PENSOFT

SENCKENBERG
world of biodiversity

Leibniz Association

A systematic review of the Neotropical social wasp genus *Angiopolybia* Araujo, 1946 (Hymenoptera: Vespidae): species delimitation, morphological diagnosis, and geographical distribution

Paulo Cézar Salgado Barroso[1], Rodolpho Santos Telles Menezes[2,3], Marcio Luiz de Oliveira[1], Alexandre Somavilla[1]

1 *Programa de Pós-Gradução em Ciências Biológicas (Entomologia), Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia (INPA), Av. André Araújo, 2.936, Petrópolis, 69067-375, Manaus, Brazil*

2 *Programa de Pós-Graduação em Biodiversidade Animal, Centro de Ciências Naturais e Exatas, Universidade Federal de Santa Maria (UFSM), Av. Roraima, 1000, Camobi, 97105-900, Santa Maria, Brazil*

3 *Laboratório de Biologia Comparada e Abelhas, Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras (FFCLRP), Universidade de São Paulo (USP), Av. Bandeirantes, 3900, Monte Alegre, 14040-901, Ribeirão Preto, SP, Brazil*

http://zoobank.org/F85F11D5-313D-4A75-B390-7FDCCCA9376F

Corresponding authors: Paulo Cézar Salgado Barroso (pc.salgadobarroso@gmail.com), Rodolpho Santos Telles Menezes (rstmenezes@gmail.com)

Received 12 July 2021
Accepted 03 February 2022
Published 02 March 2022

Academic Editors Beny Wipfler, Mónica M. Solórzano-Kraemer

Citation: Barroso PCS, Menezes RST, de Oliveira ML, Somavilla A (2022) A systematic review of the Neotropical social wasp genus *Angiopolybia* Araujo, 1946 (Hymenoptera: Vespidae): species delimitation, morphological diagnosis, and geographical distribution. Arthropod Systematics & Phylogeny 80: 75–97. https://doi.org/10.3897/asp.80.e71492

Abstract

For the Neotropical genus *Angiopolybia* Araujo 1946, several phenotypic forms were previously described, however, they have not been studied within an integrative taxonomic framework. Here, we used molecular data (variation of two mitochondrial genetic markers with molecular species delimitation methods) and morphology (adult morphology, male genitalia, and scanning electron microscopy images) to test the number of species within *Angiopolybia*. Specifically, we investigated the taxonomic validity of the morphological variants *A. pallens* dark morph, *A. paraensis* morph *paraensis*, *A. paraensis* morph *ruficornis*, and *A. paraensis* morph *obscurior*. Moreover, we reviewed the taxonomy and geographic distribution of the genus. Our results of morphological and molecular analyses are compatible with the current classification of *Angiopolybia*, and we did not find reasons to propose the morphological variants of *A. pallens* and *A. paraensis* as valid species. Additionally, we reassess the spatial range of the four *Angiopolybia* species and provide refined maps of their geographical distributions.

Keywords

Integrative taxonomy, morphological variation, mtDNA, paper wasps, phylogenetic systematics, swarm-founding social wasps.

1. Introduction

Species boundaries are frequently hard to delimit due to intraspecific morphological variation. Hence, the use of different sources of biological information such as biogeography, behavior, ecology, molecular data, and morphology is generally regarded as a good practice for species delimitation (Bickford et al. 2007; Padial et al. 2010). Intraspecific polymorphism has been designated as "morph" for swarm-founding social wasps (Vespidae: Polistinae: Epiponini) (Richards 1978), but taxonomic investigations using a variety of characters from independent datasets are scarce for the group (Menezes et al. 2015; Lopes and Menezes 2017; Somavilla et al. 2021).

Angiopolybia Araujo, 1946 is a neotropical swarming-founding social wasp genus composed of four species: *A. pallens* (Lepeletier, 1836), *A. paraensis* (Spinola, 1851), *A. obidensis* (Ducke, 1904), and *A. zischkai* Richards, 1978. *Angiopolybia* is recovered as the sister lineage of all remaining Epiponini genera (Menezes et al. 2020; Noll et al. 2021). From a morphological perspective, *Angiopolybia* is characterized by the pronotum with lateral fovea, scutum with posterolateral lamella absent anteriorly and not adjacent to the tegula, mesoepisternum with dorsal groove, clypeus with square lateral lobes, and sharply pointed apex (Carpenter 2004). According to Andena et al. (2007), the monophyly of the genus is supported by six synapomorphies: prestigma about as long as wide, proepisternum with reduced carina, scutal lamella reduced, scutellum without an impressed line, practically straight dorsal groove, and flattened metapleural basalar area. Phylogenetic studies recovered two clades with the following relationship for *Angiopolybia* species: ((*A. paraensis* + *A. obidensis*) + (*A. pallens* + *A. zischkai*)) (Andena et al. 2007; Noll et al. 2021).

The genus occurs from Costa Rica to the south-central region of Brazil (Richards 1978), and *A. pallens* is the only species that occurs in the Amazon region and the Brazilian Atlantic Forest (Carvalho et al. 2014, 2015, 2021). The nests of *Angiopolybia* are characterized as exposed on leaves, branches, and stone slabs and consisting of several stacked combs (Ducke 1914), fused or suspended from each other by a central pedicel, and the combs gradually grow along the margins (Wenzel 1998). The nests of *Angiopolybia* species have a single envelope, which can be ovoid shape or bottle-shaped, with a single entry at the lower part with a tubular form and horizontally curved (Richards 1978; Wenzel 1998). Morphological difference between queens and workers is subtle (Richards 1978), and only the male of *A. pallens* was described by Richards (1978).

Morphological differences between *A. paraensis* and *A. obidensis* and between *A. pallens* and *A. zischkai* are subtle, such as the height of the anterior pronotal lamella and the development of the pronotal lobe, respectively (Richards 1978; Andena et al. 2007). Moreover, Richards (1978) characterized multiple morphological variants of *A. pallens* and *A. paraensis* as "morph", such as *A. pallens* dark morph, *A. paraensis* morph *paraensis*, *A. paraensis* morph *ruficornis*, and *A. paraensis* morph *obscurior*. However, Andena et al. (2007) made the following comment about the "morphs" of *A. paraensis*: "is a category without nomenclatural standing, hence these morphs are synonyms of *A. paraensis*".

Here, we analyzed the variation of mitochondrial genetic markers with molecular species delimitation methods, adult morphology, male genitalia, and scanning electron microscopy images to characterize in detail the species limits within *Angiopolybia*. Thus, we tested whether the "morphs" of *A. pallens* and *A. paraensis* can be recognized based on morphological and molecular data, as well as providing diagnostic features for *Angiopolybia* species and a reassessment of their geographical distribution.

2. Material and Methods

2.1. Taxonomic sampling

We obtained type material through loans from the Natural History Museum (NHM, London, England) and Museu de Zoologia da Universidade de São Paulo (MZUSP, São Paulo, Brazil). Additionally, we obtained images of type specimens deposited at the following institutions: American Museum of Natural History (AMNH, New York, USA), Harvard Museum of Comparative Zoology (MCZ, Cambridge, MA, USA), and Muséum National d'Histoire Naturelle (MNHN, Paris, France). We also obtained supplementary material from the following scientific institutions: AMNH, Coleção de Hymenoptera do Museu de Zoologia da Universidade Federal da Bahia (MZUFBA, Salvador, Brazil), Coleção Entomológica da Universidade Federal do Espírito Santo (UFES, Vitória, Brazil), Instituto Nacional de Biodiversidad (INABIO, Quito, Ecuador), Instituto Nacional de Pesquisas da Amazônia (INPA, Manaus, Brazil), Museo de Zoología - Pontificia Universidad Católica del Ecuador (QCAZ, Quito, Ecuador), MZUSP, Museu Paraense Emílio Goeldi (MPEG, Belém, Brazil), and NHM. All specimens were identified using the identification keys proposed by Richards (1978) and Andena et al. (2007), and also by comparison with the type material and original descriptions of Lepeletier (1836), Spinola (1851), Ducke (1904), and Richards (1978).

2.2. Morphological analysis

We used adult specimens for a redescription of the female and description of the male. We examined 469 females and 32 males of *A. pallens* (eight males for genitalia analysis), four females of *A. zischkai*, 104 females and three males of *A. obidensis* (two males for genitalia analysis), and 80 females and six males of *A. paraensis* (four males for genitalia analysis). We also analyzed images of five

type specimens of the species. They were analyzed under a Nikon SMZ645 stereo microscope with an accessory magnifying lens of Nikon G-AL 2x. We obtained the proportions and morphological measurements with the ocular lens AmScope reticulated WF10X/22 and the measurements in the images using the IMAGEJ 1.52a (Rasband 2019). The explanation of how each measurement was performed is described in Supplementary Material (Table S1). For the morphological terminology, we followed Richards (1978), and for male terminalia, we used Richards (1978), Buck et al. (2012), and Somavilla et al. (2018). We obtained the images of specimens and morphological characters with the aid of a Leica DMC4500 digital camera coupled to a Leica M205A stereomicroscope with a self-assembly system, using the Leica Application Suite v.4.10.0-Montage® software. We edited the images and assembled the plates using the software ADOBE PHOTOSHOP® CS6 v.6.1. We employed scales of 1 mm and 0.5 mm for images of adults and male genitalia, respectively. We also generated Scanning Electron Microscopy images (equipment Oxford Instruments INCAx-act, model 51-ADD0007) without the use of preparation technique of coating. Finally, we built a matrix of morphological characters based on the studies of Ducke (1914), Richards (1943, 1978), Carpenter (1991), and Andena et al. (2007), as well as proposing new morphological characters for *Angiopolybia* species.

2.3. Molecular dataset

We extracted total DNA from a mid and a hind leg of specimens preserved in ethanol and pinned museum specimens. We extracted DNA from a single specimen of *A. pallens*, *A. zischkai*, *A. obidensis*, *A. paraensis* yellow, *A. paraensis* brown and yellow and *A. paraensis* dark brown, the complete list of specimens used in our analyses is presented in Supplementary Material (Table S2). For extraction, we used the DNeasy® Blood & Tissue extraction kit (QIAGEN®, Valencia, California, USA) following the manufacturer's protocol. We amplified two mitochondrial gene fragments, Cytochrome Oxidase subunit I (*Cox*1) and 16S ribosomal DNA (16S). Specific primers and conditions for PCR amplification are described by Menezes et al. (2015, 2017). The PCR products were purified using exonuclease I and shrimp alkaline phosphatase. Sanger sequencing was conducted by the Centro de Recursos Biológicos e Biologia Genômica (CREBIO), Universidade Estadual Paulista 'Júlio de Mesquita Filho' (UNESP, Jaboticabal, São Paulo, Brazil). The sequencing was carried out in both directions, and the consensus sequences were assembled on GENEIOUS R7 (Kearse et al. 2012). All sequences were deposited at GenBank (access numbers are MZ496308–MZ496314 and MZ513916 for *Cox*1, and MZ496381–MZ496387 and MZ513917 for 16S). We performed the alignment using the MUSCLE algorithm (Edgar 2004), implemented in the program MEGA X (Kumar et al. 2018) and with default parameters. We visually inspected and corrected all alignments. We concatenated the *Cox*1 and 16S sequences using the software MESQUITE v.3.61 (Maddison and Maddison 2019). The most appropriate model of nucleotide evolution and the best-fitting partitioning scheme were selected using PARTITIONFINDER2 (Lanfear et al. 2016) under the Bayesian information criterion (see Table S3).

2.4. Phylogenetic and molecular species delimitation analyses

Phylogenetic inference was conducted by Maximum Likelihood (ML) using the IQ-TREE v.1.6.12 (Nguyen et al. 2015) with a concatenated morphological and molecular dataset. We calculated branch supports with 1000 replicates of SH-like approximate likelihood ratio test (SH-aLRT) (Guindon et al. 2010) and Ultrafast Bootstrap approximation (UFBoot) (Minh et al. 2013). We used *Apoica thoracica* du Buysson, 1906 and *Agelaia fulvofasciata* (DeGeer, 1773) as outgroups based on previous phylogenetic studies (Andena et al., 2007; Menezes et al. 2020; Noll et al. 2021). Visualization and edition of the phylogenetic trees were performed using the program FIGTREE v.1.4.2 (http://tree.bio.ed.ac.uk/software/figtree). We also performed analysis under Maximum Parsimony (MP) with our concatenated matrix using the program TNT – Tree analysis using New Technology v.1.5 (Goloboff and Catalano 2016). We performed a Traditional search by Wagner trees with 1 random seed, 1000 replicates, saving 30 by replication, and collapsing the tree after the search. The polarization of states was carried out by comparison with outgroups (Nixon and Carpenter 1993). The visualization of the MP phylogenetic tree was performed using the program WINCLADA v.1.00. 08 (Nixon 2002).

We used four species delimitation methods for *Cox*1 and 16S data separately and also concatenated as follows: Automatic Barcode Gap Discovery (ABGD) (Puillandre et al. 2012), Assemble Species by Automatic Partitioning (ASAP) (Puillandre et al. 2021), bayesian Poisson Tree Processes (bPTP) (Zhang et al. 2013) and multi-rate Poisson Tree Processes (mPTP) (Kapli et al. 2017). For ABGD and ASAP, we used the online platforms https://bioinfo.mnhn.fr/abi/public/abgd and https://bioinfo.mnhn.fr/abi/public/asap respectively, using the Kimura Two-Parameter (K2P) model (Kimura 1980). We used the phylogenetic trees generated by IQ-Tree ver.1.6.12 for the bPTP and mPTP methods. For the bPTP and mPTP, we used the online platforms https://species.h-its.org and https://mptp.h-its.org/#/tree respectively, removing the outgroups and with default parameters, except for the number of generations of Monte Carlo Markov Chains (MCMC) of 300,000 in bPTP. Additionally, we analyzed the genetic distance among the specimens for both mitochondrial markers in MEGA X using the K2P model.

2.5. Geographic distribution maps

We used the recorded localities for *Angiopolybia* specimens to build a geographical database of species occur-

rence. The recorded localities were based on the label data of all analyzed specimens and information obtained in the literature with the precise locality. We avoided the use of non-geo-located information, such as presence data in states or provinces. The Google Maps platform was used to determine each specimen's geographical coordinates and convert them to decimal degrees. We used the resulting database to characterize in detail the geographic range of each *Angiopolybia* species with the software QGIS v.3.10.11 (QGIS.org, 2020, Geographic Information System, http://www.qgis.org 2020) and a biome map reported by Dinerstein et al. (2017).

3. Results

To characterize in detail the species limits within *Angiopolybia*, we considered several morphological characters, including females, males, male genitalia, and nest architecture (Figs 1–8), and two mitochondrial markers, *Cox*1 and 16S, under a phylogenetic and molecular species delimitation approach (Fig. 9). Additionally, we performed a taxonomic revision for *Angiopolybia* and characterized the geographical range of each species (Fig. 10). Moreover, we proposed an identification key with new morphological characters and images.

3.1. Revision of *Angiopolybia* Araujo, 1946

Rhopalidia Lepeletier, 1836: 538 (a genus with two species); ICZN, 1976: 240, 241 (Opinion 1051 - suppressed under the powers of the plenary, nº. 2072 in the Official Index of Rejected and Invalid Generic Names in Zoology). Type species, *Rhopalidia pallens* Lepeletier, 1836, subsequent designation by Schulz, 1912: 60.

Angiopolybia Araujo, 1946: 166, 169 (designation of new name for *Stelopolybia* Ducke, 1914). Specie-type, *Rhopalidia pallens* Lepeletier, 1836 (original designation).

Stelopolybia (*Angiopolybia*) Richards and Richards, 1951: 69; Richards, 1973: 49 (suppression of *Rhopalidia* Lepeletier, 1836 by ICZN, 1976).

Diagnosis. Lateral ocellus separated from the eye by two times its diameter. Compound eyes with bristles. Clypeus with acute apex, lateral margins parallel in part upper and rectangular lateral lobes. Short malar space. Occiput with carina. Labial palpus with four segments. Proepisternum with reduced lateral carina. Pronotal carina limited to a small length in the center of the pronotum and acute. Pronotum with lateral fovea. Mesoscutum with reduced posterolateral lamella. Dorsal groove of the mesoepisternum present and transverse to the sclerite. Metasomal tergum I, in dorsal view, with lateral margins diverging gradually from the base to apex.

Additional comments. Considering the *Gymnopolybia* description (currently *Agelaia*) from *Stelopolybia* species (currently *Angiopolybia*) by Ducke (1914), these genera are not well-defined by the proposed characters. Based on this, some morphological characters that had been proposed to separate *Angiopolybia* from *Agelaia* such as stelocyttarous nest (with envelope) (Ducke 1914), very weak or absent occipital carina (Richards 1943), and flat metapleural basalar area (Richards 1978; Andena et al. 2007) were not considered here because they are not exclusive to *Angiopolybia*, since they are present in few species of *Agelaia*. Moreover, the scutellum with line or depression (Richards 1943; Andena et al. 2007) was not considered because they are not exclusive to *Agelaia*, since some *Angiopolybia* species present the line, despite it is inconspicuous. Richards (1943) commented that the characters determined by him, isolated, had no effect on separating the taxa.

Based on previous and this study, *A. pallens* and *A. zischkai* are closer, as are *A. paraensis* and *A. obidensis*. *Angiopolybia pallens* and *A. zischkai* are distinguished by rounded gena and propodeum with posterior submedian translucent mark inserted in a depression, whereas the other species have angled gena and submedian translucent mark of the propodeum not inserted in a depression. We documented other differences in the step 1 of the identification key for the genus (see below).

Geographic distribution. Bolivia, Brazil, Colombia, Costa Rica, Ecuador, French Guiana, Guyana, Panama, Peru, Suriname, Trinidad and Tobago, Venezuela.

Angiopolybia pallens (Lepeletier, 1836)

Figs 1a–f, 2a–c, 6a–e, 7a–g

Rhopalidia pallens Lepeletier, 1836: 539; Spinola, 1851: 63 (nest); de Saussure, 1854: 189 (synonym of *Polybia pallipes* (Olivier, 1792)); du Buysson, 1906: 342 (synonym of *Apoica pallida* var. *pallens* (Fabricius, 1804)); Ducke, 1910: 542 (specimen of the collection of Spinola = *S. infernalis* (de Saussure,1854)); Schulz, 1912: 60 (synonym: *S. infernalis* (de Saussure, 1854)).

Polistes rufina Erichson, 1848: 590; Spinola, 1851: 79 (synonym of *Rhopalidia pallens* Lepeletier, 1836).

Polybia infernalis de Saussure, 1854: 195, plate XXV: fig. 3 (in division *My*); Ducke, 1905a: 662 (synonym: *P. ampullaria* Möbius, 1856); Richards, 1943: 45 (invalid designation of the type species of *Stelopolybia*); Richards, 1978: 232 (lectotype designation). Type locality: "Le Para", female (MNHN, Paris) [examined by images].

Polybia ampullaria Möbius, 1856: 133, 155 (key identification of nests), 165 (plate VII), VII (figs. 1–8 - female, nest).

Eumenes flavopectus Provancher, 1888: 422.

Stelopolybia infernalis; Ducke, 1910: 519 (key), 524 (synonym: *Polybia ampullaria* Möbius, 1856), 525 (fig. 12 - nest); Ducke, 1913: 331 (synonym: *R. pallens* Lepeletier, 1836).

Stelopolybia pallens; Bequaert, 1944: 293 (key), 294 (synonym: *Polybia infernalis* Saussure, 1854, *Polybia ampullaria* Möbius, 1856, *Polistes rufina* Erichson, 1884, *Eumenes flavopectus* Provancher 1888).

Angiopolybia pallens; Araujo, 1946: 169; Richards, 1978: 231 (key), 232 (description of male, and diagnose of female and male); Andena

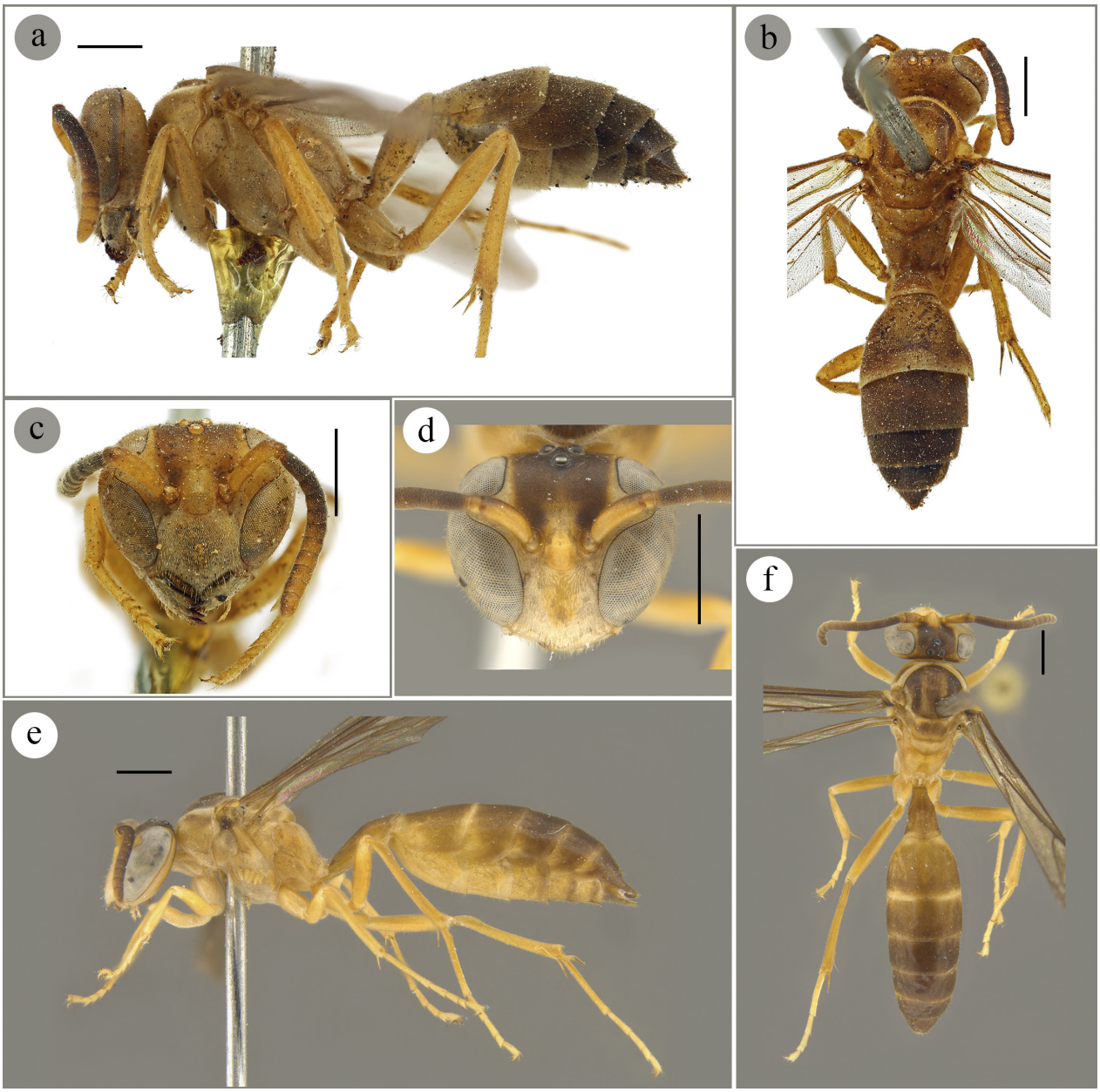

Figure 1. Lectotype, female of *Polybia infernalis* de Saussure, 1856 [currently *Angiopolybia pallens* (Lepeletier, 1836)]: **a.** lateral view, **b.** dorsal view, **c.** head in frontal view. Male: **d.** head in frontal view**, e.** lateral view, **f.** dorsal view. Scale: 1 mm. Source: Agnièle Touret-Alby MNHN for images **a**, **b**, and **c**.

et al., 2007: 59 (phylogenetic discussion), 60 (table 2 – characters matrix), 61 (figs. 1A, 2A), 62 (figs. 3B, 5 – cladogram), 63 (key), 64 (locality of examined material); Carvalho et al., 2014, 2021 (evolutionary hypothesis of species distribution).

Stelopolybia (*Angiopolybia*) *pallens*; Richards and Richards, 1951: 77 (list and notes about the nests).

Angiopolybia infernalis; Overal, 1978: 9 (list of species).

Type locality. Cayenne, French Guiana.

Diagnosis. Anterior wing of 7–8.5 mm; eyes with medium-sized and sparse bristles; rounded gena; pronotal lamella low on the anterior margin, one fifth of the height of antennal socket; pronotal lobe developed in the anterior lateral region, below the pronotal fovea; defined and deep pronotal fovea; axillary fossa with anterior margin directed to the posterior region; posterior submedian translucent mark of the propodeum inserted in a round depression; basal metapleural area with parallel upper and lower margins.

Redescription of female (Fig. 1a, b, c). Size. (1) Head 1.27 mm long, 2 mm high, and 2.27 mm wide; (2) mesosoma 3.50 mm long, anterior wing 8.11 mm long, and posterior wing 5.27 mm long; (3) metasoma 5.53 mm long. **Head.** (1) Lateral ocelli with 0.15 mm and median ocellus with 0.17 mm of diameter, not inserted in a declivity of the vertex, and the lateral ocelli separated from the eyes for twice its diameter. (2) Compound eyes with medium-sized and sparse bristles. (3) Frons with interantennal space about twice the height of antennal socket. Anterior tentorial fovea closer to the antennal socket

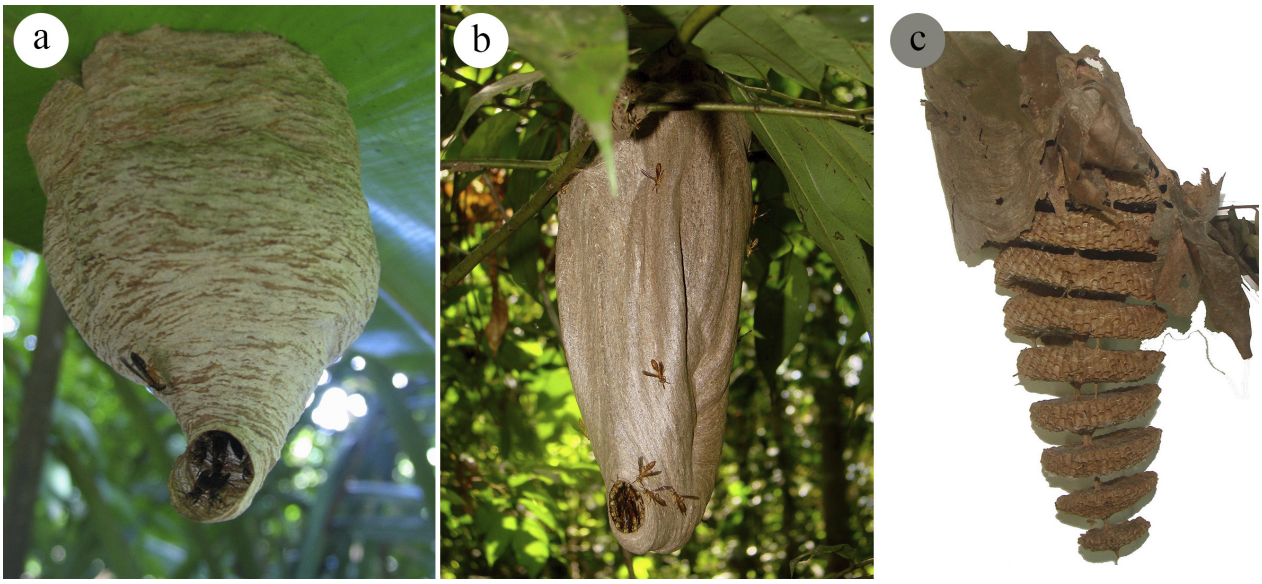

Figure 2. Structure variation of the nest of *Angiopolybia pallens*: **a.** typical form in external view, **b.** and **c.** variation found in external and internal view, respectively.

than to the eye. The central region of the frons with long bristles. (4) Antennal socket 0.22 mm high. (5) Clypeus as high as wide, contact with eyes for a distance greater than twice the height of antennal socket, and lateral lobe touching the eye. Medium bristles in the basal half and long bristles in the apical half. (6) Gena with half of the width of the eye at the level of the ocular sinus. **Mesosoma.** (1) Anterior lamella of pronotum with a height of one fifth of the height of antennal socket. Pronotal fovea with a circular shape, deep and with slight anterior prominence. (2) Mesoscutum convex and as long as wide. (3) Tegula 1.7 times longer than wide. (4) Axillary fossa with anterior margin directing to the posterior region. (5) Propodeum with translucent posterior submedian mark, anterior to the propodeal valve, inserted in a round depression. Propodeal valve complete and expanded, median region with half of the height of antennal socket. (6) Anterior wing with prestigma 1.4 times longer than wide. (7) Posterior wing with eight hamuli. **Metasoma.** (1) Metasomal tergum I two times longer than broad. Tergum with angulation in the posterior third, in lateral view. (2) Metasomal tergum II 0.82 times longer than broad. **Color.** Brown in general. Yellow: lateral of the apex, lateral of the front, interantennal region, disc of the clypeus, mandibles, gena, antennal segments: scape, dorsal of FL6 (flagellomere 6) and 7, FL8–10, band contouring the posterior margin of the pronotum, tegula, thin bands in the posterior margins of the metasomal terga I, II and III, and metasomal sterna II and III. Yellowish brown: central longitudinal and lateral region of the mesoscutum, tibiae and tarsi, femora median and posterior, metasomal tergum I, anterior half of metasomal tergum II, metasomal sterna I–IV. Black: FL1–5, ventral of FL 6 and 7, metasomal terga 4–6 and metasomal sterna 5 and 6. Wings with hyaline cells, pterostigma and venation in general yellowish-brown, except brown in the veins C, Sc+R, M+Cu and M.

Redescription of male (Fig. 1d, e, f). Size. (1) Head 1.01 mm long, 1.83 mm high, and 2.09 mm wide; (2) mesosoma 2.87 mm long, anterior wing 7.1 mm long, and posterior wing 4.5 mm long; (3) metasoma 6.08 mm long. **Head.** (1) Lateral ocelli with 0.17 mm and median ocellus with 0.18 mm of diameter. (2) Compound eyes with small-sized and sparse bristles. (3) Frons with interantennal space with 1.85 times the height of antennal socket. Anterior tentorial fovea closer to the eye that to the antennal socket. (4) Antennal socket with 0.21 mm high. (5) Clypeus as high as wide and apex less acute than in the female. Pubescence stronger than in the female. (6) Gena with half of the width of the eye at the level of the ocular sinus. **Mesosoma.** (1) Mesoscutum 0.9 times longer than wide. (2) Propodeum with translucent posterior submedian mark, anterior to the propodeal valve, inserted in a not round depression. (3) Anterior wing with prestigma 1.6 times longer than wide. **Metasoma.** (1) Metasomal tergum I 1.9 times longer than broad. (2) Metasomal tergum II 0.8 times longer than wide. **Genitalia (Fig. 6a–e). Paramere** 1.6 mm long and 0.6 mm wide; parameral spine with one fifth of the paramere, curved upwards and with small-sized and sparse bristles; lobe with a rounded apex and slightly curved downwards. **Aedeagus** 1.2 mm long; enlarged valve with a small emargination in the tip; apical portion 0.42 mm long and straight, ventral margin with denticles directed for the anterior region; denticulation decreasing in size from the apex to the base and more sclerotized than the rest of the apical portion; small-sized bristles with alveolar base, closer in the lower half and sparse in the upper half; median expansion without denticles and with acute apex; lateral apodeme not flattened dorsoventrally at the apex; basal apodeme arched to the venter. **Digitus** 2.5 times longer than wide; apical process not curved in the region of the upper half and with bristles of alveolar base small and sparse; rounded anteroventral

lobe with a strip of black scale-like bristles crossing it obliquely at the base of the digitus; bristles absent in the basal articulation. **Cuspis** approximately 0.48 mm long, with five black scale-like bristles on the lateral lobe, and small bristles with alveolar base and close throughout the area of the cuspis, except sparse in the central region and on the ventral margin.

Morphological variation (Fig. 7a–g). Anterior wing between 7–8.5 mm in length. Anterior margin of the pronotum (below the fovea) more curved. Pronotum, in lateral view, with frontal region more projected forward. Coloration varied between populations from black with yellow marks [like *A. pallens* dark morph (sensu Richards, 1978)] to yellowish brown.

Nest (Fig. 2a–c). The nest of *A. pallens* was initially described by Möbius (1856) for *Polybia ampullaria* (junior synonym of the taxon), and later described by Wenzel (1998) as a nest with a flask-shaped envelope and with a long downward entrance with its hole horizontally; pedicel initially single and later being able to be multiple; flexible card with long fibers, usually yellow or amber; and adjacent combs, suspended or fused from each other and without contact with the envelope. Additionally, the following nest variation was found: built on an irregular substrate (thin branch with several leaves), connected to the substrate by a central pedicel (thick) and several support pedicels (fines); 11 combs overlapping and also connected by a central pedicel and multiple support, with the third and fourth combs with the largest circumferences and combs decreasing in circumference towards the ends, and without contact with the envelope; hexagonal cells of the combs with diameter of 2.5 mm; single envelope with long fibers arranged longitudinally, circumference gradually decreasing towards the entrance and without entrance of tubular shape.

Comparative comments. *Angiopolybia pallens* is distinguished by the presence of a lobe in the lateroanterior region of the pronotum, absent in *A. zischkai*, and metapleural basalar area with parallel upper and lower margins, diverging in *A. zischkai*. Some *A. pallens* specimens can be confused with *A. zischkai* because it can resemble the typical form of *A. zischkai*, of color darker.

Additional comments. Despite the geographic disjunction by thousand kilometers in the distribution of *A. pallens* between the Amazon and Atlantic Forest (Carvalho et al. 2014, 2021), considering the morphological analysis of specimens collected in both biomes, we verified that the differences, when found, are very subtle and follow the variation found between different populations. Considering the populations from the Atlantic Forest, the color varied from yellow with brown marks to completely brown, while among the populations from the Amazon Forest it varied from black with yellow marks to yellowish brown, with some forms existing in both biomes. The occipital carina present in *A. pallens*, despite weak or not, found in this study not reported by Richards (1978) and Andena et al. (2007). They treated the occipital carina absent for the taxon. The prestigma longer than wide, also, was not cited by Richards (1978) and Andena et al. (2007). However, this character was found by Silveira and Carpenter (1995) for some specimens, and here we also found the two forms, prestigma about as long as wide and longer than wide. The redescription of *A. pallens* was made based on the lectotype of *Polybia infernalis* de Saussure, 1854 (junior synonym of *A. pallens*). The information about the male specimen described is: BRA, Roraima, Amajarí, Serra do Tepequém, SESC Tepequém. 1–16.i.2016 / Malaise grande, J.A. Rafael, F.F. Xavier Filho col.

Lectotype. ♀, TYPE / MUSEUM PARIS, Amérique, Leprieur 1834 / *Polybia infernalis* Sauss., Type. / 289694 / *Polybia infernalis* Sauss., Lectotype ♀, Richards, 1971 (MNHN, Paris), record MNHN, Paris EY25588 (Fig. 1a, 1b, 1c). *Polybia infernalis* is a junior synonym of *Rhopalidia pallens* Lepeletier, 1836, but here we used it to the redescription of the species. Type specimen analyzed by images.

Additional material examined. We examined 469 females and 32 males for *A. pallens*; see supplementary material S1.

Geographic distribution. Bolivia: Beni, Cochabamba; Brazil: Acre, Alagoas (**new record**), Amapá, Amazonas, Bahia, Ceará, Espírito Santo, Maranhão, Mato Grosso, Pará, Pernambuco, Piauí, Rio de Janeiro, Rondônia, Roraima, Santa Catarina, São Paulo Sergipe; Colombia: Meta, Caquetá, Nariño, Vaupés, Putumayo, Amazonas; Ecuador: Esmereldas, Napo, Pichincha; French Guiana; Guyana; Panama; Peru: Loreto, San Martin, Huánuco, Pasco, Junín, Cuzco; Suriname; Trinidad and Tobago; Venezuela: Monagas (Fig. 10a).

Angiopolybia zischkai Richards, 1978

Figs 3a–d, 7h

Angiopolybia zischkai Richards, 1978: 30 (list of mimicry), 231 (key, fig. 94), 234 (description); Andena et al., 2007: 59 (phylogenetic discussion), 60 (table 2 - character matrix), 62 (fig. 3A, 5 - cladogram), 63 (key), 64 (locality of examined specimens) [examined by images].

Type locality. Zumbi, Ecuador.

Diagnosis. Anterior wing of 8–9.5 mm; eyes with medium-sized and sparse bristles; rounded gena; pronotal lamella low on the anterior margin, one fifth of the height of antennal socket; pronotal lobe not developed in the lateral anterior region, below of the pronotal fovea; defined pronotal fovea, but little deep; axillary fossa with anterior margin directed to the posterior region; posterior submedian translucent mark of the propodeum inserted in

Figure 3. Holotype, female of *Angiopolybia zischkai* Richards, 1978: **a.** lateral view, **b.** head in frontal view, **c.** dorsal view, **d.** labels of type specimen. Scale: 1 mm. Source: Steve Thurston, AMNH.

a round depression; metapleural basalar area with divergent upper and lower margins.

Redescription of female (Fig. 3a–c). Size. (1) Head 1.03 mm long, 2.09 mm high, and 2.24 mm wide; (2) mesosoma 3.54 mm long, anterior wing 9.42 mm long, and posterior wing 6.10 mm long; (3) metasoma 5.9 mm long. **Head.** (1) Lateral ocelli with 0.16 mm and median ocellus with 0.18 mm of diameter, not inserted in a declivity of the vertex and the lateral ocelli separated from the eyes for twice its diameter. (2) Compound eyes with medium-sized and sparse bristles. (3) Frons with interantennal space with 1.75 times the height of antennal socket. Anterior tentorial fovea closer to the antennal socket than to the eye. Central region of the frons with long bristles. (4) Antennal socket 0.24 mm high. (5) Clypeus 0.9 times higher than wide, contact with eyes for a distance greater than twice the height of antennal socket, and lateral lobe touching the eye. Long bristles all over the clypeus and very long bristles on the apical margin. (6) Gena with half of the width of the eye at the level of the ocular sinus. **Mesosoma.** (1) Anterior lamella of pronotum with height of one fifth of the height of antennal socket. Pronotal fovea with ellipsoid shape, little deep and with slight anterior prominence. (2) Mesoscutum subconvex and as long as wide. (3) Tegula 1.5 times longer than wide. (4) Axillary fossa with anterior margin directing to the posterior region. (5) Propodeum with translucent posterior submedian mark, anterior to the propodeal valve, inserted in a round depression. Propodeal valve complete and expanded, median region with two thirds of the height of antennal socket. (6) Anterior wing with prestigma as long as wide. (7) Posterior wing with eight hamuli. **Metasoma:** (1) Metasomal tergum I 2.1 times longer than wide. Tergum with angulation in the posterior third, in lateral view. (2) Metasomal tergum II 0,82 times longer than broad. **Color.** Dark brown in general. Yellow: lateral of the vertex, lateral of the frons, clypeus (but dark brown disc), interantennal region, mandibles, malar space, gena, slender band contouring the posterior margin of the pronotum, outer margins of the tegula, wide spot at along the anterior margin of the scrobal furrow and along the dorsal groove of the mesoepisternum, anterior half of the metanotum, submedian longitudinal band on the propo-

deum, lateral margin of the propodeum, upper region of the metapleural basalar area. Yellowish brown: FL7–10 of the antenna, anterior and median coxae, trochanters, femora, tibiae and tarsi (but with dorsal brown spots). Black: ocellar area, FL1–6 of the antenna, mesoscutum and metasoma. Wings with hyaline cells, except yellow in the costal, medial, submarginal I and marginal; and yellowish-brown venation, except brown in the veins C, Sc+R, M+Cu, M and in the beginning of the Cu.

Male. Unknown.

Morphological variation (Fig. 7h). We found a specimen with yellow color and black marks, and the abdomen, apparently, wider in dorsal view.

Nest. Not described, but Valverde et al. (2019) in the identification key of social wasps from Costa Rica commented that the nest envelope resembles an inverted flask.

Comparative comments. *Angiopolybia zischkai* resembles *A. pallens*, but it is distinguished by the pronotum without a developed lobe in the lateroanterior region, which is present in *A. pallens*; metapleural basalar area with divergent upper and lower margins, which are parallel in *A. pallens*; and pronotal fovea with translucent mark of elliptical shape, which is circular in *A. pallens*.

Additional comments. One specimen designated as holotype of *Angiopolybia brunnescens* (Fig. 7h) but not described by Richards (specimen deposited in the NHM) is an *A. zischkai* specimen with more yellowish coloration, similar to the color of some *A. pallens*. The two specimens with the labels: Paratype / PERU: 1.609, Maracapata [Marcapata] (Perú) / *Stelopolybia infernalis* Ducke rev.11. [1911] (1 ♂, MZUSP), and 1.609, Maracapata [Marcapata] (Perú) / *Stelopolybia infernalis* Ducke rev.11. [1911] / *A. pallens* (Lep.) f. *zischkai*, Rich. 4 ♀ (1 ♀, MZUSP), that are two of the paratypes of *A. zischkai*, are specimens of *A. pallens* with coloration resemble to the holotype of *A. zischkai*. Although Gomes et al. (2018, 2020) reported *A. zischkai* samples from the Brazilian states Rondônia and Acre, we did not find *A. zischkai* for these regions.

Holotype. ♀, Holotype / Zumbi, Rio Zamora, 700M, Ecuador / XI.2.41, D.B.Laddey / *Angiopolybia pallens* ssp., *zischkai* Rich., ♀ Holotype / AMNH_IZC 00332335 (AMNH, New York) (Fig. 3). Type specimen analyzed by images.

Type material examined. Paratype: Paratype / PERU: Dept. Huanuco, Divisoria, 7.viii.1949, J.M.Schuncke., B.M.1952-645 / *Angiopolybia zischkai* Rich., ♀, paratype (1 ♀, NHM).

Additional material examined. We examined three females of *A. zischkai*; see supplementary material S1.

Geographic distribution. Bolivia: Cochabamba; Colombia: Amazonas, Cundinamarca, Magdalena, Putumayo, Valle del Cauca (**new record**); Costa Rica: Heredia; Ecuador: Orellhana, Zamora-Chinchipe; Panama: Colón; Peru: Cuzco, Huánuco, Junín, Loreto, Pasco, Ucayali (Fig. 10b).

Angiopolybia obidensis (Ducke, 1904)

Figs 4a–f, 6f–j, 7i

Polybia obidensis Ducke, 1904: 348 (key), 354; Ducke, 1907: 140 (synonym: *P. paraensis* var. *luctuosa* Schulz, 1905); Richards, 1978: 234 (lectotype designation) [examined by images].

Polybia paraensis luctuosa Schulz, 1905: 132; Ducke, 1907: 140 (synonym of *P. obidensis* Ducke, 1904); Richards, 1978: 234 (lectotype designation) [examined].

Stelopolybia obidensis; Ducke, 1910: 519 (key), 526.

Angiopolybia obidensis; Araujo, 1946: 169; Richards, 1978: 231 (key), 234; Andena et al., 2007: 59 (phylogenetic discussion), 60: (table 2 - characters matrix), 61 (fig. 2B), 62 (fig. 4A, 5 - cladogram), 63 (key) e 64 (locality of examined material).

Stelopolybia (*Angiopolybia*) *obidensis* Richards and Richards, 1951: 81 (list of species).

Type locality. Óbidos, Pará, Brazil.

Diagnosis. Anterior wing of 12–14 mm; eyes with very small-sized and sparse bristles; angulate gena with enlarged lower and upper region; pronotal lamella very elevated along the anterior margin, one third of the height of antennal socket; axillary fossa with anterior margin directed to the anterior region; posterior submedian translucent mark not inserted in a depression.

Redescription of female (Fig. 4a, b, c). Size. (1) Head 1.77 mm long, 3.13 mm high, and 3.56 mm wide; (2) mesosoma 5.69 mm long, anterior wing 13.38 mm long, and posterior wing 8.55 mm long; (3) metasoma 8.57 mm long. **Head.** (1) Lateral ocelli with 0.26 mm and median ocellus with 0.28 mm of diameter, inserted in a declivity of the vertex, and the lateral ocelli separated from the eyes for 1.7 times its diameter. (2) Compound eyes with very small-sized and sparse bristles. (3) Frons with interantennal space with 1.7 times the height of antennal socket. Anterior tentorial fovea closer to the antennal socket than to the eye. Central region of the frons with very long bristles. (4) Antennal socket 0.34 mm high. (5) Clypeus as high as wide, contact with eyes for a distance of approximately the height of antennal socket and lateral lobe not touching the eye. Clypeus with long bristles, but with very long bristles on the apical margin. (6) Gena wider than half of the width of the eye at the level of the ocular sinus. **Mesosoma.** (1) Anterior lamella of pronotum with height of one third of the height of antennal socket. Pronotal fovea with ellipsoid shape, shallow and without anterior prominence. (2) Mesoscutum convex and as long as wide. (3) Tegula 1.5 times longer than wide. (4) Axillary fossa with anterior margin directing to the anterior region. (5) Propodeum with translucent posterior submedian mark, anterior to the propodeal valve, not

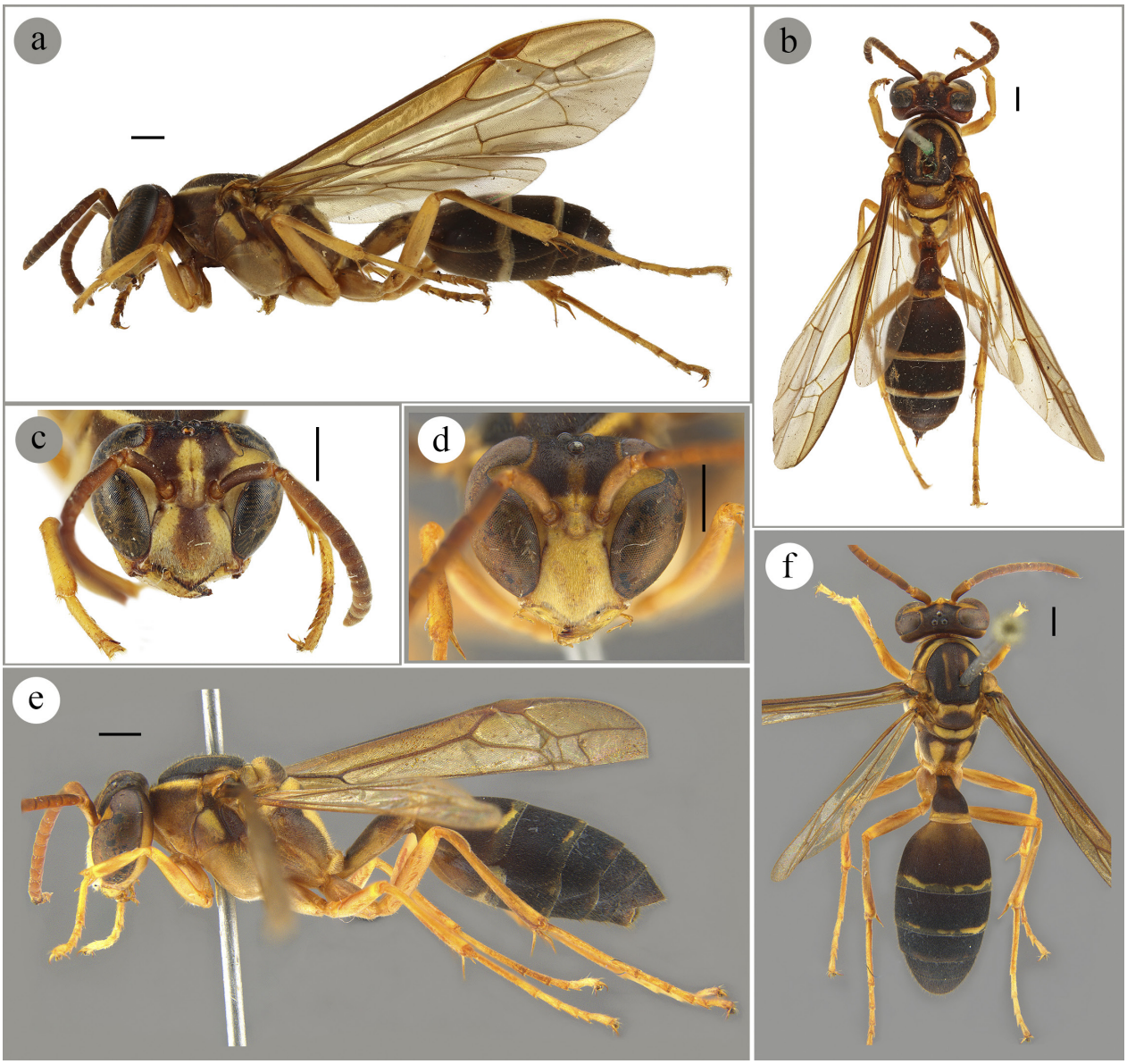

Figure 4. Lectotype, female of *Angiopolybia obidensis* (Ducke, 1904): **a.** lateral view, **b.** dorsal view, **c.** head in frontal view. Male: **d.** head in frontal view, **e.** lateral view, **f.** dorsal view. Scale: 1 mm. Source: Agnièle Touret-Alby MNHN for images **a**, **b**, and **c**.

inserted in a depression. Propodeal valve complete and expanded, median region with two third of the height of antennal socket. (6) Anterior wing with prestigma as long as wide. (7) Posterior wing with 11 hamuli. **Metasoma.** (1) Metasomal tergum I 1.7 times longer than broad. Tergum with angulation in the posterior third, in lateral view. (2) Metasomal tergum II 0.8 times longer than broad and without a row of very long bristles on the posterior margin. **Color.** Brown in general. Yellow: median longitudinal band and lateral of the frons, interantennal elevation, band surrounding the disc of the clypeus, mandibles, lower quarter of the gena, malar space, band contouring the posterior margin of the pronotum, tegula, spot anterior to the scrobal furrow of the mesepisternum, longitudinal submedian band and thin lateral band in the mesoscutum, axilla, anterior half of the scutellum, metanotum, submedian band in the propodeum, margin anterior to the propodeal valve, upper region of the metapleural basalar area, apex of the coxae, femora, tibiae and tarsi, bands along the posterior margins of the metasomal terga I–III and sternum II. Yellowish-brown: vertex and gena. Black: metasomal terga II–VI and metasomal sterna II–VI. Reddish-brown: inferior margin of the clypeus and the mandibular teeth. Wings with yellowish-brown in the cells and venation, except reddish-brown in the veins C, Sc+R, M+Cu, M and in the beginning of the Cu.

Description of male (Fig. 4d, e, f). Size. (1) Head 1.6 mm long, 2.7 mm high, and 3.2 mm wide; (2) mesosoma 5.2 mm long, anterior wing 12.4 mm long, and posterior wing 8.10 mm long; (3) metasoma 8.3 mm long. **Head.** (1) Lateral ocelli with 0.24 mm and median ocellus with 0.27 mm of diameter. (2) Frons with interantennal space with 1.5 times the height of antennal socket. Anterior tentorial fovea closer to the eye than to the antennal socket. (3) Antennal socket 0.31 mm high. (4) Clypeus 1.2 times higher than wide and apex less acute than in the female. Pubescence stronger than in the female. (5) Gena with

half of the width of the eye at the level of the ocular sinus. **Mesosoma.** (1) Mesoscutum 1.1 times longer than wide. **Metasoma.** (1) Metasomal tergum I 1.7 times longer than broad. (2) Metasomal tergum II 0.8 times longer than wide. Posterior margin with slight emargination in the center. **Genitalia (Fig. 6f–j). Paramere** 2 mm long and 0.81 mm wide; parameral spine with one fifth of the paramere, straight and with long bristles; lobe with rounded apex and slightly curved downwards. **Aedeagus** 1.72 mm long; enlarged valve with a small emargination in the tip; apical portion 0.66 mm long and curved to the venter, ventral margin with denticles directed for the anterior region; denticulation with large and conical denticles in the basal and apical thirds and small denticles with widened bases in the median third, more sclerotized than the rest of the apical portion; small-sized bristles with alveolar base, closer in the lower half and sparse in the upper half; median expansion with one denticle and with acute apex; lateral apodeme not flattened dorsoventrally at the apex; basal apodeme arched to the venter. **Digitus** 3.4 times longer than wide; apical process little curved in the region of the upper half and with bristles of alveolar base small and sparse; rounded anteroventral lobe with a strip of black scale-like bristles crossing it obliquely at the base of the digitus; bristles absent in the lower margin and basal articulation. **Cuspis** approximately 0.44 mm long, with 16 black scale-like bristles on the lateral lobe, and long bristles with alveolar base and close throughout the area of the cuspis, except sparse in the central region and on the ventral margin.

Morphological variation (Fig. 7i). Some *A. obidensis* specimens found in São Gabriel da Cachoeira (Amazonas) and Parque Nacional Serra da Mocidade (Roraima) are darker, like *A. paraensis* of coloration transitional between the yellow form and the black and yellow forms, which also occurs in these regions.

Nest. Unknown.

Comparative comments. *A. obidensis* resembles *A. paraensis*, but it is distinguished by the lamella along the anterior margin of the pronotum which is very elevated (one third of the height of antennal socket) in *A. obidensis*, and low (one fifth of the height of antennal socket) in *A. paraensis*; pronotum with prominence absent in front of the fovea, but slight prominence in front of the fovea in *A. paraensis*; angulate gena with enlarged lower and upper region, but gena with only enlarged lower region in *A. paraensis*; parameral spine straight, but spine curved upwards in *A. paraensis*; aedeagus with lateral apodeme not flattened dorsoventrally at the apex, but apex of the lateral apodeme flattened in *A. paraensis*.

Additional comments. The label information of the male specimen described is Brazil, AM, Itacoatiara, Mil Madeireira. 16.xii.1999, *Malaise*, J. Vidal *Leg*.

Lectotype. ♀, TYPE / Obidos / *Polybia obidensis* Ducke, ♀ typ. / MUSEUM PARIS, Brésil, Obidos, A. Ducke 1904 (MNHN, Paris), record MNHN, Paris EY25586 (Fig. 4a, b, c). Type specimen analyzed by images.

Type material examined. PARALECTOTYPE / Surinam, ex.coll. Fruhstorfer / spec. Typ. / *Polybia paraensis luctuosa* Schlz. ♀ an ♀, W. A. Schulz det. / Schulz Coll., 1908-157. / B.M. TYPE, HYM., 18.767b / (1 ♀, NHM). *Polybia paraensis luctuosa* is a junior synonym of *Polybia obidensis* Ducke, 1904, redescribed species here.

Additional material examined. We examined 102 females and three males for *A. obidensis*; see supplementary material S1.

Geographic distribution. Brazil: Acre, Amapá, Amazonas, Mato Grosso, Pará, Roraima (**new record**); French Guiana; Guyana; Suriname (Fig. 10c).

Angiopolybia paraensis (Spinola, 1851)

Figs 5a–f, 6k–o, 7j–l

Polistes paraensis Spinola, 1851: 60.

Polybia paraensis; de Saussure, 1854: 185, pl. XXIII fig. 2 (in division *Phi*).

Polybia ruficornis Ducke, 1905b: 20; Ducke 1910: 526 (synonym of *paraensis* (Spinola, 1953)); Richards, 1978: 235 (lectotype designation) [examined by images].

Stelopolybia paraensis; Ducke, 1910: 519 (key), 526 (nest, synonym: *P. ruficornis* Ducke, 1905b); Bequaert, 1944: 293 (key), 294 (typical *paraensis*).

Stelopolybia paraensis var. *ruficornis*; Ducke, 1910: 526.

Stelopolybia paraensis var. (or subspecies) *obscurior* Bequaert, 1944: 295 [examined by images].

Angiopolybia paraensis; Araujo, 1946: 169; Andena et al., 2007: 60 (characteres matrix), 61 (fig. 1B), 62 (fig. 4B, 5 - cladogram), 63 (key), 64 (locality of examined material).

Stelopolybia (*Angiopolybia*) *paraensis* Richards and Richards, 1951: 80 (list).

Angiopolybia paraensis obscurior; van der Vecht, 1972: 737.

Type locality. Pará, Brazil.

Diagnose. Anterior wing of 13–15 mm; eyes with very small-sized and sparse bristles; angulate gena with enlarged lower region; pronotal lamella low on the anterior margin, one fifth of the height of antennal socket; axillary fossa with anterior margin directed to the anterior region; posterior submedian translucent mark not inserted in a depression.

Redescription of female (Fig. 5a, b, c). Size. (1) Head 2.01 mm long, 3.35 mm high, and 3.71 mm wide; (2) mesosoma 6 mm long, anterior wing 14.78 mm long, and posterior wing 10.37 mm long; (3) metasoma 10.8 mm long. **Head.** (1) Lateral ocelli with 0.27 mm and median ocellus with 0.29 mm of diameter, inserted in a declivity of the vertex and the lateral ocelli separated from the eyes for two times its diameter. (2) Compound eyes with very small-sized and sparse bristles. (3) Frons with inter-

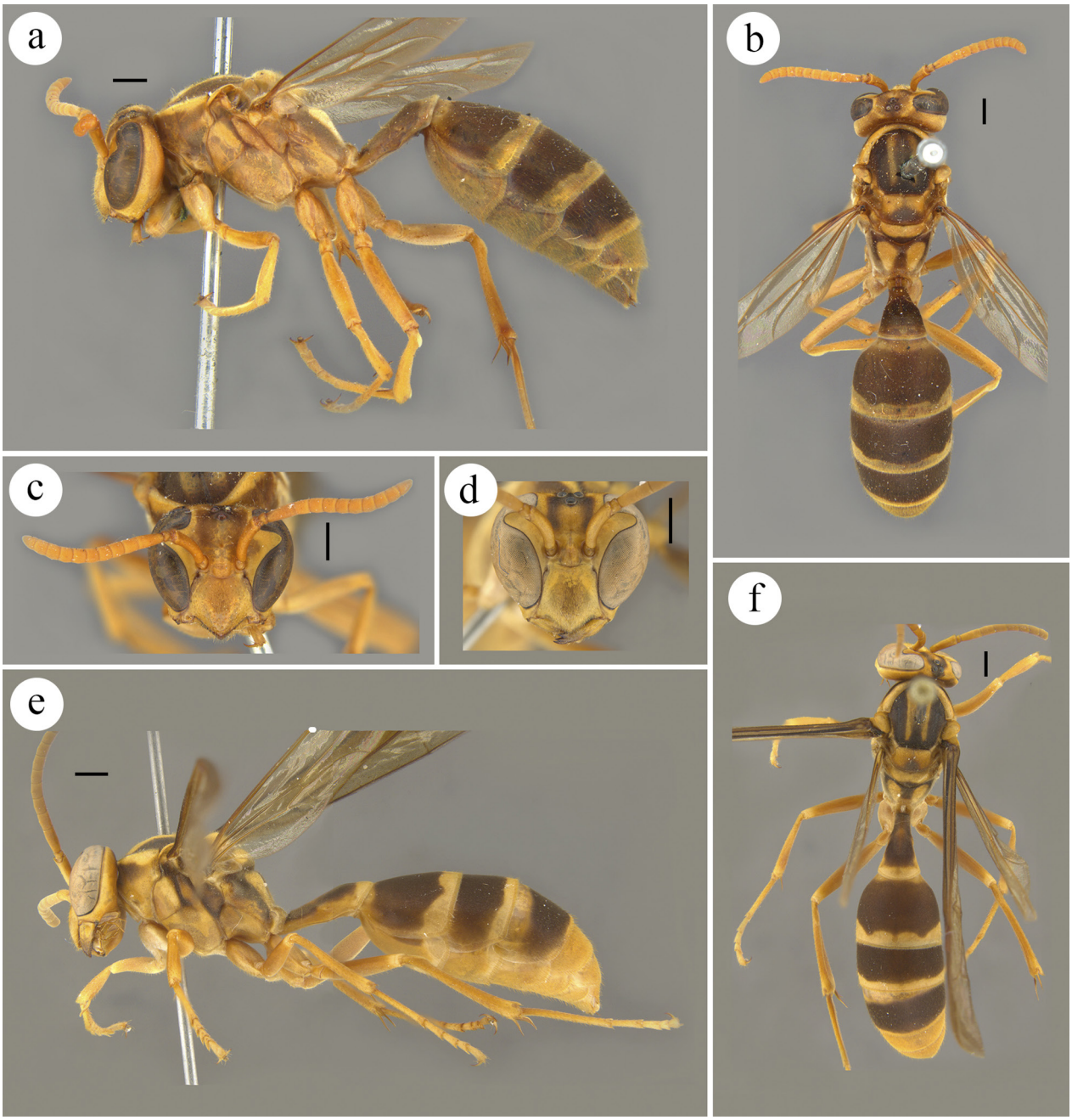

Figure 5. Female of *Angiopolybia paraensis* (Spinola, 1951) used in the redescription of the species: **a.** lateral view, **b.** dorsal view, **c.** head in frontal view. Male: **d.** head in frontal view**, e.** lateral view, **f.** dorsal view. Scale: 1 mm.

antennal space with 1.7 times the height of antennal socket. Anterior tentorial fovea closer to the antennal socket than to the eye. Central region of the frons with very long bristles. (4) Antennal socket 0.37 mm high. (5) Clypeus as high as wide, contact with eyes for a distance of approximately the height of antennal socket and lateral lobe not touching the eye. Clypeus with long bristles, but with very long bristles on the apical margin. (6) Gena wider than half of the width of the eye at the level of the ocular sinus. **Mesosoma.** (1) Anterior lamella of pronotum with height of one fifth of the height of antennal socket. Pronotal fovea with ellipsoid shape, shallow, and with slight anterior prominence. (2) Mesoscutum convex and 1.2 times longer than wide. (3) Tegula 1.6 times longer than wide. (4) Axillary fossa with anterior margin directing to the anterior region. (5) Propodeum with translucent posterior submedian mark, anterior to the propodeal valve, not inserted in a depression. Propodeal valve complete and expanded, median region with half of the height of antennal socket. (6) Anterior wing with prestigma as long as wide. (7) Posterior wing with 13 hamuli. **Metasoma.** (1) Metasomal tergum I 1.5 times longer than broad. Tergum with angulation in the posterior third, in lateral view. (2) Metasomal tergum II 0.7 times longer than broad and with a row of very long bristles on the posterior margin. **Color.** Yellowish-brown in general. Yellow: lateral of the vertex, lateral of the frons, interantennal elevation, lateral and the lower margin of the clypeus, mandibles, gena, anterior half of the lower quarter of the gena, malar space, band contouring the posterior margin of the pronotum,

Figure 6. Male genitalia of three *Angiopolybia* species. *Angiopolybia pallens*: **a.** paramere, **b.** aedeagus in left lateral view, **c.** aedeagus in ventral view, **d.** digitus, **e.** cuspis (image mirrored). *Angiopolybia obidensis*: **f.** paramere, **g.** aedeagus in left lateral view, **h.** aedeagus in ventral view, **i.** digitus, **j.** cuspis. *Angiopolybia paraensis*: **k.** paramere, **l.** aedeagus in left lateral view, **m.** aedeagus in ventral view, **n.** digitus, **o.** cuspis. Scale: 0.5 mm.

tegula, spot anterior to the scrobal furrow of the mesepisternum, longitudinal submedian band and thin lateral band in the mesoscutum, axilla, metanotum, submedian band in the propodeum, margin anterior to the propodeal valve, upper region of the metapleural basalar area, apex of the femora, tibiae and tarsi, bands on the posterior margins of the metasomal terga I–V, in the anterior margin of the sternum II, and in the posterior margins of the sterna

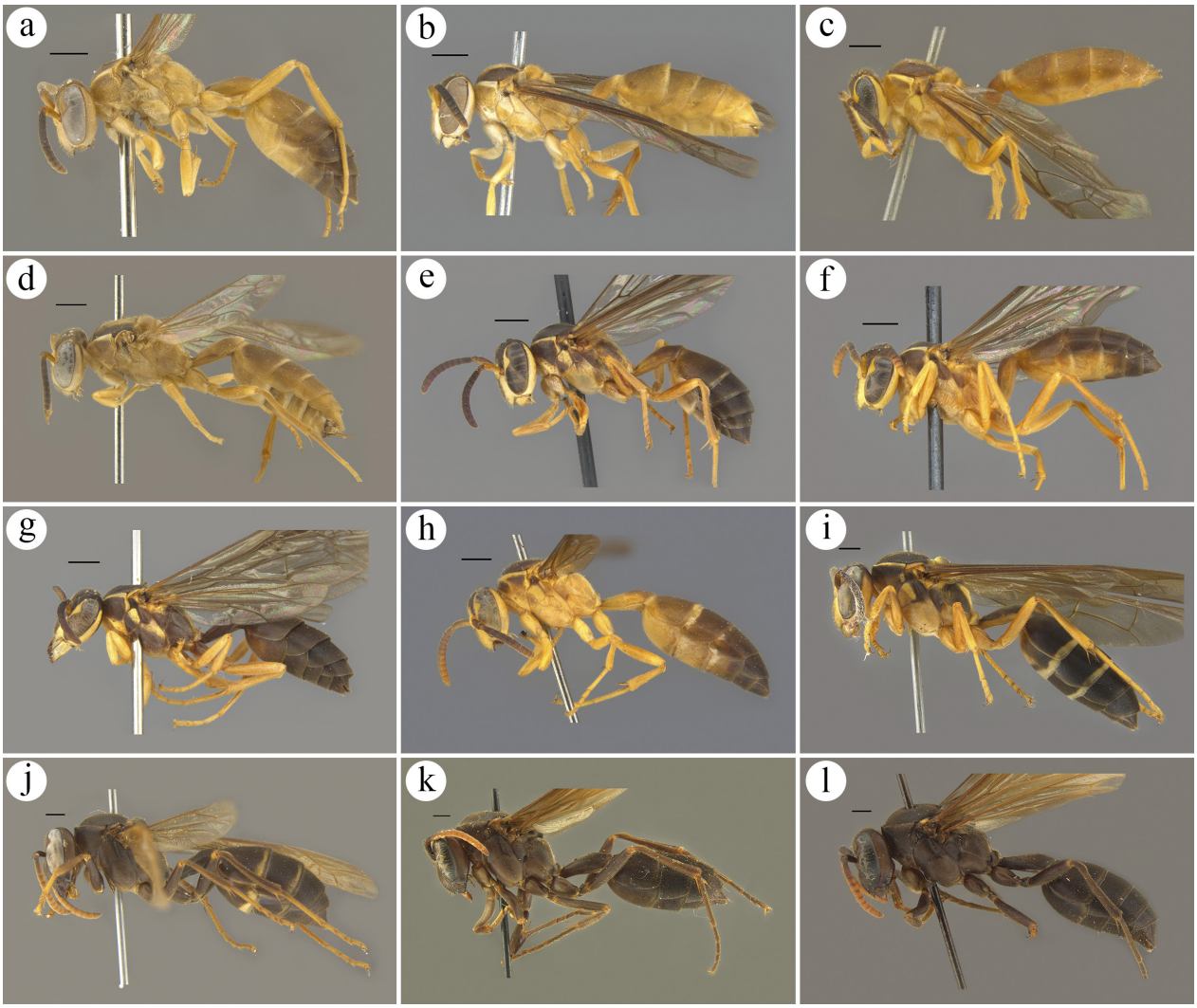

Figure 7. Morphological variation of *Angiopolybia* species. *Angiopolybia pallens*: **a.** Cayenne, French Guiana; **b.** Amazonas, Brazil; **c.** Bahia, Brazil; **d.** São Paulo, Brazil; **e.** Loreto, Peru; **f.** Napo, Ecuador; **g.** Chaparé, Bolivia. *Angiopolybia zischkai*: **h.** Pipeline, Panama. *Angiopolybia obidensis*: **i.** Roraima, Brazil. *Angiopolybia paraensis*: **j.** Roraima (brown and yellow specimen), Brazil; **k.** Napo, Ecuador (brown specimen); **l.** Crique Alama, French Guiana (dark brown specimen). Scale: 1 mm.

II–IV. Brown: a spot that extends from the vertex to the middle of the frons, transversal band in the pronotum, scrobal furrow, region posterior to the scrobal furrow, metapleural basalar area, lateral bands of the propodeum, and metasomal terga I and II. Dark brown: ocellar area, mesoscutum, posterior half of the scutellum, posterior margin of the metanotum, bands in furrow and in anterior marginal of the propodeum, and metasomal terga III and IV. Reddish-brown: lower margin of the clypeus and mandibular teeth. Reddish yellow antenna. Wings with yellowish-brown in cells and in venation, except reddish-brown in the veins C, Sc+R, M+Cu, M, at the beginning of the Cu and pterostigma.

Description of male (Fig. 5d, e, f). Size. (1) Head 1.40 mm long, 3.08 mm high, and 3.47 mm wide; (2) mesosoma 5.28 long, anterior wing 14.2 mm long, and posterior wing 9.9 mm long; (3) metasoma 10.5 mm long. **Head.** (1) Lateral ocelli with 0.24 mm and median ocellus with 0.28 mm of diameter, and lateral ocelli separated from the eyes for 1.7 times its diameter. (2) Frons with interantennal space with 1.5 times the height of antennal socket. Anterior tentorial fovea closer to the eye than to the antennal socket. (3) Antennal socket with 0.34 mm high. (4) Clypeus 1.2 times higher than wide and apex less acute than in the female. Pubescence stronger than in the female. (5) Gena with half of the width of the eye at the level of the ocular sinus. **Mesosoma.** (1) Mesoscutum 1.1 times longer than wide. (2) Propodeum without translucent posterior submedian mark. Propodeal valve with a median region with two third of the height of antennal socket. (3) Anterior wing with prestigma as long as wide. (4) Posterior wing with 14 hamuli. **Metasoma.** (1) Metasomal tergum I 1.7 times longer than broad. (2) Metasomal tergum II 0.8 times longer than wide. **Genitalia (Fig. 6k–o). Paramere** 2.3 mm long and 0.9 mm wide; parameral spine with one fifth of the paramere, curved upwards and with long bristles; lobe with rounded apex and not curved. **Aedeagus** 1.68 mm long; enlarged valve with a small emargination in the tip; apical portion 0.72 mm long and curved to the venter, ventral margin with denticles directed for the anterior region; denticula-

tion with large and conical denticles in the basal and apical thirds and denticles reduced in the middle third, more sclerotized than the rest of the apical portion; small-sized bristles with alveolar base, closer in the lower half and sparse in the upper half; median expansion without denticles and with acute apex; lateral apodeme flattened dorsoventrally at the apex; sinuous basal apodeme. **Digitus** 2.7 times longer than wide; apical process little curved in the region of the upper half and with bristles of alveolar base small and sparse; rounded anteroventral lobe with a strip of black scale-like bristles crossing it obliquely at the base of the digitus; bristles absent in the lower margin and in the basal articulation. **Cuspis** approximately 0.46 mm long, with 26 black scale-like bristles on the lateral lobe, and long bristles with alveolar base and close throughout the area of the cuspis, except sparse in the central region.

Morphological variation (Fig. 7j–l). Anterior wing of 13–15 mm; posterior wing of 13–19 hamuli; *Angiopolybia paraensis* occurs in three color variants, identified by Richards (1978) as *A. paraensis* morph *paraensis* (yellow specimens), *A. paraensis* morph *ruficornis* (brown and yellow specimens) and *A. paraensis* morph *obscurior* (brown specimens). *Angiopolybia paraensis* show small changes between yellow populations and between brown and yellow populations, such as a slightly darker color or some yellow marks, respectively, but they are well-defined. Despite the color variation, the morphological characteristics of female and male adults, and male genitalia used in the description are preserved in the three forms, so they should not be treated as subspecies or differentiated as morphs. Only a few *A. paraensis* populations, with dark brown color from French Guiana and Suriname, showed morphological variations such as the absence of very long bristles in the posterior margin of the metasomal tergum II and propodeum with a region anterior to the spiracle less projected in the metapleural basalar area. However, we believe that this evidence is still insufficient to justify a new species. Moreover, the analysis of species delimitation with molecular data (see below) showed that these variants are within the intraspecific limits of *A. paraensis*.

Nest. Described by Schulz (1903) as a spherical nest about 25 mm in diameter (possibly incorrect unit of measurement was used, with centimeter (cm) being the correct). Ducke (1910) complements the description of Schulz (1903), stating that the nest is composed of four overlapping combs, joined by a central pedicel, with a simple and very resistant envelope, and with transverse streaked with light and dark colors.

Comparative comments. *Angiopolybia paraensis* resembles *A. obidensis*, but it is distinguished by the pronotum with low lamella in the anterior margin (one fifth of the height of antennal socket), being high lamella (one third of the height of antennal socket) in *A. obidensis*; pronotum with a slight prominence in front of the fovea, but prominence absent in *A. obidensis*; gena not enlarged in the upper region, but enlarged in the upper region in *A. obidensis*; parameral spine curved upwards, but straight parameral spine in *A. obidensis*; aedeagus with the apex of the lateral apodeme dorsoventrally flattened, but apex not flattened in *A. obidensis*.

Additional comments. *Angiopolybia paraensis* was described by Spinola (1851) and his type specimen (or specimens) was deposited in the Museo Regionale di Scienze Naturali di Torino (MRSN, Torino, Italy). Richards (1978) did not find any *A. paraensis* type specimen during his study about the social wasps of the Americas, and we did not receive any answer from the Museum about the type specimen. Additionally, on the online page Checklist of Epiponini wasps (http://iunh2.sci.ibaraki.ac.jp/wasp/Epiponini/epiponini.htm; consulted in 2021) produced by Dr. James M. Carpenter, the presence of the type specimen in the Museum's collection is also uncertain. Based on this, the redescription of the species was carried out using a specimen identified by Ducke in 1909 and from the same locality of the type specimen (Brazil, Pará, 26.9.1901, Ducke / *Polybia paraensis* Spin. ♀, det. Ducke 1909 / Brazil., Mus.Goeldi., 1910-90. (1 ♀, NHM)). The information about the male specimen described is: BRA, Roraima, Amajarí, Serra do Tepequém, SESC Tepequém. 1–15.iii.2016 / Malaise grande, J.A. Rafael, F.F. Xavier Filho col.

Although some checklists treat *A. paraensis* as registered for Bahia state [for example, the Checklist of Epiponini wasps produced by Dr. James M. Carpenter (http://iunh2.sci.ibaraki.ac.jp/wasp/Epiponini/epiponini.htm; consulted in 2021) and Barbosa et al. (2016)], we did not confirm this information.

Type specimen. Without information.

Additional material examined. We examined 79 females and six males for *A. paraensis*; see supplementary material S1.

Geographic distribution. Bolivia: Cochabamba, La Paz; Brazil: Acre, Amapá, Amazonas, Maranhão, Mato Grosso, Pará, Rondônia, Roraima; Colombia: Amazonas, Caquetá; Ecuador; French Guiana; Guyana; Peru: Cuzco, Huánuco, Junín, Loreto, Madre de Dios, Pasco, San Martin; Panama; Suriname; Venezuela: Amazonas, Bolívar (Fig. 10d).

3.2. Key to *Angiopolybia* species

The following key is a revised and adapted version with few modifications of the keys provided by Richards (1978) and Andena et al. (2007).

1 Anterior wing 7–9.5 mm long; compound eyes with medium bristles, between 0.05 and 0.09 mm long (Fig. 8e); lateral lobe of clypeus touching the eye (Fig. 8g); anterior margin of the axillary fossa directed to the posterior region (Fig. 8u) **2**

1' Anterior wing 12.5–16 mm long; compound eyes with tiny bristles, approximately 0,015 mm long (Fig. 8f); lateral lobe of clypeus not touching the eye (Fig. 8h); anterior margin of the axillary fossa directed to the anterior region (Fig. 8t) **3**

2 Pronotum with lobe developed below the pronotal fovea (Fig. 8n); metapleural basalar area with parallel upper and lower margins ..... ***A. pallens***

2' Pronotum without lobe below the pronotal fovea (Fig. 8o); metapleural basalar area with divergent upper and lower margins ..... ***A. zischkai***

3 Pronotum with high lamella along the anterior margin, with about one third of the height of antennal socket; gena enlarged in the upper region (Fig. 8k) ..... ***A. obidensis***

3' Pronotum with low lamella along the anterior margin, with about one fifth of the height of antennal socket; gena not enlarged in the upper region (Fig. 8j) ..... ***A. paraensis***

3.3. Phylogeny and molecular species delimitation

Our concatenated data matrix of 934 aligned base pairs (bp) contained 166 variable sites, composed of 415 bp of *Cox*1 and 519 bp of 16S. Our morphological dataset was composed of 17 binary characters, six multi-state characters, and two contingent characters. The characters 1–18 and 19–25 are from female and male adults, respectively, as listed below and shown in Fig. 8 (coded in Table S4). The characters 2, 4, 12, 14 were modified from the study of Andena et al. (2007), and the characters 7–10, 13, 15–17, 19–25 are proposed in this study.

Morphological characters

1. Vertex, lateral ocelli, height: elevated (0); intermediate height (1) (Fig. 8a, b); low, at the declivity (2) (Fig. 8c, d).
2. Eyes, bristles, sizes: medium (0) (Fig. 8e); very small (1) (Fig. 8f).
3. Clypeus, lateral lobe, contact with the eye: in contact (0) (Fig. 8g); without contact (1) (Fig. 8h).
4. Gena, shape: rounded with upper region wider (0); rounded with middle region more wide (1) (Fig. 8i); angulated with inferior region wider (2) (Fig. 8j); angulated with inferior and upper region broad (3) (Fig. 8k).
5. Proepisternum, lateral carina, extension: complete (0); incomplete (1).
6. Pronotum, dorsal carina, length: extended laterally (0); mesal (1).
7. Pronotum, fovea, translucent mark: absent (0); present (1).
8. Pronotum, fovea, translucent mark, shape: circular (0) (Fig. 8l); elliptical (1) (Fig. 8m).
9. Pronotum, fovea, depth: shallow (0) (Fig. 8p, q); deep (1) (Fig. 8n, o).
10. Mesoscutum, curvature: convex (0) (Fig. 8r); subconvex (1) (Fig. 8s).
11. Mesoscutum, posterolateral carina, extension: complete (0); reduced (1).
12. Mesepisternum, dorsal groove, disposition: oblique (0); perpendicular (1).
13. Axillary fossa, anterior margin, direction: directed to the anterior region (0) (Fig. 8t); directed to the posterior region (1) (Fig. 8u).
14. Scutellum, median region, longitudinal line, impression: conspicuous (0); inconspicuous (1); absent (2).
15. Propodeum, posterior submedian translucent mark, insertion: in a depression (0); not in a depression (1).
16. Metasomal tergum I, lateral view, shape: angled in the posterior dorsal quarter (0) (Fig. 8v); less angled in the posterior dorsal third (1) (Fig. 8w); more angled in the posterior dorsal third (2) (Fig. 8x).
17. Metasomal tergum II, posterior margin, row of very long bristles: present (0) (Fig. 8y); absent (1) (Fig. 8z).
18. Anterior wing, prestigma, length/width ratio: 1.5 or greater (0); less than 1.5 (1).
19. Clypeus, contact with eye, extension: greater than the height of antennal socket (0) (Figs 1d, 4d); smaller than the height of antennal socket (1) (Fig. 5d).
20. Paramere, base of the parameral spine, ventral margin, shape: angulated (0); not angulated (1).
21. Digitus, strip of scale-like bristles, position: apical (0); medial (1); basal (2) (Fig. 6d, i, n).
22. Digitus, anteroventral lobe, shape: acute (0); rounded (1) (Fig. 6d, i, n).
23. Aedeagus, apical portion, denticulation: absent (0); present (1).
24. Aedeagus, apical portion, median region of the denticulation, height: not reduced (0) (Fig. 6b); reduced (1) (Fig. 6g, l).
25. Aedeagus, apical portion, curvature to the venter: not curved (0) (Fig. 6b); curved (1) (Fig. 6g, l).

Our phylogenetic inference based on ML (Fig. 9) using a concatenated matrix of morphological and mitochondrial DNA data recovered the following relationship among the *Angiopolybia* species: ((*A. pallens* + *A. zischkai*) + (*A. obidendis* + *A. paraensis*))) with high support (SH-aLRT: 97.4% and UFboot: 97%) (Fig. 9). The genus was recovered on MP (Bootstrap support: 96%) (Fig. S1) by the following synapomorphies: proepisternum with incomplete lateral carina (character 5, state 1), pronotum with mesal dorsal carina (character 6, state 1), mesoscutum with re-

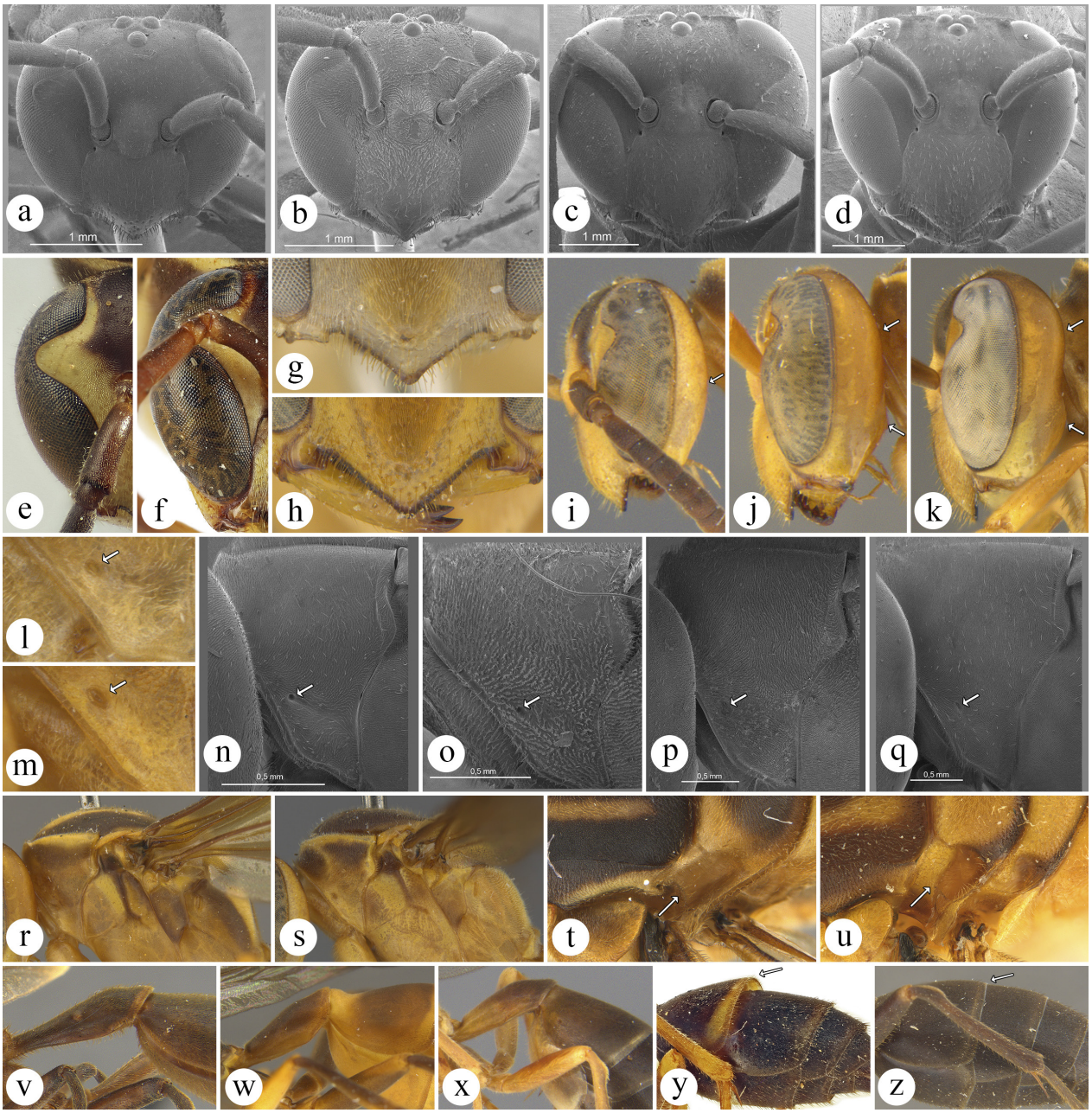

Figure 8. Morphological structures used in the matrix of characters. Head in frontal view obtained by SEM: **a.** *A. pallens*, **b.** *A. zischkai*, **c.** *A. obidensis*, **d.** *A. paraensis*. Eye bristles: **e.** *A. zischkai*, **f.** *A. obidensis*. Lateral lobe of the clypeus: **g.** *A. pallens*, **h.** *A. paraensis*. Gena: **i.** *A. zischkai*, **j.** *A. paraensis*, **k.** *A. obidensis*. Pronotal fovea: **l.** *A. pallens*, **m.** *A. zischkai*. Pronotum in lateral view obtained by SEM: **n.** *A. pallens*, **o.** *A. zischkai*, **p.** *A. obidensis*, **q.** *A. paraensis*. Mesoscutum in lateral view: **r.** *A. paraensis*, **s.** *A. zischkai*. Axillary fossa with arrow indicating the anterior margin: **t.** *A. obidensis*, **u.** *A. zischkai*. Metasomal tergum I in lateral view: **v.** *Ap. thoracica*, **w.** *Ag. Fulvofasciata*, **x.** *A. pallens*. Posterior margin of metasomal tergum II with arrow indicating row of very long bristles: **y.** *A. paraensis* brown-yellow, **z.** *A. paraensis* dark brown.

duced posterolateral carina (character 11, state 1), paramere spine with base of the ventral margin non-angulate (character 20, state 1), digitus with rounded anteroventral lobe (character 22, state 1) (Fig. S1). The genus has two well-defined clades. The first clade is formed by *A. pallens* and *A. zischkai* (with anterior wing 7–9.5 mm long) (SH-aLRT: 95.3%, UFboot: 97%, and MP Bootstrap: 96%). These two species were recovered as sister groups on MP by the synapomorphy of the axillary fossa with anterior margin directed to the posterior region (character 13, state 1). The second clade is formed by *A. paraensis* and *A. obidensis* (with anterior wing 12–16 mm long) (SH-aLRT: 99.8%, UFboot: 100%, and MP Bootstrap: 93%. These two species were recovered as sister groups on MP by the following synapomorphies: lateral ocelli on a declivity at the vertex (character 1, state 2), eyes composed with very small bristles (character 2, state 1), angulate gena with lower region broader (character 4, state 2), apical portion of the aedeagus with the median region of the reduced denticulation (character 24, state 1), apical portion of the aedeagus curved to the venter (character 25, state 1) (Fig. S1).

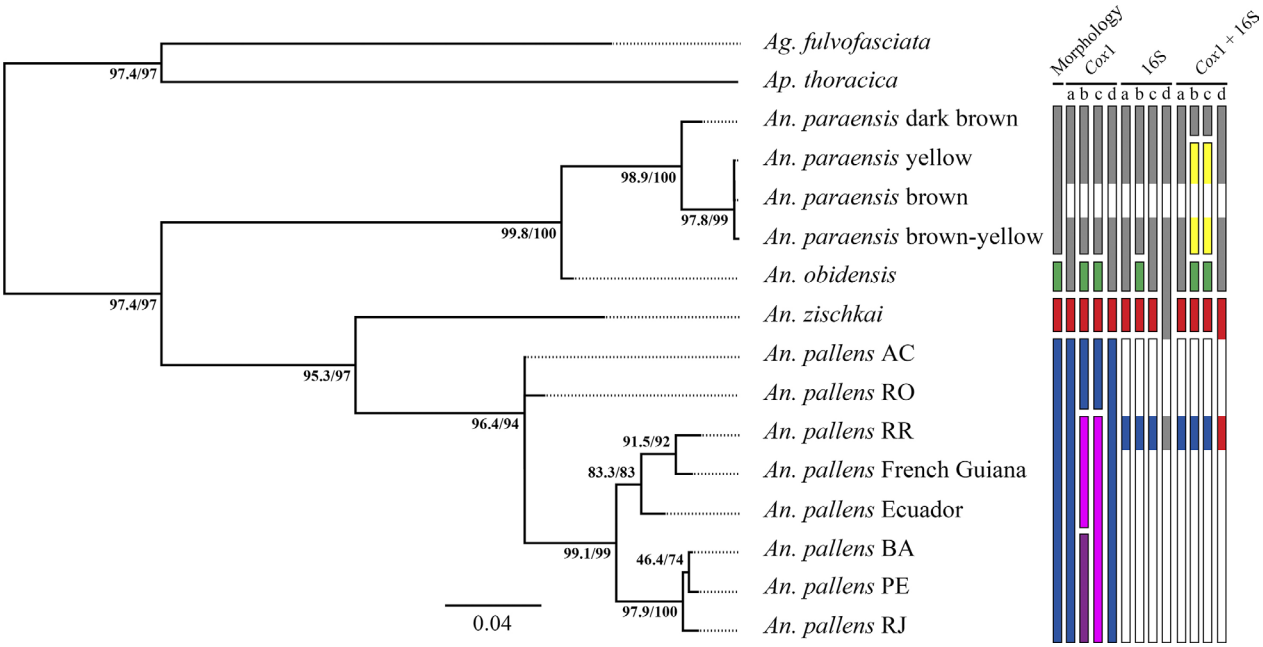

Figure 9. Phylogeny of *Angiopolybia* reconstructed by Maximum Likelihood analysis. Numbers above or below branches indicate SH-aLRT (first number) and UFBoot (second number) values. The species delimitation methods are identified by **a.** ABGD; **b.** ASAP; **c.** bPTP; and **d.** mPTP. The colored bars represent the results of the species delimitation methods and the white bars represent the absence of genetic data for the analyses. Brazilian states are abbreviated as follows: AC: Acre, BA: Bahia, PE: Pernambuco, RJ: Rio de Janeiro, RO: Rondônia and RR: Roraima.

The four molecular species delimitation hypotheses (ABGD, ASAP, bPTP, and mPTP) ranged from three to six species (Fig. 9). The *Cox*1 and 16S showed different results such as *Cox*1 delimiting between 3 (ABGD and mPTP) and 6 lineages (ASAP), the 16S between 1 (mPTP) and 4 lineages (ASAP), and the concatenated fragments (*Cox*1 + 16S) between 2 (mPTP) and 5 lineages (ASAP and bPTP). *Angiopolybia obidensis* and *A. paraensis* showed the lowest interspecific genetic distance, 5.37% for *Cox*1 and 1.89% for 16S. The highest interspecific genetic distance is between *A. paraensis* dark brown and *A. pallens* from Ecuador with 18.14% for *Cox*1. Between *A. zischkai* and *A. pallens* the lowest genetic distance is 10.15% for *Cox*1. The highest intraspecific genetic distance was found for *A. pallens*, with 9.49% among specimens from the Brazilian states Rondônia and Bahia (all values of genetic distance of *Cox*1 and 16S are listed in Table S5). Unfortunately, the intraspecific genetic distance of *A. zischkai* and *A. obidensis* was not analyzed because only one specimen of both species had the DNA extracted. These species, despite showing slight variation in the color of some populations, are morphologically corroborated considering the validity of their taxonomic status.

4. Discussion

Our ML and MP inferences with concatenated data corroborate the monophyly of *Angiopolybia* (Wenzel and Carpenter 1994; Andena et al. 2007; Menezes et al. 2020; Noll et al. 2021). The phylogenetic relationships recovered in our study for *Angiopolybia* species were similar to those found in the phylogenetic hypothesis proposed by Andena et al. (2007) based only on morphological data. Richards (1978) also described the morphological approximation among *Angiopolybia* species, despite not using a phylogenetic approach. Based on the morphological and molecular analysis, the variants of *A. paraensis* described as *Polybia ruficornis* Ducke, 1904 (*A. paraensis* morph *ruficornis* denominated by Richards, 1978) and *Stelopolybia paraensis* var. (or subspecies) *obscurior* Bequaert, 1944 (*A. paraensis* morph *obscurior* denominated by Richards, 1978), and variant *A. pallens* dark morph described by Richards, 1978 are not distinct, and we do not recommend the use of the term for species, as also suggested by Andena et al. (2007).

A high genetic diversity of *A. pallens* was also found by Carvalho et al. (2021) using three mitochondrial markers. However, the genetic relationship found by the authors between the populations from Acre and Rondônia with those from Bahia, Pernambuco, and Rio de Janeiro was smaller than the relationship with other populations from the Amazon Forest. The high genetic distance detected in *A. pallens* is possibly due to its wide geographical distribution, timing of colonization, and climatic stability in remote areas in both Amazon and Atlantic forests (for details see Carvalho et al., 2021).

Based on our morphological and molecular results, the color variation found in *A. pallens*, showing a gradient from yellow to black (Fig. 7a–g), represent only intraspecific variation for this species. In social wasps, phenotypic variants related to color can be derived from genetic differences, abiotic factors, aposematism, and

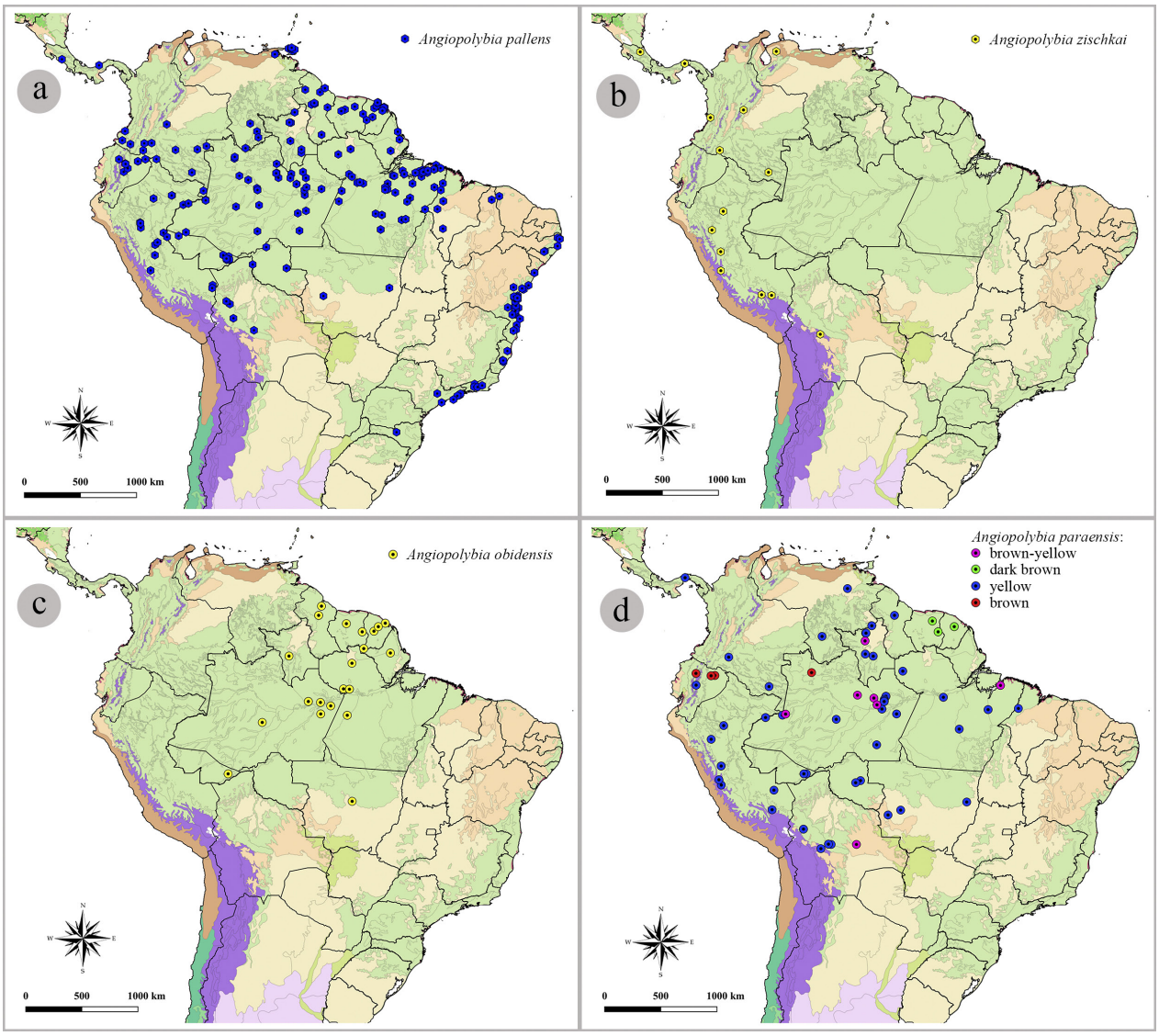

Figure 10. Map of South and Central America showing the geographic distribution of *Angiopolybia* species: **a.** *Angiopolybia pallens*, **b.** *Angiopolybia zischkai*, **c.** *Angiopolybia obidensis*, and **d.** *Angiopolybia paraensis*.

Müllerian mimicry (Perrard et al. 2014; Badejo et al. 2020). A study investigating the color variation versus altitude for *Agelaia pallipes* (Olivier, 1792) verified an interesting melanization process of the tegument related to the elevation of the Andean altitude, suggesting that the darkest color in this species is associated to thermoregulation and photoprotection (Souza et a. 2020). Further research is necessary to understand the possible causes of color variations in *A. pallens*, since both yellow and dark forms were found at low and high altitudes (see Fig. S2 and Supplementary material S1). For instance, species with darker coloration of velvet ants (Mutillidae) are frequent in habitats with higher humidity, more vegetation, and UV-B radiation (Lopez et al. 2021). For *A. paraensis*, the color variants found are well-defined because they occurred in geographic-close regions and often in the same locality (Fig. 10d).

The different results by the four molecular species delimitation methods used for *Angiopolybia* species can be interpreted by the limitations to the dataset and approach used here as well as a possible overlap between intraspecific and interspecific limits, as verified in the cicada *Tettigettalna* (Nunes et al. 2014). The missing information considering both taxonomic sampling and molecular dataset may have reduced the statistical power of our analyses. Additionally, because we used only mitochondrial markers (they are supposed to be linked, non-recombining locus with maternal inheritance, and likely evolved under similar constraints) and a category of species delimitation methods threshold-based that propose species hypotheses from a single-locus, our molecular species delimitation results should be viewed with some caution. Following the general lineage concept (de Queiroz 2007) in the search for separately evolving lineages that represent the species of *Angiopolybia*, we opted to be conservative considering our molecular species delimitation results, as recommended by Carstens et al. (2013), since here we take advantage of using both morphology-based taxonomy and molecular-based approaches. Although *A. paraensis* dark brown can be considered as such an intraspecific evolutionary lineage, additional molecular and morphological (e.g., male genitalia) data

will be necessary to propose as a new taxon. Our results are useful for future biogeographical studies and provide an integrative framework that could be applied to the taxonomy of other Neotropical social wasps.

5. Competing interests

The authors have declared that no competing interests exist.

6. Authors' contributions

P.C.S.B. designed the study, collected samples, carried out the molecular laboratory work, and led the writing of the manuscript. A.S., R.S.T.M., and M.L.O. funding acquisition. P.C.S.B., R.S.T.M., M.L.O., and A.S. performed the analyses. All authors gave final approval for publication.

7. Acknowledgements

We are thankful to the curators and assistants of the zoological collections Dr. James Michael Carpenter and Christine LeBeau (AMNH), Dr. Gavin Broad (NHM), Dra. Claire Villemant (MNHN), Dra. Crystal Maier (MCZ), Dr. Carlos Roberto Brandão and Dra. Kelli Ramos (MZUSP), Dr. Marcelo Tavares and Ricieri Dall'Orto (UFES Entomological Collection), Dra. Favízia Oliveira (MZUFBA Hymenoptera Collection), Dr. Orlando Tobiais Silveira (MPEG), Instituto Nacional de Biodiversidad (INABIO), Instituto Nacional de Pesquisas da Amazônia (INPA), and Museo de Zoología de la Pontificia Universidad Católica del Ecuador (QCAZ) by the loans of specimens. We are thankful to Steve Thurston (AMNH), Charles Farnum (MCZ), and Agnièle Touret-Alby (MNHN) by the support in obtaining the images. We are thankful to the Dr. Eduardo Almeida for the access to the Laboratório de Biologia Comparada e Abelhas for molecular procedures. We also thank Dr. James Carpenter and Dr. Antônio F. Carvalho for suggestions and comments that improved the manuscript. PCSB is grateful to the Fundação de Amparo à Pesquisa do Estado do Amazonas (FAPEAM) process POSGRAD/INPA 006/2020 and the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) process number 132264/2018-8 by scholarships. AS is thankful to FAPEAM (FIXAM, process number 062.01427/2018) and CNPq (PCI, process number 317786/2021-0). MLO is thankful to CNPq for productivity grant (process 305150-2020-0). RSTM is grateful to Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) for grant 2015/02432–0, and to CNPq for grant no. 431249/2018-0. This work was carried out with the support of the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001. We would like to thank three anonymous reviewers for valuable suggestions.

8. References

Andena SR, Noll FB, Carpenter JM (2007) Phylogenetic analysis of the Neotropical social wasps of the genus *Angiopolybia* Araujo, 1946 (Hymenoptera, Vespidae, Epiponini). Zootaxa 1427: 57–64. https://doi.org/10.11646/zootaxa.1427.1.4

Araujo RL (1946) *Angiopolybia* nom. n., para o conceito revalidado de "*Stelopolybia* Ducke, 1914" (Hym. – Vespidae – Polybiinae) (*). Papéis Avulsos 7: 165–170.

Badejo O, Skaldina O, Gilev A, Sorvani J (2020) Benefits of insect colours: a review from social insect studies. Oecologia 194: 27–40. https://doi.org/10.1007/s00442-020-04738-1

Barbosa BC, Detoni M, Maciel TT, Prezoto F (2016) Studies of social wasp diversity in Brazil: Over 30 years of research, advancements and priorities. Sociobiology 63(3): 858–880. https://doi.org/10.13102/sociobiology.v63i3.1031

Bequaert JC (1944) The social Vespidae of the Guianas, particularly of British Guiana. Bulletin of the Museum of Comparative Zoology 94: 247–304.

Bickford D, Lohman DJ, Sodhi NS, Ng PK, Meier R, Winker K, Ingram KK, Das I (2007) Cryptic species as a window on diversity and conservation. Trends in ecology & evolution 22(3): 148–155. https://doi.org/10.1016/j.tree.2006.11.004

Buck M, Cobb TP, Stahlhut JK, Hanner RH (2012) Unravelling cryptic species diversity in eastern Nearctic paper wasps, *Polistes* (*Fuscopolistes*), using male genitalia, morphometrics and DNA barcoding, with descriptions of two new species (Hymenoptera: Vespidae). Zootaxa 3502:1–48. https://doi.org/10.11646/zootaxa.3502.1.1

Buysson R du (1906) Monographie de Vespides appartenant aux genres *Apoica* et *Synoeca*. Annales de la Société Entomologique de France 75: 333–362.

Carpenter JM (1991) Phylogenetic relationships and the origin of social behavior in the Vespidae. In: Ross KG, Matthews RW (Eds) The Social Biology of Wasps. Cornell University Press, Ithaca, New York, 7–32.

Carpenter JM (2004) Synonymy of the genus *Marimbonda* Richards, 1978, with *Leipomeles* Möbius, 1856 (Hymenoptera: Vespidae; Polistinae), and a new key to the genera of paper wasps of the New World. American Museum Novitates 3465: 1–16.

Carstens BC, Pelletier TA, Reid NM, Satler JD (2013) How to fail at species delimitation. Molecular ecology 22(17): 4369–4383. https://doi.org/10.1111/mec.12413

Carvalho AF, Menezes RST, Miranda EA, Costa MA, Del Lama MA (2021) Comparative phylogeography and palaeomodelling reveal idiosyncratic responses to climate changes in Neotropical paper wasps. Biological Journal of the Linnean Society 132(4): 955–969. https://doi.org/10.1093/biolinnean/blaa215

Carvalho AF, Menezes RST, Somavilla A, Costa MA, Del Lama MA (2015) Neotropical Polistinae (Vespidae) and the progression rule principle: the round-trip hypothesis. Neotropical entomology 44(6): 596–603.

Carvalho AF, Santos GMM, Menezes RST, Costa MA (2014) Genetic diversity of *Angiopolybia pallens* (Lepeletier) (Hymenoptera, Vespidae, Polistinae) explained by the disjunction of South American rainforests. Genetics and Molecular Research 13(1): 89–94. https://doi.org/10.4238/2014.January.8.7

de Queiroz K (2007) Species concepts and species delimitation. Systematic Biology 56(6): 879–886. https://doi.org/10.1080/10635150701701083

de Saussure H 1853–1858 (1854) Monographie des Guêpes Sociales ou de la Tribu des Vespiens, ouvrage faisant suite à la Monographie des guêpes solitaries. Publishing companies: V. Masson, Paris and J. Kessmann, Genève, 97–256.

Dinerstein E, Olson D, Joshi A, Vynne C, Burgess ND, Wikramanayake E, Hahn N, Palminteri S, Hedao P, Noss R, Hansen M, Locke H, Ellis EC, Jones B, Barber CV, Hayes R, Kormos C, Martin V, Crist E, Sechrest W, Price L, Baillie JEM, Weeden D, Suckling K, Davis C, Sizer N, Moore R, Thau D, Birch T, Potapov P, Turubanova S, Tyukavina A, Souza N, Pintea L, Brito JC, Llewellyn OA,

Miller AG, Patzelt A, Ghazanfar SA, Timberlake J, Klöser H, Shennan-Farpón Y, Kindt R, Lillesø J-PB, van Breugel P, Graudal L, Voge M, Al-Shammari KF, Saleem M (2017) An Ecoregion-Based Approach to Protecting Half the Terrestrial Realm. BioScience 67 (6): 534–545. https://doi.org/10.1093/biosci/bix014

Ducke A (1904) Sobre as vespidas sociais do Pará. Extracto do Boletim do Museu Goeldi 4: 317–374.

Ducke A (1905a) Sobre as vespidas sociaes do Pará (Supplemento I). Boletim do Museu Goeldi 4: 652–698.

Ducke A (1905b) Nouvelles Contributions a la Connaissance des Vespides Sociaux De I'Amiérique du Sud. Revue D'Entomologie 24: 1–49.

Ducke A (1907) Zur Synonymie einiger Hymenopteren Amazoniens. Zeitschrift für systematische Hymenopterologie und Dipterologie 2: 137–144.

Ducke A (1910) Révision des guêpes sociales polygames d'Amérique. Annales Musei Nationalis Hungarici 8: 449–544.

Ducke A (1913) Zur Synonymie einiger Hymenopteren. Deutsche Entomologische Zeitschrift Heft 3: 330–333.

Ducke A (1914) Über Phylogenie und Klassifikation der sozialen Vespiden. Zoologische Jahrbücher - Abteilung für Systematik, Geographie und Biologie der Tiere 36: 303–330.

Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32(5): 1792–1797. https://doi.org/10.1093/nar/gkh340

Erichson WF (1848) Hymenoptera. In: Schomburgk R (Ed.) Reisen in Britisch-Guiana in den Jahren 1840–1844. Part 3. J.J. Weber Publisher, Leipzig, 587–593.

Goloboff PA, Catalano SA (2016) TNT version 1.5, including a full implementation of phylogenetic morphometrics. Cladistics 32: 221–238. https://doi.org/10.1111/cla.12160

Gomes B, Knidel SVL, Moraes HS, Silva M (2018) Survey of social wasps (Hymenoptera, Vespidae, Polistinae) in Amazon rainforest fragments in Acre, Brazil. Acta Amazonica 48(2): 109–116. https://doi.org/10.1590/1809-4392201700913

Gomes B, Lima CS, Silva M, Noll FB (2020) High Number of Species of Social Wasps (Hymenoptera, Vespidae, Polistinae) Corroborates the Great Biodiversity of Western Amazon: a Survey from Rondônia, Brazil. Sociobiology 67(1): 112–120. https://doi.org/10.13102/sociobiology.v67i1.4478

Guindon S, Dufayard J-F, Lefort V, Anisimova M, Hordijk W, Gascuel O (2010) New algorithms and methods to estimate maximum-likelihood phylogenies: assessing the performance of PhyML 3.0. Systematic Biology 59(3): 307–321. https://doi.org/10.1093/sysbio/syq010

International Commission on Zoological Nomenclature (1976) Opinion 1051: *Rhopalidia* Lepeletier, 1836 (Insecta: Hymenoptera): Suppressed under the plenary powers. The Bulletin of Zoological Nomenclature 32: 240–241.

Kapli P, Lutteropp S, Zhang J, Kobert K, Pavlidis P, Stamatakis A, Flouri T (2017) Multi-rate Poisson tree processes for single-locus species delimitation under maximum likelihood and Markov chain Monte Carlo. Bioinformatics 33(11): 1630–1638. https://doi.org/10.1093/bioinformatics/btx025

Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Meintjes P, Drummond A (2012) Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28(12): 1647–1649. https://doi.org/10.1093/bioinformatics/bts199

Kimura M (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. Journal of Molecular Evolution 16: 111–120. https://doi.org/10.1007/BF01731581

Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: Molecular Evolutionary Genetics Analysis across Computing Platforms. Molecular Biology and Evolution 35(6): 1547–1549. https://doi.org/10.1093/molbev/msy096

Lanfear R, Frandsen PB, Wright AM, Senfeld T, Calcott B (2016) PartitionFinder 2: New Methods for Selecting Partitioned Models of Evolution for Molecular and Morphological Phylogenetic Analyses. Molecular Biology and Evolution 34(3): 772–773. https://doi.org/10.1093/molbev/msw260

Lepeletier A (1836) Histoire Naturelle des Insectes: Hyménoptères. Librairie Encyclopédique de Roret Publisher, Paris, 547pp.

Lopes RB, Menezes RST (2017) *Synoeca ilheensis* sp. nov., a new social wasp (Hymenoptera, Vespidae, Polistinae) from Brazilian lowland Atlantic Forest. Zootaxa 4300(3): 445–450. https://doi.org/10.11646/zootaxa.4300.3.8

Lopez VM, Tosta TAA, Silva GG, Bartholomay PR, Williams KA, Ferreira G-F (2021) Color lightness of velvet ants (Hymenoptera: Mutillidae) follows an environmental gradient. Journal of Thermal Biology 100(103030): 1–9. https://doi.org/10.1016/j.jtherbio.2021.103030

Maddison WP, Maddison DR (2019) Mesquite: a modular system for evolutionary analysis. Version 3.61. http://www.mesquiteproject.org

Menezes RST, Brady SG, Carvalho AF, Del Lama MA, Costa MA (2015) Molecular Phylogeny and Historical Biogeography of the Neotropical Swarm-Founding Social Wasp Genus *Synoeca* (Hymenoptera: Vespidae). PLoS ONE 10(3): e0119151. https://doi.org/10.1371/journal.pone.0119151

Menezes RST, Brady SG, Carvalho AF, Del Lama MA, Costa MA (2017) The roles of barriers, refugia, and chromosomal clines underlying diversification in Atlantic Forest social wasps. Scientific reports 7(7689): 1–16. https://doi.org/10.1038/s41598-017-07776-7

Menezes RST, Lloyd MW, Brady SG (2020) Phylogenomics indicates Amazonia as the major source of Neotropical swarm-founding social wasp diversity. Proceedings of the Royal Society B 287(1928): 20200480. https://doi.org/10.1098/rspb.2020.0480

Minh BQ, Nguyen MA, von Haeseler A (2013) Ultrafast approximation for phylogenetic bootstrap. Molecular Biology and Evolution 30(5): 1188–1195. https://doi.org/10.1093/molbev/mst024

Möbius K (1856) Die Nester der geselligen Wespen. Abhandlungen aus dem Gebiete der Naturwissenschaften 3: 117–171.

Nguyen L-T, Schmidt HA, von Haeseler A, Minh BQ (2015) IQ-TREE: A Fast and Effective Stochastic Algorithm for Estimating Maximum-Likelihood Phylogenies. Molecular Biology and Evolution 32(1): 268–274. https://doi.org/10.1093/molbev/msu300

Nixon KC (2002) WinClada ver. 1.00. 08. Published by the author, Ithaca, New York.

Nixon KC, Carpenter JM (1993) On outgroups. Cladistics 9: 413–426. https://doi.org/10.1111/j.1096-0031.1993.tb00234.x

Noll FB, da Silva M, Soleman RA, Lopes RB, Grandinete YC, Almeida EAB, Wenzel JW, Carpenter JM (2021) Marimbondos: systematics, biogeography, and evolution of social behaviour of neotropical swarm-founding wasps (Hymenoptera: Vespidae: Epiponini). Cladistics 0: 1–19. https://doi.org/10.1111/cla.12446

Nunes VL, Mendes R, Marabuto E, Novais BM, Hertach T, Quartau JA, Seabra SG, Paulo OS, Simões PC (2014) Conflicting patterns of DNA barcoding and taxonomy in the cicada genus *Tettigettalna* from Southern Europe (Hemiptera: Cicadidae). Molecular Ecology Resources 14: 27–38. https://doi.org/10.1111/1755-0998.12158

Overal WL (1978) Designaçao de lectótipos de onze espécies de vespas sociais descritas por Adolpho Ducke, e notas sobre a Coleçao Ducke (Hymenoptera: Vespidae). Boletim do Museu Paraense Emílio Goeldi 94: 1–14.

Padial JM, Miralles A, De la Riva I, Vences M (2010) The integrative future of taxonomy. Frontiers in Zoology 7(16): 1–14. https://doi.org/10.1186/1742-9994-7-16

Perrard A, Arca M, Rome Q, Muller F, Tan J, Bista S, Nugroho H, Baudoin R, Baylac M, Silvain J-F, Carpenter JM, Villemant C (2014) Geographic variation of melanisation patterns in a hornet species: genetic differences, climatic pressures or aposematic constraints? PLoS ONE 9(4): e94162. https://doi.org/10.1371/journal.pone.0094162

Provancher L 1889 (1888) Faune Entomologique du Canada: Traitant des Hyménopteres. Additiones et corrections au volume II. Typographie de C. Darveau, Québec, 475pp.

Puillandre N, Brouillet S, Achaz G (2021) ASAP: assemble species by automatic partitioning. Molecular Ecology Resources 21: 609–620. https://doi.org/10.1111/1755-0998.13281

Puillandre N, Lambert A, Brouillet S, Achaz G (2012) ABGD, Automatic Barcode Gap Discovery for primary species delimitation. Molecular Ecology 21(8): 1864–1877. https://doi.org/10.1111/j.1365-294X.2011.05239.x

Rasband WS (2019) ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, 1997–2018. https://imagej.nih.gov/ij/index.html

Richards OW (1943) A new species of *Gymnopolybia* Ducke (Hymen., Vespidae). Proceedings of the Royal Entomological Society of London 12: 45–49. https://doi.org/10.1111/j.1365-3113.1943.tb00745.x

Richards OW (1973) *Rhopalidia* Lepeletier, 1836 (Hymenoptera: Vespidae): proposed suppression under the plenary powers. The Bulletin of Zoological Nomenclature 30: 49–50.

Richards OW (1978) The social wasps of the Americas: excluding the Vespinae. British Museum (Natural History) London, 580 pp.

Richards OW, Richards MJ (1951) Observations on the social wasps of South America (Hymenoptera, Vespidae). Transactions of the Royal Entomological Society of London 102: 1–169. https://doi.org/10.1111/j.1365-2311.1951.tb01241.x

Schulz WA (1903) Hymenopteren Amazoniens. Sitzungsberichte der mathematisch-physikalischen Klasse 33: 757–832.

Schulz WA (1905) Hymenopteren-Studien. Wilhelm Engelmann, Leipzig, 147 pp.

Schulz WA (1912) Aelteste und alte Hymenopteren skandinavischer Autoren. Berliner Entomologische Zeitschrift 57: 52–102.

Silveira OT, Carpenter JM (1995) A new species of *Agelaia* Lepeletier from Brazilian Amazonia (Hymenoptera: Vespidae; Polistinae). Journal of the New York Entomological Society 103(1): 69–72.

Somavilla A, Barroso PCS, Aragão M, Mateus S, Menezes RST (2021) An integrative taxonomic and phylogenetic approach reveals a new Neotropical swarm-founding social wasp, *Pseudopolybia cryptica* sp. n. (Vespidae: Polistinae: Epiponini). Arthropod Systematics & Phylogeny 79: 25–35. https://doi.org/10.3897/asp.79.e64304

Somavilla A, Oliveira ML, Andena SR, Carpenter JM (2018) An illustrated atlas for male genitalia of the New World *Polistes* Latreille, 1802 (Vespidae: Polistinae). Zootaxa 4504(3): 301–344. https://doi.org/10.11646/zootaxa.4504.3.1

Souza AR, Mayorquin AZ, Sarmiento CE (2020) Paper wasps are darker at high elevation. Journal of Thermal Biology 89 (102535): 1–6. https://doi.org/10.1016/j.jtherbio.2020.102535

Spinola M 1853 (1851) Compte rendu des Hyménoptères inédits: provenants du voyage entomologique de M. Ghiliani dans le Para en 1846. Memorie della Reale Accademia delle Scienze di Torino 13: 19–94.

Valverde JP, Hanson P, Carpenter JM (2019) Keys to the Costa Rican species of paper wasps (Hymenoptera: Vespidae: Polistinae). Revista de Biología Tropical 67(2) Suppl.: 174–199. https://doi.org/10.15517/RBT.V67I2SUPL.37229

Vecht J van der (1972) The social wasps (Vespidae) collected in French Guyana by the mission du Muséum National d'Historie Naturelle with notes on the genus *Apoica* Lepeletier. Annales de la Societé Entomologique de France 8: 735–743.

Wenzel JW (1998) A generic key to the nests of Hornets, Yellowjackets, and paper wasps worldwide (Vespidae: Vespinae, Polistinae). American Museum Novitates 3224: 1–39.

Wenzel JW, Carpenter JM (1994) Comparing methods: adaptive traits and tests of adaptation. In: Eggleton P, Vane-Wright R (Eds) Phylogenetics and Ecology. Academic Press, London, 79–101.

Zhang J, Kapli P, Pavlidis P, Stamatakis A (2013) A general species delimitation method with applications to phylogenetic placements. Bioinformatics 29(22): 2869–2876. https://doi.org/10.1093/bioinformatics/btt499

Supplementary material 1

Supplementary Tables S1–5, Supplementary Figures S1–2, and Supplementary material S1

Authors: Barroso PCS, Menezes RST, Oliveira ML, Somavilla A (2022)
Data type: .docx
Explanation note: Supplementary Table S1: Measurements of morphological structures gathered in this study. — **Supplementary Table S2:** Information about all specimens used in the molecular analyses. — **Supplementary Table S3:** Data partitions, nucleotide substitution models implemented in the Maximum likelihood analysis. — **Supplementary Table S4:** Morphological matrix. — **Supplementary Table S5:** Pairwise genetic divergence between sequences of *Angiopolybia* species. — **Supplementary Figure S1:** Analysis of Maximum Parsimony with concatenated morphological and molecular (Cox1+16S) data. — **Supplementary Figure S2.** Altitude variation of *Angiopolybia pallens* specimens. — **Supplementary material S1.** *Angiopolybia* specimens examined.

Link: https://doi.org/10.3897/asp.80.e71492.suppl1