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# Systematics and mimicry of the genus *Neocorynura*: an example of two species from Central America (Hymenoptera: Halictidae)

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Abstract. A case of probable mimicry in two species of bees in the genus *Neocorynura* (*Neocorynura rufa* MICHENER, 1954 and *N. panamensis* ENGEL, 1997) is described; diagnostic characters and a key to separate the species of Central American bees with black-red (aposematic) pattern of coloration are also provided. The phylogeny of selected species groups and the evolution of different mimicries in the genus are discussed.

Key words: Batesian and Müllerian mimicry, phylogeny, Panamă, Costa Rica, Augochlorini.

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## I. INTRODUCTION

Mimicry (Batesian and Müllerian) in insects and its relation with aposematic colors has been studied broadly in insects (TURNER 1984, 1987; WALDBAUER 1988; EDMUNDS 2000; SRYGLEY 2004), largely in butterflies (RITLAND 1991; SMITH et al. 1993; WEST 1994; OHSAKI 1995; SIMMONS & WELLER 2002; SIMMONS & WELLER 2002; PINHEIRO 2003; NAISBIT et al. 2003; FLANAGAN et al. 2004), flies (HOWARTH & EDMUNDS 2000; HOLLOWAY et al. 2002; LONDT 2003; HOWARD et al. 2004), beetles (FISHER & TUCKERMAN 1986; HETZ & SLOBODCHIKOFF 1988; HETZ & SLOBODCHIKOFF 1990; DEL-CLARO 1991; MACHADO et al. 2001) and to some extent in hymenopterans, especially in ants (HESPENHEIDE 1986), and wasps (WALDBAUER 1985; QUICKE et al. 1992; BIÈIK & LÁSKA 1997). Studies related to mimicry in bees are limited to comments on the similarity of some bees to other bees (DRESSLER 1979, 1982; ROUBIK 1989; MICHENER 2000), or bees to wasps and other stinging insects (EICKWORT 1969; SARMIENTO 1993; MICHENER 2000).

Resemblance of bees to wasps typically occurs among parasitic bees (MICHENER 2000), but it is uncommon in non-parasitic lineages; some of the few examples documented of non-parasitic bees resembling wasps are in the genus *Neocorynura* (Hymenoptera: Halictidae). This genus is highly diverse in morphology, nesting behavior (some of its species nest in the soil or rotten wood), altitudinal distribution (can be found from the sea level to the high mountains about 2.500 m: GONZALEZ

& ENGEL 2004) and relationships with plants (broadly polylectic) (MOURE & HURD 1987; EICKWORT 1969; ENGEL 2000).

I used the word mimicry entirely without behavioral justification. In reality, I merely mean to indicate resemblance to my eyes, based on dead specimens on pins (see discussion).

The genus *Neocorynura* provides an excellent opportunity for studies in mimetic behavior of bees. It is highly speciose (~100 spp); some species of which mimic vespid social wasps, mostly of the genus *Polybia* (Hymenoptera: Vespidae), while others mimic crabronid wasps (Hymenoptera: Crabronidae), or pompilid wasps (Hymenoptera: Pompilidae, spider-hunter wasps). Furthermore, there are at least four different groups within *Neocorynur*a, two of which are mimetic, the two other groups are "typical" *Augochlora*-like bees, but one is more setose (fuzzy) than the other.

One group of mimetic *Neocorynura* (here referred as the "crabronid/ pompilid-like" *Neocorynura* mimetic group) includes two species (*Neocorynura rufa* MICHENER and *N. panamensis* ENGEL). They are possible mimics of *Paratetrapedia calcarata* (CRESSON) (an abundant bee species) and of several genera of wasps of the families Pompilidae, Vespidae, and Crabronidae (the models), that have similar aposematic coloration (head and thorax black and metasoma red). All of them are largely sympatric in Panamá and Costa Rica. Furthermore, there are some other species of non-related bees (Apidae: Meliponini) co-occurring in the same region with the same pattern of coloration (Table 1, Fig. 3).

In this paper I will discuss the phylogenetic placement of the two species of crabronid/pompilid-like *Neocorynura* and the evolution of mimicry in the genus as a whole. In addition, I present diagnoses for the two mimetic species of *Neocorynura* from Panamá and Costa Rica and provide keys to separate them from one another and from other species of bees with the same pattern of coloration (Appendix 1).

A c k n w l e d g e m e n t s. This work is dedicated to my mother Aida to whom I owe all I am. I would like to thank Charles D. MICHENER and Michael S. ENGEL for their comments and suggestions on earlier versions of the manuscript, and the curators of the various institutions loaning material. Daniel J. BENNETT and Victor GONZALEZ commented on the manuscript. This paper is a contribution of the Division of Entomology, Natural History Museum and Biodiversity Research Center, University of Kansas.

## II. MATERIAL AND METHODS

Morphological observations, measurements and illustrations were made using an ocular micrometer on an Olympus SZ60 microscope. The abbreviation PD is used for puncture diameter. Morphological terminology follows that of MICHENER (2000), ENGEL (2001), and HARRIS (1979) for surface sculpturing. The word "imbricate" is used for the microsculpturing of the cuticular surface, usually between punctures or other coarser sculpturing. Diagnosis format follows that used for other augochlorine bees (e.g., ENGEL 1999; ENGEL & SMITH-PARDO 2004; SMITH-PARDO & ENGEL 2005).

The phylogenetic analysis presented here is part of a more comprehensive study (SMITH-PARDO, in prep.) focusing on the evolutionary relationships among the species of the genus *Neocorynura*. In this analysis a total 63 taxa and 188 characters (morphological, ecological, and behavioral) were used. All characters were equally weighted and considered nonadditive. The cladistic analysis was performed using the programs WinClada V. 1.00.08 (NIXON 1999-2002) and NONA (GOLOBOFF 1993), with the following criteria: heuristic, and unrestricted search (multiple TBR + TBR) with 1000 replications, with a maximum of 10000 trees to be kept. The trees were visualized using WinClada and edited and printed using Adobe Illustrator Ver. 10. A complete account of the phylogenetic study as well as diagnostic characters for all the species of *Neocorynura* employed here will be presented elsewhere.

The specimens used for this study are in the following institutions:

**CUIC,** Cornell University Insect Collection (J. K. LIEBHERR, E. R. HOEBEKE); American Museum of Natural History, New York (J. G. ROZEN, Jr.); **SEMC**, Entomology Division, Natural History Museum, University of Kansas, Lawrence (M. S. ENGEL, Z. H. FALIN); **USNMNH**, United States National Museum of Natural History, Smithsonian Institution, Washington D.C. (T. SCHULTZ).

## III. TAXONOMY

### *Neocorynura panamensis* ENGEL

Fig. 1

*Neocorynura panamensis* ENGEL, 1997: 20-22

D i a g n o s i s. *Neocorynura panamensis* is most similar to *N. rufa* in overall appearance: black head and mesosoma, and reddish to orange metasoma. In addition to those characters mentioned by ENGEL (1997), these species can be separated by the following characters: sides of base of propodeum imbricate and poorly punctate, sides of pronotum produced and angular, mesopleura sparsely punctate (punctures separated by 1 PD), and first recurrent vein of forewing connected to third submarginal cell.

C o m m e n t s. In the remarks following the description of the species, ENGEL (1997) described *N. panamensis* as a relative of *N. rufa* (based on the overall similarity) and considered the two species "almost indistinguishable from one another". ENGEL was right to affirm that these two species are the only ones known having a completely fulvous metasoma, which in combination with a black head/ mesosoma leads me to consider them as having "black-red" aposematic coloration.

M a t e r i a l e x a m i n e d. This species is only known from the type material, collected in Panamă:

**Holotype** female: **Panamă:** ***Herrera Province***, Las Minas, Cerro Alto, Higo. 20 May 1987. D. ROUBIK Coll. (CUIC). **Paratype** female: same data as holotype (CUIC).

### *Neocorynura rufa* MICHENER

Fig. 2

*Neocorynura rufa* MICHENER, 1954: 79, 82

*Neocorynura* (*Neocorynura*) *rufa*: MOURE & HURD 1987: 227

D i a g n o s i s. *Neocorynura rufa* can be easily separated from *N. panamensis* by having the base of the propodeum strongly striate, sides of the pronotum not strongly produced and obtuse, the mesopleura densely punctate, and the first recurrent vein of forewing meeting 1r-m.

C o m m e n t s. MICHENER (1954) separated this species from other species of *Neocorynura* by the "largely red abdomen of the female and other characters indicated in the accompanying key", the key includes in addition to the coloration of the metasoma, only the integument of mesoscutum: "…anterior part of the mesoscutum with punctures coarser than elsewhere and separated by dull ground", a character that is variable among species of the genus and that can be hardly used to separate specimens within the genus if not accompanied by other characters.

M a t e r i a l e x a m i n e d. **Holotype** female and allotype male: **Panamă:** ***Chiriquí Province***, Potrerillos. May 8, 1935. MACSWAIN Coll. (USNMNH). **Paratypes:** 1 male: same as holotype, except January 3 to 4; 1 female: ***Coclé Province:*** Valle de Antón, June 5, 1945. 2500ft. (not seen). Other specimens. **Costa Rica**: ***Cartago Province*****:** Tapanti. 2 July 1963, 4000 ft. C. D. MICHENER Coll.(3 ♂♂ SEMC); *Idem*, except: 12 June 1963, 1250 m. C. D. & D. R. MICHENER Colls. (3 ♀♀ SEMC).

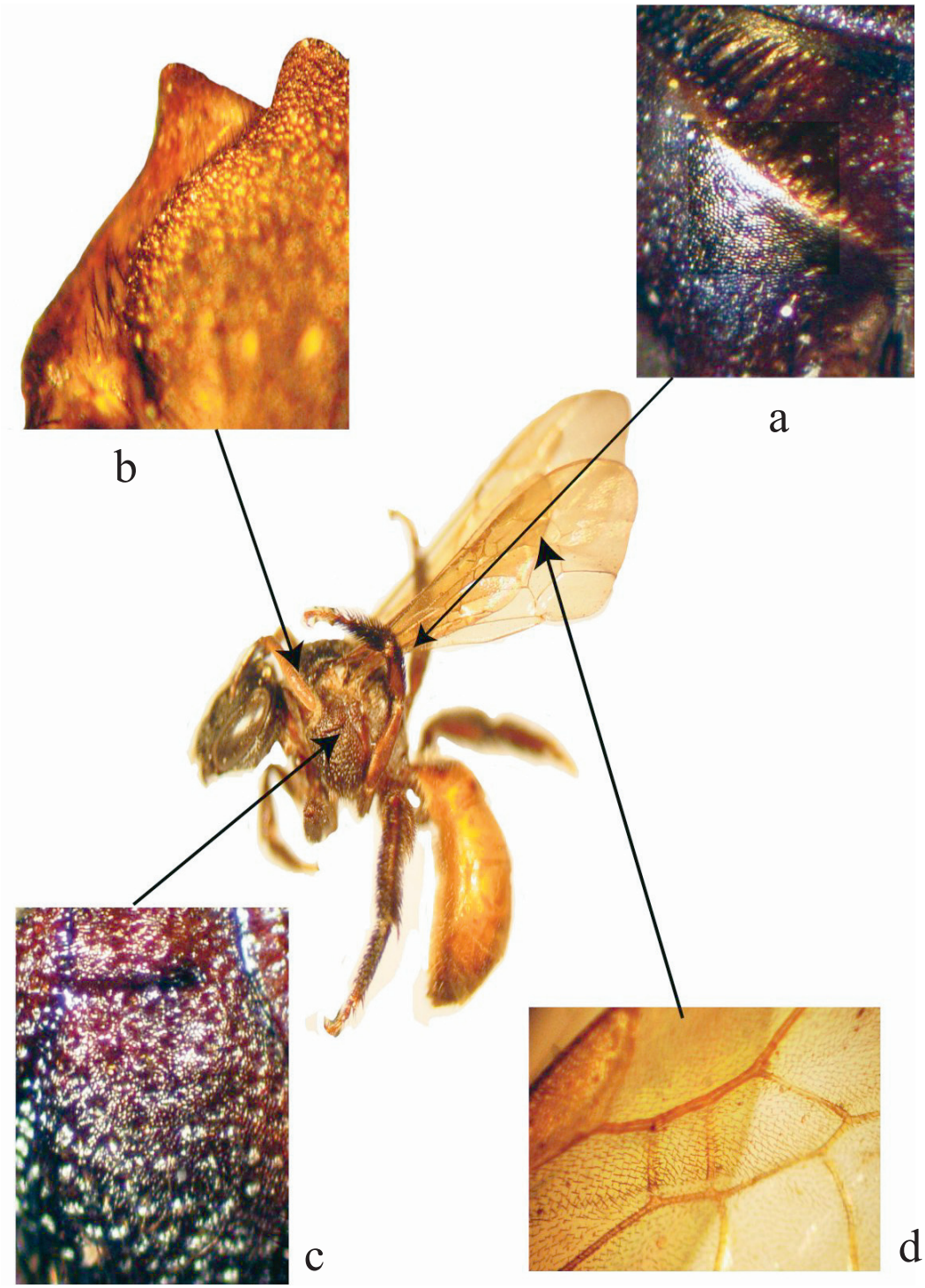


Fig. 1. Lateral habitus and some diagnostic characters of *N. panamensis* ENGEL (a – pronotum, b – base of propodeum, c – mesopleura, d – submarginal cells and recurrent vein).

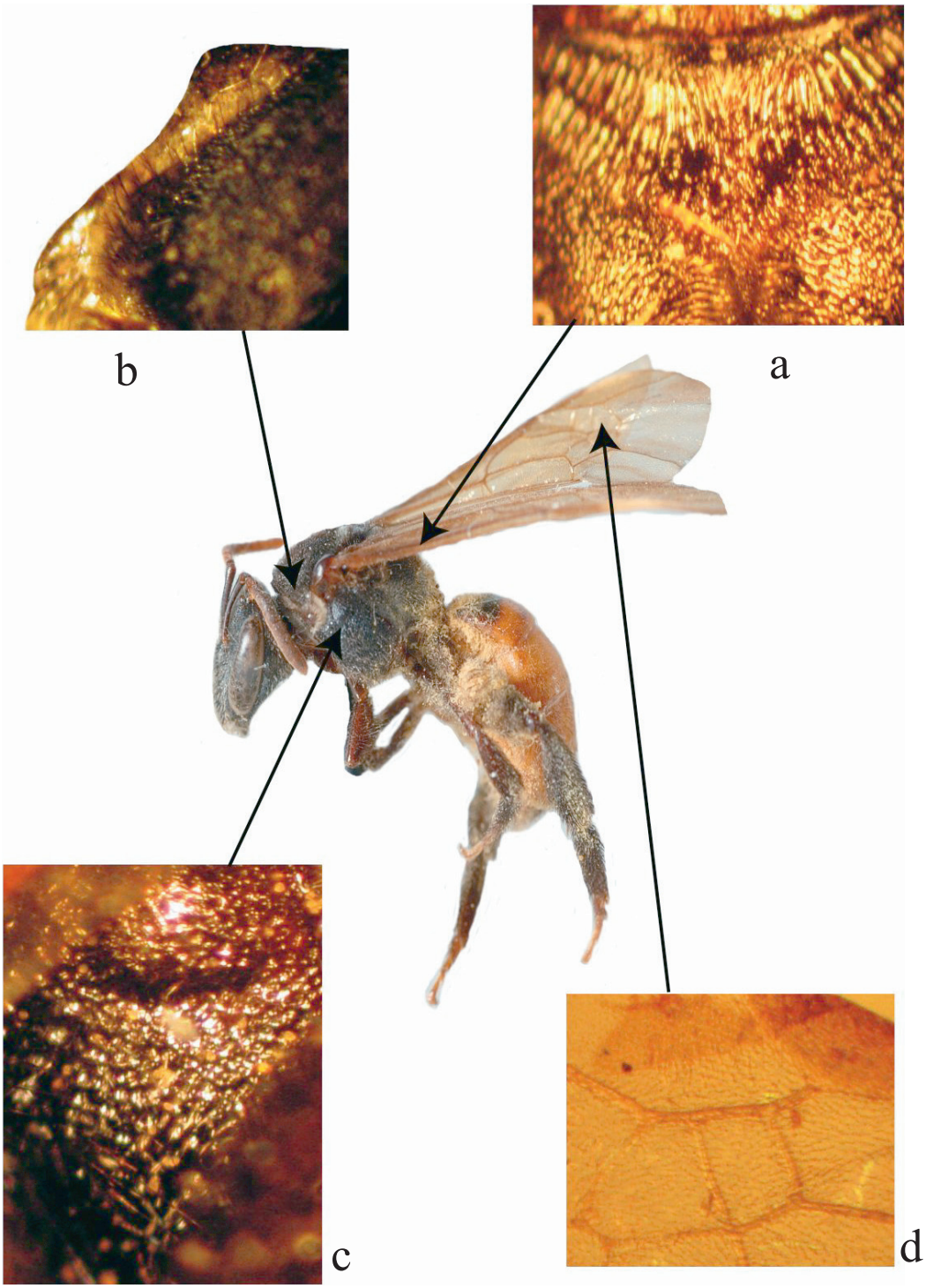


Fig. 2. Lateral habitus and some diagnostic characters of *N. rufa* MICHENER (a – pronotum, b – base of propodeum, c – mesopleura, d – submarginal cells and recurrent vein).

**Keys to black and red (crabronid/pompilid-like) bees of Panamă and Costa Rica based on females and workers**

1 Hind tibia modified bearing a corbicula . . . . . 2
– Hind tibia not modified, with or without scopae . . . . . 4
2 With some branched setae on margins of corbicula; malar area shorter than scape diameter . . . . . *Trigona fulviventris* GUÉRIN-MÉNEVILLE
– Without branched setae along margins of corbicula; malar area as long or longer than scape diameter . . . . . 3
3 Body length between 1-1.5 cm; interantennal distance greater than antennal insertion, clypeus strongly punctate, preoccipital carina present . . . *Cephalotrigona zexmeniae* (COCKERELL)
– Body length much less than 1 cm; interantennal distance shorter than antennal insertion, clypeus not strongly punctate, preoccipital carina absent . . . . *Oxytrigona daemoniaca* CAMARGO
4 Face with yellow maculation; forewing with basal vein straight; propodeum rounded in lateral . . . . . *Paratetrapedia calcarata* (CRESSON)
– Face without yellow; forewing with basal vein arched; propodeum angular in lateral view . . . . 5
5 Hind leg without scopa; mandible not toothed . . . . . *Sphecodes* sp.
– Hind leg with scopa; mandible with inner subapical toot . . . . . 6
6 Side of pronotum not strongly angular; mesopleura densely punctate, distance between punctures 1PD); first recurrent vein of forewing meeting 1r-m . . . . *Neocorynura rufa* MICHENER
– Sides of pronotum more angular; mesopleura with punctures separated by more than 1PD; first recurrent vein meting third submarginal cel . . . . . *Neocorynura panamensis* ENGEL

Table 1

Taxa involved in the probable mimetic complex in Panama and Costa Rica

| Category | Family | Genera |
|---|---|---|
| *Sting protected Models*: | Pompilidae | *Ageniella* spp., *Priocnessus* sp., *Sericopompilus* sp.?., *Caliadurgus* sp. |
| | Vespidae | *Polybia* sp., *Apoica* sp., *Brachygastra* spp.?, *Odynerus* sp.?, |
| | Crabronidae | *Philanthus* sp., *Larra* ( *L. bicolor* FABRICIUS), *Trachysphe* sp.?. |
| | Sphecidae | *Ammophila* spp. |
| | Apidae | *Paratetrapedia calcarata* (CRESSON). |
| *Probable mimics*: | Halictidae | *Neocorynura rufa* MICHENER,<br>*Neocorynura panamensis* ENGEL |
| | Apidae | *Cephalotrigona zexmeniae* (COCKERELL)<br>*Trigona fulviventris* GUERÍN-MENEVILLE<br>*Oxytrigona daemoniaca* CAMARGO |

?: presence not confirmed but suspected (present in other countries of Central America)
spp: more than one species found

**Phylogenetic analysis**

Analysis of the data matrix (SMITH-PARDO, in prep.) resulted in six most parsimonious topologies (Fig. 4), with the following descriptive statistics: length = 3396 steps; C. I. = 14; R. I. = 38. The two species used herein as an example form a clade with *Neocorynura nuda* MICHENER (also from Central America); this species has, however, a different pattern of coloration, and superficially resembles some other species of *Neocorynura* in other clades, identified as the "*Polybia*-like" mi-

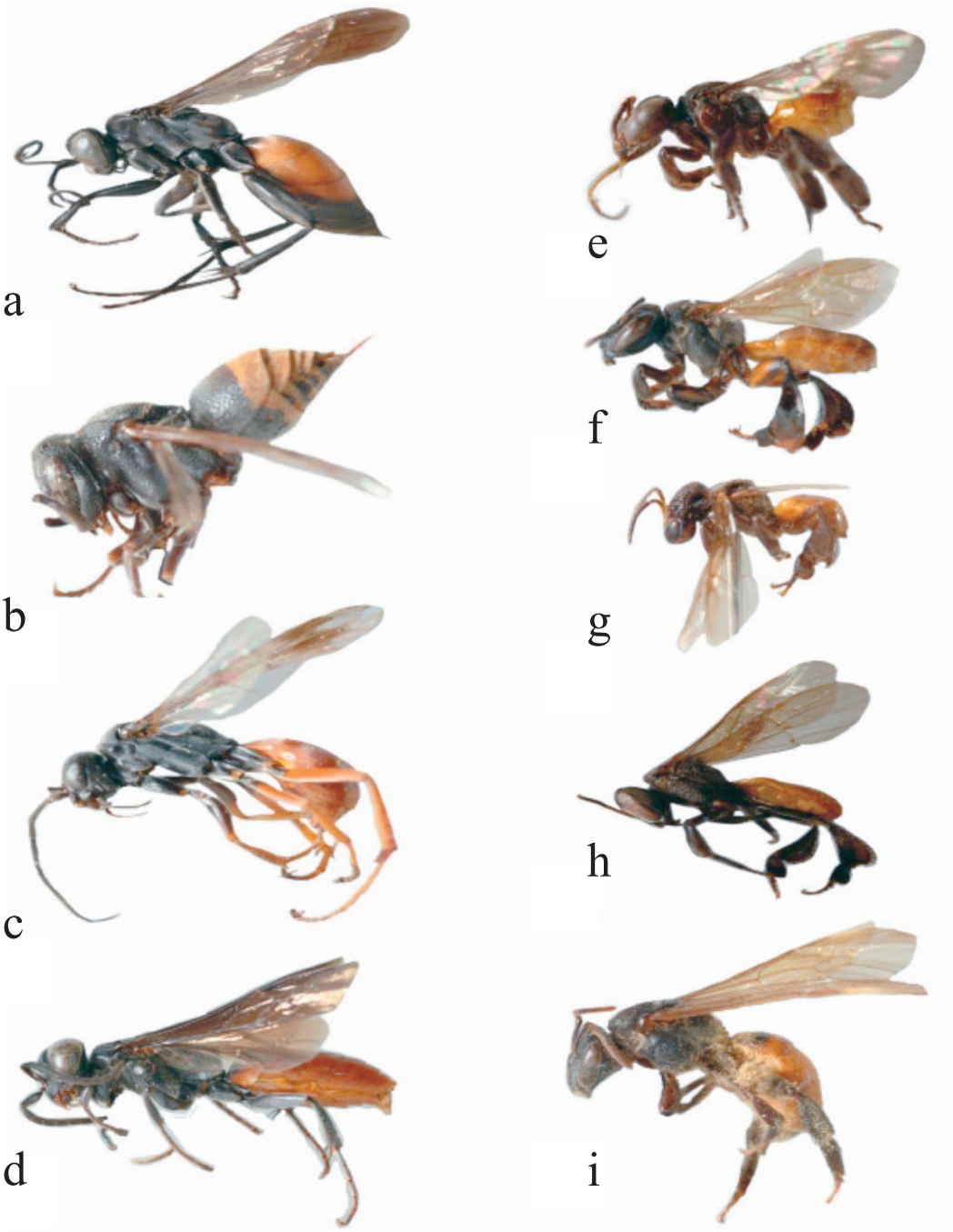


Fig. 3. Lateral habitus of bees and wasps with the black-red aposematic coloration involved in the crabronid/vespid-like mimicry (models on left side: a – *Anoplius* sp. (Pompilidae), b – *Brachygastra* sp. (Vespidae), c – *Caliadurgus* sp. (Pompilidae), d – *Larra* sp. (Crabronidae); bees on the right side: e – *Paratetrapedia calcarata* (CRESSON) (model), below it probable mimics: f – *Cephalotrigona zexmeniae* (COCKERELL), g – *Oxytrigona daemoniaca* CAMARGO, h – *Trigona fulviventris* GUÉRIN -MENEVILLE, and i – the mimic *Neocorynura* (*N. rufa* MICHENER and *N. panamensis* ENGEL).

metic groups in Fig. 4. The *N. rufa* (*N. rufa* + *N. panamensis* + *N. nuda*) clade is supported by the combination of the following homoplasious characters present in adult females (numbers correspond to the characters and those in parentheses to their character states, in SMITH-PARDO, in prep.): **30(0):** posterior margin of S2 straight, **25(0):** wings completely translucent, **26(0)**: basal bands of setae on metasomal terga absent, **36(1):** punctation on T1 broadly ( 1PD) and uniformly distributed, **42(3):** gonangulum elongated and arrowhead-like, **53(0)**: coloration of last antennal flagellomere uniform, **57(1):** first recurrent vein (1m-cu) of forewing meeting second submarginal cell and close to 1rs-m, **118(2):** integument of postgena close to mandibular articulation broadly striated, **121(1)**: mid ocellus of spheroid shape, **158(0):** first labial palpomere as long as combined lengths of the following two, and **169(3):** arms of stipes elongated close to articulation with cardines.

**Mimetisms**

A total of at least fifteen species belonging to at least 13 genera of hymenopterans (including a species of bees) was found to be possible models of the two species of *Neocorynura* (*Neocorynura rufa* and *Neocorynura panamensis*) used in this study (Table 1, Fig. 3). In addition, at least two types of mimicry within the genus *Neocorynura* were recognized in the phylogenetic analysis: crabronid/ pompilid-like, and *Polybia*-like (Fig. 4).

The resulting topology of the phylogenetic analysis shows some interesting aspects on the evolution of mimicry within the genus *Neocorynura* when the different types of probable mimics where included (in parenthesis) and associated to the different species groups. The black-red aposematic coloration on *Neocorynura* used here as example, arose only once in the evolution of the genus. Furthermore, it is also clear that the most primitive forms of *Neocorynura* species belong to the setose "*Augochlora*-like" group (similar to the genus *Andinaugochlora* sensu MICHENER 2000) and perhaps like the common ancestor for the two genera. The same phylogeny also shows how the most basal species in the clades where the mimetisms occur (*N. polybioides* and *N. aenigma*) are "*Polybia*-like" mimics.

## IV. DISCUSSION

The possible mimetic relations described here are hypothetical and mostly based in the observations of the color patterns and shapes of the specimens in collections and supported by the fact that the stings of the models are strong and can inflect pain/ deter predators. Besides the raw observations in flight behavior (slow and "tranquil" of at least other *Neocorynura* species – not observed for *N. rufa* or *N. panamensis*- and all the models) and stings of models when handling specimens, there is no conclusive field data on the effect such defenses may have on predators/ parasites; there are however, substantial data supporting the abundance of the models compared to the two possible mimics in the genus *Neocorynura,* one of the requirements for Batesian mimicry.

The two species of *Neocorynura* and the unrelated and related species sympatric with them in Panamá and Costa Rica constitute a possible Batesian mimetic complex with the wasps and *Paratetrapedia* relationship possible being Müllerian. Other bees in the complex include *Cephalotrigona zexmeniae*, *Oxytrigona daemoniaca*, and *Trigona fulviventris* (Fig. 2, Table 1). These bees have a weak sting apparatus (as in all Meliponini) but may protect themselves from predators because they have appearances similar to those of aggressive, strong and well-equipped wasps and bees (e.g. *Paratetrapedia calcarata* CRESSON). On the other hand, the Meliponini may well be protected by chemical attributes (e.g. *Trigona fulviventris* GUÉRIN).Thus they, too, would be members of the group of models. The relative high abundance of social wasps such as those in the family Vespidae and of *Trigona* bees is also a possible factor involved in these kind of interactions, because for a Batesian mimic to be successful, it must have more models than mimics, so there is continuous re-

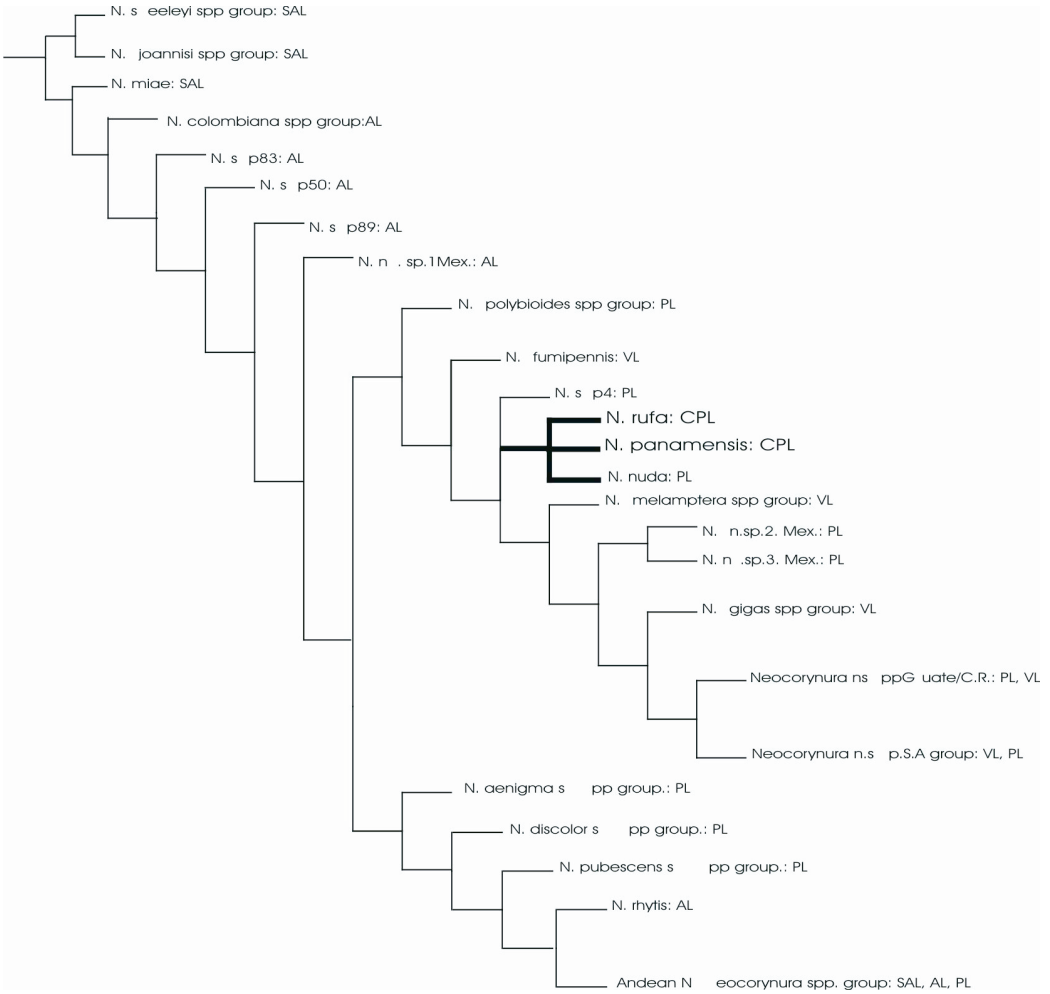


Fig. 4. Phylogenetic hypothesis (strict consensus) of the relationships among species of *Neocorynura* sensu SMITH-PARDO (letters in parentheses represent the different groups: ***SAL*** – setose *Augochlora*-like, ***AL*** – *Augochlora*-like, ***CPL*** – crabronid/pompilid-like, ***PL*** – *Polybia*-like, ***VL*** – *Vespa*-like).

inforcement of what a bad taste or sting "looks like". In this case, the supposed mimics are rare while the supposed models are among the common insects in the area.

In the course of evolution an *Augochlora*-like ancestor gave rise to the types of mimetisms (i.e."*Polystes*-like", and "crabronid/ pompilid-like") found in *Neocorynura*, although some species remained with the green *Augochlora*-like appearance.

*Neocorynura* is a highly diverse genus, with a broad latitudinal and altitudinal distribution, indicating some success in occupying many different ecosystems with their own intra- and interspecific interactions (such as competition and predation/ parasitism). One of the possible reasons for such success may be that so many species in the genus have evolved these kinds of mimicry. This strategy is one of the ways in which some species can protect themselves from possible predators or parasites, and may be one of the driving forces in diversity of bees.

From a historical-biogeographic point of view, the results showed here are in agreement with EICKWORT's hypothesis (1969) that the origins of the tribe and the genus *Neocorynura* are in tropical South America (where the most primitive species groups of the genus are restricted, and where most of the species diversity occurs). From tropical South America they most have radiated north to Central and North America and south to northern Argentina and Paraguay. This same hypothesis may help to explain why most of the species in the most northern and southern zones are restricted to those areas (e.g. in Mexico most of the species are endemic, SMITH-PARDO in pres.).

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