



**Phylogenetic Analysis of The Neotropical Pseudopolybia De Saussure, 1863, with Description of The Male Genitalia of Pseudopolybia Vespiceps (Hymenoptera: Vespidae, Epiponini)**

Authors: ANDENA, SERGIO R., NOLL, FERNANDO B., CARPENTER, JAMES M., and ZUCCHI, RONALDO

Source: American Museum Novitates, 2007(3586) : 1-11

Published By: American Museum of Natural History

URL: [https://doi.org/10.1206/0003-0082\(2007\)3586\[1:PAOTNP\]2.0.CO;2](https://doi.org/10.1206/0003-0082(2007)3586[1:PAOTNP]2.0.CO;2)

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

# AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY  
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024

Number 3586, 11 pp., 4 figures, 2 tables

September 6, 2007

## Phylogenetic Analysis of the Neotropical *Pseudopolybia* de Saussure, 1863, with Description of the Male Genitalia of *Pseudopolybia vespiceps* (Hymenoptera: Vespidae, Epiponini)

SERGIO R. ANDENA,<sup>1</sup> FERNANDO B. NOLL,<sup>2</sup> JAMES M. CARPENTER,<sup>3</sup> AND  
RONALDO ZUCCHI<sup>1</sup>

### ABSTRACT

The male genitalia of *Pseudopolybia vespiceps* are described and compared to congeners. Characters of the male genitalia are combined with morphological characters of the females and nests and used in a phylogenetic analysis. The single cladogram resulting supports monophyly of the genus *Pseudopolybia* and interrelationships among the species as: *P. langi* + (*P. difficilis* + (*P. compressa* + *P. vespiceps*)). A new, illustrated identification key is presented.

### INTRODUCTION

*Pseudopolybia* is a genus of neotropical swarm-founding wasps (Tribe Epiponini), distinguished by the third segment of the labial palpi bearing a short, stout, curved bristle near its apex, and the number of palpal segments being six maxillary and four labial (Richards, 1978). The genus comprises four species, which range from Nicaragua to

southern Brazil, and they are found mainly in rainforest (Hanson and Gauld, 1995; Richards and Richards, 1951; Richards, 1978). Although there are few species, they present several taxonomic problems, because both *P. compressa* and *P. vespiceps* occur in striking color forms that “in some respects look like species, though they show no structural differences” (Richards, 1978: 224). In the most recent revision, Richards (1978)

<sup>1</sup> FFCLRP-USP. Av. Bandeirantes, 3900, Ribeirão Preto-SP, CEP 14040-901, Brazil (sandena@usp.br).

<sup>2</sup> Departamento de Zoologia e Botânica, Instituto de Biociências, Letras e Ciências Exatas, UNESP, Rua Cristóvão Colombo, 2265; 15054-000, São José do Rio Preto, SP, Brazil (noll@ibilce.unesp.br).

<sup>3</sup> Curator, Division of Invertebrate Zoology, American Museum of Natural History (carpente@amnh.org).

treated these color variants as “morphs”: *P. compressa* comprised the morphs *compressa*, *luctuosa* and *laticincta*, and *Pseudopolybia vespiceps* comprised the morphs *vespiceps* and *testacea*. These names had been first described as distinct species or varieties; they were later reduced to varieties of the respective species (Bequaert, 1938) and are now synonyms, as the term “morph” is without taxonomic standing.

Nests of three of the species of *Pseudopolybia* have been described (Wenzel, 1998): *P. compressa*, *P. difficilis* and *P. vespiceps*. They are usually arboreal, with the pedicel fibrous and cell marginal and lower combs hanging from the upper ones, normally by a single more or less central petiole (Richards, 1978). The spherical or tapering envelope is not in contact with the combs, and is laminar or imbricate, with downwardly opening pockets built on the outside of the envelope. The entrance hole is a simple hole at the lowest point of the envelope. A nest of *P. langi* from French Guiana is mentioned in the literature (Dejean et al., 1998), and the specimen is now in the collection of the American Museum of Natural History (AMNH). It is an incipient nest, arboreal, a single comb lacking an envelope and attached by a pedicel to the substrate (a leaf). A more complete specimen was obtained in Amapá, Brazil, by Orlando Tobias Silveira, who kindly sent us a photograph. Although the specimen is damaged, essential aspects of its architecture are visible: the nest consists of several combs attached to the substrate (a leaf), evidently with some degree of stacking present; there is an envelope that is not in contact with the combs and that consists of a simple sheet, without pockets and without a spoutlike entrance. In the absence of the imbrications in the envelope, *P. langi* is primitive relative to the other species in the genus, a conclusion that is true for other characters, as will be seen.

Carpenter and Mateus (2004) presented the first detailed descriptions of male genitalia of *Pseudopolybia* and related genera (see also Charnley, 1973). Probably due to intermittent male production in social wasps (Jeanne, 1991), few works on male genitalia have been published. This type of character seems to be

important in phylogenetic investigation, an issue not well explored for the Polistinae (Carpenter, 1991; Wenzel and Carpenter, 1994). In this work, a phylogenetic analysis of *Pseudopolybia* using male genitalia and other characters is presented.

## MATERIALS AND METHODS

Specimens were examined at the AMNH and at the Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto da Universidade de São Paulo, and were obtained by loans from Museu Paraense Emílio Goeldi, Belém, Pará, Brazil (MPEG); Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZSP); Universidade Federal do Paraná, Curitiba, Paraná, Brazil (UFPR); and Instituto de Investigación de Recursos Biológicos Alexander Von Humboldt, Bogotá, Colombia (IIRBAVH). Additional material was examined in the Hymenoptera Collection of the Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil (INPA). Localities of specimens are listed in appendix 1.

Specimens dissected and illustrated by Carpenter and Mateus (2004) were available in the present study. In addition, males of *Agelaia cajennensis* (from promenades St. Jean-du-Maroni, French Guiana), *Parachartergus fraternus* (from Valle Chanchamayo, San Ramon, Peru), and *Pseudopolybia vespiceps* (from São Paulo, Brazil) were relaxed and the genitalia extracted. The genital capsule was cleared in lactophenol and examined under glycerin. The genitalia of these taxa are illustrated in figure 4; the specimens are deposited in the AMNH. Figures of the genitalia of *Apoica gelida* and *Angiopolybia pallens* (both based on specimens from Arima Valley, Trinidad), given to Carpenter by the late J. van der Vecht, were also examined. Finally, nest characters were taken from Wenzel (1998).

Measurements and illustrations were taken using a Leica MZ 7.5 stereomicroscope with drawing tube, Leica model DFC 280 digital camera, and Leica IM 50 software.

Twenty morphological characters of the females, six from male genitalia, and three nest characters for the species of *Pseudopolybia* were assembled in a data matrix

TABLE 1  
**Character Matrix for *Pseudopolybia***  
 The following symbols are used: ? (not seen); - (inapplicable)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	
<i>Apoica gelida</i>	0	0	0	0	1	0	0	0	0	0	3	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	-	
<i>Agelaia cajennensis</i>	0	0	0	0	1	0	1	0	0	1	0	3	0	0	0	0	0	0	1	1	0	1	0	0	1	0	0	1	-	
<i>Angiopolybia pallens</i>	0	0	0	0	1	0	0	0	0	0	3	0	0	0	1	0	0	0	0	0	0	1	0	1	0	0	1	1	0	
<i>Pseudopolybia langi</i>	1	0	0	1	1	0	0	0	0	1	2	0	0	0	0	0	1	0	0	0	?	?	?	?	?	?	1	1	1	
<i>Pseudopolybia vespiceps</i>	1	0	0	0	0	1	1	1	1	1	1	1	0	0	0	1	1	1	1	0	2	0	0	0	1	1	2	1	1	
<i>Pseudopolybia compressa</i>	1	0	0	0	1	0	0	1	0	1	1	1	0	0,1	0	1	1	1	0	0	2	0	0	0	1	1	2	1	1	
<i>Pseudopolybia difficilis</i>	1	0	0	0	0	0	0	1	0	1	1	1	0	0	0	0	1	0	0	0	2	0	0	0	0	0	1	2	1	1
<i>Parachartergus fraternus</i>	1	0	1	0	1	0	0	0	0	0	0	0	1	1	0	0	2	1	1	0	1	0	0	1	0	1	1	1	0	
<i>Leipomeles dorsata</i>	1	1	1	0	0	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	1	1	1	0	1	1	1	0	
<i>Nectarinella</i>																														
<i>xavantinensis</i>	1	1	1	1	0	1	0	0	0	1	0	0	0	1	0	2	3	1	0	0	0	1	0	1	1	1	1	0	0	
<i>Chartergellus punctator</i>	1	1	1	1	1	1	0	0	1	1	0	0	0	1	0	1	3	1	0	0	0	0	0	0	0	1	1	1	1	0

for phylogenetic reconstruction (table 1). Analysis of the data matrix was undertaken with the program NONA (Goloboff, 1999a), using WINCLADA as the interface (Nixon, 1999); the resulting cladogram is shown in fig. 1. Multistate character was treated as non-additive except for characters 16 and 27, in which nested similarity was observed. Characters were polarized by rooting with outgroups (Nixon and Carpenter, 1993), represented herein by species of the distantly related genera *Apoica*, *Agelaia*, and *Angiopolybia*, as well as *Chartergellus*, *Leipomeles*, *Nectarinella*, and *Parachartergus*, the other four genera of Epiponini that have the curved bristle on the labial palpi. Characters and states are listed in table 2, and illustrated in figures 2–4.

## RESULTS AND DISCUSSION

Figures of the male genitalia of *P. compressa* and *P. difficilis* were presented by Carpenter and Mateus (2004: figs. 8–9). The male genitalia of *P. vespiceps* are illustrated in figure 4. Richards (1978) described males of *P. vespiceps* as being similar to females but yellower: head mostly yellow except the upper part of frons, antennae black above, scape yellow beneath, flagellum brownish beneath, the mesosoma with many small yellow marks, the metasoma browner. The clypeus also has silvery hairs, and the gena is narrow. (Typically, most epiponine males, including *Pseudopolybia*, have the gena relatively nar-

row and the clypeus with silvery hairs; they also have an extra antennal article and the extra, seventh metasomal sternum flattened.) We noted some specimens of *P. vespiceps* that have the antenna completely yellow or brownish, which may reflect regional variation. Male genitalia of *P. vespiceps* (fig. 4) have long and numerous hairs on the parameral spine; the basal angle of the paramere obtuse (fig. 4c3); the apical angle of the paramere broad (fig. 4b3); the ventral process of the aedeagus short and angular (fig. 4a3); the digitus apically broadly pointed; and the basal process of the digitus present. Apparently, this species has less numerous hairs on the paramere than other *Pseudopolybia* species (cf. fig. 4 with Carpenter and Mateus: figs. 8–9), while the pointed digitus places this species closer to *P. compressa*, which also has this feature, than to *P. difficilis* (see the discussion below).

Analysis of the matrix, using implicit enumeration, resulted in a single cladogram (fig. 1), of length 56, consistency index 0.64, and retention index 0.70. This tree is stable to both successive (using the rescaled consistency index) and implied weighting (default concavity in the program Piwe; Goloboff, 1999b). *Pseudopolybia* is supported as a monophyletic group, with relationships among the species showing *P. langi* as relatively basal, and *P. difficilis* as sister-group to a clade composed of *P. vespiceps* + *P. compressa*.

According to previous authors (Carpenter, 1991; Wenzel and Carpenter, 1994), the third

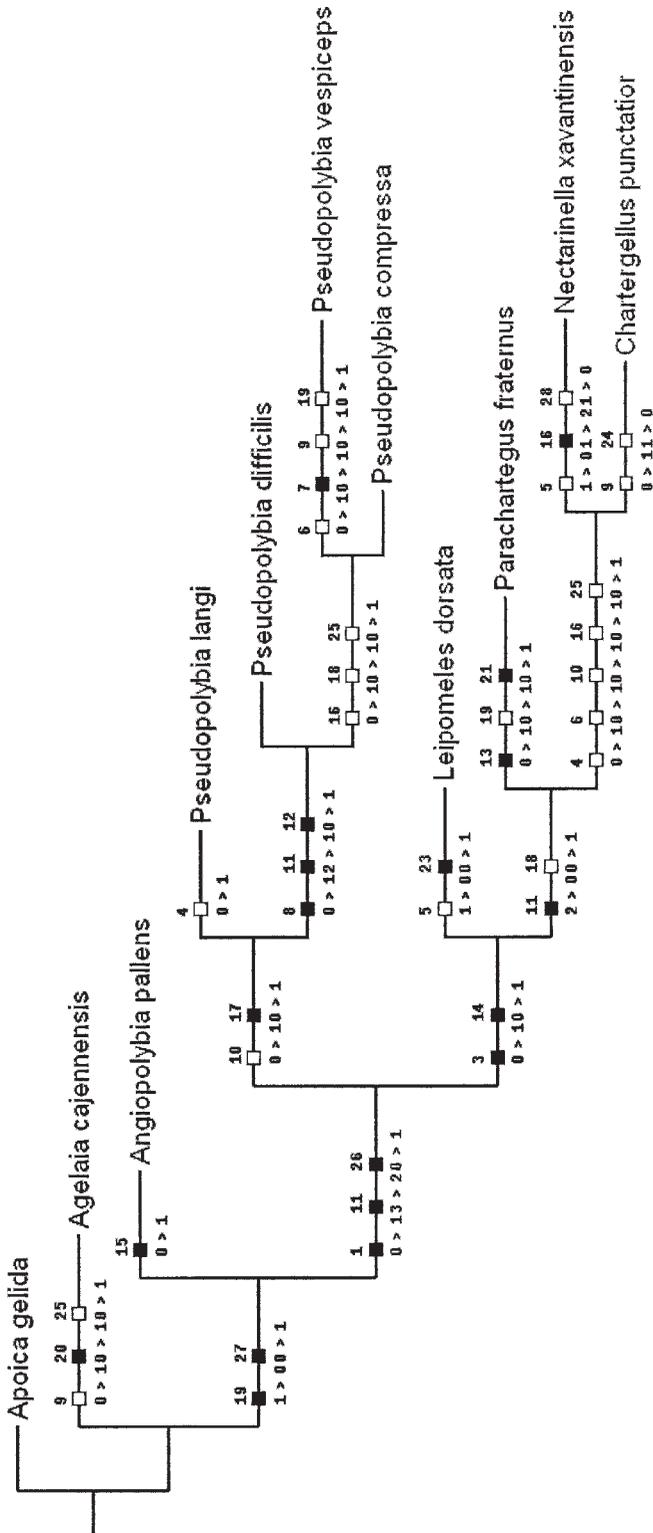


Fig. 1. The single cladogram for *Pseudopolybia*, with a length of 56, consistency index of 0.64, and retention index of 0.70; based on the data matrix from table 1. Character numbers (see table 2) are placed above hash marks, with the state numbers below, separated by ">" to indicated the transitions between states. Filled hash marks indicate an uncontroverted step, while open hash marks indicate homoplastic change.

TABLE 2  
 Character list for *Pseudopolybia*. Numerical scores for each state follow the “=”

---



---

1.	<i>Third labial palpomere</i> : without curved bristle = 0; with curved bristle = 1.
2.	<i>Maxillary palpi</i> : 6 segments = 0; 5 segments = 1.
3.	<i>Labial palpi</i> : 4 segments = 0; 3 segments = 1.
4.	<i>Third antennal article</i> : twice as long as fourth article = 0; about 1,5 times as long as fourth article = 1.
5.	<i>Eyes</i> : bare = 0; with bristles = 1.
6.	<i>Clypeus</i> : touching the eyes = 0; not touching the eyes = 1.
7.	<i>Clypeal apex</i> : sharply pointed = 0 (fig. 2A1); feebly pointed = 1 (fig. 2A2).
8.	<i>Gena</i> : at bottom of eyes, narrower than eyes = 0; at bottom of eyes, angled, wider than eyes = 1.
9.	<i>Malar space</i> : shorter than or equal to 4th antennal article = 0 (fig. 2B1); longer than 4th antennal article = 1 (fig. 2B2).
10.	<i>Occipital carina</i> : present = 0; absent = 1.
11.	<i>Dorsal pronotal carina</i> : ending close to posterior margin of pronotum = 0; ending close to midpoint of pronotum = 1 (fig. 2C1); weak, evanescent = 2 (fig. 2C2); trace, absent = 3.
12.	<i>Pronotal fovea</i> : in a shallow concavity = 0; in a deep concavity = 1.
13.	<i>Scrobal sulcus</i> : present = 0; absent = 1.
14.	<i>Dorsal groove</i> : present = 0; absent = 1.
15.	<i>Scutellum</i> : with impressed line = 0; without impressed line = 1.
16.	<i>Metanotum</i> : long, curved = 0; short, compressed = 1 (fig. 2D1, 2D2); vertical = 2.
17.	<i>Propodeal concavity</i> : narrow = 0; broad, shallow = 1; broad, deep = 2; propodeum nearly flat = 3.
18.	<i>First metasomal segment</i> : longer than wide = 0 (fig. 3A1); wider than long = 1 (fig. 3A2).
19.	<i>Prestigma</i> : as long as wide = 0; longer than wide = 1.
20.	<i>Tip of prestigma</i> : truncate = 0; rounded = 1.
21.	<i>Paramere hairs</i> : absent = 0; present, short hairs = 1; present, long hairs = 2.
22.	<i>Paramere basal angle</i> : obtuse (fig. 4c2, 4c3) = 0; acute = 1 (fig. 4c1).
23.	<i>Paramere apical angle</i> : broad (fig. 4b1, 4b2, 4b3) = 0; narrow = 1.
24.	<i>Ventral process of aedeagus</i> : short, angular = 0 (fig. 4a1, 4a3); narrow, reduced = 1 (fig. 4a2).
25.	<i>Digitus shape</i> : rounded = 0; pointed = 1.
26.	<i>Basal process of digitus</i> : absent = 0; present = 1.
27.	<i>Nest envelope</i> : absent = 0; present, single sheet = 1; present, laminar to imbricate = 2.
28.	<i>Nest pedicels</i> : absent = 0; present = 1.
29.	<i>Nest entrance</i> : downward spout = 0; simple hole = 1.

---

labial palpomere with a curved bristle (character 1, state 1; see character list) is apomorphic for the clade *Pseudopolybia* + (*Leipomeles* + (*Parachartergus* + (*Nectarinella* + *Chartergellus*))), and that is also our result (fig. 1).<sup>4</sup> The loss of the occipital carina (character 10, state 1) is a derived character found in *Nectarinella*, *Chartergellus* and all *Pseudopolybia* species, with two independent origins (fig. 1). In previous analyses, this feature was the only synapomorphy for

*Pseudopolybia*. Here, a broad, shallow propodeal concavity (character 17, state 1) is an additional synapomorphy for *Pseudopolybia*. Several other morphological characters are potentially synapomorphies, but because *P. langi* is unknown for male genitalia, the optimizations are ambiguous on figure 1. One feature of nest architecture, nest entrance a simple hole (character 29, state 1), is optimized as a synapomorphy for *Pseudopolybia*.

Richards (1978) placed *Chartergellus*, *Leipomeles*, *Parachartergus* and *Pseudopolybia* in a group with long hairs on the paramere spine (character 21, state 2, in the character list), but, as pointed out by Carpenter and Mateus (2004), this is a characteristic exclusive to *Pseudopolybia*. In fact, *Parachartergus fraternus* (fig. 4), *P. apicalis* and *P. griseus* (see Carpenter and Mateus, 2004: figs. 6–7)

<sup>4</sup>Note that the relationships of these five genera differ from the topology in Wenzel and Carpenter (1994), which shows *Pseudopolybia* + (*Parachartergus* + (*Leipomeles* + (*Chartergellus* + *Nectarinella*))). In either case, *Pseudopolybia* is the most basal genus, and both because that is the focus of this study, and due to the small number of species sampled in our outgroup, we will defer discussion.

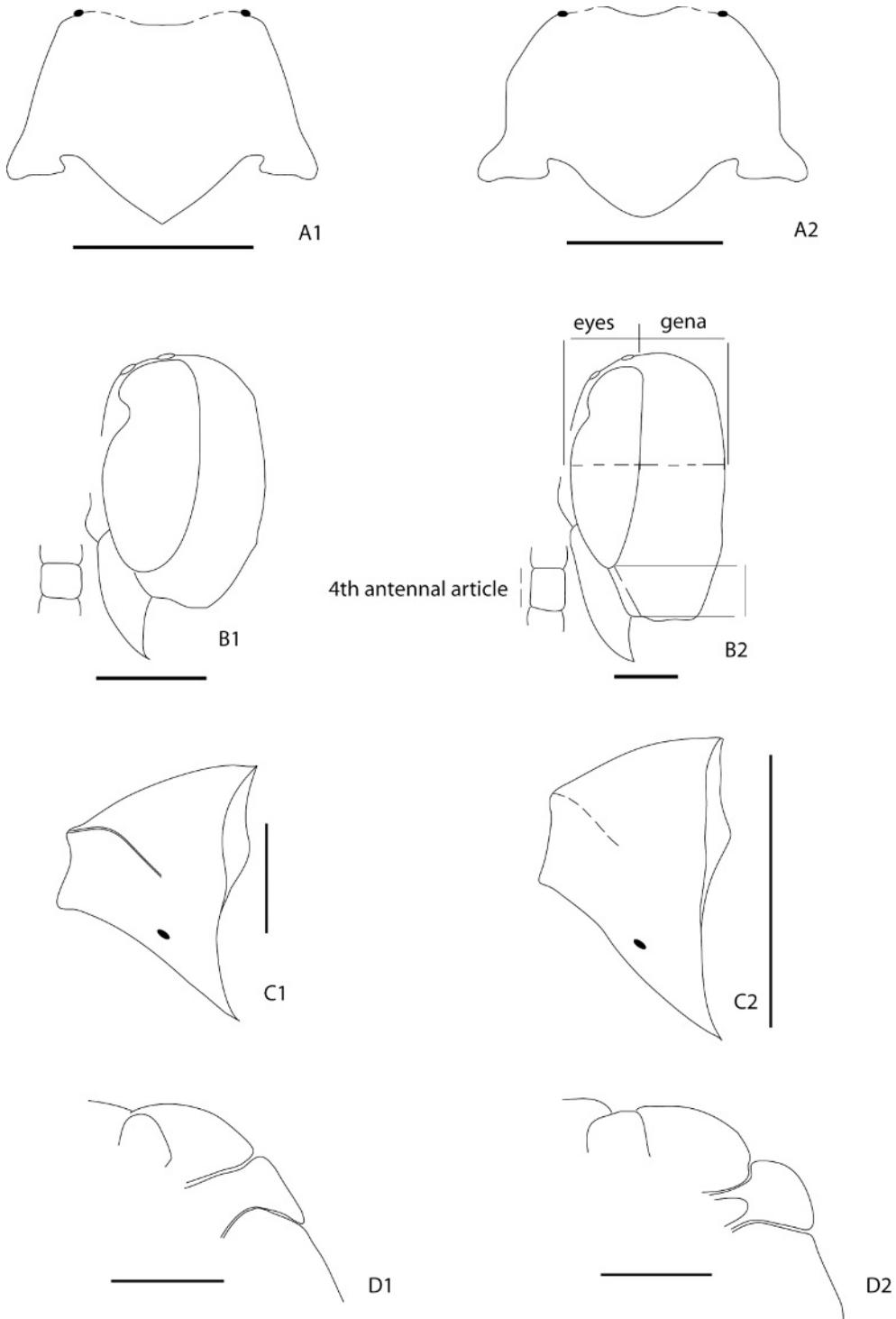


Fig. 2. Characters of *Pseudopolybia*. A, clypeus in frontal view. A1, *P. compressa*; A2, *P. vespiceps*. B, head in lateral view. B1, *P. compressa*; B2, *P. vespiceps*. C, pronotum in lateral view. C1, *P. compressa*; C2, *P. langi*. D, metanotum in lateral view. D1, *P. compressa*; D2, *P. vespiceps*. Scale bars = 1.0 mm.

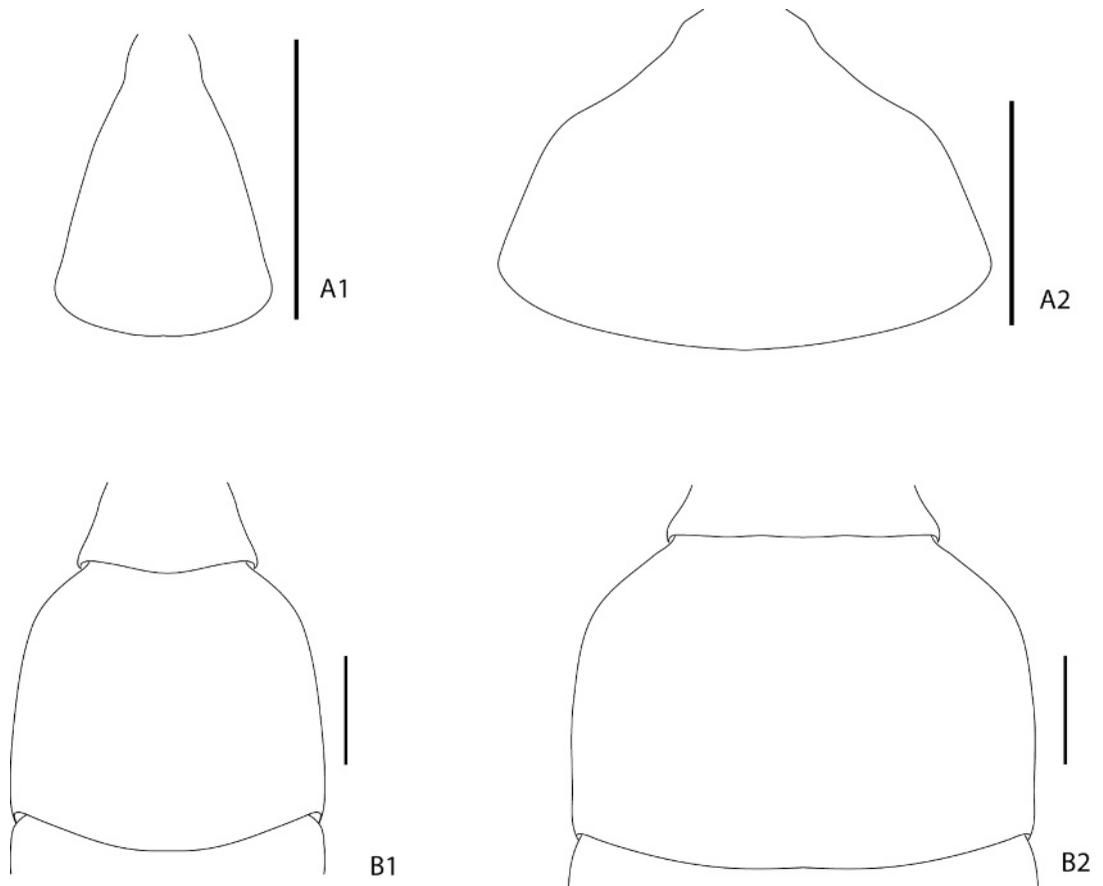


Fig. 3. Characters of *Pseudopolybia*. A, first metasomal segment in dorsal view. A1, *P. langi*; A2, *P. vespiceps*. B, second metasomal segment in dorsal view. B1, *P. difficilis*; B2, *P. vespiceps*. Scale bars = 1.0 mm.

have hairs, but they are shorter and less numerous than in *Pseudopolybia*, as Carpenter and Mateus (2004) also pointed out. *Pseudopolybia vespiceps* is less hairy than *P. difficilis* and *P. compressa* but clearly shows long hairs (fig. 4). Because of the fact that the male genitalia of *P. langi* have not been described, it is not clear whether the state “long and numerous hairs” is synapomorphic for *Pseudopolybia* as a whole, or just for the clade *P. difficilis* + (*P. vespiceps* + *P. compressa*). The state “short hairs” is possibly synapomorphic for *Parachartergus* (fig. 1). All other taxa considered here have no hairs on the parameral spine. Carpenter and Mateus (2004: 298) considered the state of hairs on the parameral spine as of uncertain polarity,

stating, “Study of additional genera besides those considered here is required to settle this.” In our results (fig. 1), which includes three other genera than those studied by Carpenter and Mateus (2004), the primitive state is “hairs absent”, and this may be general for Epiponini. Hence, the loss of hairs cannot support the grouping of genera besides *Pseudopolybia* which have lost the fourth labial palpomere (character 2, state 1), as suggested by Carpenter and Mateus (2004). We conclude that the different types of “hairs on the parameral spine” had independent origins in *Pseudopolybia* and *Parachartergus*.

According to Carpenter and Mateus (2004), a very narrow, reduced, almost hooking shape

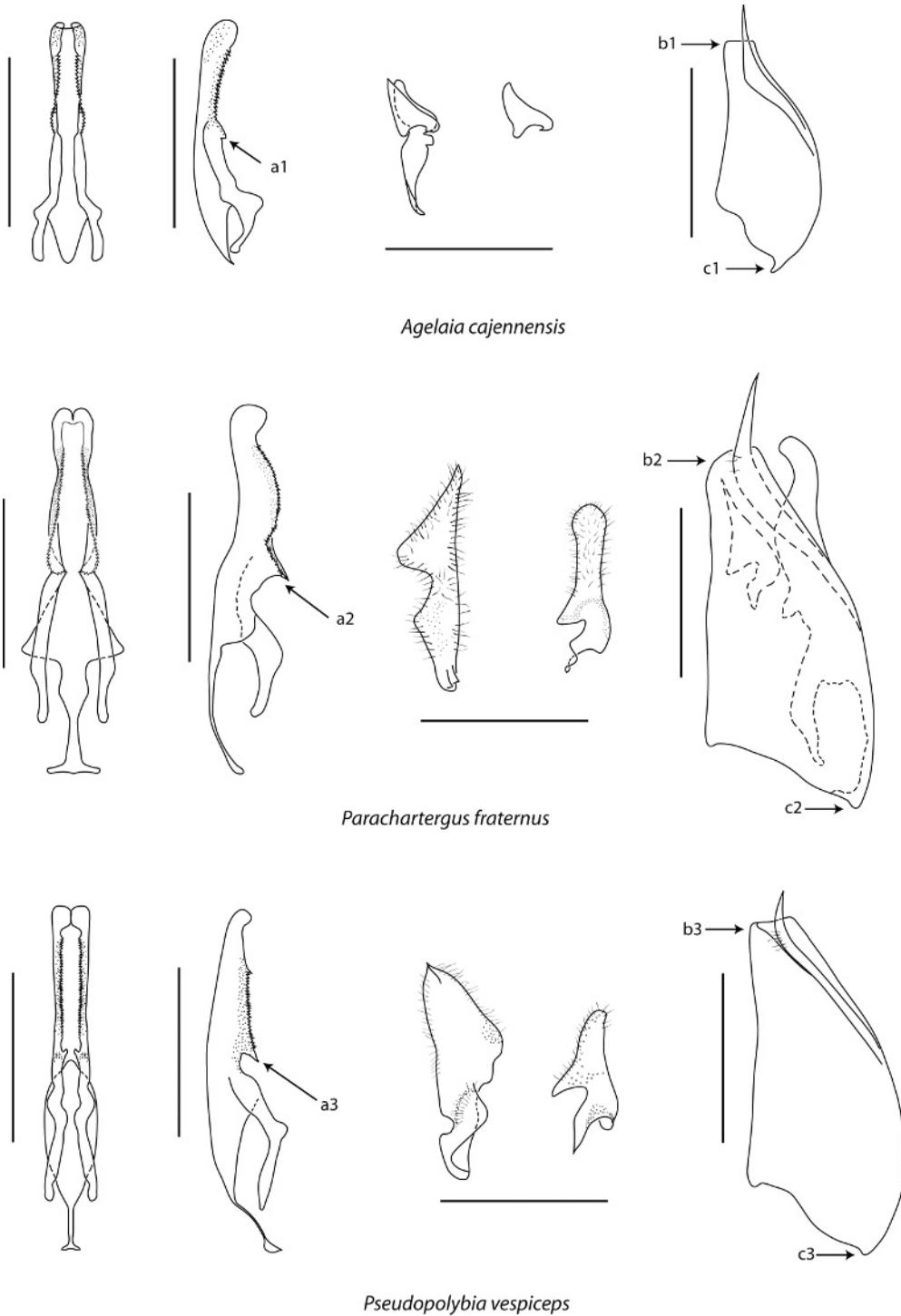


Fig. 4. Male genitalia: from left to right side = aedeagus in ventral view; aedeagus in lateral view; cuspid; digitus and paramere in lateral view. Scale bars = 1.0 mm.

of the ventral process of the aedeagus (character 24, state 1, in the character list; fig. 4a2) in most of these genera contrasts with the short angular process (character 24, state 0; fig. 4av) in *Pseudopolybia*, but this is also found in *Chartergellus*. If the narrow reduced shape is apomorphic, then *Chartergellus* either shows a reversal or is misplaced (Carpenter and Mateus, 2004). Because *P. langi* was not observed, the shape of the ventral process of aedeagus is ambiguous on our cladogram, but the apomorphic condition (narrow, reduced) is found in *Angiopolybia*, *Leipomeles*, *Parachartergus* and *Nectarinella*. Regardless of whether we assume that *P. langi* has the ventral process of aedeagus short, angular, as in other species of *Pseudopolybia* and *Chartergellus*, the character optimizes as two independent acquisitions of the state short, angular.

The shape of the digitus (character 25 in the character list) is variable in *Pseudopolybia*. *Pseudopolybia compressa* and *P. vespiceps* have the digitus pointed apically; it is also pointed in *Nectarinella* and *Chartergellus*. It is rounded in the remaining taxa. As stated by Carpenter and Mateus (2004), this is not a readily interpretable pattern. In our analysis, this character is homoplastic but supports the clade of *P. compressa* + *P. vespiceps*, with an independent origin in *Nectarinella* + *Chartergellus*.

The basal angle of the paramere acute (character 22, state 1, in the character list; fig. 4c1) seems to be plesiomorphic, as the most basal genera have this state (*Apoica*, *Agelaia* and *Angiopolybia*), with a reversal in *Nectarinella* and *Leipomeles*. The optimization of this character is ambiguous on the cladogram of figure 1, and because *P. langi* has not been observed for the male genitalia, it is not clear whether a reversal to basal angle of the paramere obtuse could be apomorphic for *Pseudopolybia*.

Carpenter and Mateus (2004) mentioned that the apical angle of the paramere (character 23 in the character list) is homoplastic at the generic level, because *Leipomeles*, *Parachartergus griseus*, and, to some extent, *P. apicalis* and *Marimbonda* (= *Leipomeles*) have a narrow apical angle. Inasmuch as *P. fraternus* (fig. 4b2) possesses a broad apical

angle of the paramere, as in the other species studied here, this character is homoplastic within the genus *Parachartergus*.

We did not observe a small sclerite basad of aedeagus in *Pseudopolybia vespiceps*, as in congeners studied by Carpenter and Mateus (2004: figs. 8–9). The dissections on which those figures are based are not extant, but when we dissected an additional *P. compressa*, we did not observe such a sclerite as depicted in Carpenter and Mateus (2004: fig. 8). We are unable to say what the structure might be and must, for the present, consider it dubious. We have therefore omitted it from the matrix.

*Pseudopolybia langi* seems correctly placed as the most basal species of *Pseudopolybia* (see fig. 1), because this species retains several symplesiomorphies shared with the outgroups. The pronotal fovea is in a shallow concavity in *P. langi*, whereas it is in a deep concavity in other species of *Pseudopolybia*; the gena is relatively narrow below (wide in the other species); and the weak pronotal carina leads to optimization of the short pronotal carina of the other species as a synapomorphy, because the state found in the basal species of Epiponini analyzed here is absence of the carina. The nest envelope lacks the imbrications found in the other species of *Pseudopolybia*, which is clearly a primitive condition.

*Pseudopolybia difficilis* differs from *P. compressa* and *P. vespiceps* in three characters, all of them homoplastic, which unite the latter two as a clade. These are the metanotum (long, curved versus compressed), first metasomal segment (longer than wide versus wider than long) and digitus shape (rounded versus pointed). The derived condition in each character is convergently acquired in *P. compressa* + *P. vespiceps*. These two species are certainly very similar, and their placement in the same clade is reasonable, but there are several diagnostic characters that can separate the species, as indicated in the key.

The data on male genitalia published by Carpenter and Mateus (2004) and the new data described here proved phylogenetically informative and, together with other morphological characters, helped in elucidating the relationships of the species of *Pseudopolybia*. We hope that this study stimulates other such analyses within Epiponini.

IDENTIFICATION KEY TO SPECIES OF  
THE GENUS *PSEUDOPOLYBIA*

An identification key to *Pseudopolybia* species is provided below, excluding the "morphs" of Richards (1978), which we conclude do not merit any treatment other than as synonyms. Ducke (1910) had reported that the forms of *P. compressa* can be found on the same nest, and while Richards (1978) stated that he felt this needed more verification, a colony collected by James M. Carpenter (from Napo Province, Ecuador, 8 km west of Misahuallí) contained both *laticincta* and *luctuosa*. Figures 2 and 3 show some characters to aid in species recognition.

- 1 Dorsal pronotal carina very weak (fig. 2C2); first metasomal segment much longer than wide (fig. 3A1); eyes densely haired; small species (6–8 mm); yellow with three brown stripes on the scutum; metasoma brownish  
..... ***P. langi* Bequaert**
- 1' Dorsal pronotal carina lamellate laterally (fig. 2C1); first metasomal tergum nearly as broad (fig. 3A1) as or much broader than long (fig. 3A2); eyes with or without hairs; larger species (13–15 mm); yellow to black ..... **2**
- 2 First and second metasomal segment a little longer than wide (figs. 3A1 and 3B1); metanotum not compressed; yellow with black marks on the head and mesosoma; three black stripes on the scutum; metasoma brownish. .... ***P. difficilis* (Ducke)**
- 2' First and second metasomal segment about twice as wide as long (figs. 3A2, 3B2); metanotum slightly to strongly compressed; dark yellow with three black stripes on the scutum or blackish species with pale marks ..... **3**
- 3 Blackish species with pale marks; prestigma about as long as wide; clypeus touching the eyes; eyes with hairs; tip of the clypeus sharply pointed (fig. 2A1); metanotum strongly compressed (fig. 2D1); malar space about as long as fourth antennal article (fig. 2B1) ..... ***P. compressa* (de Saussure)**
- 3' Dark yellow species with brown to blackish marks; prestigma much longer than wide; clypeus narrowly separated from eyes; eyes bare; tip of the clypeus weakly pointed (fig. 2A2); malar space longer than fourth antennal article (fig. 2B2); metanotum slightly compressed (fig. 2D2). .... ***P. vespiceps* (de Saussure)**

ACKNOWLEDGMENTS

The authors thank Orlando T. Silveira (MPEG), Augusto Henriques and Marcio Oliveira (INPA), Gabriel Melo and Marcel Hermes (UFPR), Carlos R. Brandão (MZUSP), and Carlos Sarmiento (IIBAVH) for loans of specimens; Kurt M. Pickett and Ward Wheeler for assistance at the AMNH; Sidnei Mateus for assistance in fieldwork; Orlando T. Silveira for sending the photograph of the nest of *P. langi*; and the Fundação de Amparo à Pesquisa do Estado de São Paulo (grants 01/02491-4 and 04/01117-0), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPQ), and Collection Study Grant Program (AMNH) for support.

REFERENCES

- Bequaert, J.C. 1938. A new *Charterginus* from Costa Rica, with notes on *Charterginus*, *Pseudocharterginus*, *Pseudopolybia*, *Epipona*, and *Tatua* (Hymenoptera, Vespidae). *Revista de Entomologia* (Rio de Janeiro) 9: 99–117.
- Carpenter, J.M. 1991. Phylogenetic relationships and the origin of social behavior in the Vespidae. In K.G. Ross and R.W. Matthew (editors), *The social biology of wasps: 7–32*. Ithaca, NY: Cornell University Press.
- Carpenter, J.M., and S. Mateus. 2004. Males of *Nectarinella* Bequaert (Hymenoptera, Vespidae, Polistinae). *Revista Brasileira de Entomologia* 48(3): 297–302.
- Dejean, A., B. Corbara, and J.M. Carpenter. 1998. Nesting site selection by wasps in the Guianese rain forest. *Insectes Sociaux* 45: 33–41.
- Ducke, A. 1910. Révision des guêpes sociales polygames d'Amérique. *Annales Historico-Naturalis Musei Nationalis Hungarici* 8: 449–544.
- Goloboff, P.A. 1999a. NONA ver 2.0, program and documentation. Fundación e Instituto Miguel Lillo, Tucumán.
- Goloboff, P.A. 1999b. PIWE ver 3.0, program and documentation. Fundación e Instituto Miguel Lillo, Tucumán.
- Hanson, P.E., and I.D. Gauld. 1995. *The Hymenoptera of Costa Rica*. Oxford: Oxford University Press.
- Jeanne, R. L. 1991. The swarm-founding Polistinae. In K.G. Ross and R.W. Matthew (editors), *The social biology of wasps: 191–231*. Ithaca, NY: Cornell University Press.
- Nixon, K.C. 1999. Winclada, software version 0.9 99i Beta (<http://www.cladistics.com>).

- Nixon, K.C., and J.M. Carpenter. 1993. On outgroups. *Cladistics* 9: 413–426.
- Richards, O.W. 1978. The social wasps of the Americas excluding the Vespinae. London: British Museum (Natural History).
- Richards, O.W., and M.J. Richards. 1951. Observations on the social wasps of South America (Hymenoptera, Vespidae). *Transactions of the Royal Entomological Society of London* 102: 1–170.
- Wenzel, J.W. 1998. A generic key to the nests of hornets, yellowjackets, and paper wasps worldwide (Vespidae: Vespinae, Polistinae). *American Museum Novitates* 3224: 1–39.
- Wenzel, J.W., and J.M. Carpenter. 1994. Comparing methods: adaptive traits and tests of adaptation. In P. Eggleton and R. Vane-Wright (editors), *Phylogenetics and ecology*: 79–101. London: Academic Press.

## APPENDIX 1

### LOCALITIES FOR SPECIMENS OF *PSEUDOPOLYBIA* STUDIED

***P. compressa*:** Rio Juruá, Ducke Reserve, and Manaus, Amazonas, Brazil (MPEG, AMNH); Espirito Santo (locality not specified), Brazil (MZUSP); Chapada dos Guimarães, Mato Grosso, Brazil (MPEG); Represa Rio Grande, Guanabara [Rio de Janeiro], Brazil (UFPR); Paramaribo, Suriname (IIBAVH); Arima Valley, Trinidad (AMNH); Madre de Dios, Tambopata National Reserve, Peru (AMNH); LaChorarra-Putumayo, Peru (AMNH); Napo Province, Ecuador (AMNH); and Changuinola, Bocas del Toro, Panama (AMNH).

***P. difficilis*:** Mato Grosso (locality not specified), Brazil (MPEG); Melgaço, Pará, Brazil (MPEG); Manaus, Amazonas, Brazil (UFPR); Ouro Preto do

Oeste, Rondônia, Brazil (MPEG); and LaChorerra-Putumayo, Peru (AMNH).

***P. langi*:** Laranjal do Jarí Marinho, Amapá, Brazil (MPEG); Manaus, Amazonas, Brazil (UFPR); and Kamakusa, Guyana (AMNH).

***P. vespiceps*:** Espirito Santo state (locality not specified), Brazil (MZUSP); Franca, São Paulo, Brazil (MZUSP); Parque Itaituba, Amazonas, Brazil (MPEG); Amazonas, (AM 01 Km 31 and Km 64; ZF 02 Km 20,7; ZF 03 km 23; Amá Station Km 06; Queraí (Pelotão); Ducke Reserve), Brazil (INPA); Rio Trombetas, Amapá, Brazil (INPA); Ouro Preto do Oeste, Rondônia, Brazil; (Garofire, Serra Norte, Mosqueiro and Belém-Mocambo), Pará, Brazil (MPEG); Pernambuco (locality not specified), Brazil (AMNH); São Paulo (locality not specified), Brazil (male genitalia dissected; AMNH); Oxapampa, Peru (AMNH).

Complete lists of all issues of the *Novitates* and the *Bulletin* are available at World Wide Web site <http://library.amnh.org/pubs>. Inquire about ordering printed copies via e-mail from [scipubs@amnh.org](mailto:scipubs@amnh.org) or via standard mail from: American Museum of Natural History, Library—Scientific Publications, Central Park West at 79th St., New York, NY 10024. TEL: (212) 769-5545. FAX: (212) 769-5009.

 This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper).