed; cuspis with short and sparse bristles; ventral process of aedeagus approximately angular, not laterally produced in dorsal view, very sclerotized and laterally serrated (Fig. 19); pre-apical region of aedeagus not angular.

**Material examined.** Paratypes: PERU: San Ramon, Valle Chanchamayo 800m, 2m#, 45f#, 01.ii.1940 (W. Weyrauch) (AMNH). **Other material.** PERU: Valle Chanchamayo 800m 2f#, 3m#, 1939 (UFRJ-MN), 12f# (BMNH).

**Distribution.** Peru: Junin.

### Key to species of the *Protopolybia sedula* species-group

1. Mesoscutum and scutellum with strong and dense micropunctuation and shallow mesopunctuation (Fig. 28); color brown, richly marked with yellow to whitish spots (Figs. 10 and 12), metanotum triangular, metanotal process elongate (Fig. 11); pronotal fovea distinct, preceded by anterior prominence relatively distant from the pronotal carina (Fig. 21) ..... *P. weyrauchi* Bequaert
  - Mesoscutum and scutellum with moderate micropunctuation and shallow mesopunctuation (Fig. 25–27); scutellum with more sparse mesopunctuation; color variable, not brown; metanotal process not elongate (Fig. 1 and 4); anterior prominence in front of the pronotal fovea extending above and close to pronotal carina, nearly collinear with fovea (Fig. 22–24).....2
2. Pronotal carina weakly lamellate, little extended below (Fig. 23); petiole of T1 narrow, without wing-like processes; species almost entirely black (form dark) or black moderately marked with yellow spots (form *sedula*) (Fig. 7 and 9); front with two small yellow spots (Fig. 8) ..... *Protopolybia sedula* (de Saussure)
  - Pronotal carina blunt, non-lamellate, distinctly extending downwards at side (Fig. 22 and 24); petiole of T1 reduced, wing-like processes not very sharp (Fig. 3).....3
3. Species yellow, with light ferruginous and very few black markings, commonly on mesoscutum; pronotal fovea distinct and deep, metanotal lobe with apex pointed (Fig. 4–6)..... *Protopolybia amarella* Bequaert
  - Species black, richly marked with yellow spots; front with extensive Y-shaped mark (Fig. 2); pronotal fovea distinct, but shallow; metanotal lobe with apex slightly rounded (Fig. 1).... *Protopolybia acutiscutis* (Cameron)

### Acknowledgements

We are very grateful to all the institutions, facilitators of loans and the two anonymous reviewers for their corrections and suggestions. The first author is also very grateful to Dr. Gavin Broad, Jaswinder Boparai and Natalie Dale-Skey for their collaboration and hospitality during the visit to BMNH and to CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico, grant 140080/2015-5) for their financial support.

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### Figure legends

**Figures 1–6.** 1, 2, 3. *Protopolybia acutiscutis*. wp, wing-like processes; 4, 5, 6. *Protopolybia amarella*.

**Figures 7–12.** 7, 8, 9. *Protopolybia sedula*; 10, 11, 12. *Protopolybia weyrauchi*, Paratype.

**Figures 13–20.** 13, 14, 15, 16. *Protopolybia sedula*; 17, 18, 19, 20. *Protopolybia weyrauchi*; 13, 17. Parameres of male genitalia. 14, 15, 18, 19. Aedeagus in dorsal and lateral views. 16, 20. Volsella of male genitalia in lateral view. Scale 0.2 mm.

**Figures 21–24.** 21. *Protopolybia acutiscutis*, pronotum, lateral view; 22. *P. amarella*; 23. *P. sedula*; 24. *P. weyrauchi*.

**Figures 25–28.** 25. *Protopolybia acutiscutis*, mesoscutum, dorsal view; 26. *P. amarella*; 27. *P. sedula*; 28. *P. weyrauchi*. Red arrows, micropunctuation and mesopunctuation.

Plate 1



Plate 2



Plate 3

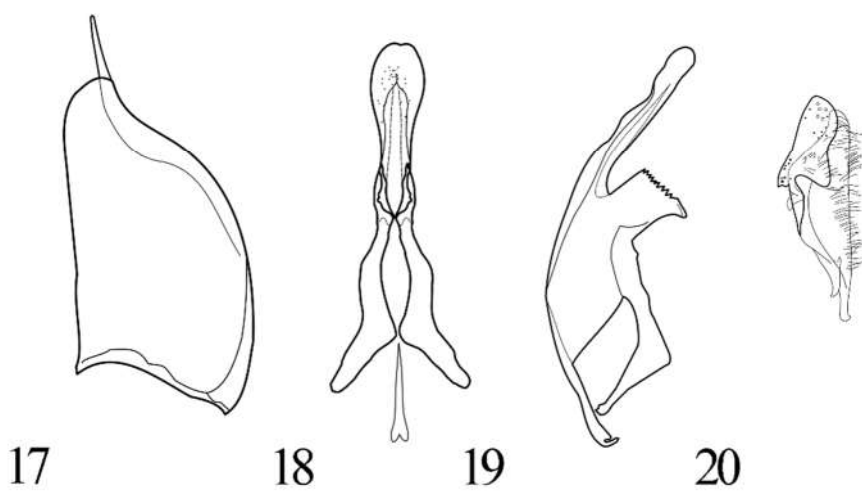
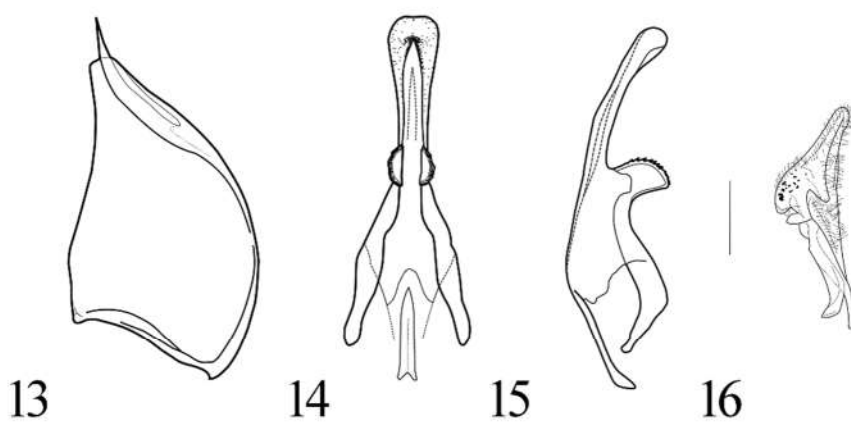


Plate 4



Full title of manuscript: **Taxonomic revision of the *Protopolybia sedula* species-group (Hymenoptera, Vespidae, Polistinae), with an new identification key to species**

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Family name of first author: **SANTOS**

File name of manuscript: **Santos\_et\_al\_Psedula**

Number of plates: [dropbox link] **Five**

Number of references cited in this ms: **53**

Number of new taxa described in this article: **Zero**

Did you use m# and f# symbols (♂♀): **Yes**

High taxon: Hymenoptera: Vespoidea: **Vespidae**

AUTHOR NAMES FOR RUNNING TITLE (USE & AND CAPS): **SANTOS ET AL.**

PREFERRED SHORT RUNNING TITLE (CAPS): **P. SEDULA SPECIES GROUP**

Accepted by Kevin A. Williams: February 6, 2018; published in April 3, 2018



# Capítulo 3

## **Taxonomic revision of the *Protopolybia picteti-emortualis* species-group (Richards, 1978) (Hymenoptera: Vespidae, Polistinae), with the description of two new species**

O capítulo 3 desta tese foi elaborado e formatado conforme as normas da publicação científica *Zootaxa*, as quais se encontram em anexo.

## Taxonomic revision of the *Protopolybia picteti-emortualis* species-group (Richards, 1978), with descriptions of two new species (Hymenoptera: Vespidae, Polistinae)

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### ABSTRACT

A taxonomic revision of the *Protopolybia picteti-emortualis* species-group now demonstrates that this group is possibly the largest of *Protopolybia*, comprising 15 species: *P. eldinari* **sp. nov.**; *P. djaneteae* **sp. nov.**; *P. cameranii* (Zavattari 1906) = *P. bella* (Von Ihering 1903) **syn. nov.**; *P. fulvotincta* **stat. nov.**; *P. biguttata*, *P. nitida*, *P. alvarengai*, *P. iheringi*, *P. perfulvula*, *P. steinbachi*, *P. weeleri*, *P. rotundata*, *P. picteti*, *P. emortualis* and *P. duckei*. Male and female genitalia are illustrated for *P. biguttata* Bequaert, *P. bella*, *P. nitida*, *P. fulvotincta* and *P. picteti*. New collection records and a new identification key are presented to this species-group.

**Key words:** Neotropical region, social wasps, Epiponini, diversity, male genitalia.

### Introduction

*Protopolybia* (Ducke 1905) is a Neotropical genus of social wasps in the tribe Epiponini, distributed from México to Argentina (Carpenter & Marques 2001), whose species can be recognized by the presence of a distinct metanotal process and the second rami of the sting apparatus with an adjacent area very wide and sclerotized (Carpenter & Wenzel 1989, Silveira & Silveira 1994, Santos-Junior et al. 2015).

*Protopolybia* comprises 39 known species that are divided into four groups (Santos-Junior et al. 2015, 2017). Richards (1978) proposed the group of *P. picteti* based on morphological characters of the clypeus, pronotum, pronotal fovea, hairs on the dorsal surface, and metasomal marks, though only one of these characters is a synapomorphy for this group of species (Santos-Junior et al. 2015). Here we consider the clade that gathers the *P. emortualis* and *P. picteti* species-groups (see Santos-Junior et al. 2015), composed of 15 species, two of them described herein.

The *Protopolybia picteti-emortualis* species-group is composed of 15 species characterized by several unique traits such as the gena very wide, apex of metanotal process truncated, whole distal area of female mandible subjacent to teeth 1–4 appearing as a nearly vertical plane in frontal view, and the shape of mandible mesial median denticle greatly reduced and mainly transversal (Santos-Junior et al. 2015). Besides these, the *picteti* subclade presents the unique traits of genal margin complete and very strong, pretegular carina high, mesoscutum integument very smooth and shining with sparse mesopunctuation and sparse very long hairs (Santos-Junior et al. 2015).

In this paper a taxonomic revision of the *P. picteti-emortualis* species-group is presented, based on external morphology of females, males and characters of the nest structure.

### Material and Methods

Acronyms of collections which provided specimens for this study are cited according to Evenhuis (2007), followed by the name of their respective curators: American Museum of Natural History, New York, USA (AMNH), Dr. J.M. Carpenter; Natural History Museum (British Museum), London, England (BMNH), Dr. G. Broad; Muséum National D'histoire Naturelle, Paris, France (MNHN), Dr. C. Villemant; Naturhistorisches Museum Wien, Vienna, Austria (NHM), Dr. D. Zimmermann; Naturhistorisches Museum der Burgergemeinde

Bern, Bern, Switzerland (NMBE), H. Baur; Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil (INPA), Dr. A.L. Henriques; Museu Paraense Emílio Goeli (MPEG), Belém, Pará, Brazil, Dr. O.T. Silveira; Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP), Dr. C.F. Brandão; Universidade Estadual Paulista Julio de Mesquita Filho, São José do Rio Preto, São Paulo, Brazil (UNESP-IBILCE), Dr. F.B. Noll; Fundação Osvaldo Cruz, Rio de Janeiro, Brazil (FIOC), Dr. J.M.C. Von Sydow.

#### *Morphological studies, measurements and terminology*

Specimens of the *P. picteti-emortualis* group were examined using a Leica MZ16 stereomicroscope equipped with an ocular micrometer and camera lucida. Morphological structures were photographed using a Leica DFC 420 digital camera coupled to the stereomicroscope. Images were processed using LAS software and edited using the Helicon Focus 6.2 and Photoshop CS5. The genitalia of males were extracted and immersed in 10% KOH solution for 8 hours, washed in running water, and subsequently stored in glycerin in Eppendorf tubes. When available, the genitalia of males were drawn under an optical microscope equipped with camera lucida.

Detailed descriptions or redescriptions were made of *P. wheeleri* Bequaert, *P. rotundata* Ducke, *P. iheringi* Ducke, *P. alvarengai* Richards, and *P. steinbachi* Richards (Bequaert 1944a, Richards 1978), and here only a diagnose of these species is given, followed by descriptions of the male, male genitalia, and new records. It was not possible to make the drawing of the aedeagus of *P. picteti* (de Saussure) in dorsal view, so this is presented only in lateral view. Measurements were made of body structures using a stereomicroscope with an ocular micrometer, using abbreviations proposed in part by Silveira (2006) and modified by Santos-Junior et al. (2015).

The terminology utilized by Santos-Junior et al. (2015) was adopted to describe the external morphology of specimens. Structural characteristics of the nest were described following Wenzel (1991, 1998). The terminology of Carpenter and Mateus (2004) and Andena et al. (2007) were adopted for the morphology of male genitalia. The abbreviation T refers to numbered metasomal terga. New records in geographical distributions are asterisked (\*).

#### **Genus *Protopolybia* Ducke, 1905**

*Protopolybia* Ducke, 1905a: 7, 9, 17. Type species: *Polybia bella* R. von Ihering, 1903 by subsequent designation (Bequaert 1944a).

*Pseudochartergus* Ducke 1905a: 8, 9, 15. Type species *Charterginus cinctellus* Fox, 1898 (= *Nectarina chartergoides* Gribodo, 1892) by subsequent designation (Bequaert 1938). Junior subjective synonym of *Protopolybia* Ducke, 1905 according to Carpenter and Wenzel (1989: 185)

*Protopolybia* Ducke: Bequaert 1938: 103.

*Pseudochartergus* Ducke: Bequaert 1938: 103.

*Protopolybia* Ducke: Bequaert 1944a: 97, 98, 99 (part.).

*Protopolybia* Ducke: Bequaert 1944b: 252, 265 (part.).

*Pseudochartergus* Ducke: Bequaert 1944b: 252, 264 (part.).

*Protopolybia* Ducke: Richards 1978: 8, 136.

*Pseudochartergus* Ducke: Richards 1978: 8, 154.

*Protopolybia* Ducke: Santos-Junior et al. 2015: 154, 172.

#### **Taxonomy of the *Protopolybia picteti* species-group**

The *Protopolybia picteti-emortualis* species-group consists of social wasps with average length 4.57 mm, with several independent unique states such as the gena very wide, apex of metanotal process truncated, distal area of female mandible as a nearly vertical plane in frontal view, and the shape of mandible mesial median denticle greatly reduced and mainly transversal (Santos-Junior et al. 2015). The *picteti* subclade presents the unique traits of genal margin complete and very strong, pretegular carina high, mesoscutum integument very smooth and shining with sparse mesopunctuation and sparse very long hairs (Santos-Junior et al. 2015). Detailed descriptions of *P. rotundata* Ducke, *P. wheeleri* Bequaert, *P. alvarengai* Richards, *P. steinbachi* Richards, *P.*

*iheringi* Ducke are provide by Bequaert (1944) and Richards (1978). Carpenter et al. (2001) revalidated *Protopolybia duckei* and presented an excellent combination of characters that makes it possible to easily distinguish this species from *P. emortualis*. For these two species, only a diagnosis and additional data of collection records are presented here.

### ***Protopolybia alvarengai* Richards, 1978**

*Protopolybia alvarengai* Richards, 1978: 139, 146. (holotype: f#, Brasil: RO, Pimenta Bueno, xi.1960 (M. Alvarenga) (UFPR), examined.

**Diagnosis.** Length of fore wing 4.37 mm; clypeus wide, with ventral margin approximately rounded; front margin of pronotum distinctly angled a little below the fovea; metanotal process with apex truncated; propodeum with wide and deep excavated cavity, like a central channel; species black to brownish, with few yellow marks; vertex and mesoscutum black; scutellum with two spots, scutellum, metanotum, propodeum and T2 anteriorly, yellow.

**Material examined.** BRAZIL: Pará, 4f#, Santarém, Taperinha, 1974 (R.L. Jeanne) (BMNH), 1f#, Belterra, 23.xi.1993 (G.C. Venturieri), 3f#, 12.xii.1999 (MPEG).

**Distribution.** Brazil: Rondônia, \*Pará; Colombia: Nariño.

**Remarks.** Richards (1978) considered the individuals that occur in Pará, as structurally close to *P. alvarengai*. Examining these specimens, there is in fact a great similarity between the populations from Taperinha (Santarém, Pará) and the type locality, presenting only slight variation in the pattern of spots on the scutellum and T2.

### ***Protopolybia bella* (R. von Ihering, 1903)**

(Figs 1, 2, 3, 4, 33, 34, 35, 36)

*Polybia bella* R. von Ihering, 1903: 146. (holotype: f#, Surinam, xii.1923? (MZUSP), examined.

*Polybia bella* R. von Ihering 1904: 177; Dalla Torre 1904: 77.

*Protopolybia bella*: Ducke 1905a: 18; 1905b: 674; 1907: 165, 166; 1910: 469, 473; 1918: 324; Richards 1978: 139, 146; Overall 1978: 11; Silveira & Carpenter 1995: 49; Rasmussen & Asenjo 2009: 49.

*Polybia cameranii*: Zavattari 1906: 10. **Syn. nov.**

*Protopolybia cameranii*: Ducke 1918: 324 (synonymized with *bella*); Richards 1978: 145.

*Protopolybia picteti* var. *bella*: Bequaert, 1944a: 117, 118; 1944b: 266; Araujo 1960: 252.

**Diagnosis.** Length of fore wing 4.0 mm; humerus distinctly projecting and shortened, carina lamellate and recurved forwards at extremity, not extending downwards. Metanotal process with apex truncated (Fig. 1); propodeum with wide and deep excavated cavity, heart-like shape (Fig. 1); color black to brownish moderately with marks yellow, scutellum with two small spots, metanotum partially, yellow; T2 with three spots anteriorly and narrow band posteriorly (Fig 1–4); preapical region of aedeagus angular, parameral spine laterally expanded at base (Fig. 33).

**Redescription.** FEMALE. Length of fore wing 4.0 mm; clypeus wide (HClp=0.56; MxWClp=0.78; TeW=0.50; MiWClp=0.75 mm), with ventral margin acute; tentorial pit closer to antennal socket than to eye margin; interantennal area relatively wide, approximately 2 × diameter of antennal socket; mandibles relatively short with length 0.81 × distance between eyes at vertex; occipital carina distinct, very strong and salient throughout; humerus distinctly projecting and shortened, carina lamellate and recurved forwards at extremity, not extending downwards; length of mesoscutum approximately 0.95 × its width; mesepisternal groove absent; scutellum with short and marked median line inconspicuous; metanotum triangular, length of median axis 0.73 × width of central disk, metanotal process with apex truncated (Fig. 1); propodeum with wide and deep excavated cavity, heart-like shape (Fig. 1), propodeal valves narrow; T1 in dorsal view with petiole very short and distal margin wider and nearly straight, cup-like.

Frons, mesoscutum, scutellum and metanotum with more sparse micropunctuation and deeper and stronger mesopunctuation, mesopleuron and T2 to T5 with distinct punctures; clypeus with short golden bristles, except

on ventral margin, which has elongated bristles; eyes glabrous; vertex, mesoscutum, scutellum and metanotum with more sparse and quite long hairs.

Species black to brown, moderately marked with yellow spots (Fig. 1–4); antennae ventrally testaceous, dorsally brown to black; mandibles brown, clypeus almost entirely yellow (Fig. 3), inner and outer orbit with wide bands that extend to ocular sinus, frons with bilobate mark, two marks on vertex, small marks on pronotal carina and fovea, mesoscutum without marks, tegulae almost entirely brown, spots on mesepisternum and area below scrobe, scutellum with two spots, metanotum partially, propodeum commonly with small paired dorsal marks, T1 without marks, three basal spots and distal band on T2 (Fig. 1, 2 and 4); T3 with distal band yellow; T4 and T5 black to brown. Coxae, femora and tibiae brown to black; tarsi brown; wings hyaline, venation brown.

MALE. Length of fore wing 4.80 mm; eyes wide, strongly produced inwards; clypeus narrow, longer than wide, with silvery bristles, ventral margin acute; tentorial pit closer to eye margin than to the antennal socket; gena narrow; color like the female. Parameral spine laterally expanded at base and without elongate bristles (Fig. 33); basal and apical angle of paramere widened (Fig. 33); digitus narrow, with apical margin rounded, basal margin with dense punctures, basal process acuminate; cuspis moderately with elongated bristles (Fig. 36); ventral process of aedeagus angular, not projecting laterally, strongly sclerotized and serrated, laterally (Fig. 34 and 35); preapical region of aedeagus angular (Fig. 35).

**Material examined.** BRAZIL: Amazonas, 1f#, Parque Nac. do Jaú, 17–19.xi.2005 (M.L. Oliveira & F. Pereira), 1f#, 19.iii–05.iv.2003 (M.L. Oliveira & J.A. Cunha) (INPA), 2f#, 4m#, Rio Japurá, 14.ix.1904 (Ducke) (MPEG), 1f#, 1.v.1904 (Ducke, A.) (BMNH), 1f#, Presidente Figueiredo, 20.vi.2004 (Noll, F.B.) (UNESP-IBILCE); Pará, 1f#, Belterra, 13.xii.1999 (G.C. Venturieri) (MPEG); PERU: Tingo Maria, 24f#, Huan., 670m, i.1947 (W. Weyrauch), 1m#, Rio Hualaga, x.1948 (AMNH), 4f#, 670m (W. Weyrauch) (FIOC), 15f# (W. Weyrauchi), 1f#, Iquitos, 11.viii.1906 (Ducke) (MPEG).

**Distribution.** Panama; Suriname; Peru: Huánuco, Junín, Iquitos; Brazil: Amapá, Amazonas, \*Pará; Bolivia.

**Remarks.** The type specimen of *P. cameranii* was not examined, but in the original description it is very congruent with *P. bella*. Silveira & Carpenter (1995) examined one specimen of *P. bella* from Panama, the same type locality of *P. cameranii*, however they did not comment on a possible synonymy between these two species. Thus, based on the observations of Silveira & Carpenter (1995), *P. cameranii* is here treated as a junior synonym of *Protopolybia bella*.

The male genitalia of *P. bella* is described herein, and it is possible to see large differences in the shape of the aedeagus: ventral process of aedeagus angulated, not projecting laterally, strongly sclerotized and serrated laterally, when compared to *P. biguttata*, a species that is structurally closely related to *P. bella*, that presents ventral process of aedeagus approximately lobed, not projecting laterally, strongly sclerotized and laterally serrated.

### ***Protopolybia biguttata* Bequaert, 1944** (Figs 37, 38, 39, 40)

*Protopolybia picteti* var. *biguttata* Bequaert, 1944: 116, 119 (holotype: 1f#, Peru, Junin, El Campamiento, Col. Perene (Univ. Cornell, Ithaca), examined female specimen from the type locality.

*Protopolybia biguttata*: Richards 1978: 139, 148; Rasmussen & Asenjo 2009: 49.

**Diagnosis.** Length of fore wing 4.50 mm; humerus distinctly projecting and shortened, carina lamellate and recurved forwards at extremity, not extending downwards; metanotal process with apex truncated; propodeum with wide and deep excavated cavity; propodeal valves distinctly wide anteriorly; species black, with few yellow marks; digitus narrow, with apical margin rounded (Fig. 40).

MALE. Length of fore wing 4.70 mm; eyes wide, strongly produced inwards; clypeus narrow, longer than wide, with silvery bristles, ventral margin acute; tentorial pit approximately equidistant to eye margin and to the antennal socket; gena narrow; color like female, except by mandible yellow, and narrow mark on outer orbit extending to vertex. Parameral spine narrow, without elongate bristles; basal and apical angle of paramere widened (Fig. 37); digitus narrow (Fig. 40), with apical margin rounded; basal process of digitus narrow and acuminate; cuspis filled with dense and elongated bristles; ventral process of aedeagus approximately lobed,

not projecting laterally, strongly sclerotized and laterally serrated (Fig. 38 and 39); preapical region of aedeagus angular (Fig. 39).

**Material examined.** ECUADOR: Napo, 4f#, 3m#, 22km N Tena, 19.xii.1990 (Carpenter & Wenzel) (AMNH), 1f# (MZUSP).

**Distribution.** Peru, \*Ecuador.

**Remarks.** Specimens from Ecuador, Napo, are black, moderately marked with yellow spots. These present mesoscutum black, scutellum with a bilobated mark, metanotum partially yellow, three basal spots, and one distal band on T2.

***Protopolybia djaneteae* Santos & Silveira sp. nov.**

(Figs 5, 6, 7, 8, 9, 10, 57, 61)

**Diagnosis.** Length of fore wing 3.95 mm; front margin margin of pronotum distinctly angled below the fovea, pronotal fovea obsolete, humerus short and roundly truncate, carina with lamella reduced (Fig. 8 and 9); mesoscutum with numerous notable elongated hairs, distinctly curved apically (Fig. 8 and 57); metanotal process distinctly wider than long, with apex truncated (Fig. 10); propodeum with a wide and shallow cavity, heart-like shape (Fig. 10); T1 with petiole short but remarkable; color brownish richly marked with yellow to whitish (Fig. 6 and 7), mesoscutum reddish, generally with two stripes, scutellum with two marks, metanotum with a band anterior (Fig. 9 and 10).

**Description.** FEMALE. Length of fore wing 3.95 mm; clypeus wide (HClp=0.55; MxWClp=0.80; TeW=0.55; MiWClp=0.75 mm), with ventral margin acute; tentorial pit closer to antennal socket than to eye margin (Fig. 5); interantennal area relatively wide, approximately  $2 \times$  diameter of antennal socket; mandibles relatively short with length  $0.84 \times$  distance between eyes at vertex; occipital carina distinct, very strong and salient throughout; humerus short and roundly truncate, carina with lamella very reduced (Fig. 9); front margin of pronotum distinctly angled below the fovea (Fig. 8 and 61), pronotal fovea obsolete, preceded by a short and low prominence (Fig. 8 and 61); length of mesoscutum approximately  $0.95 \times$  its width; mesepisternal groove absent; scutellum with a short but well-marked median line; metanotum triangular, length of median axis approximately  $0.73 \times$  width of central disk, metanotal process distinctly wider than long, with apex truncated; propodeum with a wide and shallow cavity, heart-like shape (Fig. 10); T1 sessile with distal margin wider and nearly straight, cup-like.

Frons, mesoscutum, scutellum and metanotum with more sparse micropunctuation and deeper and stronger mesopunctuation; mesopleuron and T2 to T5 with distinct punctures; clypeus with short golden bristles, except on ventral margin, which has elongated bristles; vertex, mesoscutum, scutellum and metanotum with numerous notable elongated hairs, distinctly curved apically.

Species brownish richly marked with yellow to whitish spots (Fig. 5–7); antennae ventrally testaceous or brown, dorsally black; mandibles and clypeus entirely yellow, inner orbit with wide band that extend to ocular sinus, outer orbit with band that extend to vertex, frons with a trilobate mark (Fig. 5), two wide marks on vertex, extensive mark on pronotal carina and fovea, mesoscutum brown commonly with two stripes, tegulae partially, large spot on mesepisternum and on area below scrobe, large spot on metapleuron, scutellum with two spots, metanotum partially, propodeum with paired dorsal marks, distal spot on T1, basal and distal spot on T2. Fore coxae yellow to whitish, mid and hind coxae brown, femora and tibiae brown; tarsi testaceous; wings hyaline, venation brown.

**Material examined.** BRAZIL: Amazonas, 2f#, Hwy ZF 2, km 19.5, ca 60km N Manaus, 02°30'S60°15'W, 18.viii.1979 (Adis, Erwin, Montgomery) (INPA).

**Distribution.** Brazil: Amazonas.

**Remarks.** *Protopolybia djaneteae* sp. nov. presents coloration and structure similar to *P. fulvotincta*. Both of these species have the metanotal process distinctly wider than long and the propodeal median furrow wide and shallow, with a heart-like shape. *P. djaneteae* presents the frontal margin of pronotum distinctly angled, the apex of metanotal process truncated, and numerous long hairs on the mesoscutum (Figs. 8 and 57), different from *P. fulvotincta*. In addition to that, *P. fulvotincta* has only one posterior mark on T2, while *P. djaneteae* presents three anterior marks on that same segment, being one medial wide and one band posterior.

**Etymology.** The specific name is in honor of the mother of the first author, Djanete.

***Protopolybia duckei* (du Buysson, 1905)**

(Figs 11, 12, 13, 14)

*Charterginus duckei* du Buysson, 1905: 126 (holotype: f#, Brazil: Bahia (NHM-Vienna); examined).*Charterginus duckei* du Buysson: Ducke 1910: 470; Richards 1978: 144; Carpenter 1999: 17; Carpenter et al. 2001: 179, 180.*Protopolybia emortualis* var. *duckei*: Bequaert 1944a: 116; 1944b: 270; Richards & Richards 1951: 22.*Protopolybia duckei* du Buysson: Carpenter et al. 2001: 180.

**Diagnosis.** Length of fore wing 5.46 mm; occipital carina fading at some point near the middle of gena's height; gena very wide, approximately width of lower lobe of eye in lateral view; clypeus wide, with ventral margin acute; humerus short and roundly truncate (Fig. 11), pronotal carina with lamella reduced; metanotum wider than long, metanotal process short, with apex approximately acute, propodeum with shallow cavity above the valvula (Fig. 12), propodeal valves attenuate (Fig. 13); paramere dorsally slightly angular. Species black with marks yellow; scutellum with two small spots, metanotum partially yellow (Fig. 12 and 14).

**Material examined.** FRENCH GUIANA: Cayenne, Petit-Saut, 6f# xii.1997–i.1998 (A. Dejean) (AMNH); BRAZIL: Pará, 21f#, Melgaço, Caxiuanã-ECFPn, 24.xi.1998 (O. Silveira & J. Pena), 1f#, Belém, Utinga, 12.xii.1978 (F.F. Ramos) (MPEG).

**Distribution.** Brazil: Pará\*, Bahia; French Guiana.

**Remarks.** *P. duckei* has its type locality in Bahia, Brazil. Carpenter et al. (2011) revalidated *P. duckei* based on the external morphology of the female and on the male genitalia, which is different from that of *P. emortualis*. Furthermore, they recorded this species in French Guiana. Here we present the first collection record of this species from the Brazilian Amazon.

***Protopolybia eldinaris* Santos & Silveira sp. nov.**

(Figs 15, 16, 17, 18, 19, 20, 60)

**Diagnosis.** Length of fore wing 4.00 mm; humerus distinctly projecting and shortened, carina lamellate and recurved forwards at extremity, not extending downwards (Fig. 18); mesoscutum with numerous notable elongated hairs, distinctly curved apically; metanotal process long and with apex truncated; propodeum with a wide and shallow cavity, heart-like shape (Fig. 19), propodeal valves wide (Fig. 20 and 60); color black to brownish moderately marked with yellow, mesoscutum with two stripes, sometimes without; T1 and T2 marked posteriorly.

**Description.** FEMALE. Length of fore wing 4.00 mm; clypeus wide ( $HClp=0.60$ ;  $MxWC1p=0.77$ ;  $TeW=0.50$ ;  $MiWC1p=0.75$  mm), with ventral margin acute (Fig. 15); tentorial pit closer to antennal socket than to eye margin; interantennal area relatively wide, approximately  $2 \times$  diameter of antennal socket; mandibles relatively short with length  $0.80 \times$  distance between eyes at vertex; occipital carina distinct, very strong and salient throughout; humerus distinctly projecting and shortened, carina lamellate and recurved forwards at extremity, not extending downwards (Fig. 18); pronotal fovea distinct, preceded by a linear prominence short and narrow; length of mesoscutum  $0.96 \times$  its width; mesepisternal groove absent; scutellum with a short but well-marked median line; metanotum triangular, length of median axis  $0.73 \times$  width of central disk; propodeum with a wide and shallow cavity, heart-like shape (Fig. 19), propodeal valves wide (Fig. 20 and 60); T1 in dorsal view with petiole very short and distal margin wider and nearly straight, cup-like.

Frons, mesoscutum, scutellum and metanotum with more sparse micropunctuation and deeper and stronger mesopunctuation; mesopleuron and T2 to T5 with distinct punctures. Mesoscutum with numerous notable elongated hairs, distinctly curved apically (Fig. 16 and 20); clypeus covered by short golden bristles, except on ventral margin, which has elongated bristles; eyes glabrous; vertex, mesoscutum, scutellum and metanotum with more sparse and quite long hairs.

Species black, richly marked by yellow spots (Fig. 15–18); antennae ventrally brown to testaceous, dorsally black; mandibles brown to testaceous, clypeus almost entirely yellow, inner orbit with wide band that extend to

ocular sinus (Fig. 15), outer orbit with band that extend to vertex, frons with a bilobate mark, two marks on vertex, extensive mark on the pronotal carina and fovea, two stripes on the mesoscutum, sometimes without, tegulae partially, large spot on mesepisternum and on area below the scrobe, two spots on metapleuron, scutellum and metanotum partially, propodeum with paired dorsal marks, distal small spot on T1, three basal and one distal spot on T2; T3 to T5 sometimes with distal spot. Fore coxae yellow, mid and hind black to brown, femora and tibiae black to brown; tarsi brown; wings hyaline, venation black.

**Material examined.** BRAZIL: Pará, 1f#, Belterra, 6.i.2000 (G.C. Venturieri), 1f#, 13.xii.1999 (MPEG); Mato Grosso, 1f#, Barra dos Bugres, R.E. Serra das Araras, 22.i.1986 (Zanuto, M.) (MPEG); PERU: Pachitea (Ducke) (MPEG); BOLIVIA: La Paz, 1f#, Alto Rio Beni, South of Rio Inicua, 1100m, 15–18.i.1976 (L.E. Peña) (AMNH).

**Distribution.** Brazil: Pará, Mato Grosso; Bolivia; Peru: Pachitea.

**Remarks.** *Protopolybia eldinaris* sp. nov. is a species structurally similar to *P. bella*. However, *P. eldinaris* is significantly more marked with yellow spots and the fovea is more evident. In addition, different from *P. bella*, the propodeum presents a wide and shallow heart-shaped cavity.

**Etymology.** The specific name is in honor to the first author's wife, Eldinar.

### ***Protopolybia emortualis* (de Saussure, 1855)**

(Figs. 21, 22, 23)

*Chartergus emortualis* de Saussure, 1855: 374 (holotype: f#, Brazil: Santarém (BMNH); examined).

*Chartergus emortualis*: Smith 1857: 135; Dalla Torre: 1894: 168; 1904: 85; Ducke 1904: 326.

*Chartergus rufiventris*: Ducke 1904: 325, 329, 335. (lectotype: f#, Brasil, Pará, 30.vii.1899 (Ducke) (MNHN)); examined; paralectotype 1f#, same data as lectotype; not examined.

*Chartergus rufiventris*: Ducke 1905a: 18; 1905b: 662, 673; Ducke 1907: 166; Richards 1978: 144; Nascimento & Overall 1979: 9.

*Protopolybia rufiventris*: Ducke 1905b: 662, 673.

*Protopolybia emortualis*: Ducke 1907: 165, 166; 1910: 468, 470; 1914: 309; 1918: 324; Bequaert 1944a: 101, 115; 1944b: 265, 270; Richards 1978: 138, 144; Overall 1978: 11; Carpenter & Wenzel 1989: 179, 181, 184; Sarmiento 1994: 359; Carpenter et al. 2001: 179, 180; Rasmussen & Asenjo 2009: 49.

*Charterginus rufoornatus* Cameron 1912: 220 (lectotype: f#, Guyana (BMNH); examined).

*Charterginus rufoornatus*: Richards & Richards 1951: 22; Richards 1978: 144; Carpenter 1999: 18.

*Protopolybia laboriosa*: Bodkin 1918: 308. (Misidentification).

*Protopolybia rufo-ornata*: Bequaert 1944a: 131; 1944b: 270.

**Diagnosis.** Length of fore wing 5.21 mm; occipital carina distinct, extending over three fourth of height of gena in lateral view, terminating before articulation of mandibles, gena very wide, approximately width of lower lobe of eye in lateral view (Fig. 21); clypeus wide, with ventral margin acute; humerus short and roundly truncate, pronotal carina with lamella reduced. Metanotal process with apex truncated; propodeum deeply excavated above the valvula (Fig. 22), propodeal valves basally triangular (Fig. 23). Color brown to reddish, moderately marked with yellow; scutellum and metanotum partially yellow, propodeum with paired dorsal marks. Paramere dorsally smoothly rounded.

**Material examined.** COLOMBIA: Colombia amazônica, 12f#, xi.1912 (Ducke) (MPEG); BRAZIL: Amapá, 3f#, Amapari, Tucano-2, 11–15.xi.1993 (N. Bittencourt), 1f# (W. França) (MPEG); Pará, 1f#, 02.x.1900 (Ducke), 20f#, Melgaço, Caxiuanã-ECFPn, 24.iii.1998 (O. Silveira & J. Pena), 11f#, Belém, Mocambo, 03.ix.1977 (W.L. Overall) (MPEG); 1f#, Belém, Utinga, 12.xii.1978 (F.F. Ramos) (BMNH); 1f#, Bragança, Viveda Vitória 1°11'10"S46°40'21", 24.xi.2001 (Amber Reed), 1f#, Óbidos, 05.i.1905 (Ducke) (MPEG); 1f#, 22.xii.1904 (Ducke) (BMNH); 1f#, 16.vii.1949? (MZUSP); Amazonas, 1f#, Santo Antônio do Içá, 17.viii.1906, Tefé, 1f#, 25.ix.1904, 1m#, 27.ix.1904 (Ducke), 1f#, R. Japurá, 16.ix.1904, 1f#, R. Javari, 15.vii.1906 (Ducke); SURINAM: 2f#, 16.vii.1950? (MZUSP); PERU: Iquitos, 2f#, 08.viii.1906 (Ducke) (MPEG); 2f#, Tingo Maria, 1.xi.1947 (W. Weyrauch); GUYANA: 1f# (G.E. Bodkin), 1914 (BMNH).

**Distribution.** Brazil, Peru, Colombia, Suriname, French Guiana, Guyana.



***Protopolybia fulvotincta* (Cameron, 1907)**

(Figs 24, 25, 26, 41, 42, 43, 44, 56)

*Polybia fulvotincta* Cameron, 1907: 184. (lectotype: f#, Belize, Belize (BMNH), examined).*Protopolybia fulvotincta*: Ducke 1908: 696; 1910: 469, 472; Overall 1978: 11.*Protopolybia picteti* var. *fulvotincta*: Bequaert 1944: 117, 120.*Protopolybia picteti fulvotincta*: Richards 1978: 139, 147.*Protopolybia picteti*: West-Eberhard et al. 1995: 586.

**Diagnosis.** Length of fore wing 4.25 mm; pronotal fovea obsolete, humerus short and roundly truncate, carina with lamella reduced (Fig. 24); mesoscutum with sparse and notably elongated hairs; metanotal process distinctly wider than long, with apex rounded; propodeum with a wide and deeper cavity (Fig. 25); deeper and numerous mesopunctuation on mesoscutum; color brownish with marks yellow (Fig. 26), mesoscutum brownish, scutellum with two marks, metanotum with yellow band anterior; preapical region of aedeagus not angular (Fig. 43).

**Description.** FEMALE. Length of fore wing 4.25 mm; clypeus wide ( $HClp=0.55$ ;  $MxWC1p=0.80$ ;  $TeW=0.50$ ;  $MiWC1p=0.77$  mm), with ventral margin acute; tentorial pit closer to antennal socket than to eye margin; interantennal area relatively wide, approximately  $2 \times$  diameter of antennal socket; mandibles relatively short with length  $0.78 \times$  distance between eyes at vertex; occipital carina distinct, very strong and salient throughout; humerus short and roundly truncate, carina with lamella reduced (Fig. 24), pronotal fovea obsolete, preceded by a short and low prominence; length of mesoscutum approximately  $0.87 \times$  its width; mesepisternal groove absent; scutellum with a short but well-marked median line; metanotum triangular, length of median axis approximately  $0.86 \times$  width of central disk, metanotal process distinctly wider than long, with apex rounded; propodeum with a wide and deeper cavity (Fig. 25); T1 sessile with distal margin wider and nearly straight, cup-like.

Mesoscutum with more sparse micropunctuation and deeper and numerous mesopunctuation; mesopleuron and T2 to T5 with distinct punctures; clypeus with short golden bristles, except on ventral margin, which has elongated bristles; vertex, mesoscutum, scutellum and metanotum with sparse and notably elongated hairs (Fig. 24, 26 and 56).

Species ferruginous with few yellow spots (Fig. 26); antennae ventrally testaceous, dorsally brown; mandibles yellow, with apex brown, clypeus and frons entirely testaceous to yellow, inner orbit with wide band that extend to ocular sinus, two marks inconspicuous on vertex, small mark on pronotal carina and fovea, mesoscutum brownish, tegulae yellow, large spot on mesepisternum, metapleuron without spot, scutellum with two spots, metanotum partially, propodeum with paired dorsal marks, distal spot on T1 to T3. Legs testaceous to ferruginous; wings hyaline, venation brown.

MALE. Length of fore wing 4.45 mm; eyes wide, produced inwards; clypeus narrow, approximately as long as wide, with silvery bristles, ventral margin acute; tentorial pit closer to eye margin than to the antennal socket; gena narrow; color like female. Parameral spine narrow, without elongate bristles; basal and apical angle of paramere widened (Fig. 41); digitus wide, with apical margin approximately rounded; basal process of digitus narrow and acuminate; digitus and cuspis filled with dense and elongated bristles (Fig. 44); ventral process of aedeagus approximately lobed, strongly sclerotized and not serrated (Fig. 42 and 43); preapical region of aedeagus not angular (Fig. 43).

**Material examined.** 1m#, 4f#, (without data, only *Polistella picteti* Saussure) (AMNH); BELIZE: 1f# (MPEG); 2f#, Cayo, Pook's Hill, 8km S of Teakettle Village, 26.xi.2007 (J.S. Ascher) (AMNH); COSTA RICA: Limon, 1f#, Suretka, 31.v.1924 (J.C. Bradley) (AMNH); 1f#, Belize, 5578 (P. Cameron) (BMNH).

**Distribution.** Belize, Costa Rica.

***Protopolybia iheringi* Ducke, 1910**

(Figs. 45, 46, 47, 48)

*Polybia pumila*: R. von Ihering 1904: 176, 247 (part.).

*Protopolybia iheringi* Ducke, 1910: 469, 474 (lectotype: f# Peru, Maracapata (MZUSP)), examined; paralectotype: 3f# (MPEG), examined.

*Protopolybia iheringi*: Richards 1978: 139, 148 (designation of lectotype); Overal 1978: 11; Nascimento & Overal 1979: 11; Carpenter 1999: 17; Rasmussen & Asenjo 2009: 50.

**Diagnosis.** Length of fore wing 4.50 mm; metanotal process with apex truncated; propodeum with wide and deep excavated cavity; species black, with few yellow marks; T1–T3 with distal narrow bands; ventral process of aedeagus approximately trapezoid, not projecting laterally, strongly sclerotized and not serrated (Fig. 47); preapical region of aedeagus angular (Fig. 47).

**Genitalia.** Parameral spine narrow, without elongate bristles; basal and apical angle of paramere widened (Fig. 45); digitus narrow, with apical margin approximately rounded (Fig. 48); basal process and lobe posterodorsal of digitus narrow and acuminate (Fig. 48); digitus and cuspis filled with few elongated bristles; ventral process of aedeagus approximately trapezoid, not projecting laterally, strongly sclerotized and not serrated (Fig. 47); preapical region of aedeagus angular (Fig. 47).

**Material examined.** PERU: Madre de Dios, 1f#, Quincemil, on branch R. Manu, viii.1962 (L.E. Pena) (AMNH);

**Distribution.** Peru.

### ***Protopolybia nitida* (Ducke, 1904)**

(Figs 27, 28, 29, 49, 50, 51, 52)

*Chartergus nitidus* Ducke, 1904: 327, 338 (lectotype: f#, Brazil, Óbidos (BMNH)); examined; paralectotype: 4f#, same data as lectotype; examined).

*Chartergus nitidus*: Nascimento & Overal 1979: 9; Carpenter 1999: 17.

*Protopolybia nitida*: Ducke 1905a: 18; 1905b: 674; 1907: 165; 1910: 469, 473; 1918: 324; Richards 1978: 139, 145; Overal 1978: 11; Rasmussen & Asenjo 2009: 50.

**Diagnosis.** Length of fore wing 5.21 mm; clypeus wide, with ventral margin acute; humerus distinctly projecting and shortened, carina lamellate and recurved forwards at extremity, not extending downwards (Fig. 27); metanotal process with apex slightly rounded (Fig. 28); propodeum with wide and deep excavated cavity, heart-like shape (Fig. 28); ground color black or reddish, scutellum totally yellow, metanotum almost, T2 with a large and anterior yellow spot (Fig. 29); ventral process of aedeagus curved, not projecting laterally, strongly sclerotized and weakly serrated; preapical region of aedeagus angular.

**Redescription.** FEMALE. Length of fore wing 5.21 mm; clypeus wide ( $HClp=0.72$ ;  $MxWClp=0.94$ ;  $TeW=0.59$ ;  $MiWClp=0.87$  mm), with ventral margin acute; tentorial pit closer to antennal socket than to eye margin; interantennal area relatively wide, approximately  $2 \times$  diameter of antennal socket; mandibles relatively short with length  $0.86 \times$  distance between eyes at vertex; occipital carina distinct, very strong and salient throughout; humerus distinctly projecting and shortened, carina lamellate and recurved forwards at extremity, not extending downwards (Fig. 27); pronotal fovea distinct; length of mesoscutum  $0.93 \times$  its width; mesepisternal groove absent; scutellum with a short but well-marked median line; metanotum triangular, length of median axis  $0.69 \times$  width of the central disk, metanotal process with apex slightly rounded (Fig. 28); propodeum with wide and deep excavated cavity, heart-like shape (Fig. 28); propodeal valves narrow; T1 in dorsal view with petiole very short and distal margin wider and nearly straight, cup-like.

Frons, mesoscutum, scutellum and metanotum with more sparse micropunctuation and deeper and stronger mesopunctuation, mesopleuron and T2 to T5 with distinct punctures; clypeus with short golden bristles, except on ventral margin, with elongated bristles; eyes glabrous; vertex, mesoscutum, scutellum and metanotum with more sparse and quite long hairs.

Species black or reddish richly marked by yellow spots (Fig. 27–29); antennae ventrally testaceous or brown, dorsally black; mandibles black, clypeus almost entirely yellow, inner and outer orbit with wide bands that extend to ocular sinus, frons with a bilobate mark, two marks on vertex, small marks on pronotal carina and fovea, mesoscutum without stripes, tegulae almost entirely black, large spot on mesepisternum, scutellum yellow, metanotum partially (Fig. 28), propodeum without paired dorsal marks (Fig. 28), T1 sometimes with

distal spot, extensive basal spots and narrow distal mark on T2, T3 to T5 black. Coxae, femora, tibiae brown to black; tarsi brown; wings hyaline, venation brown.

**MALE.** Length of fore wing 5.06 mm; eyes wide, strongly produced inwards; clypeus narrow, longer than wide, with silvery bristles, ventral margin acute; tentorial pit closer to eye margin than to the antennal socket; gena narrow; mandible and clypeus yellow; eyes internally bordered by a band that continues to ocular sinus; anterior margin of T2 with extensive spot, yellow. Parameral spine without elongate bristles; basal angle of paramere widened, apical angle narrower (Fig. 49); digitus narrow, with apical margin rounded; basal process of digitus approximately acuminate; cuspis moderately filled with elongated bristles (Fig. 52); ventral process of aedeagus curved, not projecting laterally, strongly sclerotized and weakly serrated, laterally; preapical region of aedeagus angular (Fig. 51).

**Material examined.** FRENCH GUIANA: Cayenne, Barrage de Petit Saut, 1f#, 5°02'N53°02'W, 19.xi.1996 (Dejean & Corbara), 8f#, xii.1997–i.1998 (A. Dejean), Plateaux des Mines, 9f#, E St. Jean, 5°21'N54°03'W, 30m, 28.ix.1996 (Wenzel & Carpenter) (AMNH); BRAZIL: Pará, Óbidos, 1f#, 1m#, 30.v.1911 (Ducke), 1f#, 31.xii.1906, Amazonas, 1f#, Manaus, ZF-2, 07–21.xi.1994 (J.A. Rafael & J. Vidal) (INPA), 2f#, 22.xii.1912 (Ducke) (MPEG), 2f#, EMBRAPA, 02°43'S09°59'W, 07.xii.2012 (K. Schoeninger) (INPA), Acre, 1f#, Rio Branco, 25.x–08.xi.1991 (F. Ramos, A. Henriques, I. Gorayeb, N. Bitencourt) (MPEG)

**Distribution.** Ecuador: Napo; Peru: Huánuco; \*French Guiana; Brazil: Amapá, Pará, \*Amazonas, \*Acre.

**Remarks.** *Protopolybia nitida* presents black color with yellow marks on scutellum and metanotum (Ducke, 1904; Bequaert, 1944; Richards, 1978). Were analyzed three individuals from Pará, Brazil, that are structurally similar to *P. nitida*, but with distinct coloration, brown and with more marks on T2. We consider this population as a variation of Ducke's species, but additional studies are necessary to determine its real status.

### ***Protopolybia perfulvula* Bequaert, 1944**

(Figs 30, 31, 32)

*Protopolybia picteti* var. *perfulvula* Bequaert, 1944: 117, 121. (holotype: f#, Panama, Rio Agua Salud (MCZ), not examined; paratype: 1f# Panama, Rio Agua Salud (AMNH), examined).

*Protopolybia perfulvula*: Richards 1978: 139, 147; Sarmiento 1994: 359; West-Eberhard et al. 1995: 586.

**Diagnosis.** Length of fore wing 4.80 mm; pronotal fovea obsolete, humerus short and roundly truncate, carina with lamella reduced (Fig. 30); few and shallow mesopunctuation on mesoscutum (Fig. 30); with sparse and notably elongated hairs distinctly curved apically; metanotal process distinctly wider than long, with apex rounded; propodeum with a wide and deep cavity, like a central channel (Fig. 31); color ferruginous moderately marked with yellow (Fig. 32), mesoscutum reddish, generally with two yellow stripes, scutellum with two marks, metanotum with yellow band anterior.

**Description.** FEMALE. Length of fore wing 4.80 mm; clypeus wide (HC1p=0.60; MxWC1p=0.90; TeW=0.60; MiWC1p=0.87 mm), with ventral margin acute; tentorial pit closer to antennal socket than to eye margin; interantennal area relatively wide, approximately 2 × diameter of antennal socket; mandibles relatively short with length 0.77 × distance between eyes at vertex; occipital carina distinct, very strong and salient throughout; humerus short and roundly truncate, carina with lamella reduced (Fig. 30); pronotal carina little developed, but visible laterally, pronotal fovea obsolete, preceded by a short and low prominence; length of mesoscutum approximately 0.89 × its width; mesepisternal groove absent; scutellum with a short but well-marked median line; metanotum triangular, length of median axis approximately 0.76 × width of central disk; propodeum with a wide and deep cavity, like a central channel (Fig. 31); T1 sessile with distal margin wider and nearly straight, cup-like.

Mesoscutum with more sparse micropunctuation and few and shallow mesopunctuation; mesopleuron and T2 to T5 with distinct punctures; clypeus with short golden bristles, except on ventral margin, which has elongated bristles; vertex, mesoscutum, scutellum and metanotum with sparse and notably elongated hairs distinctly curved apically.

Species ferruginous moderately marked with yellow spots (Fig. 32); antennae ventrally testaceous or brown, dorsally brown; mandibles brown, clypeus entirely, inner orbit with wide band that extend to ocular

sinus, frons with a bilobate mark, two marks on vertex, small mark on pronotal carina and fovea, mesoscutum ferruginous to brown, tegulae partially, large spot on mesepisternum and small on area below scrobe, scutellum almost entirely yellow, metanotum partially, propodeum with paired dorsal marks, distal spot on T1 to T3. Legs ferruginous; wings hyaline, venation brown.

**Material examined.** PANAMA: Barro Colorado, 18f#, 9–10.xi.1923, F. 4855H (without collector) (AMNH); COLOMBIA: Atlântico, 3f#, Cuatro Bocas, 22.i.1959 (J.F. Clarke) (BMNH).

**Distribution.** Costa Rica, Panama, Colombia: Atlantico, Valle.

### ***Protopolybia picteti* (de Saussure, 1854)**

(Figs 53, 54, 55)

*Polybia picteti* de Saussure, 1854: 168. (holotype: f#, Colombia, Tolima, Libano, (MNHN), examined.

*Polybia picteti*: Smith 1857: 124; Dalla Torre 1894: 165; Rudow 1901: 341; Dalla Torre 1904: 78.

*Protopolybia picteti*: Ducke 1905a: 18; 1910: 468, 471; Bequaert 1944a: 117; 1949 (1948): 131.

*Protopolybia picteti picteti* (de Saussure): Richards 1978: 139, 147; Sarmiento 1994: 359.

**Diagnosis.** Length of fore wing 4.0 mm; mesoscutum with sparse and notably elongated hairs; humerus not much distinctly projecting and shortened, carina lamellate and recurved forwards at extremity, not extending downwards; metanotal process with apex truncated; propodeum with wide and deep cavity, like a central channel; propodeal valves narrow; species blackish to brown, richly marked with yellow spots; frons with a mark, butterfly-like shape; T2 with yellow spots on each side anteriorly. Preapical region of aedeagus angular (Fig. 54); parameral spine not laterally expanded at base (Fig. 53).

**MALE:** Length of fore wing 4.0 mm; eyes wide, strongly produced inwards; clypeus narrow, longer than wide, with silvery bristles, ventral margin acute; tentorial pit approximately equidistant to eye margin and to the antennal socket; gena narrow; color like female, except by mandible, clypeus and front yellow. Parameral spine narrow, without elongate bristles; basal and apical angle of paramere widened (Fig. 53); digitus narrow (Fig. 55), with apical margin rounded; basal process of digitus narrow and acuminate; cuspis filled with dense and elongated bristles; ventral process of aedeagus approximately lobed, not projecting laterally, strongly sclerotized and not laterally serrated (Fig. 54); preapical region of aedeagus angular (Fig. 54).

**Material examined.** COLOMBIA: Sevilla, 1f#, 1.v.1926 (C.G. Gowdey); Magdalena, 38f#, 20m#, 14.ii.1976 (F. Schremmer); 1f#, N. Sierra Nevada, Rio Don Diego, 22–24.xii.1976 (M. Cooper); 1f#, Rio Buritaca, 14.ii.1974; 1f#, Santa Marta, 14.ii.1976 (without collector) (BMNH); COSTA RICA: Heredia, 1f#, La Selva Biol. Sta., 3km S Pto. Viejo, 10°26N, 84°01W, 28.vii-02.viii.1992 (G. Wright), 1f#, 19.vii.1992 (H.A. Hespeneide) (AMNH).

**Distribution.** Panama, \*Costa Rica; Colombia: Magdalena, Tolima; Venezuela: D.F.

**Remarks.** Richards (1978) treats both *P. picteti* and *P. fulvotincta* as subspecies, considering the color pattern as the only difference between these two species. These species also share the presence of sparse and notably elongated hairs on the mesoscutum. The male genitalia present clear differences (on the aedeagus apex and on the parameral spine), showing that these are clearly two distinct species.

### ***Protopolybia rotundata* Ducke, 1910**

*Protopolybia rotundata* Ducke, 1910: 469, 472. (lectotype: f#, French Guiana, La Mana (MNHN), not examined: paralectotype: 1f#, same data as lectotype (MPEG), examined).

*Polybia pumila* Fox: 1898: 449 (part.).

*Protopolybia rotundata*: Richards 1978: 138, 145; Overall 1978: 11; Nascimento & Overall 1979: 11; Carpenter & van der Vecht 1991: 215; Carpenter 1999: 18.

*Protopolybia pumila* var. *rotundata*: Bequaert 1944a: 123, 126; 1944b: 270.

**Diagnosis.** Length of fore wing 4.35 mm; humerus short and roundly truncate, carina with lamella reduced; pronotal fovea obsolete, like as puncture; scrobal groove not strong; metanotal process with apex truncated;

propodeum with wide and deep excavated cavity; species black with few yellow spots. Scutellum yellow, posterior margin of T1 and T2 with yellow spot.

**Material examined.** GUYANE: road to Kaw, 20f#, 300m, 4°32'N52°10'W, 2.x.1996 (Wenzel & Carpenter) (AMNH); BRAZIL: Pará, 2f#, Belterra, 13.xii.1999 (G.C. Venturieri) (MPEG), Pará, 1f#, Serra de Carajás, Ápice Oeste, 10.07.2014 (G.C. Ferreira) (MPEG); COLOMBIA: 1f#, Narino, Barbacoas, 20.iii.1974 (M. Cooper).

**Distribution.** French Guiana; Brazil: Mato Grosso, Pará; \*Guyana, \*Colombia.

### ***Protopolybia steinbachi* Richards, 1978**

*Protopolybia steinbachi* Richards, 1978: 139, 148. (holotype: f#, Bolivia (J. Steinbach) (BMNH), examined; paratype: 2f#, same data as holotype (BMNH), examined).

**Diagnosis.** Length of fore wing 4.55 mm; humerus distinctly projecting and shortened, carina lamellate and recurved forwards at extremity, not extending downwards; metanotal process with apex truncated; propodeum with wide and deep excavated cavity, heart-like shape; propodeal valves wide; species black, vertex, mesoscutum, scutellum, metanotum and propodeum with marks; T1 and T2 ferruginous with yellow marks.

**Material examined.** BOLIVIA: Alto Beni, 2f#, S. Rio Inicua, i. 1976 (Peña), 1f#, i.1967 (AMNH).

**Distribution.** Bolivia.

### ***Protopolybia wheeleri* Bequaert, 1944**

*Protopolybia picteti* var. *wheeleri* Bequaert, 1944a: 121. (holotype: f#, Panama, Frijoles, Canal Zone (MCZ), not examined; paratype: 1f#, same data as holotype (BMNH), 1f# (AMNH), examined).

*Protopolybia wheeleri*: Richards 1978: 139, 146.

**Diagnosis.** Length of fore wing 4.50 mm; humerus distinctly projecting and shortened, carina lamellate and recurved forwards at extremity, not extending downwards; pronotal fovea very wide and deep; metanotal process with apex truncated; propodeum with a wide and shallow cavity; species black to brownish, very richly marked with yellow spots; mesoscutum with four stripes; T2 with apical band and three proximal spots, being central pyriform.

**Material examined.** PANAMA: Frijoles, 1f#, Canal Zone (AMNH); 1f# (BMNH); Champion, 87f#, Tolé (Godman-Salvin).

**Distribution.** Nicaragua, Panama.

### **Key to the species of the *Protopolybia picteti-emortualis* species-group.**

1. Occipital carina strong, fading at some point near the middle of gena's height; mesoscutum with dense moderately elongated erect hairs; pronotal pretegular carina not strongly developed ..... 2
  - Occipital carina very strong and salient from top to the insertion of the mandibles; mesoscutum with notably elongated hairs; pronotal pretegular carina strongly developed, adjacent area wider.....3
2. Metanotal process with apex truncated; propodeum deeply excavated above the valvula (Fig. 22), propodeal valves basally triangular (Fig. 23); color brown to reddish, moderately marked with yellow; scutellum and metanotum partially yellow, propodeum with paired dorsal marks; male genitalia with paramere dorsally smoothly rounded. Nest construction material composed by mud, plant material and saliva.... *P. emortualis* (de Saussure)
  - Metanotal process short, with apex approximately acute; propodeum with shallower above the valvula (Fig. 12), propodeal valves attenuate (Fig. 13); color black with marks yellow; scutellum with two small spots, metanotum partially yellow; male genitalia with paramere dorsally slightly angular..... *P. duckei* (du Buysson)
3. Mesoscutum with notably elongated hairs and sparse (Fig. 56).....4
  - Mesoscutum with numerous notable elongated hairs, distinctly curved apically (Fig. 8, 20 and 57).....5

4. Mesoscutum with few and sparse elongated hairs, metanotal process distinctly wider than long, with apex rounded (Fig. 25); color brownish with marks yellow (Fig. 26) mesoscutum brownish, scutellum with two marks, metanotum with yellow band anterior; preapical region of aedeagus not angular (Fig. 43)..... *P. fulvotincta* (Cameron)  
 – Metanotal process with apex truncated; propodeum with wide and deeper cavity, with a central channel; propodeal valves narrow (Fig. 58); species blackish to brown, richly marked with yellow spots; frons with a mark, butterfly-like shape; T2 with yellow spots on each side anteriorly. Preapical region of aedeagus angular (Fig. 54); parameral spine not laterally expanded at base..... *Protopolybia picteti* (de Saussure)
5. Metanotal process distinctly wider than long, with apex truncated (Fig. 10); front margin of pronotum distinctly angled below the fovea (Fig. 8 and 61); T1 with petiole short but remarkable; color brownish richly marked with yellow to whitish (Fig. 6 and 7), mesoscutum reddish, generally with two stripes, scutellum with two marks, metanotum with yellow to whitish band anterior ..... *P. djaneteae* **sp. nov.**  
 – Metanotal process approximately as long as wide with apex truncated or rounded.....6
6. Pronotal fovea very wide and deep; frontal margin of pronotum, distinctly angled in approximately 120 degree, near to fovea; species black to brownish, very richly marked with yellow spots; mesoscutum with four stripes; T2 with three spots anteriorly, being the central pyriform..... *P. wheeleri* Bequaert  
 – Pronotal fovea narrow, small and shallower.....7
7. Species black, T1 and T2 ferruginous with yellow marks; vertex, mesoscutum, scutellum, metanotum and propodeum with marks; metanotal process with apex truncated; propodeal valves wide..... *P. steinbachi* Richards  
 – Species entirely black, brown or ferruginous, with yellow marks.....8
8. Propodeum with a wide cavity shallow, heart-like shape (Fig. 19); metanotal process with apex truncated; propodeal valves wide (Fig. 20 and 60); color black to brownish moderately marked with yellow, mesoscutum with two stripes, sometimes without, T2 with three spots anteriorly .... *P. eldinaris* **sp. nov.**  
 – Propodeum with a wide and deep cavity, sometimes like a channel.....9
9. Scutellum totally yellow, metanotum almost; metanotal process with apex slightly rounded (Fig. 28); propodeum with wide and deep excavated cavity (Fig. 28); ground color black or reddish, T2 with a large and anterior yellow spot; ventral process of aedeagus curved, not projecting laterally, strongly sclerotized and weakly serrated; preapical region of aedeagus angular... *P. nitida* (Ducke)  
 – Scutellum not totally yellow, metanotum partially marked or without marks.....10
10. Humerus not projecting, shortened to roundly truncate, generally indicated by yellow band (Fig. 9) .....11  
 – Humerus distinctly projecting and shortened, carina lamellate and recurved forwards at extremity, not extending downwards (Fig. 18).....12
11. Propodeal valves basally triangular; front margin of pronotum not angled (Fig. 62); scrobal groove not strong; species black with few yellow spots. Scutellum with a wide yellow mark, posterior margin of T1 and T2 with yellow spot..... *P. rotundata* Ducke  
 – Propodeal valves attenuate (Fig. 59), front margin of pronotum distinctly angled a little below the fovea; species black to brownish, with few yellow marks; vertex and mesoscutum black; scutellum, metanotum and propodeum with two spots, T1 and T2 with a yellow spot posterior.... *P. alvarengai* Richards
12. Scrobal groove shallow and abbreviated; propodeal valves narrow; color ferruginous moderately marked with yellow (Fig. 32), mesoscutum reddish, generally with two yellow stripes, scutellum with two marks, metanotum with yellow band anterior. Metanotal process with apex rounded (Fig. 31); propodeum with a wide and deep cavity, like a central channel (Fig. 31); few and shallow mesopunctuation on mesoscutum (Fig. 30); with sparse and notably elongated hairs distinctly curved apically..... *P. perfulvula* Bequaert  
 – Scrobal groove strongly marked; propodeal valves wide.....13
13. Scutellum without marks; T1–T3 with distal narrow bands, T2 with three spots anteriorly, being a small anterior central mark, and narrow band posteriorly; species black, with few yellow marks; ventral process of aedeagus approximately trapezoid, not projecting laterally, strongly sclerotized and not serrated (Fig. 47); preapical region of aedeagus angular (Fig. 47)... *P. iheringi* Ducke  
 – Scutellum with a mark, three basal spot and one distal band on T2 .....14
14. Propodeum with wide and deep excavated cavity; mesoscutum black, scutellum with a bilobated mark, metanotum partially, three basal spot and one distal band on T2; ventral process of aedeagus approximately lobed, not projecting laterally, strongly sclerotized and laterally serrated (Fig. 39); preapical region of aedeagus angular (Fig. 39); parameral spine narrow (Fig. 37); digitus narrow, with apical margin rounded (Fig. 40) ..... *P. biguttata* Bequaert

– Propodeum with a wide and deep cavity, heart-like shape; species black to brownish richly marked; scutellum with two small spots, metanotum partially yellow; ventral process of aedeagus angular, not projecting laterally, strongly sclerotized and serrated, laterally (Fig. 34 and 35); preapical region of aedeagus angular; parameral spine laterally expanded at base (Fig. 33).... *P. bella* (Von Ihering)

### Acknowledgements

We are grateful to all the institutions, facilitators of loans, and two anonymous reviewers for their corrections and suggestions. The first author is also very grateful to Dr. Gavin Broad, Jaswinder Boparai, and Natalie Dale-Skey for their hospitality during his visit to the Natural History Museum (London) and to the CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico, grant 140080/2015-5) for financial support.

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### Figure legends

**Figures 1–4.** *Protopolybia bella*. *mp*, metanotal process.

**Figures 5–10.** *Protopolybia djaneteae* **sp. nov.** yellow arrow= front margin of pronotum.

**Figures 11–14.** *Protopolybia duckei*.

**Figures 15–20.** *Protopolybia eldinaris* **sp. nov.**

**Figures 21–26.** 21, 22, 23. *Protopolybia emortualis*. *pv*, propodeal valve; 24, 25, 26. *Protopolybia fulvotincta*.

**Figures 27–32.** 27, 28, 29. *Protopolybia nitida*; 30, 31, 32. *Protopolybia perfulvula*.

**Figures 33–44.** 33, 34, 35, 36. *Protopolybia bella*; 37, 38, 39, 40. *Protopolybia biguttata*; 41, 42, 43, 44. *Protopolybia fulvotincta*. 33, 37, 41. Parameres of the male genitalia. 34, 35, 38, 39, 42, 43. Aedeagus in dorsal and lateral view. 36, 40, 44. Volsella of male genitalia in lateral view. Scale 0.2mm.

**Figures 45–55.** 45, 46, 47, 48. *Protopolybia iheringi*; 49, 50, 51, 52. *Protopolybia nitida*; 53, 54, 55. *Protopolybia picteti*. 45, 49, 53. Parameres of the male genitalia. 46, 47, 50, 51, 54. Aedeagus in dorsal and lateral view. 48, 52, 55. Volsella of male genitalia in lateral view. Scale 0.2 mm. *ps*, parameral spine; *par*, preapical region.

**Figures 56–62.** 56. *Protopolybia fulvotincta*; 57. *Protopolybia djaneteae*. Mesoscutum in lateral view. 58. *Protopolybia picteti*; 59. *Protopolybia alvarengai*; 60. *Protopolybia eldinaris*. Metapleuron in lateral view. 61. *P. djaneteae*. 62. *P. rotundata*. Pronotum in lateral view. Scale 0.2 mm. *fmp*, front margin of pronotum.

### Plate 1



### Plate 2



Plate 3



Plate 4

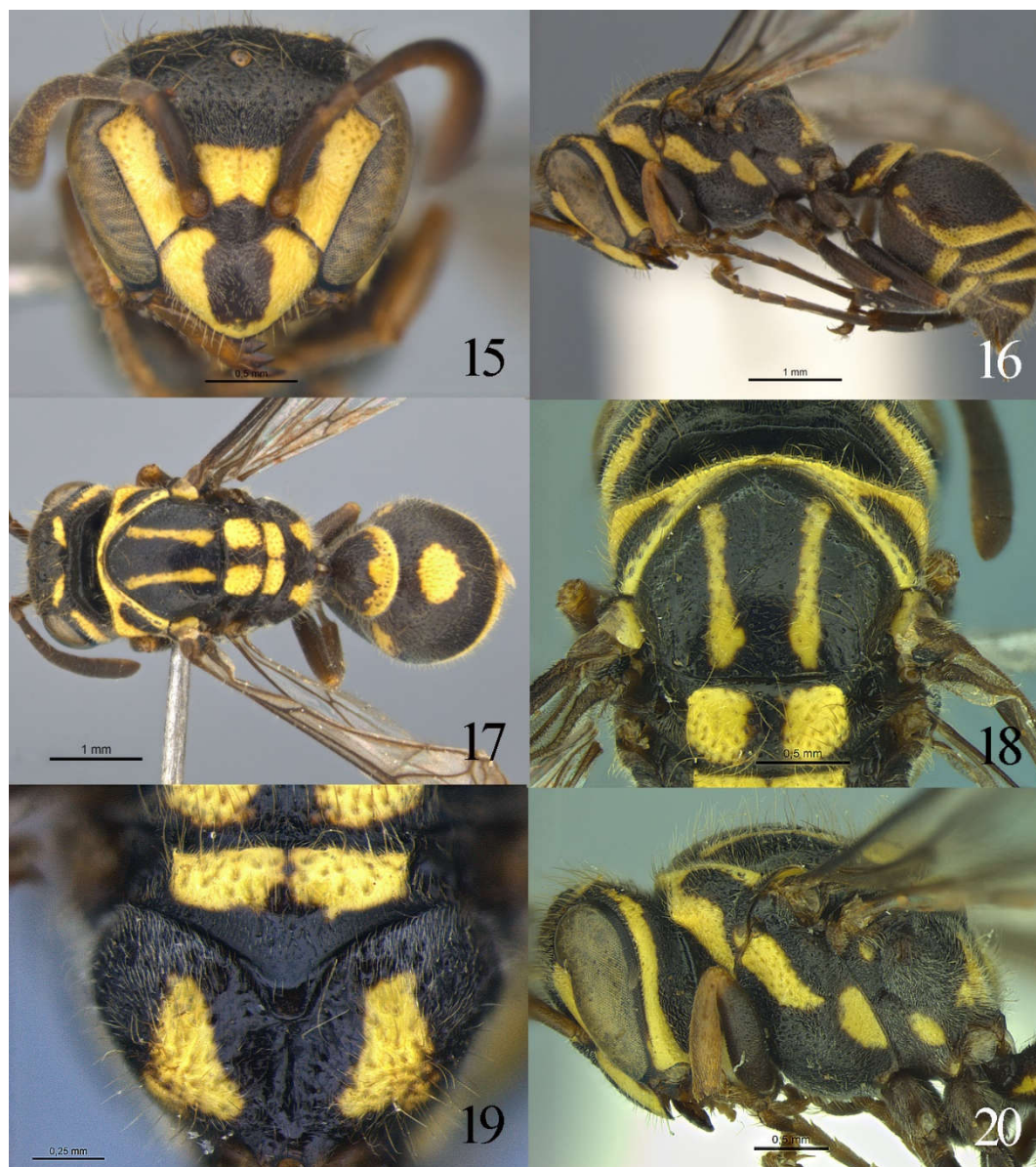


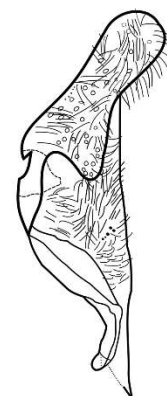
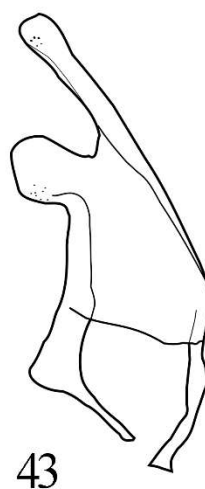
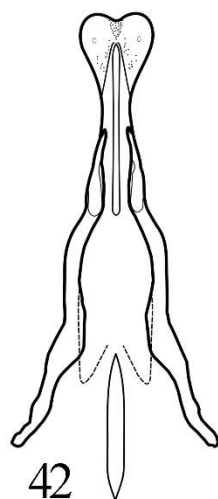
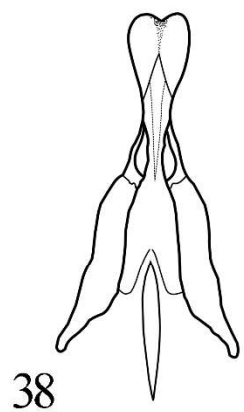
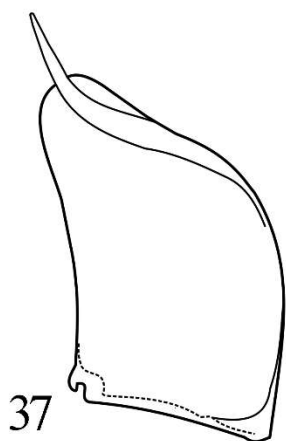
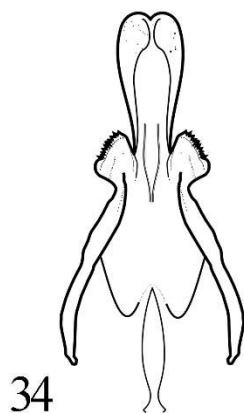
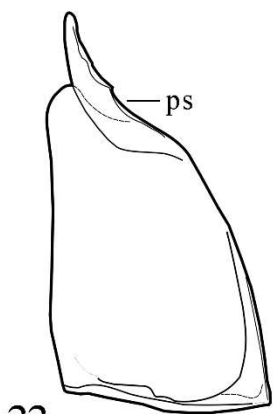
Plate 5

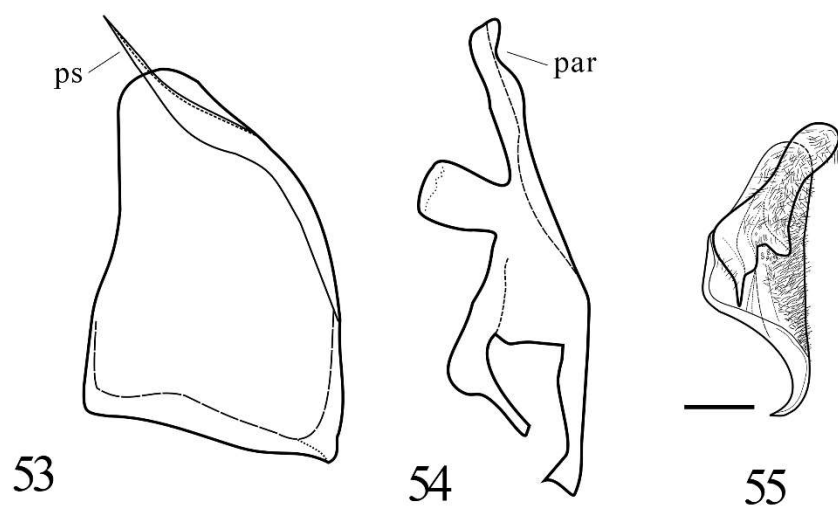
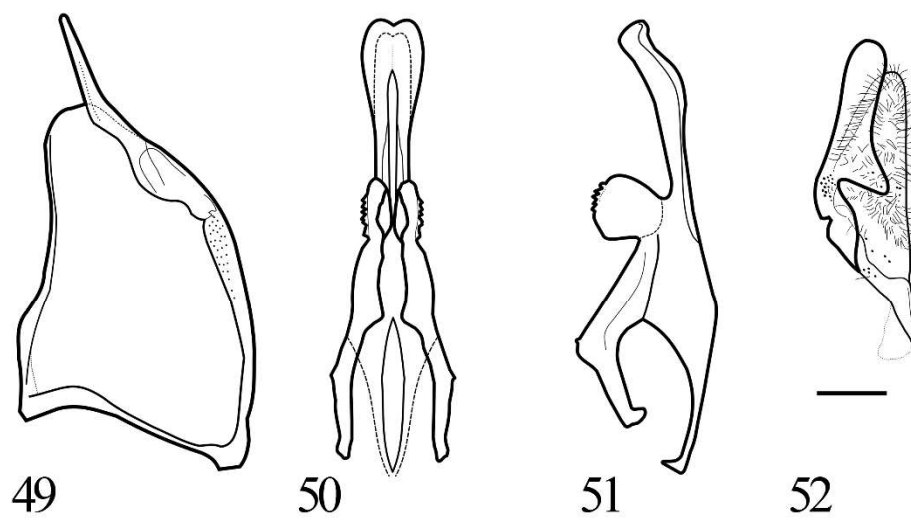
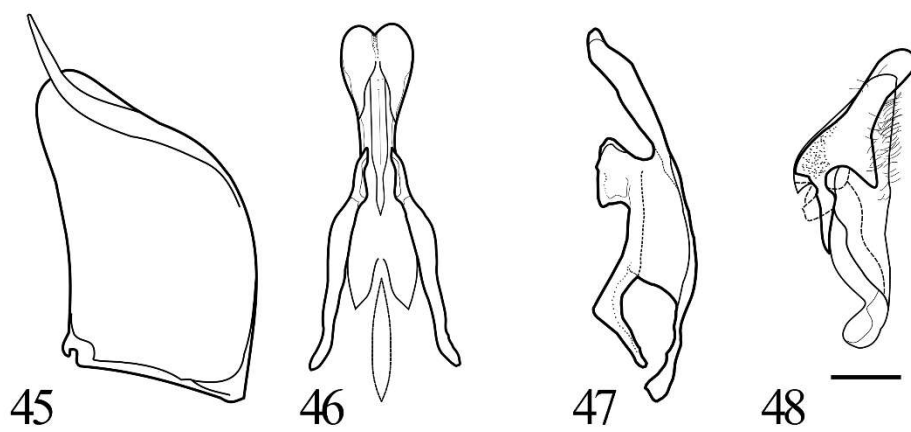


Plate 6

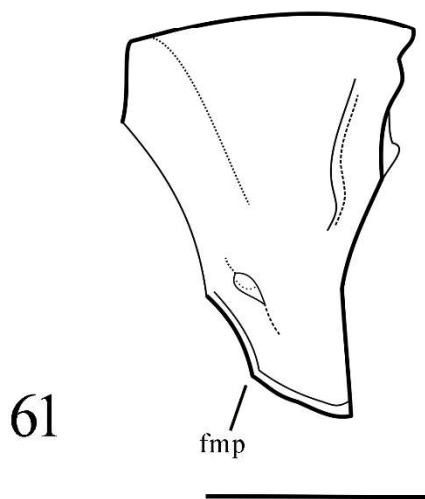
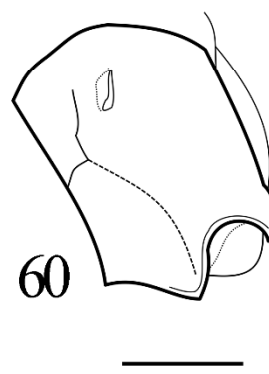
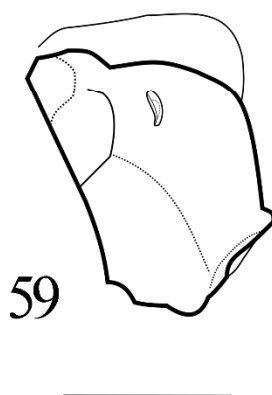
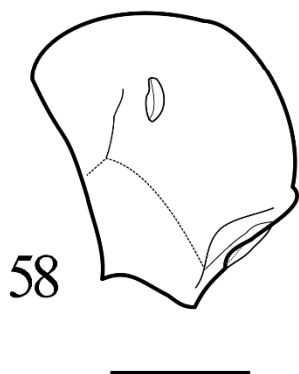
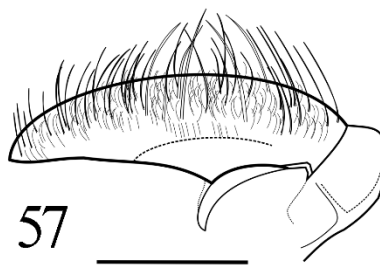
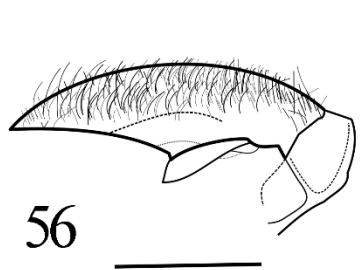


Plate 7





## Plate 9





# Capítulo 4

**Taxonomic revision of the *P. chartergoides*  
species-group of the genus *Protopolybia* Ducke,  
1905 (Hymenoptera: Vespidae, Polistinae)**

O capítulo 4 desta tese foi elaborado e formatado conforme as normas da publicação científica *Zootaxa*, as quais se encontram em anexo.

## Taxonomic revision of the *P. chartergoides* species-group of the genus *Protopolybia* Ducke, 1905 (Hymenoptera: Vespidae, Polistinae)

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### ABSTRACT

A taxonomic revision of the *Protopolybia chartergoides* species-group was undertaken. *Protopolybia isthmensis* **stat. nov.** is elevated to the level of species. *P. chartergoides boshelli* Bequaert 1938 is a junior synonymy of *P. chartergoides* (Gribodo 1891). The male genitalia of *P. chartergoides*, *P. fuscata*, and *P. pallidibalteatus* are illustrated and described. New collection records and a new identification key to the *P. chartergoides* species-group are presented.

**Key words:** Social wasps, Epiponini, diversity, male genitalia, synonymy.

### Introduction

The genus *Pseudochartergus* Ducke, 1905 was described based mainly on body shape: "...metanotum with a narrow upper horizontal zone, then vertically steep, its lower margin penetrating the base of the middle segment as an acute angle". Ducke (1907) presented a few notes for *Pseudochartergus*, such as the characterization of *P. chartergoides* and *P. fuscatus*, distribution data for the genus, and the synonymy of *P. cinctellus* Fox with *P. chartergoides*. Ducke (1910) recognized the close relationship between *Pseudochartergus* and *Protopolybia* based on the form of metanotum, previously treated as diagnostic for both genera in kinship diagrams (Ducke 1914).

Bequaert (1938) questioned the validity of this taxon, suggesting that they were "poorly differentiated, both morphologically and biologically." However, Bequaert (1944a) later cited W. Weyrauch for the existence of fundamental differences in the nest architecture. Bequaert (1944b) presented an identification key that distinguished *Pseudochartergus* and *Protopolybia* based on the shape of the clypeus, the external orbits and form of the metanotum. Richards (1978) also considered *Pseudochartergus* as a genus, primarily because of nest characters (absence of envelope, number of combs, combs built between the leaves of the substrate plant). Carpenter and Wenzel (1990) proposed the synonymy of the two genera, considering the distinctive characters between them to be inconsistent.

Santos-Junior et al. (2015) proposed the first phylogenetic hypothesis for the genus, and the resulting topologies presented the species of former "*Pseudochartergus*" as a group within *Protopolybia* (not as a sister-group). However, monophyly and position of such a group within *Protopolybia* were not well established.

This article presents a taxonomic revision of the *P. chartergoides* species-group (= *Pseudochartergus* sensu Richards 1978).

### Material and methods

The acronyms of the collections that yielded specimens for this study are quoted according to Evenhuis (2007), followed by the name of their respective curator: American Museum of Natural History, New York, USA (AMNH), Dr. J.M. Carpenter; Natural History Museum (British Museum), London, UK (BMNH), Dr. G. Broad; Carnegie Museum of Natural History, Pittsburgh, USA (CM Pittsburgh), Dr. J. Rawlins; Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil (INPA), Dr. A.L. Henriques; Museu Paraense Emílio Goeldi, Belém, Pará, Brazil (MPEG), Dr. O.T. Silveira; Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP), Dr. C.R.F. Brandão.

### *Morphological studies, measurements and terminology*

Specimens of *Protopolybia* from the *P. chartergoides* group were examined using a Leica MZ16 stereomicroscope equipped with micrometer eyepiece and camera lucida. Taxonomically relevant morphological structures were photographed using the MZ16 stereomicroscope with a coupled Leica DFC 420 digital camera. The images were processed using the LAS 3.6v program and edited in Helicon Focus 6.2 and Photoshop CS5. Male genitalia were extracted and immersed in 10% KOH solution for 10 hours, washed in running water and stored in microtubes containing glycerin. Measurements were made of body structures using the stereomicroscope with micrometer eyepiece. The structure abbreviations were taken from Silveira (2006) and Santos-Junior et al. (2015). The terminology used by Santos-Junior et al (2015) was adopted to describe the external morphology of the species. The nest structures were described following the terminology of Wenzel (1991, 1998). For the male genitalia we adopted terminology of Carpenter and Mateus (2004) and Andena et al. (2007). The abbreviation T refers to the metasomal terga. New collection records are indicated by an asterisk (\*).

### **Genus *Protopolybia* Ducke, 1905**

*Protopolybia* Ducke, 1905a: 7, 9, 17. Type species: *Polybia bella* R. von Ihering, 1903 by subsequent designation (Bequaert 1944a).

*Pseudochartergus* Ducke 1905a: 8, 9, 15. Type species *Charterginus cinctellus* Fox, 1898 (= *Nectarina chartergoides* Gribodo, 1892) by subsequent designation (Bequaert 1938). Junior subjective synonym of

*Protopolybia* Ducke, 1905 according to Carpenter and Wenzel (1989: 185)

*Protopolybia* Ducke: Bequaert 1938: 103.

*Pseudochartergus* Ducke: Bequaert 1938: 103.

*Protopolybia* Ducke: Bequaert 1944a: 97, 98, 99 (part.).

*Protopolybia* Ducke: Bequaert 1944b: 252, 265 (part.).

*Pseudochartergus* Ducke: Bequaert 1944b: 252, 264 (part.).

*Protopolybia* Ducke: Richards 1978: 8, 136.

*Pseudochartergus* Ducke: Richards 1978: 8, 154.

### **Taxonomy of the *Protopolybia chartergoides* species-group**

The species of the group are small in size, average length of anterior wing=5.0mm, with robust body and black color. Santos-Junior et al. (2015) proposed a phylogeny in which one of the hypotheses presents the group of *P. chartergoides* as paraphyletic, due to the position of *P. duckeianus* Richards. However, in other topologies, *P. chartergoides* was presented as monophyletic because of a unique feature within *Protopolybia*: T2 with the profile distinctly bulged anteriorly and with the spiracles facing forward.

*Protopolybia isthmensis* Richards and *P. duckeianus* Richards were described in detail (Richards 1978). Therefore, only their diagnoses are presented here.

The distribution data of species, aside from the material examined, were taken from Richards (1978) and Carpenter et al. (2012).

### ***Protopolybia chartergoides* (Gribodo, 1891).**

(Figs. 1, 2, 11, 12, 13, 14)

*Nectarina chartergoides* Gribodo, 1891: 253. Holotype: ♀, French Guiana, Cayenne (MCSN), examined.

*Nectarina chartergoides* Dalla Torre 1904: 86; Ducke 1905a: 11; 1905b: 663; van der Vecht & Carpenter 1990: 49; Santos-Junior et al 2015: 154.

*Charterginus cinctellus* Fox, 1898: 460. Holotype: ♀, Brasil, Chapada (CM, Pittsburgh), examined.

*Charterginus cinctellus* Dalla Torre 1904: 85; Von Ihering 1904: 117, 234; van der Vecht & Carpenter 1990: 49; Santos-Junior et al 2015: 154.

*Chartergus cinctellus* Ducke 1904: 325, 329, 337; Cameron 1907: 181; Carpenter & van der Vecht 1991: 222.

*Chartergus chartergoides* Ducke 1904: 325.

*Pseudochartergus chartergoides* Ducke 1910: 466; Bequaert 1938: 104; Jeanne 1970: 56, 59, 60; Overall 1978: 11; Carpenter & Wenzel 1990: 178, 181–183; Wenzel 1991: 498, 515.

*Pseudochartergus chartergoides* var. *cinctellus* Bequaert 1938: 104; 1944: 264;

*Pseudochartergus chartergoides* var. *boshelli* Bequaert, 1938: 104. Holotype: f#, Colombia: Meta (MCZ, Cambridge), identified from the original description. **Syn nov.**

*Pseudochartergus chartergoides chartergoides* morph *cinctellus* Richards 1978: 155, 156; Almeida & Castro 1991: 47.

*Protopolybia chartergoides chartergoides* Araujo 1960: 252; Sarmiento 1994: 359.

*Pseudochartergus chartergoides chartergoides* morph *chartergoides* Richards 1978: 154, 156.

*Protopolybia chartergoides* Carpenter & van der Vecht 1991: 222; Santos-Junior et al 2015: 153, 154, 167, 174, 176, 182; Morato et al 2008: 794; Silveira & Santos-Junior 2011: 482, 483, 485, 487, 489, 500; Borges et al 2017: 9

**Diagnosis.** Length of fore wing 6.08 mm; ventral region of gena with width  $\frac{1}{4}$  smaller than its width at the midpoint; pronotal carina laterally angular, projected shoulders, indicated by yellow marks; fovea preceded by a short and low prominence (Fig. 1); pronotal fovea distinct, wide and deep; mesoscutum with conspicuous bristles; metanotum short, metanotal process with apex rounded (Fig. 2); scrobal groove obsolete; propodeal valves wide posteriorly. Color black, with few yellow marks. Ventral process of the aedeagus narrow and laterally projected. Apex rounded in dorsal view (Fig. 13).

**Redescription.** FEMALE. Length of fore wing 6.08 mm; clypeus wide, approximately as long as wide ( $HClp=0.85$ ;  $MxWClp=0.97$ ;  $TeW=0.80$ ;  $MiWClp=0.90$  mm), ventral margin narrowly subtruncated; tentorial pit closer to antennal socket than to eye margin; interantennal area relatively wide, approximately  $2 \times$  diameter of antennal socket; mandibles relatively short, with length  $0.65 \times$  times distance between eyes at vertex; occipital carina distinct, extending for approximately three fourths of height of gena, fading very close to insertion of mandible; humerus angularly projecting, carina weakly lamellate, less extending downwards at side; prominence in front of the pronotal fovea poorly developed, low, relatively distant from the pronotal carina (Fig. 1); pronotal fovea distinct, wide and deep; length of mesoscutum  $0.90 \times$  its width; scrobal groove obsolete; metanotum triangular, short, length of median axis  $0.46 \times$  width of central disk, metanotal process short, with apex rounded (Fig. 2); propodeum with wide and shallow cavity; propodeal valves distinctly wide posteriorly; T1 sessile, distinctly wider than long, approximately as wide as T2.

Frons, mesoscutum, scutellum, metanotum, propodeum and ventral region of mesopleuron with sparse micropunctuation and deeper and stronger mesopunctuation; T2–T5 with distinct punctures; clypeus with short golden bristles, except on ventral margin, which has elongated bristles; eyes with short and sparse bristles; body covered by short bristles, mesoscutum with conspicuous bristles.

Black, with few yellow spots; scape and pedicel brown ventrally, black dorsally; antennomeres black; mandibles black, clypeus almost entirely, inner orbit with band which extends to the vertex; outer orbit with band which extends to the occiput; front and vertex with two small marks, a narrow mark on pronotal carina, mesoscutum usually with two stripes, tegulae partially, meso and metapleuron without marks, scutellum and metanotum partially, propodeum black, T1–T5 with a yellow distal band. Legs black; hyaline wings, venation brown.

MALE. Length of fore wing 5.66 mm; eyes wide, strongly produced inwards; clypeus narrow, longer than wide, with gold and long bristles, ventral margin subtruncated; tentorial pit approximately equidistant to eye margin and to the antennal socket; gena narrow; color like female. *Genitalia.* Parameres without elongate bristles; basal and apical angle of paramere widened (Fig. 11); digitus narrow with apical margin approximately rounded, moderately covered by long bristles; basal process acuminate (Fig. 14); cuspis covered by long bristles; ventral process of aedeagus narrow and laterally projecting (Fig. 12), strongly sclerotized and weakly serrated; preapical region of aedeagus not angular in lateral view (Fig. 12); apex rounded in dorsal view (Fig. 13).

**Material examined.** BELIZE: Toledo, 1f#, 25m, Punta Gorda, Salamanca, 28.viii.–4.ix.1978 (P.S. Broomfield) (BMNH); BOLIVIA: 2f#, Yungas de La Paz, 16.vii.1944 (MZUSP), Beni, 4f#, Romansos, 1km, N. Junction Rio Itenes & Rio Paragua, 30.vii.1964 (Bouseman, J.R. & Lussenhop, L.) (MPEG), 1f#, Rurenabaque, 270m, 21.iv.1979 (M. Cooper) (BMNH), Cochabamba, 1f#, Villa Tumari, c. 450m, 7.vi.1979

(M. Cooper) (BMNH); BRAZIL: Acre, 1f#, Rio Branco, 25.x–8.xi.1991 (F. Ramos, A. Henriques, I. Gorayeb, N. Bittencourt), Amazonas, 1f#, Manaus, 11.iii.1976 (Ilio); 1f#, Teffé, 06.ix.1904 (Ducke), 21f#, Mamirauá, Varzea, 08.vi.1994 (I.S. Gorayeb & O.T. Silveira), 2f#, Manaus, Est. do Tarumã, v.1968 (A.F. Neto & E.V. Silva), 15f#, BR 174, km 46 est., 25.v.1978 (A.Y. Harada) (MPEG), Amapá, 1f#, Macapá, 20.v.1900 (Ducke) (MPEG); Pará, 1f#, Bujaru, 15.xii.1978 (R.B. Neto) (BMNH), 1f#, 15.i.1978 (P. Waldir) (BMNH), 1f#, Belém, Utinga, 06.xii.1978, W. França (BMNH), 1f#, Faz. Velha, 07.xii.1978, W. França (BMNH); Maranhão, 2f#, Igarapé Gurupi, Uma aldeia Araçu, 50km E. de Canindé, v.1963 (Malkin) (MZUSP); 1f#, São Luiz, 08.vi.1907 (Ducke) (MPEG), Mato Grosso, 1f#, 29.iii.1968 (OW Richards) (BMNH), 1f#, Utiariti, Rio Papagaio, x.1966 (Lenko & Pereira); 4f#, Barra dos Bugres, R. E. Serra das Araras, 22.i.1986 (M. Zanuto) (MPEG), 1f#, Rio Sasare, 4.x.1984 (J. Elias), 2f# (E. Binda) (INPA), Roraima, 1f#, Ilha de Maraca, Rio Uraricoera, 02–13.v.1987, Arm. Shannon (J.A. Rafael) (INPA), Pará, 2f#, Tucuruí, Faz. Senador, 01.xii.2001, Malaise (J.A. Rafael & J. Vidal) (INPA); 1f#, Ananindeua, i.1963 (Machado & Pereira) (MZUSP); Belém, 67f#, 20.iv.1968 (O.W. Richards) (BMNH); ECUADOR: 1f#, Tungurahua, Yanayacu 300m, 29-30.viii.1977 (L.E. Pena); COLOMBIA: A. Magdalena, 1f#, Sierra Nevada de S. Marta, Rio Dom Diego, 22-24.xii.1976 (M. Cooper), 1f#, Caqueta, Florencia, 10.i.1979 (M. Cooper) (BMNH); 1f#, Amazonas, Letícia, 4°12'S69°56'W, 14.iv.1997 (Carpenter & Davidson) (MZUSP); Buenaventura, 3f#, 22.ii.1935 (Schwarz, H.F.), Amazonas, 1f#, Letícia, 4°12'S69°56'W, 110m, 14.iv.1997 (Carpenter & Davidson) (AMNH), Meta, 12f#, Rio Guaryuriba, a tributary of Rio Meta, xii.1946 (Richter, L & Donor, F.J.) (AMNH), Putumayo, 2f#, Puerto Leguizamo, 180m, 29/x/1971 (M. Cooper), 10f#, Puerto Assis, 350m, 23.iii.1972, Cali, 1f#, Buenaventura Road, near Rio Dagua Bridge, 50m. 3.x.1971, 1f#, Magdalena, N. Sierra Nevada de S. Marta, Rio Buritaca, 100m, 14.ii.1974 (M. Cooper) (BMNH); GUYANA: Bartica, 1f#, Kartabo, 30.v.1924 (AMNH), 5f#, Mazaruni, (Clearing.), 18.vii.1937 (W. Richards) (BMNH); PERU: Cuzco, 1f#, Atalaya, Rio Tambo, 31.iii.1954 (J.M. Schunke) (BMNH), 3f#, Maracapatá (MZUSP); Loreto, 8f#, 40km NE Iquitos, 31.xii.1990 (Carpenter & Wenzel), 1f#, Pucallpa, Lake Yarina Cocha, 180m, 26–27.viii.1971 (C. & M. Vardy) (BMNH), 2f#, 80km NE Iquitos, 28.xii.1990, 7f#, Galicia, 05°25'S73°51'W, 18.iii.1999 (Carpenter & Davidson), Huanuco, 3f#, 2m#, Tingo Maria, 670m (Weyrauch).

**Distribution.** \*Belize, Bolivia, Brazil: Acre, Amazonas, Amapá, Maranhão, Mato Grosso, Rondônia, Pará; Colombia: Putumayo, Valle; Ecuador: Manabi, Napo, \*Tungurahua; Guyana; French Guiana; Peru: Cuzco, Loreto; Suriname.

**Remarks.** Richards (1978) treated *P. boshelli* as a subspecies of *P. chartergoides* but mentioned (p. 157) overlapping variation. From examination of specimens of the BMNH collection, it was observed that *boshelli* is only a variation of *P. chartergoides*. Thus, we consider them here as synonyms, *P. chartergoides boshelli* = *P. chartergoides*.

### ***Protopolybia duckeianus* Richards, 1978**

(Figs 3, 4)

*Pseudochartergus duckeianus* Richards, 1978: 154, 155. Holotype: f#, Brazil: AP, Oiapoque (BMNH), examined. *Protopolybia duckeianus*: Carpenter & Wenzel 1990: 179-181, 184. Silveira & Santos-Junior 2011: 500. Santos-Junior et al 2015: 175–179, 182.

**Diagnosis.** Length of fore wing 5.53 mm; eyes with long bristles. Gena wide. Pronotal carina weak and obtuse (Fig. 3); prominence in front of the pronotal fovea poorly developed, low (Fig. 3). Posterior region of metanotum and propodeum almost without punctures. Metanotal process very short and with apex distinctly rounded (Fig. 4); propodeal valves wide posteriorly. Color black with few yellow marks.

**Material examined.** BRAZIL: Amazonas, 1f#, [Manaus], Reserva Ducke, 21.ix.1981 (J.A. Rafael), 1f#, 23.i.1978 (L.P. Albuquerque) (INPA).

**Distribution.** Brazil: Amapá, \*Amazonas; Suriname.

### ***Protopolybia fuscata* (Fox, 1898)**

(Figs. 5, 6, 15, 16, 17, 18)

*Charterginus fuscatus* Fox, 1898: 459. Holotype: f#, Brazil: Mararú (CM, Pittsburgh), examined.

*Charterginus fuscatus* Dalla Torre 1904: 85; Carpenter & van der Vecht 1991: 222.

*Charterginus fuscatus* Ducke 1904: 325, 329, 338.

*Pseudocharterginus fuscatus*: Ducke 1910: 466; Bequaert 1938: 105; Jeanne 1970: 55, 56, 60; Richards 1978: 154, 155; Overal 1978: 11; Carpenter & Wenzel 1990: 180, 183; Wenzel 1991: 515; Downing 1991: 548

*Protopolybia fuscatus*: Carpenter & van der Vecht 1991: 222; Sarmiento 1994: 359; Santos-Junior et al 2015: 153, 154, 168, 174, 182.

**Diagnosis.** Length of fore wing 5.16 mm; eyes glabrous; gena very narrow, occipital carina developed only on upper quarter of the head; body almost completely covered by minute bristles; pronotal carina laterally very developed, angular (Fig. 5); prominence in front of the pronotal fovea developed, high (Fig. 5); pronotal fovea distinct, wide and deep; mesoscutum without conspicuous bristles. Metanotum short, metanotal process with apex narrowly rounded (Fig. 6); propodeal valves narrow. Color black with few marks on front and gena. Apical angle of paramere narrow (Fig. 15), apex of aedeagus approximately truncated in dorsal view (Fig. 17).

**Redescription.** FEMALE. Length of fore wing 5.16 mm; clypeus narrow, approximately as long as wide ( $HClp=0.91$ ;  $MxWClp=0.81$ ;  $TeW=0.63$ ;  $MiWClp=0.72$  mm), ventral margin narrowly subtruncated; tentorial pit closer to antennal socket than to eye margin; interantennal area relatively wide, approximately  $2 \times$  diameter of antennal socket; mandibles relatively short, with length  $0.54 \times$  times distance between eyes at vertex; gena very narrow; occipital carina developed only on upper quarter of the head; pronotal carina laterally very developed, angular; prominence in front of the pronotal fovea developed, high; pronotal fovea distinct, wide and deep (Fig. 5); length of mesoscutum  $1.03 \times$  its width; scrobal groove obsolete; metanotum triangular, short, length of median axis  $0.56 \times$  width of central disk, metanotal process with apex narrowly rounded (Fig. 6); propodeum with wide and shallow cavity; T1 sessile, distinctly wider than long, approximately as wide as T2.

Frons, mesoscutum, scutellum, metanotum and propodeum with sparse micropunctuation and deeper and stronger mesopunctuation; T1–T5 with mesopunctuation strong and deep; clypeus with short golden bristles, except on ventral margin, which has elongated bristles; eyes with diminute and sparse bristles; mesoscutum without conspicuous bristles; propodeum with short and sparse bristles.

Color black, scape and pedicel ventrally brown, antennomeres and mandibles black to brown; clypeus almost entirely, inner orbit with narrow band which extends to the ocular sinus, outer orbit with narrow band which extends to the occiput; tegulae partially brown, propodeum without dorsal marks; T1–T5 black. Legs black; wings hyaline, venation brown.

MALE. Length of fore wing 5.58 mm; eyes wide, strongly produced inwards; clypeus narrow, longer than wide, with silvery and long bristles, ventral margin little produced and subtruncated; tentorial pit closer to eye margin than to antennal socket; gena very narrow; color like female. *Genitalia.* Parameral spine without elongate bristles; basal angle of paramere widened, apical angle narrow (Fig. 15); digitus wide with apical margin approximately rounded, without long bristles; basal process acuminate (Fig. 18); cuspis strongly covered by long bristles; ventral process of aedeagus laterally projecting, strongly sclerotized and weakly serrated (Fig. 16); preapical region of aedeagus not angular in lateral view (Fig. 16); apex approximately truncated in dorsal view (Fig. 17).

**Material examined.** BOLIVIA: Beni, 1f#, Rurenabaque, 270m, 18.iv.1979 (M. Cooper); La Paz, 1f#, Rio, San Buenaventura, 270m, 22.iv.1979 (M. Cooper) (BMNH); BRAZIL: Pará, 9f#, Belém, Utinga, 30.xi.1967 (R.L. Jeanne), 3f#, 26.iv.1901 (Ducke), 1f#, Serra Norte, Serraria, 20.vi.1986 (M.F. Torres), 1f#, Belterra, 06.i.2000 (G.C. Venturieri) (MPEG); 1f#, 16.742 (MZUSP); COLOMBIA: Valle, 1f#, 1m#, Tulua, 25.ii.1976 (M.J.W. Eberhardt); ECUADOR: Napo, 1f#, Limonocha, 280m, 14.vii.1977 (C.W. Ruttenmeyer & R. Chadab) (BMNH); PERU: Loreto, 7f#, 80km NE Iquitos, 24.xii.1990 (Carpenter & Wenzel), 6m#, Rio Sucusari at Napo, 25.xii.1990 (AMNH).

**Distribution.** Bolivia: Beni; Brazil: Pará; Colombia: Boyaca; Ecuador; Peru.

***Protopolybia isthmensis* Richards, 1978 stat. nov.**

(Figs 7, 8)

*Pseudochartergus chartergoides isthmensis*, Richards 1978: 155, 157. Holotype: f#, Panama: Sabanas, 20.iv.1923 (R.C. Shannon) (USNM), not examined; paratype: f# Panama: Tocumen, 26.iv.1961 (N.H.L. Krauss); f# Costa Rica, Palmar, 11.v.1950 (D.O. Allen) (USNM), not examined (identified from the original description).  
*Protopolybia chartergoides isthmensis*: Carpenter et al. 2012: 269, 275.

**Diagnosis.** Length of fore wing 5.56 mm; ventral region of the gena width, about  $\frac{1}{2}$  smaller than its width at the midpoint; pronotal carina strong, oblique; prominence in front of the pronotal fovea developed, high, pronotal fovea wide and deep (Fig. 7), metanotal process with apex rounded (Fig. 8). Propodeal valves wide; propodeum deeply excavated above the valvula. Color black richly marked with yellow spots; mesoscutum black; pronotum and scutellum almost entirely yellow.

**Material examined.** BOLIVIA: Beni, 1f#, Rurenabaque, 270m, 19.iv.1979 (M. Cooper), 2f#, 25.iv.1979 (M. Cooper) (BMNH); ECUADOR: 1f#, Napo, Limonocha, 280m, 22.vi.1977 (C.W. Rutenmeyer & R. Chadab) (BMNH); PANAMA: Barro Colorado, 1f#, 13.xi.1923, Bocas del Toro, 1f#, Changuinola, vi.1924 (J.C. Bradley) (AMNH); PERU: 5f#, 2m#, Tingo Maria, 670m, (W. Weyrauch), 1m#, Cuzco, Paucartambo, 600m, 18.iv.1964 (A. Florez) (BMNH).

**Remarks.** Richards (1978) described *Pseudochartergus isthmensis* only like a variation of *P. chartergoides*. However, the external morphology, the color is distinctly different.

**Distribution.** \*Bolivia: Beni; \*Ecuador: Napo, Costa Rica: Palmar; Guatemala: Suchitupéquez; Panama: \*Barro Colorado, \*Bocas del Toro, Sabanas, Tocumen; Peru.

***Protopolybia pallidibalteatus* (Cameron, 1912)**  
 (Figs 9, 10, 19, 20, 21, 22)

*Charterginus pallidibalteatus* Cameron, 1912: 219. Holotype: f# type locality not stated, [Guyana] (BMNH), examined.

*Chartergus pallidilineatus*: Bodkin 1918: 297–321.

*Pseudochartergus pallidibalteatus*: Richards 1978: 154, 157; Carpenter and Wenzel 1990: 180, 182; Wenzel 1991: 515.

*Protopolybia pallidibalteatus*: Santos-Junior et al. 2015: 174, 182.

**Diagnosis.** Length of fore wing 5.71 mm; eyes glabrous; gena narrow; body almost completely covered by diminute bristles; pronotal carina laterally very developed, angular; prominence in front of the pronotal fovea developed, short (Fig. 9); pronotal fovea distinct, wide and deep; mesoscutum without conspicuous bristles. Metanotum short, metanotal process with apex narrowly rounded; propodeal valves narrow (Fig. 10). Color black with few marks on front and gena.

**Redescription.** FEMALE. Length of fore wing 5.71 mm; clypeus narrow, approximately as long as wide (HClp=0.82; MxWC1p=0.90; TeW=0.70; MiWC1p=0.80 mm), ventral margin narrowly subtruncated; tentorial pit closer to antennal socket than to eye margin; interantennal area relatively wide, approximately 2 × diameter of antennal socket; mandibles relatively short, with length 0.60 × times distance between eyes at vertex; occipital carina distinct, extending for approximately three fourths of height of gena, fading very close to insertion of mandibles; pronotal carina laterally very developed, angular; prominence in front of the pronotal fovea developed, short (Fig. 9); pronotal fovea distinct, wide and deep; length of mesoscutum 0.98 × its width; metanotum short, length of median axis 0.58 × width of central disk, metanotal process with apex narrowly rounded; propodeum with wide and shallow cavity; propodeal valves narrow (Fig. 10); T1 sessile, distinctly wider than long, approximately as wide as T2.

Front, mesoscutum, scutellum, metanotum and propodeum with sparse micropunctuation and deeper and stronger mesopunctuation; T1–T5 with mesopunctuation strong and deep; clypeus with short golden bristles, except on ventral margin, which has elongated bristles; eyes glabrous; mesoscutum with conspicuous bristles; propodeum with short and sparse bristles.

Color black, scape and pedicel ventrally brown, antennomeres and mandibles black to brown; mandibles black with distal region brown, clypeus almost entirely, inner orbit with narrow band which extends to the ocular sinus, outer orbit with narrow band which extends to the occiput; tegulae black, propodeum without dorsal marks; distal margin of T1–T5, with a narrow yellow band. Legs black to brown; wings hyaline, venation brown.

MALE. Length of fore wing 5.50 mm; eyes wide, strongly produced inwards; clypeus narrow, longer than wide, with silvery and long bristles, ventral margin little produced and subtruncated; tentorial pit closer to eye margin than to antennal socket; gena very narrow; color like female. *Genitalia*.

Parameral spine without elongate bristles; basal angle of paramere widened, apical angle narrow (Fig. 19); digitus narrow with apical margin approximately rounded, with few long bristles, basal process acuminate (Fig. 22); cuspis moderately covered by long bristles; ventral process of aedeagus laterally projecting, strongly sclerotized and weakly serrated; preapical region of aedeagus not angular in lateral view (Fig. 20); apex approximately truncated in dorsal view (Fig. 21).

**Material examined.** FRENCH GUIANA: Petit-Saut, 1f#, 1m#, sample 7 (xii.1997) (A. Dejean) (AMNH), 2f#, St. Jeane di Havani ou Mavani, x.1951 (P. Benno) (BMNH).

**Distribution.** French Guiana; Suriname.

### ***Protopolybia panamensis* (Zavattari, 1906)**

*Chartergus panamensis* Zavattari, 1906: 4. Holotype: f#, Panama, Colon (MRSN, Turin)?

*Chartergus acutiscutis* Cameron, 1907: 188. Holotype: f#, Belize (BMNH), examined.

*Pseudochartergus panamensis*: Richards 1978: 154, 157; Carpenter & Wenzel 1990: 181, 183.

*Protopolybia panamensis*: Sarmiento 1994: 359; West-Eberhard et al. 1995: 586; Silveira & Carpenter 1996 (1995): 49 (male, Panama).

**Diagnosis.** Length of fore wing 5.21 mm; eyes glabrous; gena narrow; pronotum and mesoscutum with conspicuous bristles; pronotal carina laterally very developed, angular, however not forming an acute carina; prominence in front of the pronotal fovea developed, but short and low; propodeal valves distinctly widened. Posterior margin of pronotum and prominence in front of the pronotal fovea marked; scutellum and metanotum with extensive yellow spots.

**Material examined.** BELIZE: 1f#, Belize (BMNH).

**Distribution.** Belize; Colombia; Costa Rica; Guatemala; Honduras; Panama.

### **Key to the species of the *Protopolybia chartergoides* species-group.**

1. Eyes with long bristles. Gena wide. Pronotal carina weak and obtuse (Fig. 3); prominence in front of pronotal fovea poorly developed, low (Fig. 3). Posterior region of metanotum and propodeum almost without punctures. Metanotal process very short and with apex distinctly rounded (Fig. 4); propodeal valves wide posteriorly. Color black with few yellow marks..... *Protopolybia duckeianus* Richards  
– Eyes glabrous or with minute bristles. Gena narrow. Pronotal carina strongly developed.....2
2. Occipital carina developed only on upper quarter of the head; prominence in front of the pronotal fovea developed, high (Fig. 5); pronotal carina laterally very developed, angular (Fig. 5); pronotal fovea distinct, wide and deep; mesoscutum without conspicuous bristles. Metanotum short, metanotal process with apex narrowly rounded. Apical angle of paramere narrow (Fig. 15), apex of aedeagus approximately truncated in dorsal view (Fig. 17)..... *Protopolybia fuscata* (Fox)  
– Occipital carina developed on more than upper quarter of the head..... 3
3. Color black, richly marked with yellow spots; pronotum almost completely; mesoscutum without outstandly yellow stripes; scutellum, usually, almost entirely yellow. Pronotal carina developed, oblique and produced ventrally in lateral view; propodeum deeply excavated above the valvula..... *Protopolybia isthmensis* Richards  
– Color black, moderately or poorly marked with yellow spots.....4
4. Propodeal valves narrow (Fig. 10); prominence in front of the pronotal fovea developed, short (Fig. 9); pronotal fovea distinct, wide and deep (Fig. 9); mesoscutum without conspicuous bristles. Metanotum short, metanotal



- process with apex narrowly rounded; eedeagus with apex approximately truncated in dorsal view.....  
*Protopolybia pallidibalteatus* (Cameron)  
 – Propodeal valves markedly enlarged; mesoscutum with remarkable bristles.....5  
 5. Metanotal process with apex rounded (Fig. 2); scrobal groove obsolete; color black, with few yellow spots;  
 propodeal angles projected posteriorly. Ventral process of aedeagus narrow and projected laterally. Apex rounded in  
 dorsal view (Fig. 13).....*Protopolybia chartergoides* (Gribodo)  
 – Metanotal process with apex almost pointed; propodeal angles not projected posteriorly; posterior margin of  
 pronotum and prominence in front of the pronotal fovea with a mark; scutellum and metanotum with extensive  
 yellow marks..... *Protopolybia panamensis* (Zavattari)

## Acknowledgements

We are grateful to all the institutions that loaned specimens, the facilitators of those loans, and two anonymous reviewers for their corrections and suggestions. The first author is also very grateful to Dr. Gavin Broad, Jaswinder Boparai, and Natalie Dale-Skey for their hospitality during his visit to the Natural History Museum (London) and to the CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico, grant 140080/2015-5) for financial support

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## Figure legends

**Figures 1–6.** 1, 2. *Protopolybia chartergoides*; 3, 4. *Protopolybia duckeianus*; 5, 6. *Protopolybia fuscata*. *ppf*, prominence in front of the pronotal fovea; *mp*, metanotal process.

**Figures 7–10.** 7, 8. *Protopolybia isthmensis*; 9, 10. *Protopolybia pallidibalteatus*. *pv*, propodeal valves.

**Figures 11–22.** 11, 12, 13, 14. *Protopolybia chartergoides*; 15, 16, 17, 18. *Protopolybia fuscata*; 19, 20, 21, 22. *Protopolybia pallidibalteatus*. Parameres. 11, 15, 19. Aedeagus in lateral and dorsal views. 12, 13, 16, 17, 20, 21. Volsella in lateral view. 14, 18, 22. Scale 0.2 mm.

Plate 1

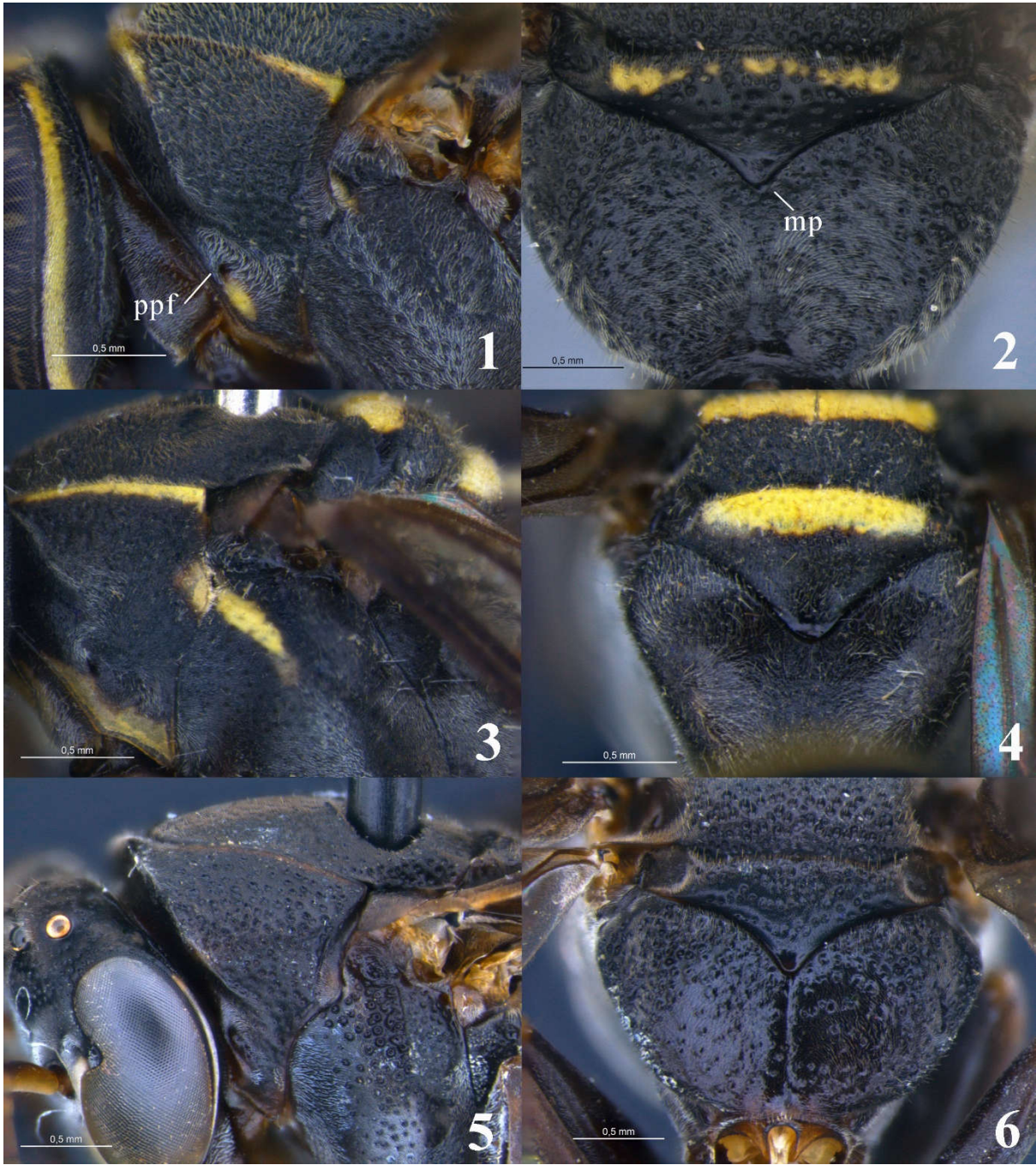


Plate 2

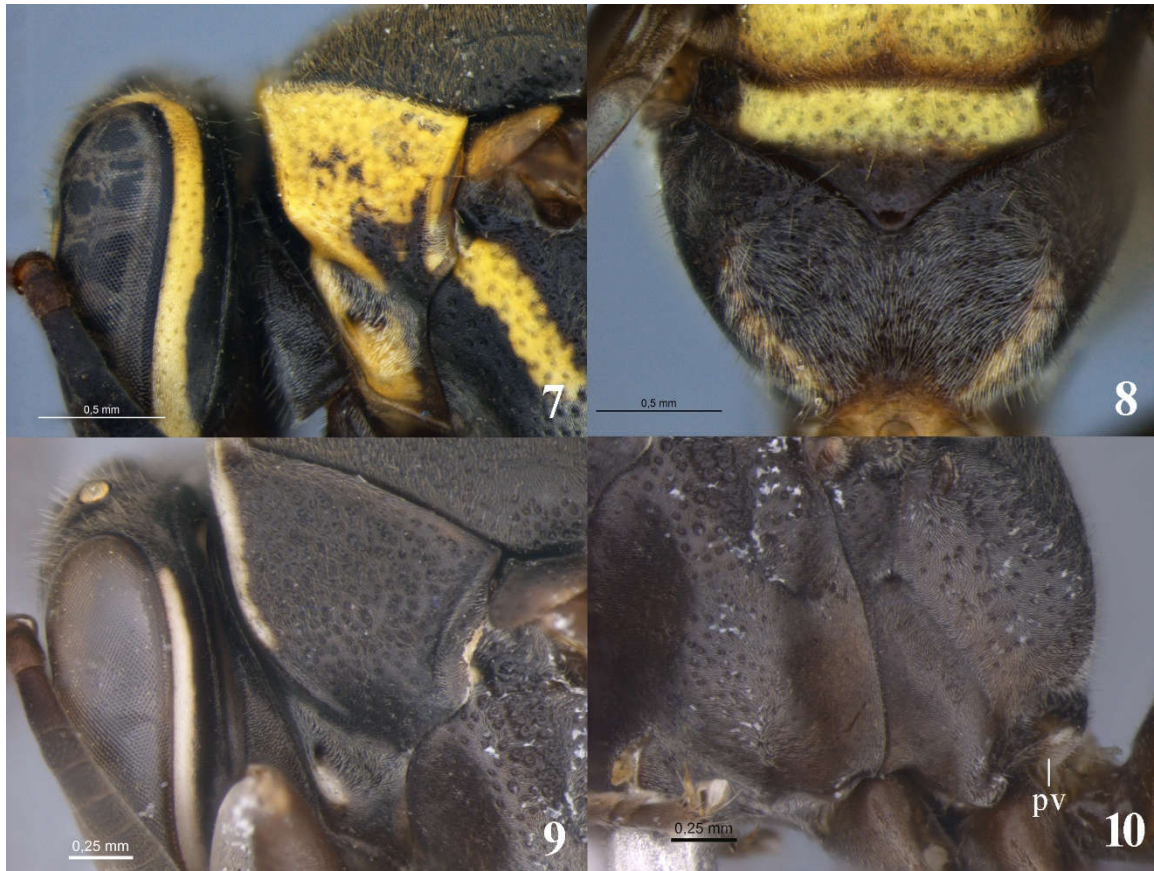


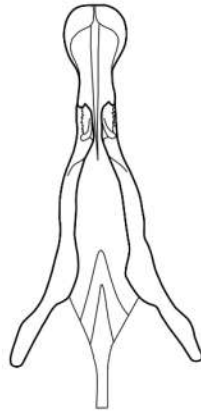
Plate 3



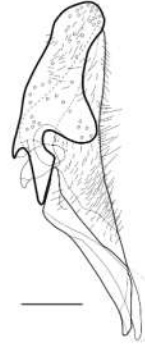
**11**



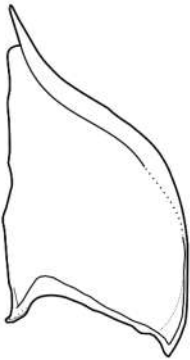
**12**



**13**



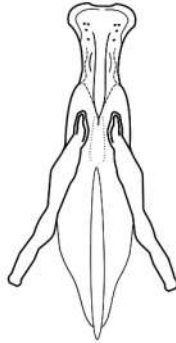
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**16**



**17**



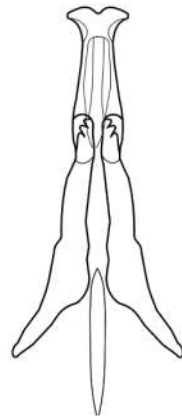
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**20**



**21**



**22**

# Capítulo 5

## **Análise filogenética do gênero *Protopolybia* Ducke, 1905 usando caracteres morfológicos e moleculares (Vespidae, Polistinae, Epiponini)**

O capítulo 5 desta tese foi elaborado e formatado conforme as normas da publicação científica *Zootaxa*, as quais se encontram em anexo.

## **Análise filogenética do gênero *Protopolybia* Ducke, 1905 usando caracteres morfológicos e moleculares (Vespidae, Polistinae, Epiponini)**

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### **Introdução**

O gênero de vespas eussociais *Protopolybia* Ducke compreende 39 espécies com ocorrência do México até a Argentina (Richards 1978, Carpenter e Wenzel 1989, Carpenter et al. 2001, Santos-Junior et al. 2015). Suas espécies são reconhecidas pela forma distinta do metanoto, que é projetado para trás em direção ao propódeo e, pelo alargamento do segundo ramo do aparato do ferrão (Carpenter & Wenzel 1989, Silveira & Silveira 1994, Santos-Junior et al. 2015).

Apresentam considerável variação entre seus grupos de espécies, principalmente no que se refere à estrutura dos ninhos (número de favos e presença de envelope) (Wenzel 1991, 1998). Considerando a variação dentro dos grupos que compõem o gênero, a identidade das espécies é feita com base na morfologia externa das fêmeas, na forma da genitália do macho e, menos frequentemente, na caracterização do ninho (Silveira e Carpenter 1995, Silveira 2004, Carpenter et al. 2001, Santos-Junior et al. 2015). No entanto, a genitália do macho e o ninho ainda são desconhecidos para algumas espécies.

A primeira hipótese filogenética proposta para *Protopolybia*, baseada apenas em caracteres morfológicos, corroborou sua monofilia e permitiu dividir o gênero em quatro grupos de espécies (grupo de *Protopolybia exigua*, *P. picteti-emortualis*, *P. sedula* e *P. chartergoides*) (Santos-Junior et al. 2015). O último grupo, contudo, resultou parafilético em 22 (de 28 árvores) e polifilético em 6 (de 28 árvores) obtidas em análise sem pesagem. Entretanto, com o uso de pesagem implícita de caracteres (Goloboff, 1993), o grupo de *P. chartergoides* resultou monofilético e mais estreitamente relacionado ao grupo de *P. picteti-emortualis*. Além desses aspectos da topologia, à exceção do grupo de *Protopolybia sedula*, em nenhum dos outros grupos se obteve resolução para as relações entre espécies.

A hipótese filogenética para *Protopolybia*, apresentada por Santos-Junior et al (2015), expôs as limitações dos dados morfológicos no que se refere à resolução das relações interespecíficas, de modo mais detalhado, e ao posicionamento do grupo de *P. chartergoides* dentro do gênero. Soluções destes problemas, sem dúvida, poderiam receber importantes contribuições da adição à matriz de dados moleculares. No que se refere ao uso de DNA em estudos filogenéticos de Vespidae, vários trabalhos têm mostrado a utilidade do método (Hines et al. 2007, Bank et al. 2017). Pickett & Carpenter (2010) propuseram uma hipótese para filogenia de Vespidae, aplicando dados moleculares para avaliar hipóteses acerca do surgimento da Eussocialidade. Ao nível de subfamília, Arevalo et al (2004) propuseram uma hipótese para relações entre gêneros de Polistinae, combinando o uso de caracteres morfológicos e moleculares, produzindo conclusões mais robustas sobre as relações entre os táxons. Para relações dentro dos gêneros, Pickett e Wenzel (2004) propuseram uma hipótese filogenética para *Polistes* Latreille, usando morfologia e sequências de DNA. Subsequentemente, Pickett et al. (2006) usaram morfologia e fragmentos adicionais de DNA (além do gene citocromo c oxidase subunidade I – COI, usado no trabalho de 2004), obtendo uma nova árvore para *Polistes* que corroborou não somente a monofilia, mais também alguns clados congruentes com os estudos tradicionais baseados unicamente em morfologia. Pickett & Wenzel (2007) também apresentaram uma filogenia com base na combinação de dados morfológicos e moleculares para o gênero *Apoica* Lepeletier, da tribo Epiponini. Mais recentemente, outros estudos estão sendo conduzidos para estudo da filogenia no gênero *Polistes* (Somavilla, tese de doutorado, 2017).

Desta forma, o objetivo desse artigo foi aprimorar o estudo filogenético feito por Santos-Junior et al. (2015), adicionando à matriz dez novos caracteres morfológicos, bem como dados moleculares referentes a 902 pares de base de dois genes mitocondriais. Originalmente, o estudo foi planejado para utilização de quatro

genes, três mitocondriais e um nuclear – RNA ribossomal subunidade 28s (nuclear), RNA ribossomal subunidade 12s (mitocondrial), RNA ribossomal subunidade 16s (mitocondrial) e COI. Entretanto, em razão da baixa qualidade do DNA extraído, somente dois genes, COI e 16s, e onze espécies (27% do total de espécies do gênero) puderam ser efetivamente utilizadas nesse estudo. Recentemente, Perrard et al (2013) trabalhando com a subfamília Vespinae, também realizaram estudo filogenético baseado em dados morfológicos e moleculares combinados, assim como no presente caso, enfrentaram os mesmos problemas sobre a extração e amplificação do DNA. Apenas 66% dos terminais utilizados na análise morfológica tiveram caracteres moleculares disponíveis para análise sob a combinação de dados morfológicos e moleculares. Apesar disso, os resultados de Perrard et al (2013) mostram que a adição de caracteres moleculares, mesmo incompletos, podem acrescentar robustez a uma hipótese filogenética.

## Material e Métodos

### *Construção da matriz*

Apesar da hipótese sobre dados morfológicos proposta por Santos-Junior et al (2015) apresentar importantes resultados para o gênero *Protopolybia*, objetivou-se aqui a construção de uma nova matriz com o programa Winclada (Nixon 2002), fazendo preenchimento dos “gaps” da matriz morfológica do trabalho supracitado e a adição de 10 novos caracteres levantados ao longo dos últimos quatro anos.

Para a construção da matriz, os caracteres utilizados foram obtidos a partir da descrição apresentada por Wenzel (1991, 1998) para os ninhos e, da morfologia externa de fêmeas e machos adultos. Para a morfologia externa dos espécimes foi adotada a terminologia usada por Santos-Junior et al. (2015). Para a genitália dos machos foi usada a terminologia de Carpenter e Mateus (2004) e Andena et al. (2007).

### *Extração, amplificação e sequenciamento do DNA*

O material utilizado foi obtido através de coleta em campo e empréstimos de coleções entomológicas institucionais (INPA e AMNH). A análise foi realizada com o uso de três dos quatro grupos de *Protopolybia* (*P. exigua*, *P. sedula* e *P. chartergoides* – ver tabela 1). *Agelaia pallipes* (Olivier) foi usado para o enraizamento da árvore, cujas sequências foram obtidas no repositório NCBI (National Center for Biotechnology Information).

Para a obtenção dos dados moleculares foi realizada a extração do DNA usando kits comerciais de extração QUIAGEN e Promega e o produto final total foi conservado em freezer a -20°C. Das 12 espécies estudadas, em cinco foi realizada a ressuspensão do produto seguindo o protocolo de Michaels et al. (1994) e, em seguida, o produto foi alíquotado na concentração de 1:50 em TE filtrado. Foram amplificados as regiões do genoma ribossomal nuclear com o marcador 28S (28 rRNA) (Simon et al. 1994), e os genes ribossomal mitocondrial, através dos marcadores 12S (12 rRNA) (Simon et al. 1994), 16S (16 rRNA) (Costa et al. 2003) e o gene mitocondrial citocromo c oxidase subunidade I (COI) (Simon et al. 1994) (tabela 2). Em razão da baixa qualidade do DNA, não foi possível obter sequências de todos os marcadores utilizados para algumas espécies. No que se refere a esta questão, algumas amostras tinham cerca de 15 anos desde a coleta e outras foram obtidas de coleções de meio seco, o que provavelmente danificou a conservação do DNA e inviabilizou o uso das sequências das espécies do gênero, particularmente para os fragmentos 12S e 28S.

Amplificações do material genômico por PCR (Reação em Cadeia Polimerase) foram realizadas utilizando-se 4μL (20ng) de DNA total extraído. Para atingir uma solução final de 25 μL foram utilizados os seguintes volumes de reagentes: 12.5μl de Master Mix 1X, 0.75μl (200ng/μl) de cada “primer” (“forward e reverse”) para cada gene completando com água. Para as amostras ressuspendidas utilizou-se o seguinte protocolo para o volume final de 25 μL: 12.5μl de Master Mix 1X, 0.75μl (200ng/μl) de cada “primer” (“forward e reverse”) para cada gene 1.0μl de BSA (Albumina de Soro Bovino) e 0.5μl de MgCl<sub>2</sub> e água para completar. Para o termociclador foi utilizado o seguinte programa: desnaturaçãõ de 94°C por 5 minutos, 35 ciclos de 94°C por 45 segundos, 50°C por 45 segundos e 68°C por 1 minuto e 20 segundos, com extensão final de 68°C por 7 minutos. Para as amostras ressuspendidas, seguiu-se o mesmo programa modificando-se apenas a extensão final para 72°C por 7 minutos. Para a visualização dos produtos de extração e amplificação foi feita a leitura



sob gel em eletroforese. Para o gel de agarose 1%, foram utilizados 5 µL de cada amostra para 2 µL de corante. Para o marcador foram usados 2 µL de ladder para cada gel.

Os produtos amplificados foram sequenciados em sequenciador automático ABI 3130 (Applied Biosystems) usando o BigDye Terminator v3.1 Sequencing Standard Kit (Applied Biosystems) [para um volume final de 10 µL foi utilizado 2 µL de produto de PCR precipitado; 2 µL de tampão; 0,5 µL de Big Dye; 0,5 µL de primer e água para completar]. Os sequenciamentos foram feitos em ambas as fitas de DNA (senso e anti-senso). Foram re-sequenciados os produtos cujas posições incertas foram evidenciadas pela comparação entre as duas fitas. A extração, amplificação e sequenciamento ocorreu no Laboratório Multidisciplinar do Museu Paraense Emílio Goeldi, em Belém, Pará. Todas as sequências obtidas serão depositadas no GenBank.

### *Análise Molecular e combinação de dados morfológicos e moleculares*

As sequências foram editadas e alinhadas no programa (MUSCLE: Edgar 2004a, 2004b). O modelo evolutivo de cada gene foi determinado a partir de análises no PartitionFinder 1.1.1 (Lanfear et al. 2012), utilizando o critério AIC (Akaike Information Criteria) para a seleção entre as combinações de partições-modelos alternativos. Em seguida, genealogias foram estimadas individualmente para cada *locus* gênico, bem como para os dois genes a partir de banco de dados concatenado.

Após essas etapas, foi construída uma matriz de dados pela concatenação de dados morfológicos e DNA mitocondrial, COI e 16s, e produzidos scripts para análise no programa EditPadLite 7.6. Subsequentemente, a análise dos dados foi realizada com o uso do programa POY versão 4 (Varón et al. 2004) utilizando-se para a obtenção do consenso estrito os comandos e ajustes dos parâmetros do seguinte modo: build (250), swap (spr), set (root: “pallipes”); para os demais critérios usou-se o default do software. No que se refere ao suporte estatístico dos ramos pelo método de bootstrap foram usados os ajustes a seguir: build (250), swap (tbr) e root (“pallipes”); para os demais critérios usou-se o default do software. Para a busca por árvores utilizou-se como critério a parcimônia.

## **Resultados**

### *Informações morfológicas e comportamentais*

**Lista de caracteres analisados.** Os últimos 10 caracteres morfológicos apresentados aqui, são adicionais à matriz de dados de Santos et al. (2015) (Apêndice 1). Os caracteres multiestado foram tratados como não aditivos, exceto quando se observou claramente a uma série de transformação linear.

- 1. Grau de torsão da região apical da mandíbula da fêmea:** (0) sem torsão significativa, em vista frontal, dente 1 aparecendo parcialmente escondido abaixo do dente 2; (1) dente 1 em vista frontal visível, área distal subjacente ao dente 3 destacada obliquamente; (2) dentes 1-3 bem separados um do outro, área distal subjacente e dentes 2-4 destacando-se obliquamente; (3) área distal subjacente aos dentes 1-4 que aparecem como um plano quase vertical em vista frontal (ver Silveira & Santos-Junior 2011). ADITIVO
- 2. Forma do perfil da margem posterior da mandíbula feminina:** (0) margem mais ou menos reta; (1) elementos proximais e distais formando um ângulo distinto; (2) margem com uma curva suave; (3) com um perfil notavelmente sinuoso (Silveira & Santos-Junior 2011).
- 3. Forma do perfil da margem anterior da mandíbula feminina:** (0) margem curvada, afiada e escurecida por toda parte; (1) margem quase reta, afiada (Silveira & Santos-Junior 2011).
- 4. Forma do dente apical 1–2 da mandíbula da fêmea:** (0) dentes 1–2 de forma semelhante e tamanho, bastante curto; (1) dente 1 mais longo que o dente 2; (2) dente 1 distintamente mais longo que o dente 2, consideravelmente mais largo (Silveira & Santos-Junior 2011). ADITIVO
- 5. Forma da carina anterior mesal e do dentículo anterior da mandíbula feminina:** (0) carena baixa, produzida de forma arredondada, sua extremidade distal convergindo para o elemento externo do dentículo anterior mesial em um ponto próximo para o ângulo marginal; (1) carena afiada para a maior parte do seu comprimento, amplamente separada e paralela à margem anterior, extremidade distal da carina formando com o elemento externo do dentículo anterior mesial um molar com estrutura muito proeminente; (2) carina

reduzida, um pouco obliquamente posicionada, apenas observada ao lado da linha de cerdas, denticulo anterior mesial desenvolvido agudamente (Silveira & Santos-Junior 2011).

**6. Forma do denticulo médio mesial:** (0) uma crista aproximadamente triangular e moderadamente alongada, com extremidade distal em forma de borda oblíqua gradualmente inclinada; (1) bastante reduzida, principalmente transversal, com bordas menos definidas (Silveira & Santos-Junior 2011).

**7. Forma do denticulo posterior mesial:** (0) linear, variável alongada e elevada, com extremidade distal abrupta ou apontando distalmente, localizado entre os dentes 1 e 2; (1) uma crista aproximadamente triangular e moderadamente alongada, com extremidade distal em forma de borda afiada gradualmente inclinada; (2) crista triangular muito curta e saliente; (3) grandemente reduzida, principalmente transversal, com bordas bastante borradas (estados como em Silveira & Santos-Junior 2011).

**8. Margem apical do clipeo:** (0) margem apical pontiaguda (Fig. 7); (1) margem apical amplamente truncada; (2) estreitamente subtruncada; (3) amplamente curvada (estados como Santos-Junior et al 2015).

**9. Largura do clipeo:** (0) relativamente larga, aproximadamente tão longa quanto larga; (1) estreito, aproximadamente duas vezes mais longa que largo (estados como em Santos-Junior et al 2015).

**10. Lobos laterais do clipeo:** (0) bem desenvolvido; (1) reduzido e arredondado (estado como em Carpenter 1991).

**11. Largura da gena no ponto medio de sua altura:** (0) muito largo, aproximadamente igual à largura do lobo inferior do olho em vista lateral; (1) menos largo,  $0,8 \times$  a largura do olho; (2) muito estreito,  $0,5 \times$  a largura do olho (Fig. 14) (estados como em Santos-Junior et al 2015). ADITIVO

**12. Carina occipital:** (0) carina ausente; (1) limitada ao topo do gena; (2) desaparecendo em algum ponto próximo ao meio da altura de gena; (3) desaparecendo muito perto da inserção da mandíbula; (4) muito forte e saliente por toda parte (estados como em Santos-Junior et al 2015). ADITIVO

**13. Occipício na visão dorsal:** (0) distintamente curvado; (1) quase reta (estados como em Santos-Junior et al 2015).

**14. Carena pronotal e região umeral:** (0) úmero normalmente produzido, alongado e estreito, carena pontiaguda não lamelar, estendendo-se menos para baixo no lado; (1) úmero normal, carena fracamente lamelar, estendendo-se menos para baixo no lado (Fig. 17); (2) úmero normal, carena sem corte, não lamelar, distintamente estendendida para baixo ao lado (Fig. 18); (3) úmero angularmente saliente, carena fracamente lamelar, estendendo-se menos para baixo ao lado (Fig. 19); (4) úmero distintamente saliente e encurtado, carena lamelar e recurvada para a frente, extremidade não se estendendo para baixo (Fig. 20); (5) úmero curto e truncado, carena com lamela reduzida (Fig. 21); (6) carena centralmente reduzida, com remanescentes laterais agudos; (7) carena ausente (estados como em Santos-Junior et al 2015).

**15. Proeminência pronotal anterior na frente da fôvea pronotal:** (0) não desenvolvida; (1) desenvolvida, relativamente distante da carena pronotal; (2) que se estende acima e perto da carena pronotal, quase colinear com a fôvea; (3) proeminência anterior à fovea desenvolvida, carena pronotal ausente (estados como em Santos-Junior et al. 2015).

**16. Carena pretercular pronotal e área adjacente posterior:** (0) carena pretegrular ausente; (1) carena evanescente; (2) carena normalmente desenvolvida, área adjacente estreita; (3) carena fortemente desenvolvida, área adjacente mais larga (estados como em Santos-Junior et al. 2015). ADITIVO

**17. Forma da entrada espiracular secundária:** (0) semelhante a uma crista; (1) como uma crista escondida anterior (parecendo como ausente); (2) em forma de cúpula (estados como em Santos-Junior et al. 2015).

**18. Escultura da placa mesepisternal dorsal e sulco scrobal:** (0) placa mesepisternal sem pontuações, sulco scrobal estreito mas bastante distinto; (1) placa com mesopontuações rasas e esparsas, sulco scrobal distinto; (2) placa com furos mais fortes que invadem o sulco scrobal, que, no entanto, é distinto; (3) placa com pontuações maiores e ainda mais densas invadindo e obliterando o sulco scrobal; (4) placa com macropontuações muito grandes, sulco scrobal bem aparente; (5) placa não-perfurada, sulco scrobal obsoleto (estados como em Santos-Junior et al. 2015).

**19. Pontuação do mesoscuto:** (0) apenas com micropontuações densas; (1) com micropontuação densa e mesopontuação superficial; (2) com micropontuação mais esparsa e mesopontuação mais profunda e mais forte;

(3) sem micropontuação, com mesopontuação esparsa (muito brilhante); (4) com macropontuação coalescente muito grande (estados como em Santos-Junior et al. 2015).

**20. Cerdas no mesoscuto:** (0) praticamente sem cerdas eretas; (1) com cerdas muito curtas e densas; (2) com cerdas eretas, densas e moderadamente alongadas; (3) com cerdas notavelmente alongadas e nitidamente curvadas apicalmente; (4) com cerdas mais esparsas e bastante longas (estados como em Santos-Junior et al. 2015).

**21. Lamela escutal:** (0) desenvolvida como uma tegula adjacente; (1) reduzida (como em Carpenter 1991).

**22. Lóbulo metanotal:** (0) ausente; (1) presente (estados como em Santos-Junior et al. 2015).

**23. Forma do metanoto e mais o propódeo em perfil:** (0) perfil oblíquo, metanoto convexo e totalmente visível a partir de cima; (1) perfil fortemente inclinado, quase vertical, porção anterior do metanoto apenas visível de cima; (2) perfil essencialmente vertical, metanoto fortemente achatado sem qualquer superfície horizontal; (3) perfil fortemente vertical, metanotum em ângulo de perfil, com uma extensa área horizontal próxima da margem anterior que apresenta um pequeno tubérculo (estados como em Santos-Junior et al. 2015).

**24. Aspecto posterior do propódeo:** (0) com uma cavidade larga e rasa; (1) suavemente convexo em torno de um sulco mediano estreito; (2) com a face posterior projetando-se simetricamente para cada lado do sulco mediano, formando duas protuberâncias moderadamente altas (como em Silveira & Carpenter, 1995).

**25. Valva propodeal:** (0) um grande lóbulo triangular arredondado; (1) um lóbulo baixo completamente amplo e redondo; (2) fortemente reduzida (como em Santos-Junior et al. 2015). ADITIVO

**26. Processos semelhantes a asas no pecíolo de T1:** (0) ausente; (1) presente (como em Santos-Junior et al. 2015).

**27. T1 em vista dorsal:** (0) com pecíolo distinto, margem distal estreita e pouco convexa; (1) pecíolo curto, margem distal estreita e muito convexa; (2) pecíolo muito curto, margem distal mais larga e quase reta, em forma de campânula; (3) margem séssil, distal, muito larga e convexa; (4) pecíolo distinto, alongado, margem distal muito larga e convexa (Santos-Junior et al. 2015).

**28. Forma de T2:** (0) normalmente alongado, aproximadamente tão longo quanto largo, contorno anterior suavemente arredondado, menos convexo em ambas as vistas dorsal e lateral; (1) tergo mais largo que longo, contorno anterior distintamente convexo em ambas as vistas dorsal e lateral; (2) tergo mais largo que longo, perfil fortemente abaulado ântero-lateralmente, espiráculos tendendo a estar virados para a frente (Santos-Junior et al. 2015).

**29. Região pré-espinal do edeago em vista lateral:** (0) não angulada; (1) angulada (como em Santos-Junior et al. 2015).

**30. Glândula de Van der Vecht:** (0) área externamente modificada presente; (1) ausente (como em Carpenter 1991).

**31. Forma do segundo ramo do aparato do ferrão:** (0) com área esclerotizada adjacente muito estreita, muitas vezes indistinta; (1) com área esclerotizada adjacente moderadamente desenvolvida; (2) segundo ramo com área esclerotizada adjacente muito ampla (baseado em Silveira & Silveira 1994). ADITIVO

**32. Material de construção do ninho:** (0) material vegetal e saliva; (1) material vegetal e saliva, alguns ninhos com paredes de secreção pura; (2) material vegetal, saliva e barro (como em Santos-Junior et al. 2015).

**33. Ligação do favo do ninho ao substrato:** (0) por pedicelos únicos ou múltiplos; (1) ninho com iniciação séssil estreita, externamente parecida com um pedúnculo robusto; (2) com iniciação séssil ampla, frequentemente em torno de substratos estreitos como ramos de plantas; (3) células construídas diretamente no substrato (como em Santos-Junior et al. 2015).

**34. Entrada do ninho e múltiplos favos:** (0) entrada única, lateral ou central; (1) múltiplas entradas laterais independentes, uma para cada favo; (2) favos em blocos separados, ou contínuos como uma espiral descendente, muitas vezes caóticos em estrutura (estado 2 como em Wenzel 1998).

**35. Ninho com incorporação de vegetação próxima:** (0) Ausente; (1) Presente (como em Wenzel 1998).

**36. Distância entre os ocelos posteriores:** (0) Muito curta, menor que o diâmetro de um ocelo (Fig. 1); (1) Média, aproximadamente duas vezes o diâmetro de um ocelo (Fig. 2); (2) Larga, aproximadamente três vezes o diâmetro de um ocelo (Fig. 3 e 4). ADITIVO

- 37. Margem ventral do pronoto:** (0) Aproximadamente aguda, e com região anterior ligeiramente sinuosa (Fig. 5); (1) Não angulada, somente acima do ponto ventral (Fig. 6); (2) Estreitamente angulada (Fig. 7); (3) Largamente angulada (Fig. 8).
- 38. Forma do ápice do processo metanotal:** (0) Estreitamente arredondado (Fig. 9); (1) Truncado (Fig. 10); (2) Agudo (Fig. 11); (3) Largamente arredondado (Fig. 12).
- 39. Ápice do edeago em vista dorsal:** (0) Aproximadamente reto, sem lóbulos; (1) Muito expandido lateralmente, mas sem formar lóbulos; (2) Pouco expandido lateralmente, sem lóbulos e com a porção mediana não bifida; (3) Pouco expandido lateralmente, sem lóbulos e com a porção mediana bifida; (4) Expandido lateralmente, formando lóbulos (Figs. 13–16); (5) Bipartido e truncado (Figs. 17 e 18).
- 40. Margem mediana do edeago:** (0) Ausente; (1) Presente (Figs. 13–18). ADITIVO
- 41. Processo ventral do edeago:** (0) Presente e posteriormente direcionado; (1) Presente e anteriormente direcionado (Fig. 19, 21, 25, 27, 29); (2) Ausente; (3) Presente e lateralmente direcionado (Figs. 22 e 31)
- 42. Cristas do processo ventral do edeago:** (0) Ausente (Fig. 19); (1) Presente, restrito somente à margem distal (Fig. 21 e 23); (2) Presente, visível nas margens lateral e distal (Fig. 25).
- 43. Margem posterior do edeago:** (0) Agudo (Fig. 20 e 26); (1) Truncado (Fig. 24); (2) Bipartido (Fig. 22).
- 44. Lóbulo posterodorsal do dígito:** (0) Desenvolvido, aproximadamente agudo (Fig. 27); (1) Não desenvolvido (Fig. 28); (2) Desenvolvido e estreitamente arredondado (Fig. 29); (3) Desenvolvido e largamente arredondado (Figs. 30–31).

### Análise filogenética de dados combinados

A matriz combinada de dados moleculares e morfológicos resultou em 946 caracteres. Desses, 44 representam informações morfológicas. A caracterização morfológica foi apresentada de acordo com dados da literatura (Silveira & Carpenter 1995, Silveira & Santos-Junior 2011, Santos-Junior et al. 2015). Os últimos 10 caracteres apresentados, são adicionais à matriz de dados de Santos et al. (2015) (Apêndice 1). Os caracteres multiestado foram tratados como não aditivos, exceto quando se observou claramente a uma série de transformação linear.

A análise com combinação dos caracteres morfológicos e DNA resultou em 164 árvores igualmente parcimoniosas cujo consenso estrito é apresentado (Fig. 39). Nele, assim como na hipótese morfológica de Santos-Junior (2015) (Fig. 38), a monofilia do gênero *Protopolybia* é corroborada. Entretanto, no presente estudo, o grupo de *P. exigua* resultou parafilético e, portanto, esta análise só permite o reconhecimento de três dos grupos taxonômicos indicados em Santos-Junior et al. (2015), a saber: *P. sedula*, *P. chartergoides* e *P. picteti*. Do mesmo modo, o clado *P. picteti-emortualis* também é suportado (Fig. 39). No que se refere ao posicionamento do grupo de *P. chartergoides* em *Protopolybia*, a análise puramente morfológica inicialmente o apresentou como grupo-irmão de *P. picteti-emortualis* (Santos-Junior et al. 2015) (Fig. 38). Diferentemente, a hipótese proposta aqui pela combinação de dados morfológicos e moleculares apresentou topologia em que *P. chartergoides* é irmão do grupo de *P. sedula* (Fig. 39).

No que se refere ao grupo de *P. exigua*, a hipótese de Santos-Junior et al. (2015) o apresentou como monofilético com base na forma estreita do clipeo e na conformação do propódeo ligeiramente convexa. Um exame visual das 164 topologias resultantes, mostrou três configurações alternativas para as relações de espécies deste grupo: (1) [elementos restantes do gr. *exigua* (*P. scutellaris* + gr. *emortualis-picteti*)]; (2) [elementos restantes do gr. *exigua* ((*P. scutellaris* + *P. similis*) + (gr. *picteti-emortualis*))]; (3) [elementos restantes do gr. *exigua* + ((*P. scutellaris* + (*P. similis* + *P. aliciae*)) + (*P. colombiana* + gr. *picteti-emortualis*))]. Conclui-se assim que, no estado atual de conhecimento, não há como garantir a monofilia do grupo de *P. exigua*, mas, por outro lado, esse resultado ainda foi obtido de análise baseada unicamente da nova matriz morfológica (i.e. acrescida dos 10 novos caracteres).

Hipóteses de relações mais estreitas entre alguns elementos do gr. *exigua* e o grupo *picteti-emortualis* parecem controversas, visto que tanto a morfologia corpórea, a biologia e os traços comportamentais representados pela arquitetura do ninho são claramente distintos (Wenzel 1998, Santos-Junior et al. 2015). Nesse sentido, vale a pena aguardar por uma condição de maior completude dos dados para se ter uma avaliação mais decisiva desse problema (a respeito de análise com dados incompletos, ver também Troyanskaya et al. 2001).

## Considerações finais

Considerando a combinação de dados morfológicos e moleculares, a monofilia do gênero *Protopolybia* foi novamente corroborada, bem como o suporte de três grupos de espécies: *P. sedula*, *P. chartergoides* e *P. picteti-emortualis*. Em contrapartida, o grupo de *P. exigua* não resultou monofilético. Além disso, este estudo apresentou resultados mais conclusivos sobre o posicionamento do grupo de *P. chartergoides*, dentro de *Protopolybia*, diferentes dos obtidos na análise de Santos-Junior et al. (2015).

A hipótese morfológica apresentada por Santos-Junior et al. (2015) propôs o grupo de *P. chartergoides* como grupo-irmão de *P. picteti-emortualis*, com base na escultura da placa mesepisternal dorsal com furos mais fortes que invadem o sulco scrobal, o qual é distinto. De outro modo, a hipótese usando a combinação de dados morfológicos e moleculares apresentada aqui indicou o grupo de *P. chartergoides* como grupo-irmão do grupo de *P. sedula*. Essa disposição parece ser mais plausível, em razão de refletir a grande semelhança existente entre a forma da cabeça das espécies que compõem os dois grupos, e principalmente a largura da gena, a qual é bem próxima em ambos.

O aprimoramento dos resultados aqui apresentados deverá buscar melhor amostragem de espécies dos grupos de *P. picteti-emortualis* e *P. exigua*, para se obter conclusões mais precisas acerca das relações internas em *Protopolybia*, sobretudo sobre a questão da parafilia do gr. *exigua*. Quanto ao grupo de *P. chartergoides*, será decisivo analisar sequência de DNA da espécie *P. duckeianus*, cuja morfologia externa parece representar traços intermediários em respeito aos outros grupos do gênero.

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## Legandas das Figuras

**Figuras 1–12.** 1, 11. *Protopolybia holoxantha*; 2. *P. amarella*; 3, 9. *P. fuscatus*; 4. *P. chartergoides*; 5. *P. acutiscutis*; 6. *P. bella*; 7. *P. rotundata*; 8. *P. chartergoides*; 10. *P. emortualis*; 12. *P. duckeianus*.

**Figuras 13–37.** 13. *Protopolybia iheringi*; 14. *P. sedula*; 15. *P. chartergoides*; 16. *P. pallidibalteatus*; 17. *P. fuscata*; 18. *P. minutissima*; 19, 20. *P. fulvotincta*; 21, 22. *P. sedula*; 23, 24. *P. chartergoides*; 25, 26. *P. diligens*; 27, 28. *P. iheringi*; 29, 30. *P. bella*; 31, 32. *P. pallidibalteatus*; 33. *P. pallidibalteatus*; 34. *P. holoxantha*; 35. *P. iheringi*; 36. *P. chartergoides*; 37. *P. fuscata*. 13–18. Ápice do eedeago em vista dorsal. 19–32. Eedeago em vista lateral e dorsal. 33–37. Volsela da genitália do macho em vista lateral. Escala 0.2mm.

**Figura 38.** Árvore de consenso estrito de 28 árvores igualmente parcimoniosas resultantes da análise sem pesagem de caracteres (retirado de Santos-Junior et al. 2015). O suporte dos ramos é dado a partir do método de reamostragem simétrica (Goloboff et al. 2003).

**Figura 39.** Árvore de consenso para *Protopolybia* estimada a partir da combinação de dados morfológicos e moleculares, usando dados morfológicos e sequências de DNA dos genes 16s e CO1. O suporte dos ramos foi estimado pelo método de Bootstrap. Nós sem suporte foram colapsados.

**Tabela 1** – Tabela de genes sequenciados por amostras. (X) DNA extraído, amplificado e sequenciado (\*\*) DNA amplificado, mas não sequenciado. (-) DNA não extraído.

**Tabela 2** – Tabela de primers utilizados para o sequenciamento dos genes 28s, 16s, 12s e COI, com suas respectivas referências para construção.

**Apêndice 1.** Matriz de caracteres editada de Santos-Junior et al. (2015). (?) não observado; (-) ambíguo. Colunas 36 a 44 correspondem aos caracteres adicionais descritos.

Figuras 1–12





Figuras 13– 37

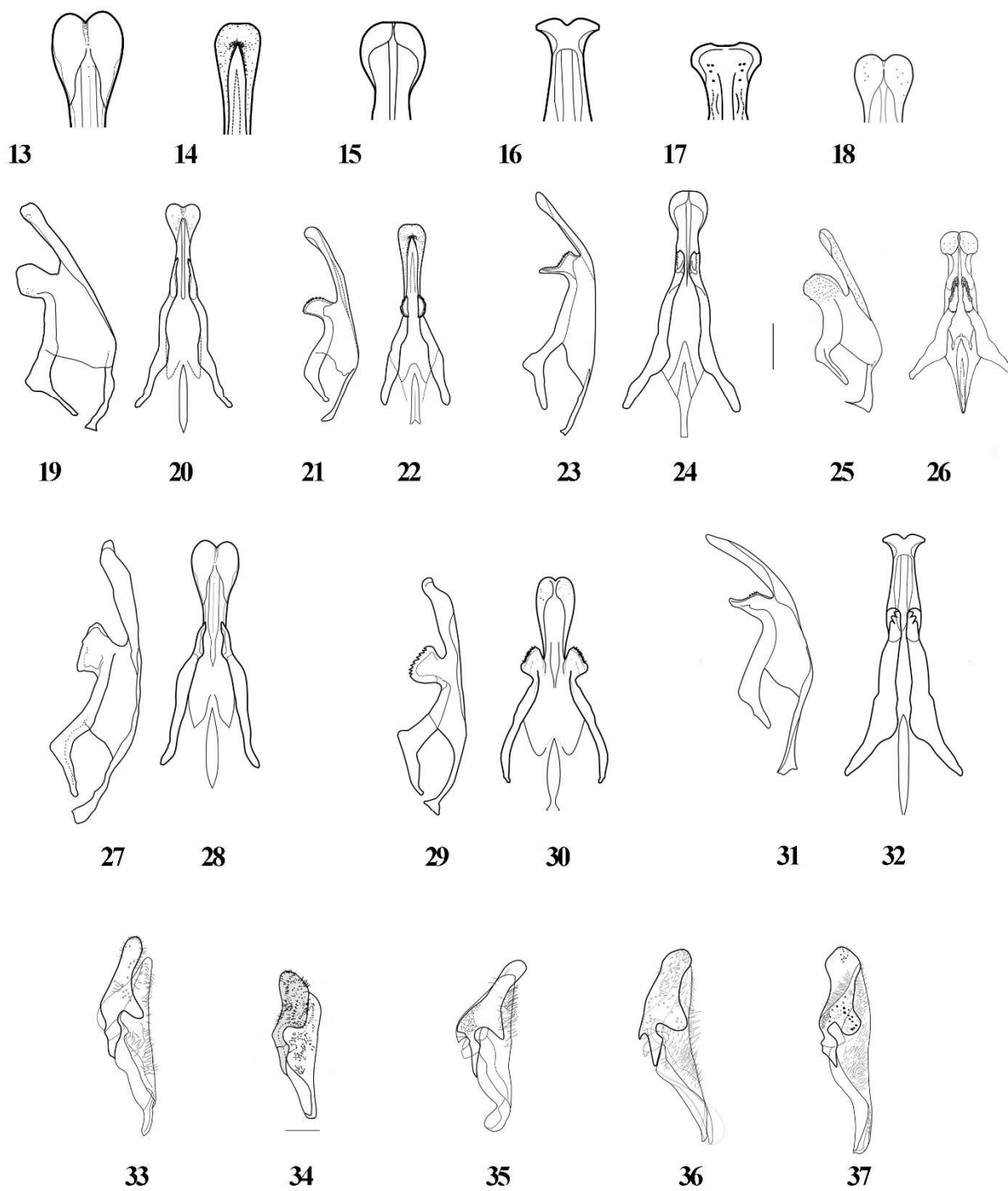


Figura – 38

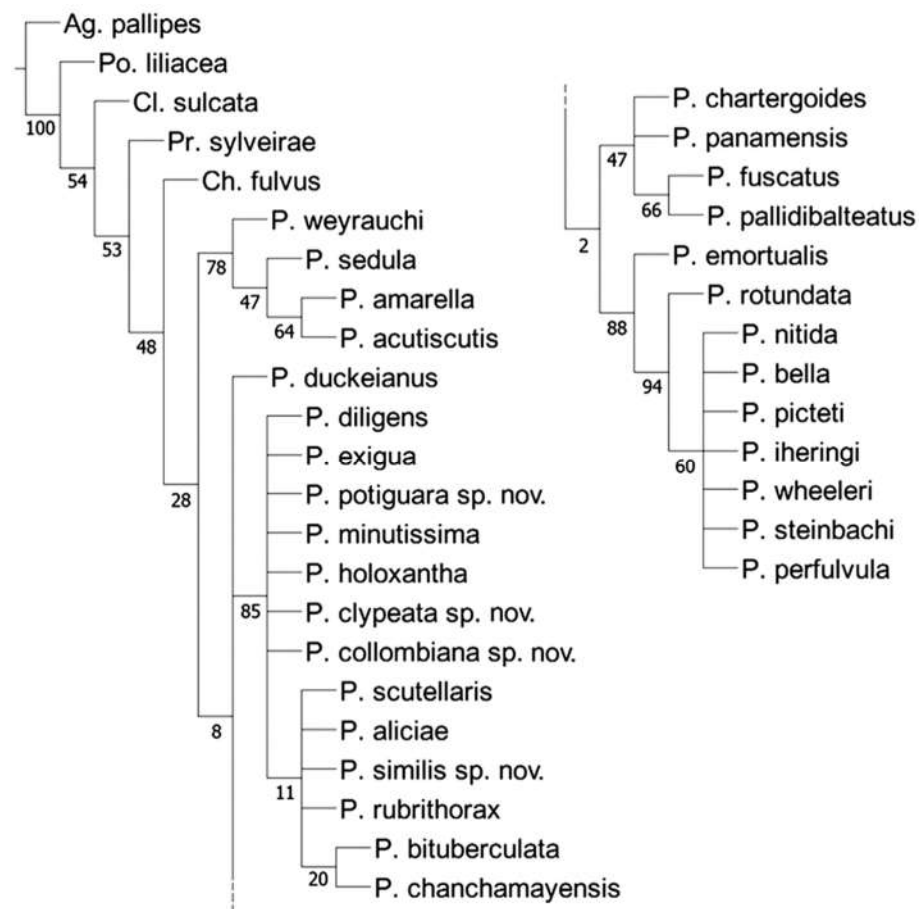


Figura – 39

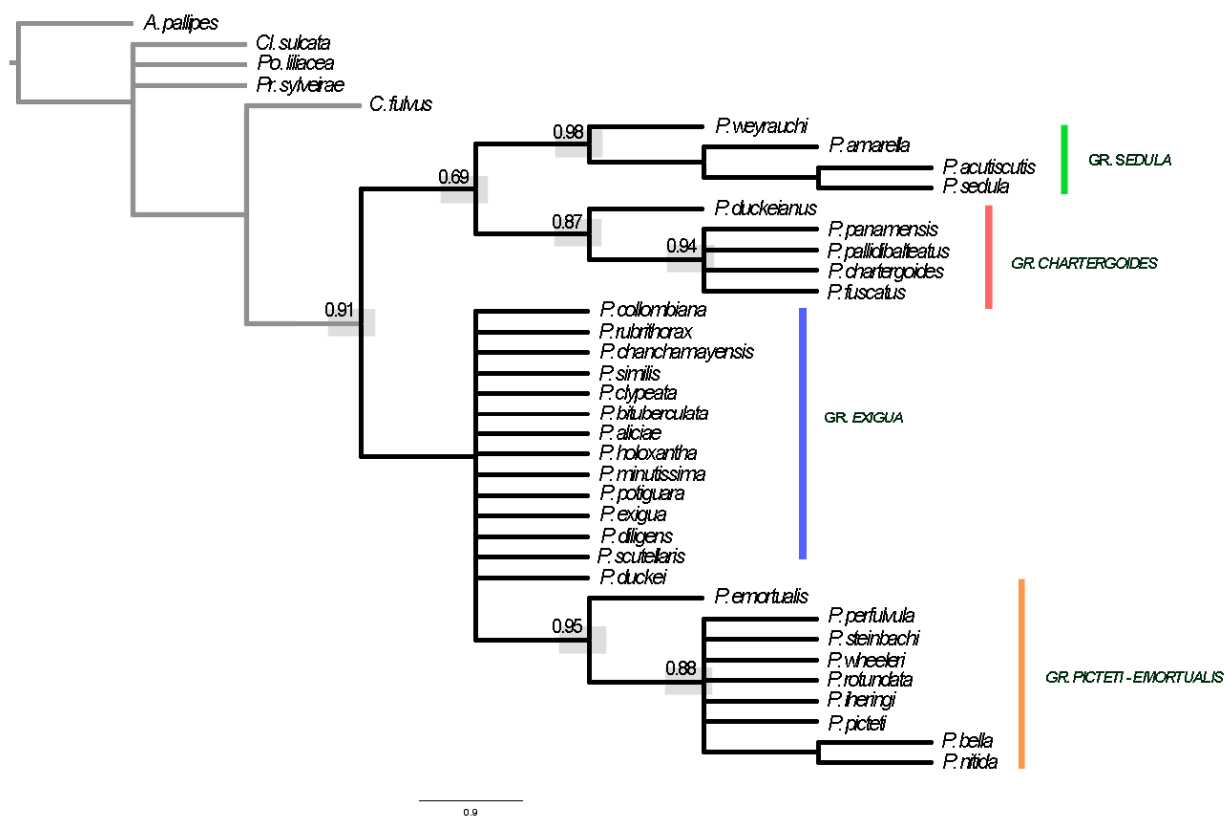


Tabela 1

| TÁXON                      | FRAGMENTOS |     |     |     | N/<br>NUCLEOTÍDEOS |
|----------------------------|------------|-----|-----|-----|--------------------|
|                            | 28S        | 16S | 12S | COI |                    |
| <i>P. pallipes</i>         | X          | X   | X   | X   | 2044pb             |
| <i>Pr. sylveirae</i>       | X          | X   | X   | X   | 2044pb             |
| <i>C. fulvus</i>           | X          | X   | X   | X   | 2044pb             |
| <i>Po. Striata</i>         | X          | X   | X   | **  | 1234pb             |
| <i>P. bituberculata</i>    | X          | X   | X   | X   | 2044pb             |
| <i>P. minutissima</i>      | X          | X   | **  | X   | 1714pb             |
| <i>P. diligens</i>         | X          | X   | X   | X   | 2044pb             |
| <i>P. exigua</i>           | -          | X   | X   | X   | 2044pb             |
| <i>P. scutellaris</i>      | X          | X   | X   | X   | 2044pb             |
| <i>P. chartergoides</i>    | X          | X   | X   | X   | 1714pb             |
| <i>P. pallidibalteatus</i> | **         | X   | -   | X   | 1714pb             |
| <i>P. sedula</i>           | **         | X   | **  | X   | 1714pb             |
| <i>P. amarela</i>          | X          | X   | **  | X   | 1714pb             |
| <i>P. acutiscutis</i>      | X          | X   | X   | X   | 2044pb             |
| <i>P. bella</i>            | -          | -   | -   | -   | 0                  |
| <i>P. nítida</i>           | **         | -   | -   | -   | 0                  |
| <i>P. duckei</i>           | X          | X   | X   | X   | 2044pb             |
| <i>P. emortualis</i>       | X          | X   | -   | X   | 1714pb             |

Tabela 2

| Gene       | Primer              | Sequência (5' - 3')        | Referência         |
|------------|---------------------|----------------------------|--------------------|
| <b>16S</b> | LR13943F            | CACCTGTTTATCAAAAACAT       | Costa et al., 2003 |
|            | LR13392R            | CGTCGATTTGAACTCAAATC       | Costa et al., 2003 |
| <b>COI</b> | F: CI-J-1718        | GGAGGATTTGGAAATTGATTAGTTCC | Simon et al., 1994 |
|            | R: CI-N-2191        | GGTAAAATTAATAAATAAACTTC    | Simon et al., 1994 |
| <b>28S</b> | For28SVesp          | AGAGAGAGTTCAAGAGTACGTG     | Simon et al., 1994 |
|            | Rev28SVesp          | GGAACCAGCTACTAGATGG        | Simon et al., 1994 |
| <b>12S</b> | 12S ai (SR-J-14233) | AAACTAGGATTAGATACCCTATTAT  | Simon et al., 1994 |
|            | 12S bi (SR-N-14588) | AAGAGCGACGGGCGATGTGT       | Simon et al., 1994 |

## Apêndice 1

|                            | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25  | 26 | 27 | 28 | 29 | 30 | 31 | 32  | 33 | 34 | 35 | 36 | 37 | 38  | 39 | 40 | 41 | 42 | 43 | 44 |   |   |   |  |
|----------------------------|---|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|-----|----|----|----|----|----|----|-----|----|----|----|----|----|-----|----|----|----|----|----|----|---|---|---|--|
| <i>Ag. pallipes</i>        | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0  | 0  | 2  | 0  | 0  | 1  | 2  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0   | 0  | 0  | 0  | 0  | 0  | 0  | 0   | 0  | 0  | 0  | 0  | -  | 0   | -  | 0  | 0  | 0  | 0  | 0  | ? | 0 | 0 |  |
| <i>Ch. fulvus</i>          | 2 | 3 | 1 | 1 | 2 | 0 | 2 | 1 | 0 | 1  | 2  | 1  | 0  | 6  | 0  | 0  | 2  | 4  | 4  | 2  | 1  | 0  | 3  | 0  | 2   | 0  | 4  | 1  | 0  | 1  | 1  | 0   | 1  | -  | 0  | -  | 0  | 1   | 1  | 0  | 0  | 0  | 1  | 1  |   |   |   |  |
| <i>Pr. sylveirae</i>       | 1 | 1 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 1  | 0  | 2  | 0  | 2  | 1  | 2  | 1  | 1  | 2  | 3  | 1  | 0  | 1  | 0  | 1   | 0  | 2  | 1  | ?  | 1  | 0  | 0   | 2  | 0  | 0  | -  | 0  | 1   | ?  | ?  | ?  | ?  | ?  | ?  |   |   |   |  |
| <i>Po. liliacea</i>        | 1 | 0 | 0 | 1 | 0 | 0 | 3 | 0 | 0 | 1  | 1  | 2  | 0  | 7  | 1  | 1  | 0  | 5  | 0  | 0  | 1  | 0  | 0  | 0  | 0   | 0  | 0  | 1  | 1  | 0  | 1  | 0   | 0  | 2  | 0  | 0  | -  | 0   | 1  | 2  | 0  | -  | 0  | 1  | 2 |   |   |  |
| <i>Cl. sulcata</i>         | 2 | 2 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 1  | 2  | 0  | 0  | 7  | -  | 2  | 2  | 1  | 1  | 2  | 1  | 0  | 0  | 0  | 0   | 0  | 0  | 1  | 1  | 0  | 1  | 0   | 0  | 3  | 0  | 0  | -  | 0   | 1  | 3  | 0  | 1  | 1  | 0  | ? |   |   |  |
| <i>P. emortualis</i>       | 3 | 2 | 1 | 2 | 2 | 1 | 3 | 0 | 0 | 1  | 0  | 2  | 0  | 5  | 1  | 2  | 2  | 2  | 2  | 2  | 1  | 1  | 2  | 0  | 2   | 0  | 3  | 1  | 0  | 1  | 2  | 2   | 0  | 1  | 0  | 1  | 0  | 1   | 0  | 1  | 4  | 1  | 1  | 1  | 1 | 3 |   |  |
| <i>P. duckeianus</i>       | 2 | 3 | 1 | 1 | 2 | 0 | 2 | 3 | 0 | 1  | 1  | 2  | 0  | 2  | 1  | 1  | 2  | 2  | 1  | 1  | 1  | 1  | 1  | 0  | 2   | 0  | 3  | 2  | ?  | 1  | 2  | ?   | ?  | ?  | ?  | ?  | 3  | 3   | 2  | ?  | ?  | ?  | ?  | ?  | ? |   |   |  |
| <i>P. fuscatus</i>         | 2 | 3 | 1 | 1 | 2 | 0 | 2 | 2 | 0 | 1  | 2  | 2  | 1  | 3  | 1  | 2  | 2  | 3  | 2  | 2  | 1  | 1  | 2  | 0  | 2   | 0  | 3  | 2  | 0  | 1  | 2  | 1   | 0  | -  | 0  | 0  | 3  | 2   | 5  | 1  | 1  | 0  | 3  | 3  |   |   |   |  |
| <i>P. chartergoides</i>    | 2 | 3 | 1 | 1 | 2 | 0 | 2 | 2 | 0 | 1  | 2  | 3  | 0  | 3  | 1  | 2  | 2  | 3  | 2  | 2  | 1  | 1  | 2  | 0  | 1,2 | 0  | 3  | 2  | 0  | 1  | 2  | 0,1 | 0  | 1  | 0  | 3  | 3  | 2   | 4  | 1  | 1  | 1  | 3  | 3  |   |   |   |  |
| <i>P. pallidibaldeatus</i> | 2 | 3 | 1 | 1 | 2 | 0 | 2 | 2 | 0 | 1  | 2  | 2  | 1  | 3  | 1  | 2  | 2  | 3  | 2  | 2  | 1  | 1  | 2  | 0  | 2   | 0  | 3  | 2  | 0  | 1  | 2  | 0,1 | 0  | 1  | 0  | 3  | 3  | 2   | 5  | 1  | 1  | 0  | 2  | 3  |   |   |   |  |
| <i>P. panamensis</i>       | 2 | 3 | 1 | 1 | 2 | 0 | 2 | 2 | 0 | 1  | 2  | 2  | 0  | 3  | 1  | 2  | 2  | 3  | 2  | 2  | 1  | 1  | 2  | 0  | 2   | 0  | 3  | 2  | ?  | 1  | 2  | 1   | 0  | -  | 0  | 3  | 3  | 1,2 | ?  | ?  | ?  | ?  | ?  | ?  |   |   |   |  |
| <i>P. nitida</i>           | 3 | 2 | 1 | 2 | 2 | 1 | 3 | 0 | 0 | 1  | 0  | 4  | 0  | 4  | 1  | 3  | 2  | 2  | 3  | 4  | 1  | 1  | 1  | 3  | 2   | 0  | 2  | 1  | 1  | 1  | 2  | 0   | 0  | 1  | ?  | 1  | 1  | 1   | 4  | 1  | 1  | 0  | 2  | 1  |   |   |   |  |
| <i>P. bella</i>            | 3 | 2 | 1 | 2 | 2 | 1 | 3 | 0 | 0 | 1  | 0  | 4  | 0  | 4  | 1  | 3  | 2  | 2  | 3  | 4  | 1  | 1  | 1  | 3  | 2   | 0  | 2  | 1  | 1  | 1  | 2  | 0   | 0  | 2  | 0  | 1  | 1  | 1   | 4  | 1  | 1  | 1  | 2  | 1  |   |   |   |  |
| <i>P. picteti</i>          | 3 | 2 | 1 | 2 | 2 | 1 | 3 | 0 | 0 | 1  | 0  | 4  | 0  | 4  | 1  | 3  | 2  | 2  | 3  | 4  | 1  | 1  | 1  | 0  | 2   | 0  | 2  | 1  | 0  | 1  | 2  | 0   | 0  | 1  | 0  | 0  | 2  | 1   | 4  | 1  | 0  | 0  | 2  | 1  |   |   |   |  |
| <i>P. iheringi</i>         | 3 | 2 | 1 | 2 | 2 | 1 | 3 | 0 | 0 | 1  | 0  | 4  | 0  | 4  | 1  | 3  | 2  | ?  | 3  | 4  | 1  | 1  | 1  | 3  | 2   | 0  | 2  | 1  | 1  | 1  | 2  | 0   | 0  | 1  | 1  | 1  | 2  | 1   | 4  | 1  | 0  | 0  | 0  | 1  |   |   |   |  |
| <i>P. rotundata</i>        | 3 | 2 | 1 | 2 | 2 | 1 | 3 | 0 | 0 | 1  | 0  | 4  | 0  | 5  | 1  | 4  | 2  | 2  | 3  | 4  | 1  | 1  | 1  | 3  | 2   | 0  | 2  | 1  | ?  | 1  | 2  | ?   | ?  | ?  | ?  | ?  | ?  | 1   | 2  | 1  | ?  | ?  | ?  | ?  | ? |   |   |  |
| <i>P. wheeleri</i>         | 3 | 2 | 1 | 2 | 2 | 1 | 3 | 0 | 0 | 1  | 0  | 4  | 0  | 4  | 1  | 4  | 2  | 2  | 3  | 4  | 1  | 1  | 1  | 0  | 2   | 0  | 2  | 1  | ?  | 1  | 2  | 0   | 0  | 1  | 0  | 1  | 2  | 1   | ?  | ?  | ?  | ?  | ?  | ?  |   |   |   |  |
| <i>P. steinbachi</i>       | 3 | 2 | 1 | 2 | 2 | 1 | 3 | 0 | 0 | 1  | 0  | 4  | 0  | 4  | 1  | 4  | 2  | 2  | 3  | 4  | 1  | 1  | 1  | 3  | 1   | 0  | 2  | 1  | ?  | 1  | 2  | 0   | 0  | 1  | ?  | 1  | 2  | 1   | ?  | ?  | ?  | ?  | ?  | ?  |   |   |   |  |
| <i>P. perfulvula</i>       | 3 | 2 | 1 | 2 | 2 | 1 | 3 | 0 | 0 | 1  | 0  | 4  | 0  | 4  | 1  | 4  | 2  | 2  | 3  | 4  | 1  | 1  | 1  | 3  | 2   | 0  | 2  | 1  | ?  | 1  | 2  | 0   | 0  | 1  | ?  | 0  | 2  | 1   | ?  | 0  | ?  | ?  | ?  | ?  |   |   |   |  |
| <i>P. sedula</i>           | 2 | 3 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 1  | 1  | 3  | 0  | 1  | 2  | 2  | 2  | 1  | 1  | 1  | 1  | 1  | 0  | 0  | 2   | 0  | 2  | 1  | 0  | 1  | 2  | 0   | 2  | 2  | 1  | 0  | 0  | 1   | 4  | 1  | 1  | 2  | 2  | 1  |   |   |   |  |
| <i>P. amarella</i>         | 2 | 3 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 1  | 1  | 3  | 0  | 2  | 2  | 2  | 2  | 1  | 1  | 1  | 1  | 0  | 0  | 2  | 1   | 2  | 1  | ?  | 1  | 2  | ?  | ?   | ?  | ?  | ?  | ?  | 0  | 0   | 1  | ?  | ?  | ?  | ?  | ?  |   |   |   |  |
| <i>P. acutiscutis</i>      | 2 | 3 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 1  | 1  | 3  | 0  | 2  | 2  | 2  | 2  | 1  | 1  | 1  | 1  | 0  | 0  | 2  | 1   | 2  | 1  | ?  | 1  | 2  | 0  | 2   | 1  | 1  | 0  | 0  | 1  | ?   | ?  | ?  | ?  | ?  | ?  | ?  |   |   |   |  |
| <i>P. weyrauchi</i>        | 2 | 3 | 1 | 1 | 2 | 0 | 2 | 0 | 0 | 1  | 1  | 3  | 0  | 2  | 1  | 2  | 2  | 1  | 1  | 1  | 1  | 1  | 0  | 0  | 2   | 0  | 2  | 1  | 0  | 1  | 2  | 0   | 2  | 1  | 1  | 0  | 0  | 1   | 4  | 1  | 1  | 2  | 2  | 1  |   |   |   |  |
| <i>P. scutellaris</i>      | 2 | 3 | 1 | 1 | 2 | 0 | 2 | 2 | 1 | 1  | 1  | 2  | 0  | 2  | 2  | 2  | 2  | 0  | 0  | 0  | 1  | 1  | 0  | 1  | 2   | 1  | 1  | 0  | 0  | 1  | 2  | 0   | 0  | -  | 0  | 2  | 0  | 1   | 4  | 1  | 2  | 0  | 2  | 1  |   |   |   |  |
| <i>P. diligens</i>         | 2 | 3 | 1 | 1 | 2 | 0 | 2 | 2 | 1 | 1  | 1  | 2  | 0  | 2  | 1  | 2  | 2  | 0  | 0  | 1  | 1  | 1  | 0  | 1  | 1   | 0  | 1  | 0  | 1  | 0  | 1  | 2   | 0  | 0  | 1  | 0  | 0  | 0   | 1  | 4  | 1  | 2  | 0  | 2  | 1 |   |   |  |
| <i>P. exigua</i>           | 2 | 3 | 1 | 1 | 2 | 0 | 2 | 2 | 1 | 1  | 1  | 2  | 0  | 2  | 1  | 2  | 2  | 0  | 0  | 1  | 1  | 1  | 0  | 1  | 1   | 0  | 1  | 0  | 1  | 0  | 0  | 1   | 2  | 0  | 0  | 1  | 1  | 0   | 0  | 1  | 4  | 1  | 2  | 0  | 2 | 1 |   |  |
| <i>P. potiguara</i>        | 2 | 3 | 1 | 1 | 2 | 0 | 2 | 2 | 1 | 1  | 1  | 2  | 0  | 2  | 1  | 2  | 2  | 0  | 0  | 1  | 1  | 1  | 0  | 1  | 1   | 0  | 1  | 0  | 1  | 0  | ?  | 1   | 2  | ?  | ?  | ?  | ?  | 0   | 0  | 1  | ?  | ?  | ?  | ?  | ? |   |   |  |
| <i>P. minutissima</i>      | 2 | 3 | 1 | 1 | 2 | 0 | 2 | 2 | 1 | 1  | 1  | 3  | 0  | 2  | 1  | 2  | 2  | 0  | 0  | 1  | 1  | 1  | 0  | 1  | 1   | 0  | 1  | 0  | 0  | 1  | 2  | 0   | 0  | 1  | 0  | 0  | 0  | 1   | 4  | 1  | 1  | 0  | 2  | 1  |   |   |   |  |
| <i>P. holoxantha</i>       | 2 | 3 | 1 | 1 | 2 | 0 | 2 | 2 | 1 | 1  | 1  | 2  | 0  | 2  | 2  | 2  | 1  | 1  | 1  | 1  | 1  | 0  | 1  | 1  | 0   | 1  | 0  | 0  | 1  | 2  | 0  | 0   | 1  | 0  | 2  | 0  | 0  | 4   | 1  | 1  | 0  | 1  | 1  |    |   |   |   |  |
| <i>P. aliciae</i>          | 2 | 3 | 1 | 1 | 2 | 0 | 2 | 3 | 1 | 1  | 1  | 2  | 0  | 2  | 1  | 2  | 2  | 0  | 0  | 0  | 1  | 0  | 1  | 1  | 1   | 1  | 0  | ?  | 1  | 2  | 0  | 0   | 1  | 0  | 0  | 0  | 1  | ?   | ?  | ?  | ?  | ?  | ?  |    |   |   |   |  |
| <i>P. bituberculata</i>    | 2 | 3 | 1 | 1 | 2 | 0 | 2 | 3 | 1 | 1  | 1  | 2  | 0  | 2  | 1  | 2  | 2  | 0  | 0  | 0  | 1  | 1  | 0  | 2  | 1   | 0  | 1  | 0  | 0  | 1  | 2  | 0   | 0  | 1  | 0  | 0  | 0  | 1   | 4  | 1  | 2  | 0  | 2  | 3  |   |   |   |  |
| <i>P. clypeata</i>         | 2 | 3 | 1 | 1 | 2 | 0 | 2 | 3 | 1 | 1  | 1  | 2  | 0  | 2  | 2  | 2  | 2  | 0  | 0  | 1  | 1  | 1  | 0  | 1  | 1   | 0  | 1  | 0  | 0  | 1  | 2  | 0   | 0  | ?  | 0  | 0  | 0  | 1   | 4  | 1  | 2  | 2  | 0  | 1  |   |   |   |  |
| <i>P. similis</i>          | 2 | 3 | 1 | 1 | 2 | 0 | 2 | 2 | 1 | 1  | 1  | 3  | 0  | 2  | 1  | 2  | 2  | 0  | 0  | 0  | 1  | 1  | 0  | 2  | 1   | 1  | 1  | 0  | 0  | 1  | 2  | ?   | ?  | ?  | ?  | ?  | 0  | 0   | 1  | 4  | 1  | 2  | 0  | 2  | 1 |   |   |  |
| <i>P. chanchamayensis</i>  | 2 | 3 | 1 | 1 | 2 | 0 | 2 | 3 | 1 | 1  | 1  | 2  | 0  | 2  | 1  | 2  | 2  | 0  | 0  | 0  | 1  | 1  | 0  | 2  | 1   | 0  | 1  | 0  | 1  | 0  | ?  | 1   | 2  | 0  | 0  | 1  | 0  | 0   | 1  | ?  | ?  | ?  | ?  | ?  |   |   |   |  |
| <i>P. rubrithorax</i>      | 2 | 3 | 1 | 1 | 2 | 0 | 2 | 3 | 1 | 1  | 1  | 2  | 0  | 2  | 1  | 2  | 2  | 0  | 0  | 0  | 1  | 1  | 0  | 1  | 1   | 0  | 1  | 0  | 1  | 0  | ?  | 1   | 2  | ?  | ?  | ?  | ?  | 0   | 0  | 1  | ?  | ?  | ?  | ?  | ? |   |   |  |
| <i>P. colombiana</i>       | 2 | 3 | 1 | 1 | 2 | 0 | 2 | 2 | 1 | 1  | 1  | 2  | 0  | 2  | 2  | 2  | 2  | 0  | 0  | 1  | 1  | 1  | 0  | 1  | 1   | 0  | 1  | 0  | 0  | 1  | 2  | 0   | 0  | 1  | 0  | 0  | 0  | 1   | 4  | 1  | 1  | 0  | 2  | 1  |   |   |   |  |

## CONCLUSÕES GERAIS

O gênero *Protopolybia* Ducke 1905 foi revisado, sendo descritas três novas espécies, *Protopolybia lidiae* sp. nov., *P. eldinaris* sp. nov. e *P. djaneteae* sp. nov. Além disso, o status taxonômico de duas espécies foi revalidado. Chaves de identificação foram propostas para os grupos de *P. sedula*, *P. picteti-emortualis* e *P. chartergoides*. Vários novos registros de coleta e novas sinonímias foram apresentados.

Quanto à proposição de uma hipótese filogenética por evidencia total para o gênero, a monofilia proposta por Santos-Junior et al. (2015) foi novamente corroborada. Em contrapartida, diferentemente da hipótese proposta unicamente por dados morfológicos, essa análise resultou o grupo de *P. exigua* como parafilético.

Além disso, a hipótese de monofilia do grupo de espécies de *P. chartergoides* é corroborada e sua posição relativa dentro de *Protopolybia* é resolvida, com indicação de uma relação mais estreita com o grupo de *P. sedula*. Esta hipótese parece ser mais plausível que a morfológica, visto refletir a grande semelhança existente entre a forma da cabeça e largura da gena das espécies que compõem os dois grupos.

## ANEXOS

**ZOOTAXA** ISSN 1175-5326 (Print Edition) & ISSN 1175-5334 (Online Edition)**Preparation of manuscripts**

- 1) *General*. All papers must be in English. Authors whose native language is not English are encouraged to have their manuscripts read by a native Englishspeaking colleague before submission. Nomenclature must be in agreement with the *International Code of Zoological Nomenclature* (4th edition 1999), which came into force on 1 January 2000. Author(s) of species name must be provided when the scientific name of any animal species is first mentioned (the year of publication needs not be given; if you give it, then provide a full reference of this in the reference list). Authors of plant species names need not be given. Metric systems should be used. If possible, use the common font New Times Roman and use as little formatting as possible (use only bold and *italics* where necessary and indentions of paragraphs except the first). Special symbols (e.g. male or female sign) should be avoided because they are likely to be altered when files are read on different machines (Mac versus PC with different language systems). You can code them as m# and f#, which can be replaced during page setting. The style of each author is generally respected but they must follow the following general guidelines.
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- 3) The name(s) of all authors of the paper must be given and should be typed in the upper case (e.g. ADAM SMITH, BRIAN SMITH & CAROL SMITH). The address of each author should be given in *italics* each starting a separate line. Email address(es) should be provided if available.
- 4) The abstract should be concise and informative. Any new names or new combinations proposed in the paper should be mentioned. Abstracts in other languages may also be included in addition to English abstract. The abstract should be followed by a list of key words that are not present in the title. Abstract and key words are not needed in short correspondence.

5) The arrangement of the main text varies with different types of papers (a taxonomic revision, an analysis of characters and phylogeny, a catalogue etc.), but should usually start with an introduction and end with a list of references. References should be cited in the text as Smith (1999), Smith & Smith (2000) or Smith et al. (2001) (3 or more authors), or alternatively in a parenthesis (Smith 1999; Smith & Smith 2000; Smith et al. 2001). All literature cited in the text must be listed in the references in the following format (see a sample page here in PDF).

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C) Book: Smith, A., Smith, B. & Smith, C. (2001) *Title of Book*. Publisher name and location, xyz pp.

D) Internet resources: Author (2002) Title of website, database or other resources, Publisher name and location (if indicated), number of pages (if known). Available from: <http://xxx.xxx.xxx/> (Date of access).

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5–7) and also geographic or name associations (Murray–Darling River; a Federal–State agreement).

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1 Seven setae present on tarsus I ; four setae present on tibia I; leg I longer than the body; legs black in color ... Genus A

- Six setae present on tarsus I; three setae present on tibia I; leg I shorter than the body; legs brown in color ... 2

2 Leg II longer than leg I ... Genus B

- Leg II shorter than leg I ... Genus C

## Zootaxa Digital Imaging Guide

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digital files. The editors only reject substandard work. Evidence of inferior illustrations published elsewhere shall not be used to argue for acceptability in Zootaxa. Peruse recent issues to judge minimal quality standards for Zootaxa. Here a somewhat lengthy guide to digital imaging specifically designed for Zootaxa is provided. The file preparation guide is given specifically for Photoshop, most likely the most widely used imaging application. Other applications may be used as long as a publication quality file is achieved. Zootaxa neither requires the usage of nor endorses any particular product.

QUICK SUMMARY Required final resolution is 300 dpi for coloured images (RGB), 300–600 dpi for black and white images and 600–1200 dpi for line art (bitmap). Adjust levels/curves in scan software, possibly correct color casts. Use ROC if necessary, do not use ICE3/ICE4.

Scan at somewhat higher resolution than is necessary, use Genuine Fractals to upsample older digital captures. Save line art generated in Illustrator, Excel, Powerpoint as .tif/.bmp files. Further process only .tif/.psd files (do not adjust jpegs/gifs). Clean images at 100%. Use dust and scratches filter with diameter 2, threshold +/- 12, then use healing brush or cloning stamp. Adjust overall tonality/contrast with levels and curves. Adjust overall color with curves (better than variations/color correction); adjust (increase) saturation. Selections for local tonality/contrast and color adjustments should be feathered. Cutouts for multi-image plates should be carried out with feathered tools in nonbackground layers. Crop excess borders. SAVE MASTER FILE. On copy file, downsample to 17 cm wide & 300/600 dpi Unsharp mask (not sharpen), diameter 1.4–1.8, threshold 10–16, amount variable. Alternatively, use outputsharpening utility/plugin such as NikSharpener. Save as uncompressed .tif file. On second copy file (submission images), downsample to 72 dpi; save as greyscale/RGB not CMYK) jpeg quality 6/10. Further instructions as to how to transmit the files will be provided once the manuscript is near acceptance.

- 2) Submission files. Duplicate all your final image files, and place them into a "submission" directory (third copy of images). Open the images, and reduce image size (Image: Image size) to 72 dpi at the original size (maximum width = 17 cm), with the resampling check box checked. Save images as good medium quality jpegs (quality 6 of 10). PLEASE save jpegs in

B&W/RGB mode; although your system may be able to handle CMYK jpegs, many cannot do so, hence doing this may increase the review period of your manuscript.