Novitates AMERICAN MUSEUM

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024 Number 3465, 16 pp., 51 figures

December 30, 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

JAMES M. CARPENTER¹

ABSTRACT

The paper wasp genus *Marimbonda* Richards, 1978, is synonymized with *Leipomeles* Möbius, 1856, n.syn. A key to all the currently recognized paper wasp genera in the Western Hemisphere is provided.

INTRODUCTION

The paper wasp genus *Marimbonda* was described by Richards (1978) for two species: the type species *M. albogrisea* Richards, 1978, and *M. pusilla* (Ducke, 1904). The recognition of this new genus was due primarily to the nest architecture of the new species *M. albogrisea*. The single nest collected was astelocyttarus (Richards and Richards, 1951: 6): the comb lacking any petiole, with the cells constructed on a flat surface

and an envelope covering the comb. Richards (1978: 10) keyed the new genus out with those genera also bearing a stout, curved bristle on the third segment of the labial palpus (figs. 1–2), and among these the genera sharing reduction in the palpal formula to five-segmented maxillary palpi and three-segmented labial palpi (fig. 1). However, his dendrogram (Richards, 1978: fig. 40) showed *Marimbonda* as intermediate between these genera and a group clade including other genera with astelocyttarus nest architecture.

¹ Curator of Hymenoptera, Division of Invertebrate Zoology, American Museum of Natural History (carpente@amnh.org).

NO. 3465

Richards (1978: 201) stated: "The genus whose relationships are shown in the dendrogram . . . and in the key . . . does not seem to be at all allied to the others which make astelocyttarus nests (*Synoeca*, *Metapolybia*, and *Clypearia*) and while it should probably be placed somewhere near the others which have the curved bristle on the labial palpus, it does not seem to be close to any of them."

The other genera with the bristle on the third labial palpomere are Pseudopolybia, Parachartergus, Chartergellus, Nectarinella, and Leipomeles. In previous cladistic analyses of paper wasp genera (Carpenter, 1991; Wenzel and Carpenter, 1994) these genera were shown to form a monophyletic group including *Marimbonda*; that bristle is a synapomorphy. Within this clade, Marimbonda and Leipomeles are sister-groups. A morphological synapomorphy is the similar form of the first metasomal segment (conically petiolate; figs. 3-4), while a possible synapomorphy in nest architecture is a central furrow built in the lines of construction of the envelope.

In the present work, Marimbonda and Leipomeles are synonymized. Although it is possible to adduce morphological apomorphies to support each genus as monophyletic (e.g., Leipomeles has the first metasomal segment forming a longer, relatively narrower petiole, fig. 4; Marimbonda has the hindwing with vein Cu₁ as long as cu-a, fig. 5, vs. Cu₁ shorter than cu-a in *Leipomeles*, fig. 6), these are all minor features, relative both to the features shared by these genera and features defining other paper wasp genera. More significantly, Marimbonda was recognized as a genus in the first place because of its nest architecture, but its astelocyttarus design is less important than other features of the nest that it shares with Leipomeles (Wenzel and Carpenter, 1994). The astelocyttarus nest obscured the relationships of Marimbonda when that genus was described—in fact was misleading, as seen from Richards' placement of the genus on his dendrogram. Moreover, as will be shown, astelocyttarus nests do not in fact separate Marimbonda from Leipomeles.

After discussion of taxonomic history and further explication of the rationale for the synonymy, a new key to the paper wasp genera is provided, which will cover all the taxa found in the New World.

TAXONOMIC HISTORY

The present generic classification of New World Polistinae owes its basic form to the work of Adolpho Ducke. A century ago, working at the Museu Goeldi in Belem, he revised the classification then prevailing, and his views were especially informed by his own extensive field work in Amazonian Brazil. Prior to Ducke the classification used was basically that in the last worldwide monograph (de Saussure, 1853–1858), which itself was a refinement of Lepeletier's (1836) classification, who began the recognition of numerous genera for Polistinae. Polistinae were separated from other Vespidae (as the Linnaean genus Vespa) by Latreille (1802), who described two genera, Polistes and Epipona. Between the time of Latreille and Lepeletier just a few isolated genera were described (Kirby, 1826: Cyclostoma²; Guérin-Méneville, 1831: Ropalidia; Perty, 1833: Brachygastra), but Lepeletier described five genera: Agelaia, Apoica, Chartergus, Polybia, and *Rhopalidia*.³ Between the time of Lepeletier and de Saussure again just a couple of genera were added (White, 1841: Anthreneida, 4 Myrapetra⁵). De Saussure (1852) added Synoeca and de Saussure (1853-1858) Raphigaster⁶ and Mischocyttarus. Subsequent to de Saussure's work a few more genera accumulated (Möbius, 1856: Leipomeles; Gribodo, 1892: Paraicaria⁷; H. von Ihering, 1896: Pseudopolybia⁸; Fox, 1898: Charterginus).

Working on the fauna of Pará, Ducke

² Junior homonym of *Cyclostoma* Lamarck, 1799; replaced by *Gyrostoma* Kirby, 1828; now a subgenus of *Polistes* (Carpenter, 1996).

³ Suppressed by Opinion 1051 of the International Commission on Zoological Nomenclature (1976); the name *Angiopolybia* Araujo, 1946, is now used for this genus

⁴ Synonymized with *Ropalidia* Guérin-Méneville, 1831, by Kojima (1997).

⁵ Now a subgenus of *Polybia* (Richards, 1978).

⁶ Junior homonym of *Raphigaster* Laporte, 1832; replaced by *Belonogaster* de Saussure, 1853.

⁷ Synonymized with *Ropalidia* Guérin-Méneville, 1831, by Kojima (1997).

⁸ Junior homonym of *Pseudopolybia* de Saussure, 1863; junior synonym of *Kappa* de Saussure, 1854, a subgenus of *Mischocyttarus*.

(1904) at first followed de Saussure's classification, adding just one genus, Megacanthopus.9 But shortly thereafter, Ducke (1905a) radically revised the generic classification of the South American Polistinae. De Saussure had recognized eight genera of Polistinae in the Neotropics; Ducke (1905a) recognized 18. In particular, he split up the genera Chartergus and Polybia, both quite heterogeneous in his 1904 study. With respect to Chartergus he added the genus Parachartergus, a genus described shortly before by R. von Ihering (1904), as well as the new genus Pseudochartergus. In addition to Polybia, he raised to generic rank Clypearia de Saussure, 1854, and *Charterginus* Fox, 1898, treated by him as subgenera of Polybia in 1904; recognized Leipomeles Möbius, 1856, treated by him as a synonym of Polybia in 1904; and added the new genera Synoecoides and Metapolybia.

Marimbonda pusilla was originally described in the genus Chartergus by Ducke (1904), from Belem and Oyapoc in Brazil. When Ducke (1905a) began to revise the generic classification, he transferred C. pusillus to Parachartergus. Möbius (1856) first used the palpal formula as a taxonomic character, when describing the genus Leipomeles, and R. von Ihering (1904: 129) cited this example in justifying his new genus. Parachartergus was described as monotypic, distinguished from Chartergus by labial palpi being three-segmented not four-segmented. Ducke (1905a, 1905b), however, argued that many species hitherto considered as Chartergus had the fourth labial palpomere rudimentary, and that therefore they could not be separated generically from Parachartergus. As defining characters of Parachartergus were cited the thick, long, curved bristle before the extremity of the labial palpus, and nests, where known, all stelocyttarus calyptodomous (terminology of de Sausure, 1853–1858, meaning petiole combs covered with an envelope and free of the latter). Interestingly, Ducke (1904: 357) had refused to accept *Lei*pomeles as a genus, deriding the importance of the palpi as a generic character: "Mas como hoje já passou o tempo em que se ba-

In 1914, Ducke transferred *pusillus* to *Pseudopolybia*, which was raised to generic rank by R. von Ihering (1913: 227; *Pseudopolybia* had been described as a division of *Polybia* by de Saussure, 1863). The species did not receive much further attention, although it was misidentified by Bequaert (1944), and following him Richards (*in* Richards and Richards, 1951), who used the name for *Leipomeles spilogastra* (Cameron) (see Carpenter, 1999: 9). Then Richards (1978: 202) studied a specimen, which he designated as lectotype, and transferred the species to his new genus, *Marimbonda*.

Ducke's (1914) definitive generic classification for neotropical Polistinae recognized 20 genera, a number that was not augmented until Richards (1978), who recognized 24. Of Richards' four additional genera, two were elevations of subgenera described by Bequaert (1938: *Chartergellus, Nectarinella*), while two were new taxa, *Marimbonda* and *Occipitalia*. The latter was subsequently syn-

seava generos novos sobre pequenas differenças no apparelho buccal ...". Under his changed view (Ducke, 1905a), the five-segmented maxillary palpi was the key character state separating Leipomeles from Parachatergus, both of which had the bristle on the labial palpus and stelocyttarus calyptodomous nests—but he did not recognize that two species he placed in Parachartergus also have that condition, namely pusillus and ater (de Saussure).¹⁰ Ducke (1905a, 1905b) recognized four species groups in Parachartergus, only one of which had the fourth labial palpomere either rudimentary or lacking. That was his first group for species now placed in Parachartergus or Chartergellus Bequaert—species that, as far as is known, all have the labial palpi three-segmented, never with a rudimentary fourth segment. Ducke's (1905a, 1905b) three other species groups within Parachartergus were all stated to have the fourth segment of the labial palpus very distinct. That is correct for two of the groups, which are species now placed in Pseudopolybia de Saussure, but incorrect for his fourth group, which consisted solely of pusillus.

⁹ Now a subgenus of *Mischocyttarus* (Richards, 1941).

¹⁰ Preoccupied; the name has been replaced by *Chartergellus amazonicus* Richards, 1978.

onymized with *Clypearia* by Carpenter et al. (1996), who showed the single species included in *Occipitalia* to be intermediate in the morphological and nest architectural characters defining *Clypearia*. Other work subsequent to Richards (Raw, 1985; Carpenter and Wenzel, 1990; Carpenter et al., 2000) has led to a number of 22 presently recognized neotropical polistine genera. Synonymy of *Marimbonda* with *Leipomeles* now reduces that number to 21.

SYNONYMY

Leipomeles and Marimbonda share numerous morphological features that are certainly derived: the third segment of the labial palpus bearing a stout, curved bristle apically, reduction in the palpal formula to fivesegmented maxillary palpi and three-segmented labial palpi, mesepisternum without dorsal groove, and first metasomal segment conically petiolate. The two genera are not keyed out together in Richards' key (1978: 10), but that is partly erroneous. Thus, the pronotal fovea is not "weak or absent" in Leipomeles; when present, it is as "strong" as other genera. Also contrary to the key, the anterior pronotal carina ("prominence") is in fact acute, and the metanotum in fact has a dorsal surface. The secondary spiracular entrance and propodeal valvula do not differ between Leipomeles and Marimbonda. This leaves the cuticle, which is less punctured and more shining in Leipomeles than Marimbonda, the form of the metasomal petiole which is more elongate in Leipomeles (cf. figs. 3 and 4), and the derived hindwing venation in Marimbonda (fig. 5). None of these features is as significant as the features shared by the two genera, and all are of less significance than the features by which other genera are differentiated (see key, below). Moreover, greater variation in all of these features is found within other genera: sharper differences in punctation occur in, for example, Polybia, Protopolybia, and Ropalidia; the form of the metasomal petiole is much more variable in, for example, *Mischo*cyttarus and Polybia, and the difference between Leipomeles and Marimbonda is less than occurs within Polistes; and the hindwing venation is much more divergent within Parapolybia and Polybioides (van der Vecht, 1966; Carpenter, 1999), with CuA vein separating from M+CuA distad of the insertion of the cu-a crossvein, instead of basad of the insertion of cu-a.

The chief justification for recognition of Marimbonda as a genus in any case was the asterlocyttarus nest architecture. Only the nest collected with the type series of M. albogrisea is definitely known; Wenzel (1998: 16) stated to have seen another nest he believed to be Marimbonda, but the identity was not certain. According to Martin Cooper (in litt.), who collected the nest identified in Wenzel (1998: fig. 23D) as Marimbonda, it was found in Colombia, and was abandoned. Cooper's initial identification was as a Leipomeles nest, but Wenzel assigned it to Marimbonda because the comb was sessile. As will be seen, that is no longer grounds for generic assignment.

As discussed by Wenzel and Carpenter (1994), the nests of Marimbonda and Leipomeles share several derived architectural components, including application of blots of colored pulp to the envelope, envelope with ridges parallel to the lines of construction, and envelope with a central, impressed, longitudinal furrow. That last character is evidently variably present within both genera according to Wenzel (1998), who keyed out both genera together. Leipomeles always nests on the undersides of leaves, whereas the nest of Marimbonda collected by Richards was on the trunk of a sapling. The putative nest of Marimbonda was on a leaf (see Wenzel, 1998: 16), but it may have been Leipomeles. That aside, the absence of a petiole on the comb of Marimbonda was the only consistent difference in nest architecture between Leipomeles and Marimbonda. The number of petioles has long been known to be variable in Leipomeles, from one to several, and their orientation with respect to the substrate (leaf veins) may be vertical or oblique. Petioles have always been thought to be present, but I have now seen nests of Leipomeles dorsata (Fabricius) that lack them. First, a nest was sent to me by James H. Hunt, along with adult wasps, collected in Costa Rica: Prov. Heredia, La Selva Biological Station, 18 Jan. 1991 (J. H. Hunt), nest no. CR91–2. The single comb was attached

to the underside of a leaf along the midrib not by a petiole, but rather by a low fibrous ridge that ran along the entire length of the comb. A hole in the ridge may possibly indicate fusion of originally separate structures, but if so these were ribbonlike rather than petiolate. Second, I have seen a nest at the Universidade de São Paulo in Ribeirão Preto, collected by Gabriel A. R. Melo in Brazil: Amazonas, Beruri, R. Purus, 16 Oct. 1991 (G. A. R. Melo), no. M89, along with adult wasps. The single comb was on the underside of a leaf of Astrocaryum, attached along its entire surface. Moreover, he collected another nest of this species in the same locality, identically attached along the entire surface.

Thus, astelocyttarus combs may occur in *Leipomeles*, and the main justification for separating *Marimbonda* collapses. Accordingly, I am synonymizing these genera. The synonymy follows, and then a new key to the genera of Polistinae of the New World.

Genus Leipomeles Möbius

Leipomeles Möbius, 1856, Nester Gesell. Wespen: 25, genus.

Type species: *Leipomeles lamellaria* Möbius, 1856 [= *Polistes dorsata* Fabricius, 1804], by monotypy.

Lipomeles Schulz, 1906, Spolia Hym.: 232. Unjustified emendation of *Leipomeles* Möbius.

Marimbonda Richards, 1978, Social Wasps Am.: v, 10, 201, genus. NEW SYNONYMY. Type species: Marimbonda albogrisea Richards, 1978, by original designation.

KEY TO THE GENERA OF NEW WORLD POLISTINAE

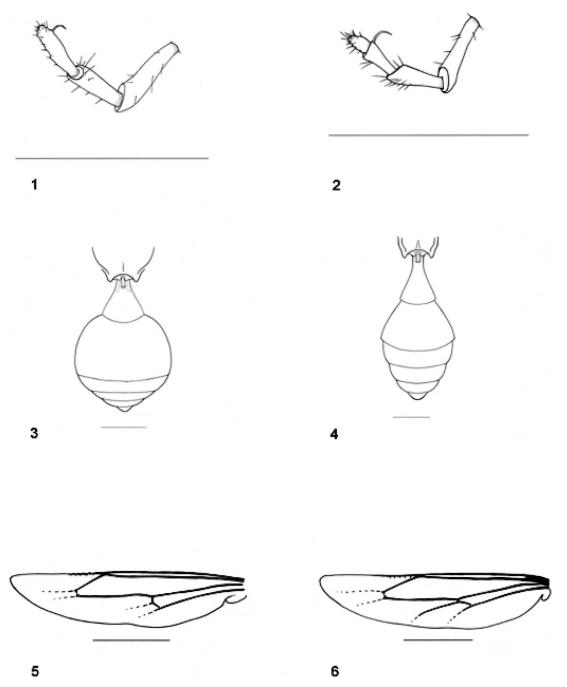
..... tribe Polistini, Polistes Latreille

Metasomal segment I differently shaped, in dorsal view basally petiolate to long-petiolate or sessile with width greater than length (figs. 3-4, 8, 27, 29, 45-47); propodeum with orifice usually more broadly rounded dorsally (figs. 8, 45); pronotum if with carina and lateral fovea, then the carina is anterior to the fovea (fig. 10) or the two are not closely approximated (fig. 18)

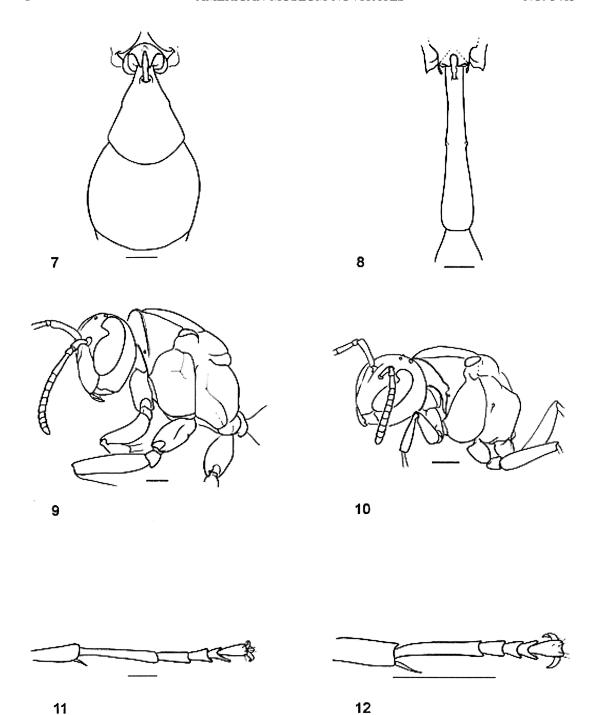
- Mid- and hindtarsi with third and fourth segments asymmetrical, inner lobe longer than outer lobe (fig. 11); forecoxa not dorsolaterally produced (fig. 13); metasomal segment I petiolate, not abruptly expanding posteriorly, in dorsal view with width half or less that of II, and at least twice as long as wide (fig. 8) . . . tribe Mischocyttarini, Mischocyttarus de Saussure
- Mid- and hindtarsi with third and fourth segments symmetrical (fig. 12); forecoxa usually dorsolaterally produced (fig. 14); metasomal seqment I variously shaped tribe Epiponini, 3
- 3. Third labial palpomere with stout, recurved bristle apically (figs. 1, 2); female clypeus with square lateral lobes and sharply pointed apex (fig. 42) 4
- Third labial palpomere without bristle; female clypeus variable 8
- 4. Head with occipital carina present (figs. 15–17) 5
- Head without occipital carina (fig. 18–19)
- Pronotum without sinuous carina (figs. 16, 18–19); forewing with prestigma shorter than pterostigma (fig. 21) Leipomeles Möbius
- 6. Metanotum vertical posteriorly (fig. 18); scutellum angular in profile (fig. 18) Nectarinella Bequaert

- 8. Pronotum without lateral fovea (figs. 22, 23)

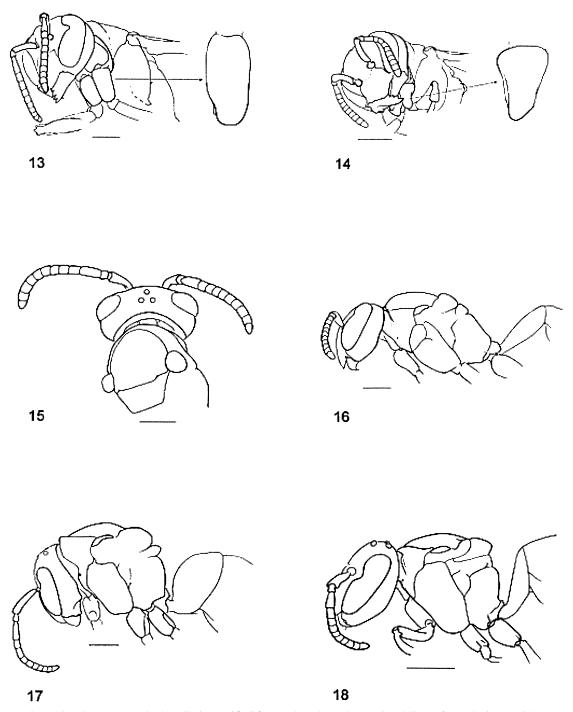
— Scutellum rounded in profile (fig. 23); projecting beyond scutellum posteriorly (figs. 23, 25); head with occipital carina present or absent; pronotum with pretegular carina (fig. 25)	 Scutum with posterolateral lamella absent anteriorly, not adjoining tegula (fig. 35)
 Propodeum without carinae (figs. 27–29); metanotum without tubercle (figs. 27–29); head without occipital carina (fig. 29) 	(fig. 39) Agelaia Lepeletier 17. Mesepisternum with dorsal groove (fig. 40); female clypeus with square lateral lobes and sharply pointed apex (fig. 42)
11. Forecoxa not dorsolaterally produced (fig. 13)	 — Angiopolybia Araujo — Mesepisternum without dorsal groove (fig. 41); female clypeus with lateral lobes
12. Propodeum posteromedially concave (fig. 28); body with some pale maculations, not metallic; head in lateral view with tempora narrower than eye at ocular sinus (figs. 48–49); clypeus longer than wide	rounded (figs. 37, 43, 44) and apex bluntly pointed (fig. 37) or rounded (fig. 43) or truncate (fig. 44)
— Propodeum posteromedially convex (fig. 29); body without pale maculations, cuticle partly to entirely bluish metallic or yellowish with some bluish highlights; head in lateral view with tempora as wide or wider than eye at ocular sinus (figs. 16, 50); clypeus at most as long as wide	 Metanotum without posterior lobe 19 19. Metasomal segment I in dorsal view with short petiole, apically abruptly broadened, wider than half the width of segment II (fig. 46); head in lateral view with tempora much narrower than eye at ocular sinus (fig. 48); pronotum with anteromedial fovea
13. Clypeus apically emarginate (fig. 30); cuticle black, bare, and shining Epipona Latreille Clypeus apically bluntly pointed (fig. 31); cuticle not shining	 Metasomal segment I in dorsal view differently shaped, narrowly petiolate to sessile (fig. 47); head in lateral view with tempora at least as wide as eye at ocular sinus (fig. 49), usually wider (fig. 50); pronotum
14. Metasomal segment I in lateral view more flattened posteriorly (fig. 32), in dorsal view with maximum width 3× basal width	without anteromedial fovea 20 20. Lateral ocelli almost as far apart as distance from each to eyes (fig. 51); eyes bristled (fig. 51); metasomal segment I not petio-
 Metasomal segment I in lateral view convex posteriorly (fig. 33), in dorsal view with maximum width 2× basal width 	late in dorsal view
15. Scutum with posterolateral lamella present adjoining tegula (fig. 34) 16	is to eyes (fig. 37); eyes usually not bristled; metasomal segment I usually petiolate in dorsal view <i>Polybia</i> Lepeletier



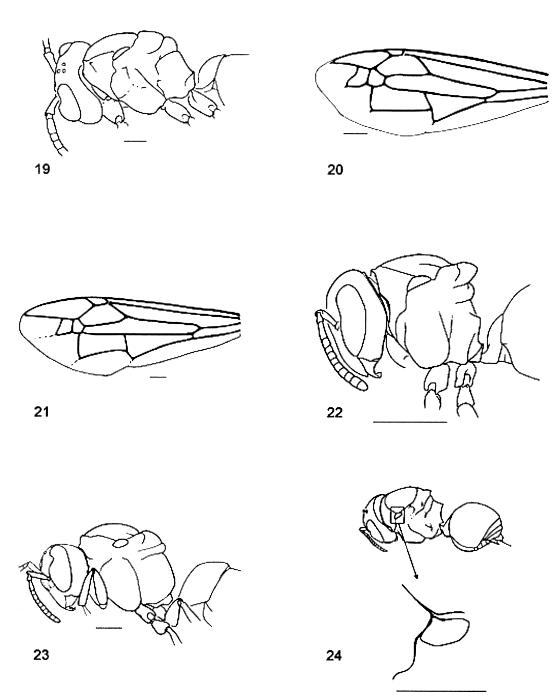
Figs. 1–6. Neotropical Polistinae. 1–2. Labial palpus. 1. Chartergellus nigerrimus Richards. 2. Pseudopolybia compressa (de Saussure). 3–4. Metasoma in dorsal view. 3. Marimbonda albogrisea Richards. 4. Leipomeles dorsata (Fabricius). 5–6. Hindwing. 5. Marimbonda albogrisea Richards. 6. Leipomeles dorsata (Fabricius). All scale bars are 1.0 mm.



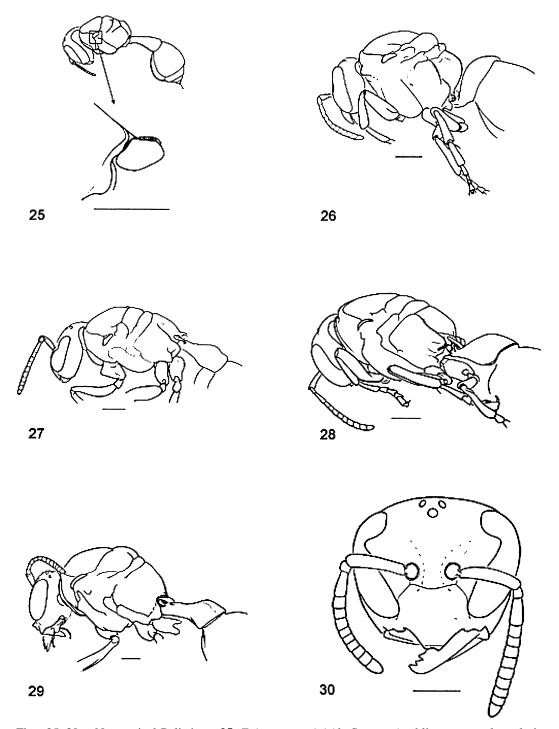
Figs. 7–12. Neotropical Polistinae. 7–8. Metasomal terga I and II in dorsal view. 7. *Polistes consobrinus* de Saussure. 8. *Mischocyttarus rotundicollis* (Cameron). 9–10. Head and mesosoma in anterolateral view. 9. *Polistes consobrinus* de Saussure. 10. *Parachartergus fraternus* (Gribodo). 11–12. Hindtarsus. 11. *Mischocyttarus rotundicollis* (Cameron). 12. *Brachygastra augusti* (de Saussure). All scale bars are 1.0 mm.



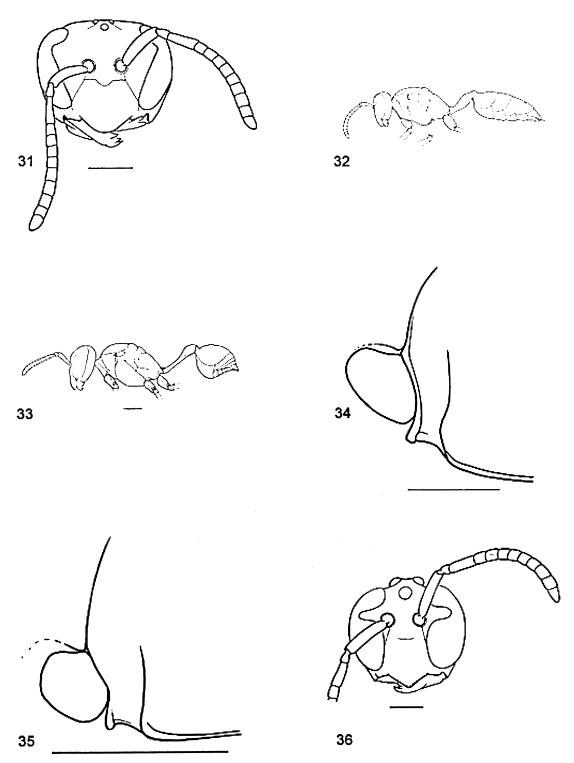
Figs. 13–18. Neotropical Polistinae. 13–14. Head and prothorax in oblique frontal view, with procoxa set off in lateral view. 13. *Mischocyttarus rotundicollis* (Cameron). 14. *Brachygastra augusti* (de Saussure). 15–16. *Agelaia multipicta* (Haliday). 15. Head and mesosoma in oblique posterior view. 16. Lateral view. 17. *Parachartergus fraternus* (Gribodo), posterolateral view. 18. *Nectarinella championi* (Dover), head and mesosoma in lateral view. All scale bars are 1.0 mm.



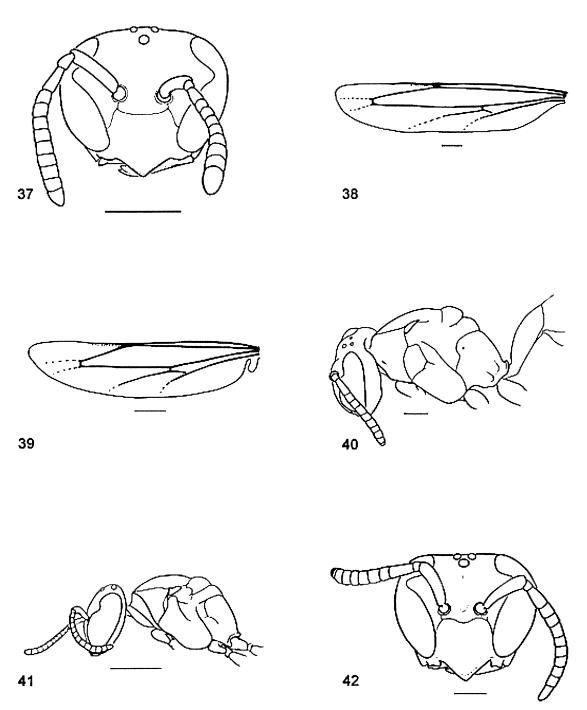
Figs. 19–24. Neotropical Polistinae. **19.** *Pseudopolybia vespiceps* (de Saussure), head and mesosoma in oblique lateral view. **20–21**. Forewing. **20.** *Parachartergus fraternus* (Gribodo). **21.** *Angiopolybia obidensis* (Ducke). **22–23**. Head and mesosoma in lateral view. **22.** *Brachygastra augusti* (de Saussure). **23.** *Chartergus artifex* (Christ). **24.** *Brachygastra augusti* (de Saussure), oblique posterolateral view, with pronotum and tegula set off. All scale bars are 1.0 mm.



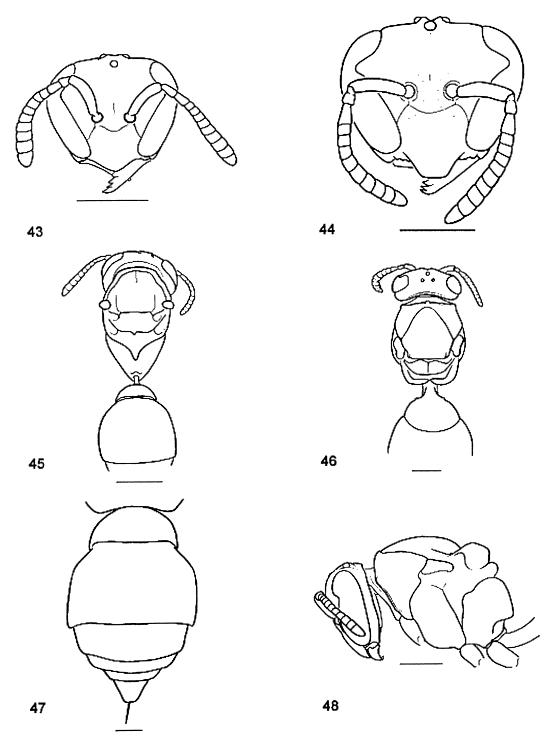
Figs. 25–30. Neotropical Polistinae. **25.** *Epipona guerini* (de Saussure), oblique posterolateral view, with pronotum and tegula set off. **26–29.** Oblique posterolateral view. **26.** *Chartergus artifex* (Christ). **27.** *Asteloeca traili* (Cameron). **28.** *Clypearia sulcata* (de Saussure). **29.** *Synoeca cyanea* (Fabricius). **30.** *Epipona guerini* (de Saussure), head in frontal view. All scale bars are 1.0 mm.



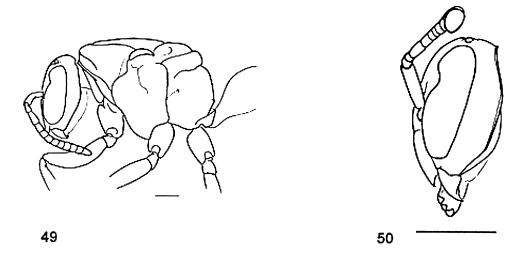
Figs. 31–36. Neotropical Polistinae. **31.** *Asteloeca traili* (Cameron), head in frontal view. **32–33**. lateral view. **32.** *Asteloeca traili* (Cameron). **33.** *Metapolybia cingulata* (Fabricius). **34–35**. Scutum and tegula in dorsal view. **34.** *Apoica pallens* (Fabricius). **35.** *Polybia bistriata* (Fabricius). **36.** *Apoica pallens* (Fabricius), head in frontal view. All scale bars are 1.0 mm.

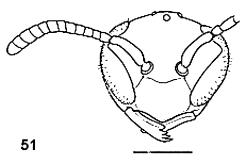


Figs. 37–42. Neotropical Polistinae. 37. Polybia bistriata (Fabricius), head in frontal view. 38–39. Hindwing. 38. Apoica pallens (Fabricius). 39. Agelaia multipicta (Haliday), hindwing. 40–41. lateral view. 40. Angiopolybia obidensis (Ducke). 41. Protopolybia sedula (de Saussure). 42. Angiopolybia obidensis (Ducke), head in frontal view. All scale bars are 1.0 mm.



Figs. 43–48. Neotropical Polistinae. 43–44. Head in frontal view. 43. *Protopolybia sedula* (de Saussure). 44. *Charterginus fulvus* Fox. 45–46. Dorsal view. 45. *Protopolybia sedula* (de Saussure). 46. *Charterginus fulvus* Fox. 47. *Polybia depressa* (Ducke), metasoma in dorsal view. 48. *Charterginus fulvus* Fox, head and mesosoma in lateral view. All scale bars are 1.0 mm.





Figs. 49–51. Neotropical Polistinae. **49.** *Polybia depressa* (Ducke), head and mesosoma in lateral view. **50.** *Protonectarina sylveirae* (de Saussure), head in lateral view. **51.** *Protonectarina sylveirae* (de Saussure), head in frontal view. All scale bars are 1.0 mm.

ACKNOWLEDGMENTS

I am very grateful to Fernando Noll and Sidnei Mateus for showing me an astelocyttarus nest of *Leipomeles*, and especially to Gabriel Melo for collecting it. I am also grateful to Jim Hunt for collecting and sending to me the nest from Costa Rica. I thank Martin Cooper, Kurt Pickett, and John Wenzel for encouragement and comments, and two anonymous reviewers of the manuscript for corrections. The illustrations for the key were provided by Molly Rightmyer and Valerie Giles.

REFERENCES

Bequaert, J.C. 1938. A new *Charterginus* from Costa Rica, with notes on *Charterginus*, *Pseu-*

dochartergus, Pseudopolybia, Epipona, and Tatua (Hymenoptera, Vespidae). Revista de Entomologia (Rio de Janeiro) 9: 99–117.

Bequaert, J.C. 1944. The social Vespidae of the Guianas, particularly of British Guiana. Bulletin of the Museum of Comparative Zoology 94: 249–300.

Carpenter, J.M. 1991. Phylogenetic relationships and the origin of social behavior in the Vespidae. *In* K.G. Ross and R.W. Matthews (editors), The social biology of wasps: 7–32. Ithaca, NY: Cornell University Press.

Carpenter, J.M. 1996. Phylogeny and biogeography of *Polistes. In S. Turillazzi* and M.J. West-Eberhard (editors), Natural history and evolution of paper-wasps: 18–57. Oxford: Oxford University Press.

Carpenter, J.M. 1999. Taxonomic notes on paper wasps (Hymenoptera: Vespidae; Polistinae). American Museum Novitates 3259: 1–44.

- Carpenter, J.M., J. Kojima, and J.W. Wenzel. 2000. *Polybia*, paraphyly and polistine phylogeny. American Museum Novitates 3298: 1–24.
- Carpenter, J.M., and J.W. Wenzel. "1989" [1990]. Synonymy of the genera *Protopolybia* and *Pseudochartergus* (Hymenoptera: Vespidae; Polistinae). Psyche 96: 177–186.
- Carpenter, J.M., J.W. Wenzel, and J. Kojima. 1996. Synonymy of the genus *Occipitalia* Richards, 1978, with *Clypearia* Saussure, 1854 (Hymenoptera: Vespidae; Polistinae, Epiponini). Journal of Hymenoptera Research 5: 157–165.
- Ducke, A. 1904. Sobre as Vespidas sociaes do Pará. Boletim do Museu Goeldi 4: 317–374.
- Ducke, A. 1905a. Nouvelles contributions à la connaissance des Vespides sociales de l'Amérique du Sud. Revue d'Entomologie 24: 5–24.
- Ducke, A. 1905b. Sobre as Vespidas sociaes do Pará. (I.º. Supplemento). Boletim do Museu Goeldi 4: 652–698.
- Ducke, A. 1914. Über Phylogenie und Klassification der sozialen Vespiden. Zoologischen Jahrbüchern, Abteilung für Systematik, Geographie und Biologie der Tiere 36: 303–330.
- Fox, W.J. 1898. Contributions to the knowledge of the Hymenoptera of Brazil. No. 5. Vespidae. Proceedings of the Academy of Natural Sciences of Philadelphia 1898: 445–460.
- Gribodo, G. "1891" [1892]. Contribuzioni imenoterologiche. Sopra alcune specie nuove o poco conosciute imenotteri diplotteri. Nota IV. Bollettino della Società Entomologica Italiana 23: 242–300.
- Guérin-Meneville, F.E. 1831. Crustacees, Arachnides et Insects. *In* L.I. Duperrey, Voyage autour du monde sur la Coquille (1882–25). Zoologie 2(2), div. 1 pls. 8–9. Paris.
- Ihering, H. von. 1896. Zur Biologie der socialen Wespen Brasiliens. Zoologischer Anzeiger 19: 449–453.
- Ihering, R. von. 1904. As vespas sociaes do Brasil. Revista do Museu Paulista 6: 97–309.
- Ihering, R. von. 1913. O genero *Parachartergus* R. v. Ih. (vespas sociaes). Revista do Museu Paulista 9: 226–228.
- International Commission on Zoological Nomenclature. 1976. Opinion 1051. *Rhopalidia* Lepeletier, 1836 (Insecta: Hymenoptera): Suppressed under the plenary powers. Bulletin of Zoological Nomenclature 32: 240–241.
- Kirby, W. 1826. In W. Kirby and W. Spence, An introduction to entomology, or elements of the natural history of insects 3(1). London: Longman, Hurst, Rees, Orme, and Brown.
- Kojima, J. 1997. Abandonment of the subgeneric concept in the Old World polistine genus Ropalidia Guérin-Méneville, 1831 (Insecta: Hy-

- menoptera: Vespidae). Natural History Bulletin of Ibaraki University 1: 93–106.
- Latreille, P.A. 1802. Histoire naturelle, générale et particulière des Crustacées et des Insectes. Paris: Sonnini's Suites à Buffon.
- Lepeletier de St. Fargeau, A.L.M. 1836. Histoire Naturelle des Insectes. Hyménoptères, 1. Paris: Roret's Suites à Buffon.
- Möbius, K.A. 1856. Die Nester der geselligen Wespen. Beschreibungen neuer Nester—und einiger neuen Wespen-arten des naturhistorischen Museums zu Hamburg nebst Betrachtungen über den Nesterbau im Allegemeinen. Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg 3: 117–171, 19 pls.
- Perty, M. 1833. Delectus Animalium Articulatorum quae Itinere per Brasiliam—Collegerunt Dr. J. de Spix et Dr. C.F. Ph. de Martius, fasc. 3. München.
- Raw, A. 1985. Asteloeca, a new neotropical wasp genus (Hymenoptera, Vespidae). Revista Brasileira de Entomologia 29: 185–188.
- Richards, O.W. 1941. The classification of the genus *Mischocyttarus* Saussure (Hymenopt., Vespidae). Proceedings of the Royal Entomological Society of London (B) 10: 124–130.
- 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.
- Saussure, H. de. 1852. Note sur un nouveau genre de guêpes. Annales de la Société entomologique de France (2) 10: 549–556.
- Saussure, H. de. 1853–1858. Monographie des guêpes sociales ou de la tribu des vespiens. Paris: Masson, and Genève: J. Cherbuliez.
- Saussure, H. de. 1863. Mélanges Hyménoptérologiques. II. Vespides. Mém oires de la Soc iété de Phys ique et d'Hist oire nat urelle de Genève 17: 171–244.
- Vecht, J. van der. 1966. The East Asiatic and Indo-Australian species of *Polybioides* du Buysson and *Parapolybia* de Saussure (Hym., Vespidae). Zoologische Verhandelingen 82: 1–42.
- 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.I. Vane-Wright* (editors), Phylogenetics and Ecology: 79–101. London: Academic Press.
- White, A. 1841. Description of a South American wasp which collects honey. Annals and Magazine of Natural History 7: 315–322.