AMERICAN MUSEUM NOVITATES

Number 3973, 42 pp. July 22, 2021

Total-evidence Phylogeny of the New World *Polistes* Lepeletier, 1836, Paper Wasps (Vespidae, Polistinae, Polistini)

ALEXANDRE SOMAVILLA,[1] BERNARDO F. SANTOS,[2] JAMES M. CARPENTER,[3] SÉRGIO RICARDO ANDENA,[4] AND MÁRCIO LUIZ OLIVEIRA[1]

ABSTRACT

The genus *Polistes* is one of the most species-rich and widely distributed groups of social wasps and a model taxon for studies of social behavior. Almost half the *Polistes* world fauna occurs in the New World, but their classification has been unstable due in part to the scarcity of phylogenetic studies. We investigated the phylogeny of the New World *Polistes* by combining a previously existing molecular dataset with a new morphological and behavioral matrix for 90 of the 93 New World species. All analyses support a single origin for the New World *Polistes*. All five traditionally defined New World subgenera (*Aphanilopterus*, *Epicnemius*, *Fuscopolistes, Onerarius*, and *Palisotius*) were monophyletic, but the relationships among them varied across datasets. Our results, with an expanded phenotypic dataset, improved taxonomic sampling, and enhanced clade support relative to previous studies, strongly support a classification based on five subgenera, which are all diagnosable groups supported by clear morphological synapomorphies. Hence, we propose the revalidation of previously proposed subgenera; we provide a taxonomic account of each subgenus and an identification key to all species of New World *Polistes*.

[1] Instituto Nacional de Pesquisas da Amazônia – INPA, Coordenação de Biodiversidade, Manaus, Amazonas, Brazil.
[2] Institut de Systématique, Evolution, Biodiversité (ISYEB), Muséum national d'Histoire naturelle, CNRS, SU, EPHE, UA, Paris, France.
[3] American Museum of Natural History, Division of Invertebrate Zoology, New York.
[4] Universidade Estadual de Feira de Santana, Museu Zoologia, Divisão de Entomologia, Bahia Brazil.

 ISSN 0003-0082

INTRODUCTION

The paper wasps (Hymenoptera, Vespidae, Polistinae) comprise over 1000 species of exclusively social wasps divided into four tribes: Polistini, with a single genus, *Polistes* Latreille; Mischocyttarini, also with a single genus, *Mischocyttarus* de Saussure; Epiponini, with 19 genera; and Ropalidiini, with four genera (Silveira et al., 2021). The genus *Polistes* is one of the most species-rich, familiar, and widespread taxa of social wasps, with 237 described species found in all habitable continents (Richards, 1978; Carpenter, 1996a, 1996b; Santos et al., 2015; Silveira et al., 2021). While the genus is distributed worldwide, its highest diversity has been recorded in tropical forests (Richards, 1973, 1978; Carpenter, 1993, 1996a, 1996b; Nguyen et al., 2017). Almost half the *Polistes* world fauna occurs in the New World, where 93 native species have been recorded (Richards, 1978; Carpenter, 1996a; Buck et al., 2012; Silveira et al., 2021).

Species of *Polistes* are characterized by having the metasomal tergum I subsessile and conical in dorsal view; propodeal orifice acute dorsally and pronotum with posterior carina lateral to the fovea (Richards, 1973, 1978; Somavilla and Carpenter, 2021). The genus has been one of the most well-documented groups of social wasps in terms of behavioral studies, largely due to the ease with which investigators can observe colony life (i.e., the nest is not surrounded by an envelope); the ease with which colonies can be located (often on human constructions); and the small size of the colonies (usually fewer than 100 individuals), all of which allow for detailed behavioral observation (Pardi, 1996; Pickett and Wenzel, 2004).

The taxonomic history of New World *Polistes* has been troublesome. Until 1973, most of the nomenclature in use was based on informal species groups with specific regional application (Carpenter, 1996a). Richards (1973) divided *Polistes* into 12 subgenera, five of them occurring in the New World (*Aphanilopterus*, *Epicnemius*, *Fuscopolistes, Onerarius*, and *Palisotius*) and seven in the Old World (*Gyrostoma*, *Stenopolistes*, *Nygmopolistes*, *Megapolistes*, *Polistella*, *Sulcopolistes*, and *Polistes*).

Carpenter (1996b), using morphological characters, presented three matrices, with up to 18 terminals that were subgenera or species groups; these were summary terminals, for more than 140 species. Cladistic analysis recovered several of the subgenera proposed by Richards (1973) as paraphyletic. For the New World, Carpenter (1996b) found that *Polistes* (*Epicnemius*), *Polistes* (*Fuscopolistes*), *Polistes* (*Onerarius*), *Polistes* (*Palisotius*), rendered *Polistes* (*Aphanilopterus*) paraphyletic, and synonymized them with *Polistes* (*Aphanilopeterus*). Later, studies incorporating molecular data or combined with morphological characters presented conflicting results, either rejecting (Arévalo et al., 2004; Pickett and Wenzel, 2004; Pickett and Carpenter, 2010) or corroborating (Pickett et al., 2006) Richards's (1973) subgeneric classification. In the latest large-scale phylogeny including species of New World *Polistes* (Santos et al., 2015), the New World subgenera were recovered as monophyletic, except for *Polistes* (*Fuscopolistes*), which was paraphyletic with respect to *Polistes (Onerarius) carnifex.*

Despite these recent advances in the understanding of the phylogeny of *Polistes*, previous studies included a relatively small portion of the New World species (40 species or fewer) and added only a few morphological characters to those of Carpenter (1996b). This study aims to propose a more complete picture of the evolutionary history of New World *Polistes* by including

a comprehensive taxonomic sampling and presenting a more detailed phenotypic matrix, adding female, male, male genitalia, larvae, and nest architecture characters to the available molecular data, assembling the largest dataset for New World *Polistes* to date.

MATERIAL AND METHODS

Material examined: There are currently 93 valid species of *Polistes* native to the New World (table 1). The ingroup for our analyses included 90 of these species. Specimens of *Polistes* (*Epicnemius*) *boharti* Snelling, *Polistes* (*Aphanilopterus*) *eburneus* Bequaert and *Polistes* (*Aphanilopterus*) *pseudoculatus* Snelling were not found, even in the published holotype depositories. Eleven Old World *Polistes* and three species of *Vespula* were employed as outgroups (table 1; Supplementary material S1, available online: https://doi.org/10.5531/sd.sp.50).

Samples from the following institutions were studied: AMNH, American Museum of Natural History, New York (J.M. Carpenter, C. LeBeau); CESC, Coleção Entomológica da Universidade de Santa Cruz do Sul, Brazil, Santa Cruz do Sul (A. Kohler); CZMA, Coleção Zoológica do Maranhão, Brazil, Caxias (F. Limeira); IBNP: Museo Nacional de Historia Natural del Paraguay, Asuncion, Paraguay (B.R. Garcete-Barrett); INPA, Instituto Nacional de Pesquisas da Amazônia, Brazil, Manaus (M.L. Oliveira); MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, MA (P.D. Perkins); MNB, Museum für Naturkunde Berlin, Germany, Berlin (M. Ohl, F. Koch); NHM, Natural History Museum, United Kingdom, London (G. Broad); NMNH, National Museum of Natural History, Smithsonian Institution, Washington, D.C. (S. Brady); MNHN, Muséum National d'Histoire Naturelle, France, Paris (C. Villemant, A. Touret-Alby); MNRJ, Museu Nacional do Rio de Janeiro, Brazil, Rio de Janeiro (F. Vivalo); MZSP, Museu de Zoologia da Universidade de São Paulo, Brazil, São Paulo (C.R. Brandão); RAM, Royal Alberta Museum, Canada, Edmonton (M. Buck); ZMC, Zoological Museum of University of Copenhagen, Denmark, Copenhagen (L. Vilhelmsen); and ZSM, Zoologische Straatssammlung München, Germany, Munich (S. Schmidt).

Data collection: A total of 140 morphological characters were delimited and coded (24 adapted from Carpenter (1996b), five from Pickett and Carpenter (2010) and 111 first presented here): 88 of adult females, 32 of adult males, including the male genitalia, 13 of larvae and seven of nest architecture (table 1; figures 5–16). Morphological terminology for adults of *Polistes* followed Richards (1973, 1978), Carpenter (1996b), and Somavilla et al. (2018). For dissection of the male genitalia we adopted the protocol of Somavilla et al. (2018). For the male genitalia we adopted the terminology of Buck et al. (2012) and Somavilla et al. (2018). Part of the larval characters was coded from information available in Richards (1978), Dias-Filho (1975), Wheeler and Wheeler (1979), Nelson (1982), Kojima and Yamane (1984), Kojima (1987), and Kojima (1998). Nest architecture characters were coded based on Richards (1978), Wenzel (1998) and on directly observed nests deposited in the AMNH. A total of 10 characters were treated as additive (See appendix 1).

Molecular characters were adopted from the matrix of Santos et al. (2015), including data from six genes: mitochondrial cytochrome oxidase I (COI), 12S rRNA (12S) and 16S rRNA

TABLE 1. *Polistes* species and out group used in phylogenetic analysis, with their distribution, number of characters used in females, males, larvae and nests, and molecular data for each gene region: COI, 12S, 16S, 28S, H3 and EF1-α.

Taxon	Distribution	Female	Male	Larvae	Nest	COI	12S	16S	28S	H3	EF1
Vespula germanica (Fabricius)	Palearctic	81	30	-	07	X	X	X	X	-	-
Vespula maculifrons (du Buysson)	Nearctic	81	30	-	07	X	X	X	X	X	-
Vespula squamosa (Drury)	Nearctic	81	30	-	07	X	X	X	X	X	-
Polistes (*Gyrostoma*) *olivaceus* (DeGeer)	Palearctic, Oriental	81	30	-	07	X	-	-	-	-	-
Polistes (*Gyrostoma*) *tenebricosus* Lepeletier	Oriental	81	30	-	07	X	X	X	X	-	-
Polistes (*Polistella*) *japonicus* de Saussure	Oriental	81	30	-	03	X	X	X	X	X	X
Polistes (*Polistella*) *sagittarius* de Saussure	Oriental	81	30	-	07	X	X	X	X	X	X
Polistes (*Polistella*) *snelleni* de Saussure	Oriental	81	30	-	07	X	X	X	X	X	-
Polistes (*Polistella*) *stigma* (Fabriciu)	Oriental	81	30	-	07	X	X	-	X	X	X
Polistes (*Polistes*) *biglumis* (Linnaeus)	Palearctic	81	30	-	07	X	-	-	-	-	-
Polistes (*Polistes*) *dominulus* (Christ)	Palearctic, Oriental	81	30	-	07	X	X	X	X	X	X
Polistes (*Polistes*) *gallicus* (Linnaeus)	Palearctic, Oriental	81	30	-	07	X	X	X	X	-	X
Polistes (*Polistes*) *marginalis* (Fabricius)	Afrotropic	81	30	-	07	X	X	X	X	-	X
Polistes (*Polistes*) *ninpha* (Christ)	Palearctic	81	30	-	07	X	X	X	X	X	X
Polistes (*Epicnemius*) *actaeon* Haliday	Neotropical	81	30	13	05	X	X	X	X	-	-
Polistes (*Aphanilopterus*) *adelphus* Richards	Neotropical	81	30	13	06	-	-	-	-	-	-
Polistes (*Epicnemius*) *angulinus* Richards	Neotropical	81	07	13	04	-	-	-	-	-	-
Polistes (*Aphanilopterus*) *annullaris* (Linnaeus)	Nearctic	81	30	13	07	X	X	X	X	X	X
Polistes (*Fuscopolistes*) *apachus* de Saussure	Nearctic	81	30	13	07	X	-	-	X	-	-
Polistes (*Aphanilopterus*) *apicalis* de Saussure	Neotropical	81	30	13	07	X	X	X	X	X	X
Polistes (*Aphanilopterus*) *arizonensis* Snelling	Nearctic	81	30	13	04	X	-	-	-	-	-
Polistes (*Aphanilopterus*) *aterrimus* de Saussure	Neotropical	81	30	13	07	-	-	-	-	-	-
Polistes (*Epicnemius*) *atrox* Richards	Neotropical	79	30	13	04	-	-	-	-	-	-
Polistes (*Fuscopolistes*) *aurifer* Saussure	Nearctic	81	30	13	07	X	X	X	X	X	-
Polistes (*Aphanilopterus*) *bahamensis* Bequaert and Salt	Nearctic, Neotropical	81	30	13	07	X	-	-	-	-	-
Polistes (*Fuscopolistes*) *bellicosus* Cresson	Nearctic, Neotropical	81	30	13	07	X	X	X	X	X	-
Polistes (*Aphanilopterus*) *bequaertellus* Snelling	Neotropical	81	07	13	04	-	-	-	-	-	-
Polistes (*Epicnemius*) *bequaertianus* Willink	Neotropical	81	07	13	04	-	-	-	-	-	-
Polistes (*Epicnemius*) *bicolor* Lepeletier	Neotropical	81	30	13	07	X	X	X	X	X	X
Polistes (*Aphanilopterus*) *biguttatus* Haliday	Neotropical	81	30	13	07	X	-	-	X	X	-

TABLE I *continued*

Taxon	Distribution	Female	Male	Larvae	Nest	COI	12S	16S	28S	H3	EF1
Polistes (*Epicnemius*) *billardieri* Fabricius	Neotropical	81	30	13	07	-	-	-	-	-	-
Polistes (*Aphanilopterus*) *binotatus* de Saussure	Neotropical	81	30	13	04	-	-	-	-	-	-
Polistes (*Epicnemius*) *boharti* Snelling	Neotropical	-	-	-	-	-	-	-	-	-	-
Polistes (*Aphanilopterus*) *brevifissus* Richards	Neotropical	81	30	13	04	-	-	-		-	-
Polistes (*Aphanilopterus*) *buyssoni* Brèthes	Neotropical	81	30	13	07	X	X	X	X	X	X
Polistes (*Aphanilopterus*) *canadensis* Richards	Nearctic, Neotropical	81	30	13	07	X	-	-	X	-	-
Polistes (*Epicnemius*) *candidoi* von Ihering	Neotropical	81	07	13	04	-	-	-	-	-	-
Polistes (*Onerarius*) *carnifex* Bequaert	Neotropical	81	30	13	07	X	-	-	-	-	-
Polistes (*Fuscopolistes*) *carolina* Linnaeus	Nearctic, Neotropical	81	30	13	07	X	X	X	X	X	X
Polistes (*Aphanilopterus*) *cavapyta* de Saussure	Neotropical	81	30	13	07	X	X	X	X	X	X
Polistes (*Aphanilopterus*) *cavapytiformis* Richards	Neotropical	81	30	13	07	-	-	-	-	-	-
Polistes (*Epicnemius*) *cinerascens* de Saussure	Neotropical	81	30	13	07	X	X	X	X	X	X
Polistes (*Epicnemius*) *claripennis* Ducke	Neotropical	81	30	13	07	-	-	-	-	-	-
Polistes (*Aphanilopterus*) *comanchus* Saussure	Nearctic, Neotropical	77	30	13	04	X	X	X	X	X	X
Polistes (*Aphanilopterus*) *consobrinus* de Saussure	Neotropical	81	30	13	06	-	-	-	-	-	-
Polistes (*Aphanilopterus*) *crinitus* Felton	Neotropical	81	30	13	07	X	X	X	X	-	X
Polistes (*Aphanilopterus*) *cubensis* Lepeletier	Neotropical	81	07	13	04	-	-	-	-	-	-
Polistes (*Epicnemius*) *davillae* Richards	Neotropical	81	07	13	04	-	-	-	-	-	-
Polistes (*Epicnemius*) *deceptor* Schulz	Neotropical	81	30	13	04	-	-	-	-	-	-
Polistes (*Aphanilopterus*) *dominicus* Vallot	Neotropical	81	30	13	04	-	-	-	-	-	-
Polistes (*Fuscopolistes*) *dorsalis* Fabricius	Nearctic, Neotropical	81	30	13	07	X	X	X	X	X	X
Polistes (*Aphanilopterus*) *eburneus* Bequaert	Neotropical	-	-	-	-	-	-	-	-	-	-
Polistes (*Aphanilopterus*) *erythrocephalus* Latreille	Neotropical	81	30	13	04	X	-	-	-	-	-
Polistes (*Aphanilopterus*) *exclamans* Viereck	Nearctic, Neotropical	81	30	13	06	X	X	X	X	X	X
Polistes (*Aphanilopterus*) *ferreri* de Saussure	Neotropical	81	30	13	04	-	-	-	-	-	-
Polistes (*Fuscopolistes*) *flavus* Cresson	Nearctic	81	30	13	04	-	-	X	-	-	-
Polistes (*Aphanilopterus*) *franciscanus* Richards	Neotropical	81	07	13	04	-	-	-	-	-	-
Polistes (*Fuscopolistes*) *fuscatus* Fabricius	Nearctic	81	30	13	07	X	X	X	X	X	X
Polistes (*Epicnemius*) *geminatus* Fox	Neotropical	81	30	13	07	X	X	X	X	X	X
Polistes (*Aphanilopterus*) *goeldii* Ducke	Neotropical	81	30	13	07	X	X	X	X	X	X
Polistes (*Aphanilopterus*) *huacapistana* Richards	Neotropical	81	07	13	04	-	-	-	-	-	-
Polistes (*Fuscopolistes*) *hirsuticornis* Buck	Nearctic	81	30	13	04	-	-	-	-	-	-

TABLE I *continued*

Taxon	Distribution	Female	Male	Larvae	Nest	COI	12S	16S	28S	H3	EF1
Polistes (*Aphanilopterus*) *incertus* Cresson	Neotropical	81	07	13	04	-	-	-	-	-	-
Polistes (*Aphanilopterus*) *infuscatus* Lepeletier	Neotropical	81	30	13	06	-	-	-	-	-	-
Polistes (*Aphanilopterus*) *instabilis* de Saussure	Neotropical	81	30	13	07	X	-	-	-	-	-
Polistes (*Aphanilopterus*) *kaibabensis* Hayward	Nearctic	81	30	13	04	-	-	-	-	-	-
Polistes (*Aphanilopterus*) *lanio* Fabricius	Neotropical	81	30	13	07	X	X	X	X	X	X
Polistes (*Aphanilopterus*) *lineonotus* Bohart	Neotropical	81	30	13	04	-	-	-	-	-	-
Polistes (*Palisotius*) *major* Palisot de Beauvois	Neotropical	81	30	13	07	X	-	X	X	X	X
Polistes (*Aphanilopterus*) *maranonensis* Willink	Neotropical	81	30	13	01	-	-	-	-	-	-
Polistes (*Epicnemius*) *melanosoma* de Saussure	Neotropical	81	30	13	07	-	-	-	-	-	-
Polistes (*Aphanilopterus*) *melanotus* Richards	Neotropical	81	07	13	07	X	X	X	X	X	-
Polistes (*Fuscopolistes*) *metricus* Say	Nearctic	81	30	13	07	X	X	X	X	X	X
Polistes (*Aphanilopterus*) *mexicanus* Bequaert	Neotropical	81	30	13	04	-	-	-	-	-	-
Polistes (*Aphanilopterus*) *minor* Palisot de Beauvois	Neotropical	81	30	13	04	-	-	-	-	-	-
Polistes (*Epicnemius*) *moraballi* Richards	Neotropical	81	07	13	04	-	-	-	-	-	-
Polistes (*Aphanilopterus*) *myersi* Bequaert	Neotropical	81	30	13	07	-	X	-	-	-	-
Polistes (*Epicnemius*) *niger* Brèthes	Neotropical	81	30	13	04	-	-	-	-	-	-
Polistes (*Aphanilopterus*) *ninabamba* Richards	Neotropical	81	30	13	04	-	-	-	-	-	-
Polistes (*Aphanilopterus*) *notatipes* Richards	Neotropical	81	07	13	04	-	-	-	-	-	-
Polistes (*Epicnemius*) *obscurus* de Saussure	Neotropical	81	30	13	04	-	-	-	-	-	-
Polistes (*Epicnemius*) *occipitalis* Ducke	Neotropical	81	30	13	07	X	X	X	X	-	-
Polistes (*Aphanilopterus*) *oculatus* Smith	Neotropical	81	30	13	04	-	-	-	-	-	-
Polistes (*Epicnemius*) *pacificus* Fabricius	Neotropical	81	30	13	07	X	X	X	X	X	-
Polistes (*Palisotius*) *palmarum* Bequaert	Nearctic, Neotropical	81	30	13	04	-	-	-	-	-	-
Polistes (*Palisotius*) *paraguayensis* Bertoni	Neotropical	81	30	13	04	-	-	-	-	-	-
Polistes (*Fuscopolistes*) *parametricus* Buck	Nearctic	81	30	13	04	-	-	-	-	-	-
Polistes (*Epicnemius*) *penai* Richards	Neotropical	81	30	13	04	-	-	-	-	-	-
Polistes (*Aphanilopterus*) *peruvianus* Bequaert	Neotropical	81	30	13	07	-	-	-	-	-	-
Polistes (*Fuscopolistes*) *poeyi* Lepeletier	Neotropical	81	30	13	04	X	X	X	X	-	-
Polistes (*Aphanilopterus*) *pseudoculatus* Snelling	Neotropical	-	-	-	-	-	-	-	-	-	-
Polistes (*Aphanilopterus*) *ridleyi* Kirby	Neotropical	81	30	13	07	-	-	-	-	-	-
Polistes (*Fuscopolistes*) *rossi* Bohart	Nearctic, Neotropical	81	30	13	04	-	-	-	-	-	-
Polistes (*Fuscopolistes*) *rubiginosus* Lepeletier	Nearctic	81	30	13	04	X	X	X	X	X	X

TABLE I *continued*

Taxon	Distribution	Female	Male	Larvae	Nest	COI	12S	16S	28S	H3	EF1
Polistes (*Aphanilopterus*) *rufidens* de Saussure	Neotropical	81	07	13	07	-	-	-	-	-	-
Polistes (*Epicnemius*) *rufiventris* Ducke	Neotropical	81	30	13	07	-	-	-	-	-	-
Polistes (*Aphanilopterus*) *satan* Bequaert	Neotropical	81	30	13	07	X	-	-	X	-	-
Polistes (*Aphanilopterus*) *simillimus* Zikán	Neotropical	81	30	13	07	X	X	X	X	-	-
Polistes (*Aphanilopterus*) *stabilinus* Richards	Neotropical	81	30	13	04	-	-	-	-	-	-
Polistes (*Epicnemius*) *subsericeus* de Saussure	Neotropical	81	30	13	04	-	-	-	-	-	-
Polistes (*Epicnemius*) *testacicolor* Bequaert	Neotropical	81	30	13	07	X	X	X	X	X	X
Polistes (*Epicnemius*) *thoracicus* Fox	Neotropical	81	30	13	04	-	-	-	-	-	-
Polistes (*Epicnemius*) *torresae* Silveira	Neotropical	81	07	13	04	-	-	-	-	-	-
Polistes (*Aphanilopterus*) *veracrucis* Richards	Neotropical	81	30	13	04	-	-	-	-	-	-
Polistes (*Aphanilopterus*) *versicolor* Olivier	Neotropical	81	30	13	07	X	-	X	-	-	-
Polistes (*Aphanilopterus*) *weyrauchorum* Willink	Neotropical	81	30	13	07	-	-	-	-	-	-
Polistes (*Aphanilopterus*) *xanthogaster* Bequaert	Neotropical	77	30	13	04	-	-	-	-	-	-

(16S), and nuclear 28S rRNA (28S), histone 3 (H3) and elongation factor 1-alpha (EF1-α) (table 1). Multiple sequence alignment was conducted in MA-FFT v.5 (Katoh et al., 2002). Default parameters were used for COI, H3, and EF1-a, for which the alignment is relatively trivial. For the three ribosomal loci, however, the E-INS-I algorithm was used, which is suitable for sequences with large unalignable regions (Katoh et al., 2005) (See Santos et al., 2015).

A total of 104 species were included in the original matrix; eight Old World species were excluded from the present analyses: *Polistes chinensis antennalis* Pérez, *P. formosanus* Sonan, *P. humilis* (Fabricius), *P. jokahamae* Radoszkowski, *P. nipponensis* Pérez, *P. riparius* Yamane and Yamane, *P. rothneyi* Cameron, and *P. variabilis* (Fabricius) because they were not scored for morphological characters.

Phylogenetic analyses: Three character matrices were assembled for phylogenetic analyses: (1) morphological data alone, scored for 104 species (Supplementary material S2, available online: https://doi.org/10.5531/sd.sp.50); (2) combined morphological and molecular, scored for 104 species; molecular data derived from a previously existing dataset for *Polistes* (Santos et al., 2015), thus with molecular data missing for 51 New World species (Supplementary material S3, available online: https://doi.org/10.5531/sd.sp.50); (3) combined morphological and molecular data, restricted to the 53 species for which molecular data was available. This third matrix was generated to allow for a total-evidence dataset with reduced missing data compared to the second matrix (Supplementary material S4, available online: https://doi.org/10.5531/sd.sp.50).

Phylogenetic analyses were undertaken using TNT version 1.5 (Goloboff et al., 2008a), under parsimony and implied weighting (Goloboff, 1993). We used the TNT script *setk.run*, written

by Salvador Arias (Instituto Miguel Lillo, San Miguel de Tucumán, Argentina) to calculate the appropriate value of the concavity constant (*k*) for each data partition (morphology + behavior and each molecular locus separately), following the reasoning of Goloboff et al. (2008b). For each matrix, tree search was performed using 100 replications, each with one hit to minimum length, 100 parsimony ratchet (Nixon, 1999) iterations (with upweighting probability of 8%, downweighting probability of 4%), 20 rounds of tree drifting, five rounds of tree fusing, and sectorial searching (Goloboff, 1999). Clade support was estimated using 10,000 pseudoreplicates of symmetric resampling (Goloboff et al., 2003) in TNT, reported as frequency differences (GC scores).

RESULTS

(1) Analysis of Morphological Data: Analysis of the morphological and behavioral characters (k = 26.748047) resulted a single most parsimonious tree (fig. 1), with Fit 34,5863 (table 2), consistency index (CI) = 0.12 and retention index (RI) = 0.57. *Polistes* (*Gyrostoma*) and *Polistes* (*Polistella*) were both monophyletic and recovered as sister groups, and *Polistes* (*Polistes*) was sister to a clade with all species from the New World. The clade with all New World *Polistes* was supported by eight synapomorphies, two of them uniquely derived: propodeal striae centrally strong, laterally evanescent (char. 63: state 2) and propodeal orifice elongate (67:2).

The topology supports the monophyly of the five subgenera proposed by Richards (1973), which were later synonimized with *Polistes* (*Aphanilopterus*) (Carpenter, 1996b). *Polistes* (*Onerarius*) was sister to all other subgenera, followed by *Polistes* (*Palisotius*). *Polistes*(*Fuscopolistes*) was sister to a clade including both *Polistes* (*Epicnemius*) and *Polistes* (*Aphanilopterus*) sensu Richards (1973). *Polistes* (*Onerarius*), comprising the single species *P. carnifex* (Fabricius) had 13 apomorphies, three of them uniquely derived: malar space longer than wide (18:2); base of metasomal sternum VII of male with anterior lobes (98:1); and larval galea bilobed with two apical sensilla on one of the lobes (133:1).

Polistes (*Palisotius*) (GC = 94) was supported by eight synapomorphies, one of them uniquely derived: epicnemial carina incomplete (45:2). In this clade, *P. palmarum* Bequaert was sister to (*P. major* Palisot de Beauvois + *P. paraguayensis* Bertoni).

Polistes (*Fuscopolistes*) (GC = 82) was supported by nine synapomorphies, one of which was uniquely derived: disc of metasomal sternum VII of male tuberculate (97:1). *P. poeyi* was recovered as sister of all other species of the subgenus, followed by *P. rossi* Bohart. The other species were divided into two clades: one with *P. carolina* Linnaeus (*P. fuscatus* (Fabricius) (*P. metricus* Say (*P. hirsuticornis* Buck + *P. parametricus* Buck))) and another with *P. rubiginosus* Lepeletier (*P. dorsalis* (Fabricius) (*P. flavus* Cresson (*P. bellicosus* Cresson (*P. apaches* de Saussure + *P. aurifer* de Saussure)))).

The clade *Polistes* (*Epicnemius*) + *Polistes* (*Aphanilopterus*) (GC = 72) was supported by eight synapomorphies, two of which were uniquely derived: tergum I conical in dorsal view, longer than wide (76:2) and anterior part of tergum I not enlarged (77:1).

Polistes (*Epicnemius*) (GC = 94) was supported by eight synapomorphies, three of which were uniquely derived: epicnemial carina complete (45:1); larval teeth robust (125:1); and larval

TABLE 2. Numerical data for the analysis of different data partitions. Columns: R, number of rearrangements tried, in millions; Fit, the best score; MPTs, number of most parsimonious trees recovered; Support, average group support recovered from 10,000 pseudoreplicates of symmetrical resampling. Support values are based on reported frequency differences (GC score) not absolute values.

Dataset	R	Fit	MPTs	Support
Morphology	6.964	34.58363	1	20.3
Combined – 53 taxa	1.017	703.17781	1	51.7
Combined – 104 taxa	6.837	783.99798	1	24.1

cuticle dark (129:0). *Polistes subsericeus* was recovered as sister to all other species of the subgenus, followed by a grade from *P. pacificus* Fabricius and *P. cinerascens* de Saussure to *P. candidoi* von Ihering. The remaining species were divided into two clades: one formed by (*P. actaeon* Haliday (*P. torresae* Silveira (*P. davillae* Richards + *P. geminatus* Fox))) + (*P. bicolor* Lepeletier (*P. billardieri* Fabricius (*P.bequaertianus* Willink + *P. obscurus* de Saussure))), and the other by (*P. angulinus* Richards (*P. atrox* Richards + *P. occipitalis* Ducke) (*P. claripenis* Ducke ((*P. melanosoma* de Saussure + *P. testaceicolor* Bequaert) (*P. moraballi* Richards (*P. thoracicus* Fox (*P. rufiventris* Ducke (*P. deceptor* + *P. niger* Brèthes)))))))).

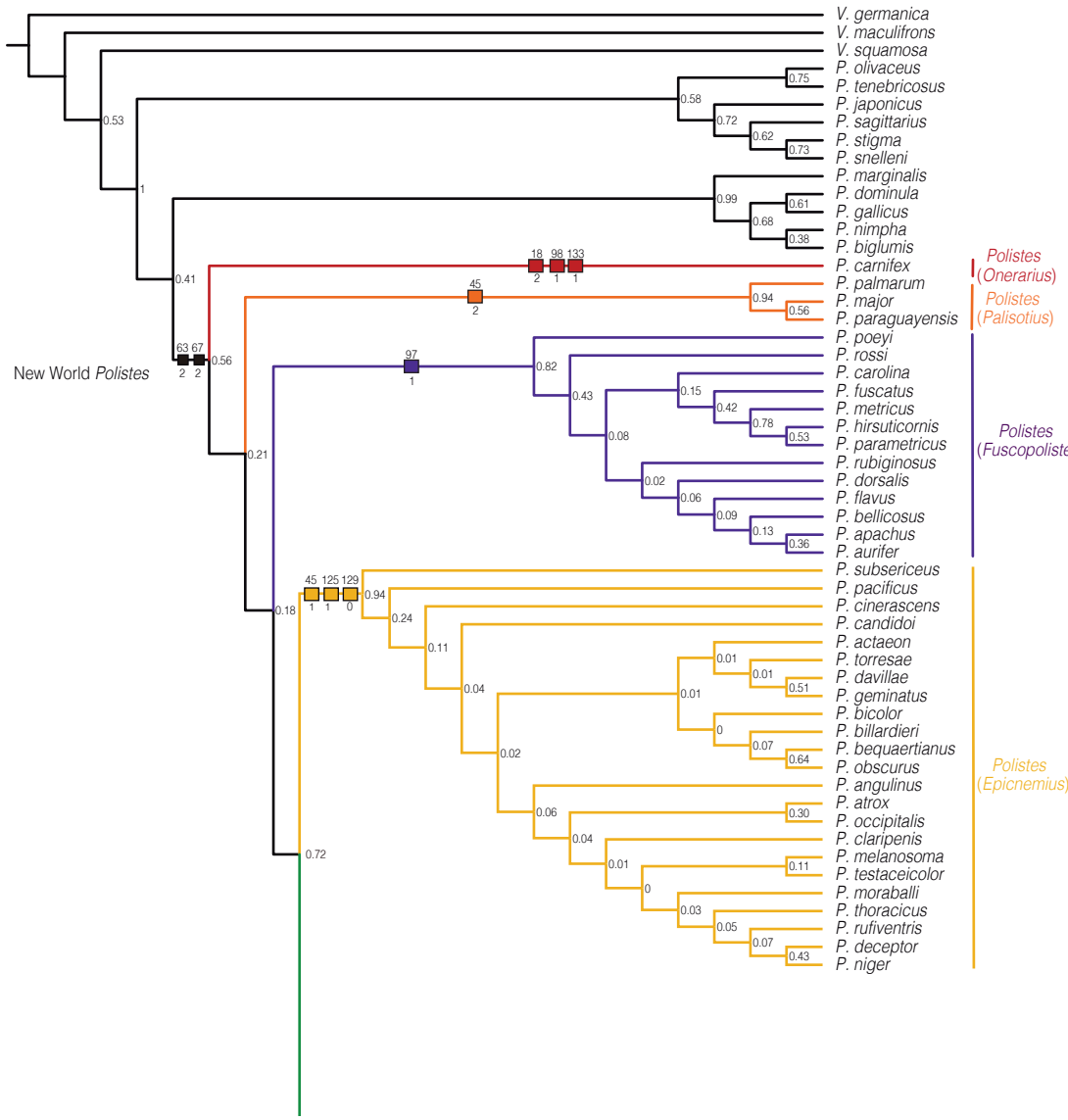
Finally, *Polistes* (*Aphanilopterus*) (GC = 93) was supported by eight synapomorphies, one of which was uniquely derived: malar space transverse (18:3). *Polistes oculatus* Smith was sister to all other species in the subgenus, with the remaining species divided into two large clades.

(2) Parsimony Combined Analysis, Complete Dataset: Analysis of the total-evidence dataset with 104 species (molecular data missing for 51 species) resulted in a single most parsimonious tree (fig. 2) with Fit 783.99798 (table 2). *Polistes* (*Polistes*) was recovered as sister to the other subgenera, and *Polistes* (*Gyrostoma*) formed by (*P. olivaceus* + *P. tenebricosus*), and *Polistes* (*Polistella*) formed by *P. stigma* + (*P. sagittarius* + (*P. japonicus* + *P. snelleni*)) were sister groups.

Within New World species, once again, all the subgenera defined by Richards (1973) were recovered as monophyletic, with higher support values than in the other analysis (GC = 90 to 96). The clade with all New World *Polistes* was supported by three morphological synapomorphies (GC = 96): occipital carina extending to middle of the eye (35:1), propodeal orifice elongate (67:2), and shape of nest comb subcircular (136:1). The clade comprising the species of *Polistes* (*Epicnemius*) was sister to all other subgenera, followed by a second clade comprising *Polistes* (*Onerarius*) and (*Polistes* (*Palisotius*) + *Polistes* (*Fuscopolistes*)), this clade being sister to *Polistes* (*Aphanilopterus*).

Polistes (*Epicnemius*) (GC = 95) was supported by one uniquely derived synapomorphies: epicnemial carina complete (45:1). *Polistes* (*Onerarius*) had one uniquely derived synapomorphy: malar space longer than wide (18:2). *Polistes* (*Palisotius*) (GC = 91) was supported by one uniquely derived synapomorphy: epicnemial carina incomplete (45:2). *Polistes* (*Fuscopolistes*) (GC = 96) was also supported by one uniquely derived synapomorphy: disc of metasomal sternum VII of male tuberculate (97:1). Finally, *Polistes* (*Aphanilopterus*) (GC = 90) was supported by two derived synapomorphies: malar space transverse (18:3) and bristles absent on the head in larva (121:0).

(3) Parsimony Combined Analysis, Restricted Dataset: Restricting the total-evidence dataset to include only species for which both molecular and morphological data were available



resulted in a matrix with 53 taxa, of which 39 were from the New World. The corresponding tree search recovered a single most parsimonious tree (fig. 3) with Fit 703.17781 (table 2). Clade support was in general much higher (average GC = 96 to 99). The clade with all New World *Polistes* was supported by four synapomorphies (GC = 96): occipital carina extending to middle of the eye (35:1), propodeal striae centrally strong, laterally evanescent (63:2) and propodeal orifice elongate (67:2) and galea bilobed, with two apical sensilla on one of lobes, or trilobed (133:1). The reduction in taxon sampling resulted in two clades: one including *Polistes* (*Onerarius*) sister to the single representative species of *Polistes* (*Palisotius*), *P. major*. The two subgenera were sister to *Polistes* (*Fuscopolistes*). The other clade including *Polistes* (*Epicnemius*) was recovered as sister to the *Polistes* (*Aphanilopterus*).

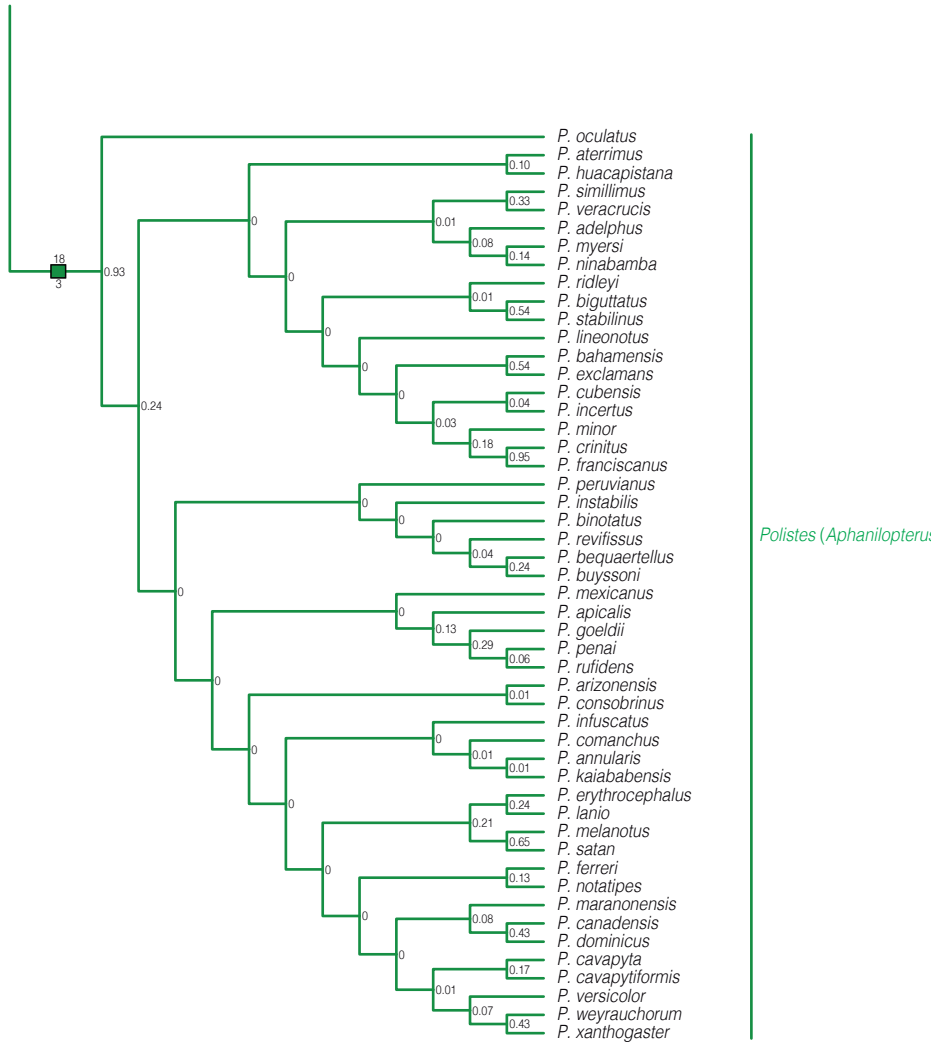
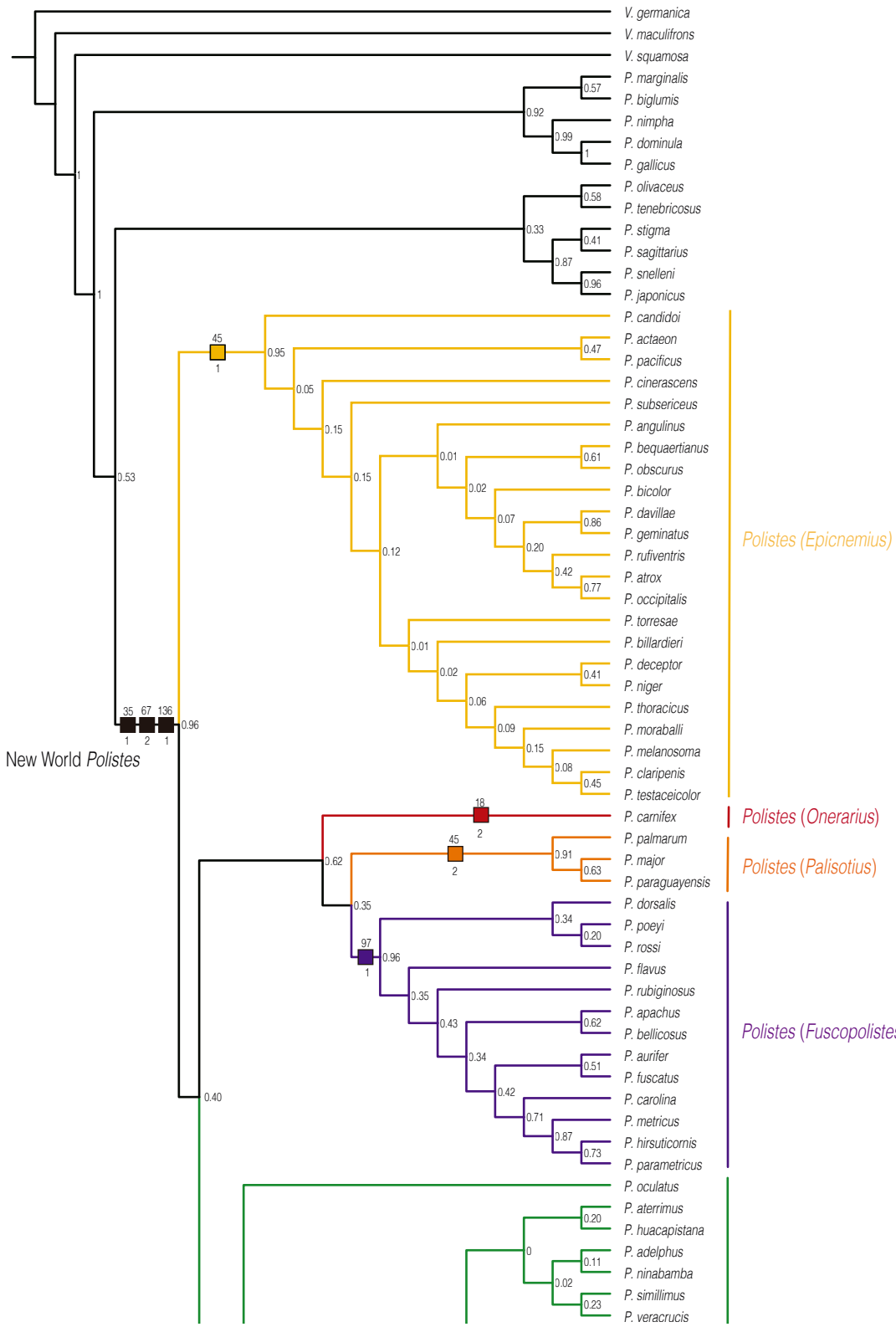


FIGURE 1. Single most parsimonious tree obtained in the analysis of morphological and behavioral data for 101 species of *Polistes* (*opposite page and continued above*). Node numbers represent support values from symmetrical resampling.

Polistes (*Onerarius*) was supported by four uniquely derived synapomorphies: malar space longer than wide (18:2); base of metasomal sternum VII of male with anterior lobes (98:1); larval cuticle mostly clear, with dark bands on the head (129:2), and shape of nest comb subcircular (136:1). *Polistes* (*Palisotius*) was supported by one uniquely derived synapomorphy: epicnemial carina incomplete (45:2). *Polistes* (*Fuscopolistes*) (GC = 99) was supported by two uniquely derived synapomorphies: clypeus narrowly separated from eye in male (92:2) and disc of metasomal sternum VII of male tuberculate (97:1). *Polistes* (*Epicnemius*) (GC = 99) was supported by three uniquely derived synapomorphies: epicnemial carina complete (45:1); larval teeth robust (125:1); and larval cuticle dark (129:0). Finally, *Polistes* (*Aphanilopterus*) (GC = 98) was supported by one uniquely derived synapomorphy: malar space transverse (18:3).


V. germanica
V. maculifrons
V. squamosa
P. marginalis
P. biglumis
P. nimpha
P. dominula
P. gallicus
P. olivaceus
P. tenebricosus
P. stigma
P. sagittarius
P. snelleni
P. japonicus
P. candidoi
P. actaeon
P. pacificus
P. cinerascens
P. subsericeus
P. angulinus
P. bequaertianus
P. obscurus
P. bicolor
P. davillae
P. geminatus
P. rufiventris
P. atrox
P. occipitalis
P. torresae
P. billardieri
P. deceptor
P. niger
P. thoracicus
P. moraballi
P. melanosoma
P. claripenis
P. testaceicolor
P. carnifex
P. palmarum
P. major
P. paraguayensis
P. dorsalis
P. poeyi
P. rossi
P. flavus
P. rubiginosus
P. apachus
P. bellicosus
P. aurifer
P. fuscatus
P. carolina
P. metricus
P. hirsuticornis
P. parametricus
P. oculatus
P. aterrimus
P. huacapistana
P. adelphus
P. ninabamba
P. simillimus
P. veracrucis
Polistes (Epicnemius)
Polistes (Onerarius)
Polistes (Palisotius)
Polistes (Fuscopolistes)
New World Polistes

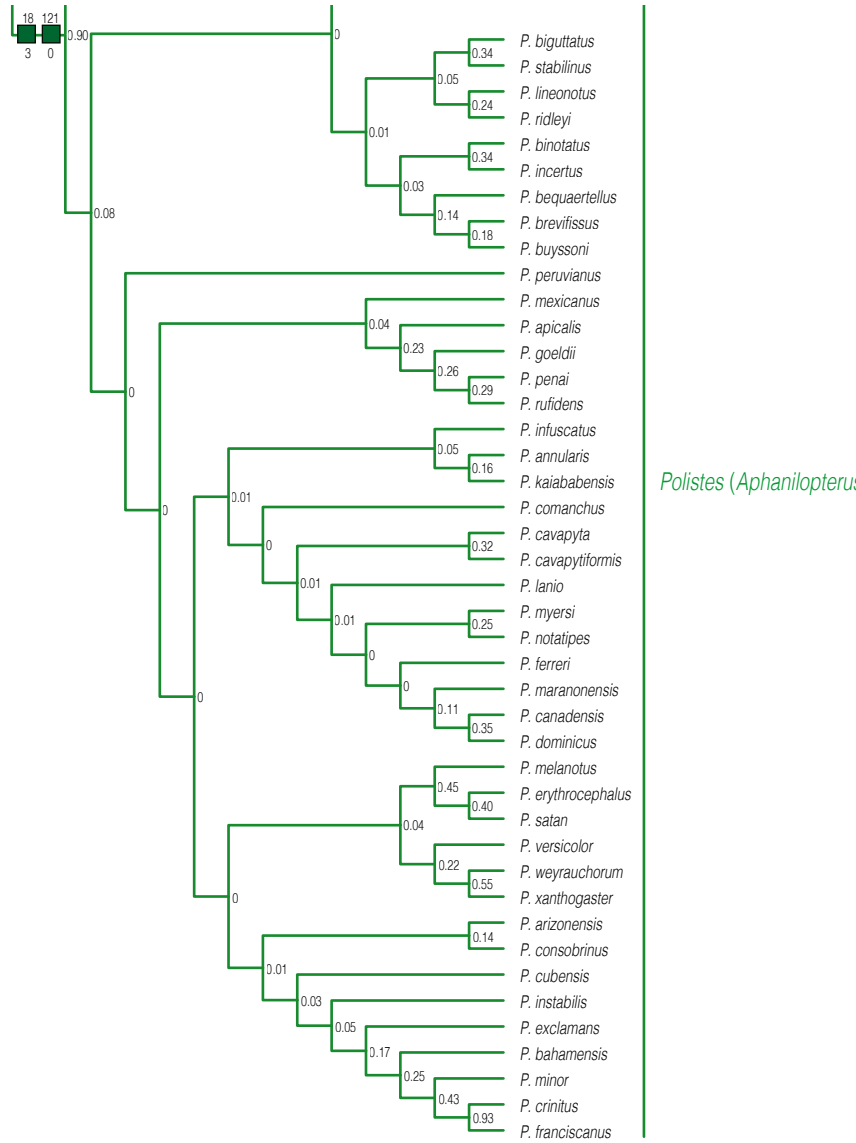


FIGURE 2. Single most parsimonious tree obtained in the analysis of morphological, behavioral and molecular data for 101 species of *Polistes* (*opposite page and continued above*). Node numbers represent support values from symmetrical resampling, reported as absolute frequencies.

DISCUSSION

Morphological Diversity in *Polistes*

Polistes has been notorious for its homogeneity in external morphology (Richards, 1978; Carpenter, 1996a, 1996b; Arévalo et al., 2004). Previous work on the phylogeny of the genus relied on relatively few morphologial characters: even when augmented by scoring of behavioral traits, most previous studies never coded more than 48 morphological traits. Pickett and

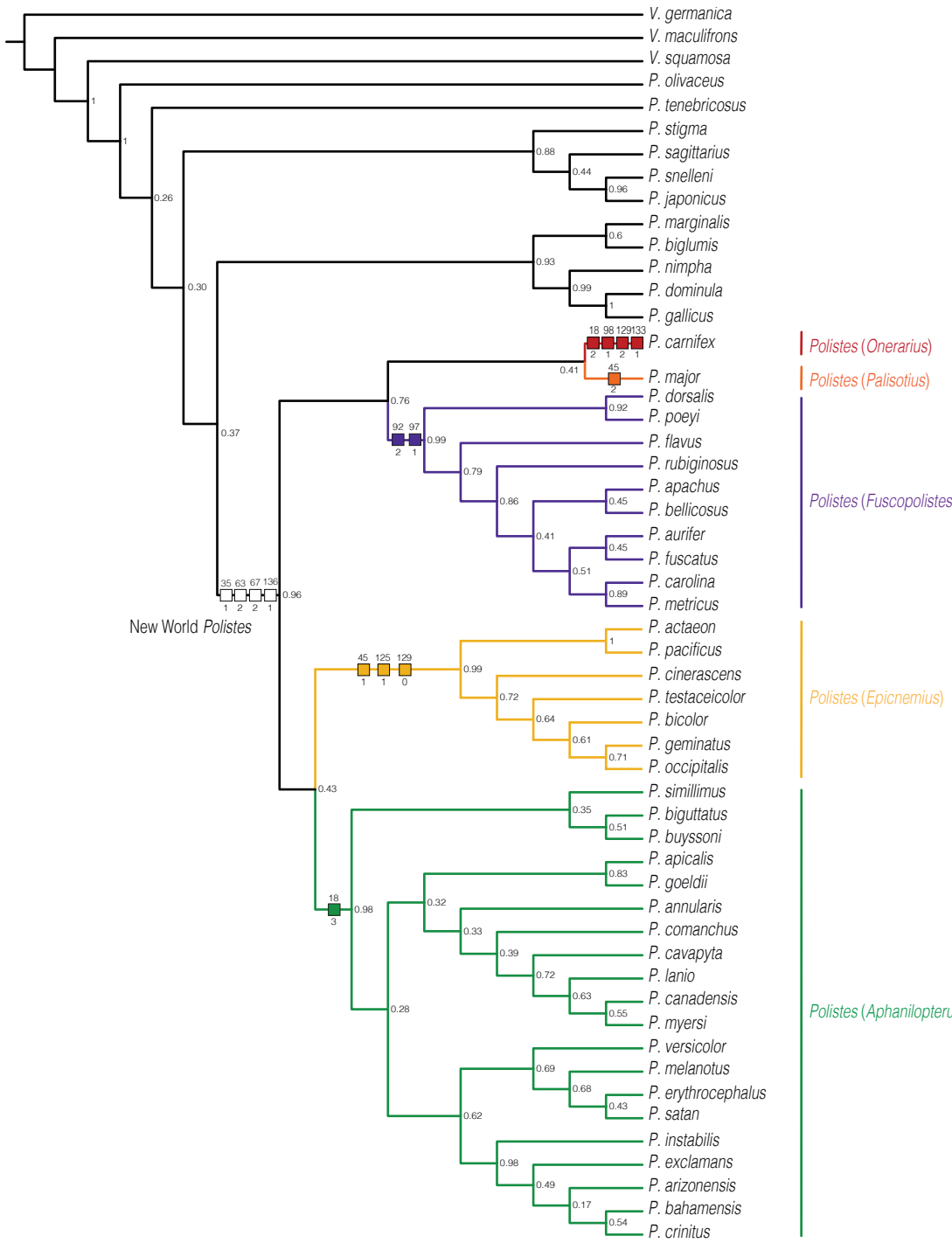


FIGURE 3. Single most parsimonious tree obtained in the analysis of morphological, behavioral, and molecular data, with the dataset restricted to the 53 species of *Polistes* for which molecular data was available. Node numbers represent support values from symmetrical resampling, reported as absolute frequencies.

Carpenter (2010), investigating the origins of eusociality in Vespidae, used 333 morphological and behavioral characters, but most of those were not informative for the internal phylogeny of *Polistes*. Historically, it has resulted in generally poorly resolved phylogenies (Arévalo et al., 2004; Pickett and Wenzel, 2004), although the adoption of DNA sequences as an additional source of characters has contributed to ameliorate this scenario. Obtaining DNA-grade specimens for a comprehensive sample of a speciose and widespread genus such as *Polistes*, however, has been challenging. The largest phylogeny of *Polistes* to date (Santos et al., 2015) included 58 species of the genus, of which 37 were from the New World. Hence, the generation of more extensive phenotypic datasets may be an important alternative to include species for which DNA-grade specimens are unavailable or hard to obtain.

Our phenotypic dataset recovered the five subgenera of New World *Polistes* as monophyletic; the same result was observed in the total-evidence phylogeny, both for the complete (104 species) and restricted (53 species) datasets. The relationships among the five subgenera, however, differed across our three analyses.

Some of the morphological characters seem to have a stronger phylogenetic signal than others, that is, have higher CI and RI values, because they are determinant in subgeneric recovery and in some groups of species. The most notable synapomorphy of *Polistes* is the conical shape of the first tergum of the metasoma, different from the other genera of Polistinae. However, we observed some variation in the shape of this tergum, which revealed an important character among the *Polistes* species. The species of *P.* (*Fuscopolistes*), *P.* (*Palisotius*) and *P.* (*Onerarius*) have the tergum as wide as long, or sometimes even wider than long, abruptly widening anteriorly; while in *P.* (*Aphanilopterus*) and *P.* (*Epicnemius*) tergum I is longer than wide, gradually widened toward the posterior portion.

The epicnemial carina on the mespisternum is present and well developed in all *P.* (*Epicnemius*) species (45:1). In *P.* (*Fuscopolistes*) it is present in few species but generally reduced (45:2). The carina is completely absent in *P.* (*Aphanilopterus*), *P.* (*Palisotius*) and *P.* (*Onerarius*) (45:0); some species of these subgenera may have a weak groove in the mesepisternum in place of the epicnemial carina.

The dorsal groove of the mesepisternum is present and well developed in all species of *P.* (*Aphanilopterus*), *P.* (*Palisotius*), *P.* (*Onerarius*) and *P.* (*Fuscopolistes*), the single exception being *P.* (*Fuscopolistes*) *poyei,* for which the dorsal groove is very weak and present only at the anterior part (44:2). For *P.* (*Epicnemius*) the dorsal groove is generally absent altogether (44:0), or when present, weak and developed only in the anterior part (44:2).

The clypeus dimensions and the extent of contact between the clypeus and the eyes also help in the separation of groups of species within the subgenera. In *P.* (*Epicnemius*) *thoracicus* the clypeus is narrowly separated from the eyes (11:2). In some species of *P.* (*Fuscopolistes*), *P.* (*Palisotius*), *P.* (*Onerarius*), the clypeus and eyes touch for an extent shorter than the width of the antennal socket (11:1); in most species of *P.* (*Aphanilopterus*) and *P.* (*Epicnemius*) the clypeus and eyes touch for an extent equal to or longer than than the width of the antennal socket (11:0). Likewise, *P.* (*Fuscopolistes*), *P.* (*Palisotius*), *P.* (*Onerarius*) and *P.* (*Aphanilopterus*) usually have the clypeus as long as wide (1:0), sometimes wider, while for some species of *P.* (*Epicnemius*) the clypeus is longer than wide (1:1).

In relation to the occipital carina (34, 35), usually in the species of *P*. (*Epicnemius*) we find the occipital carina more developed, extending to the region of the gena (35:2); in the other subgenera, the occipital carina usually presents on the central region of the head (36:0), to the middle of the eyes (35:1). In relation to the pronotal carina (37, 38), usually in the species of *P*. (*Epicnemius*) we find the pronotal carina a little sharper and more developed (38:1), reaching the end of the pronotum (37:1) or to the humeral region (37:2); in the other subgenera, the pronotal carina may be strong but rounded (30:0). Some species of *P*. (*Epicnemius*) have a central projection in the gena, becoming wider than the eye (in lateral view) and the humerus projecting laterally (39:1,2), while in most *Polistes* species, the humerus is not projected (40:0), the pronotum being almost entirely rounded.

The propodeal striae separate large groups in *Polistes*. For *P*. (*Fuscopolistes*), *P*. (*Palisotius*) and *P*. (*Onerarius*) the striae are strong and well marked (63:0), generally developed laterally, in *P*. (*Aphanilopterus*) a large group of species has these striae developed up to the border of the propodeum, however, some species have strong striae only in the center (63:1); in *P*. (*Epicnemius*) these striae may be weaker or evanescent in the center and laterally on the propodeum (63:2).

For males, the clypeus (92, 93) is usually in contact with the eye (92:0,1) in *P*. (*Aphanilopterus*) and in *P*. (*Palisotius*), however, in some species of *P*. (*Epicnemius*), *P*. (*Fuscopolistes*) and *P*. (*Onerarius*) the clypeus is separated from the eye (92:2, 3). The male's antenna (81–93) has important morphological differences for the phylogeny, generally the last flagellomeres on antenna apex can be fine (91:0) or coiling (91:1) in some *P*. (*Fuscopolistes*) and *P*. (*Epicnemius*) species.

The male genitalia were also a source of morphological characters. Previous work on vespid taxonomy indicated the possibility of the use of male genitalia in phylogenetic matrices (Andena and Carpenter, 2012; Hermes et al., 2014). More recently, Somavilla et al. (2018) described the genitalia morphology for many species of New World *Polistes*, highlighting a considerable number of variable characters of potential use in phylogenetic analyses. In the paramere, the apical spine and the apical bristles show variation across *Polistes* species, as does the length/width ratio. Structures such as the aedeagus and the digitus helped to separate large species groups; the species of *P*. (*Fuscopolistes*) have a more robust aedeagus (111:0), with the teeth in the apical portion more developed (118:3) than in species of *P*. (*Aphanilopterus*), *P*. (*Epicnemius*), *P*. (*Palisotius*), and *P*. (*Onerarius*); differences in the penis valve (113, 114) and apodeme (119, 120) were also observed. The digitus in *P*. (*Fuscopolistes*) has the apical process reduced (104:1) and punctate throughout (105:0). The species of *P*. (*Aphanilopterus*), *P*. (*Epicnemius*), *P*. (*Palisotius*), and *P*. (*Onerarius*) have the apical process well developed (104:0), sometimes with the apex varied from rounded to pointed, with reduced punctation usually placed laterally (105:1). A more detailed discussion about characters in the male genitalia of *Polistes* can be found in Somavilla et al. (2018).

Comparison with Previous Studies

All our analyses, using either solely phenotypic traits or combined phenotypic and molecular data, recovered the species of *Polistes* from the New World as a monophyletic group. The same result

was also found previously in the analyses performed by Arévalo et al. (2004), Pickett and Wenzel (2004), Pickett et al. (2006) and Santos et al. (2015), all of which had used a smaller sample of New World taxa. Pickett and Carpenter (2010), in contrast, recovered the New World species as paraphyletic, with the Old World species *P. jokahamae* and P. *tenebricosus* nested within the *P.* (*Epicnemius*) clade. The latter study was the first to include molecular data from loci other than COI, adding sequences for three ribosomal loci (12S, 16S, and 28S). At the same time, the morphological matrix in Pickett and Carpenter (2010) was focused mostly on resolving the higher-level phylogeny of Vespidae, with few characters informative for *Polistes*. Santos et al. (2015) added data from two protein-coding loci (H3 and EF1-α) and adopted the phenotypic characters from Pickett et al. (2006), which focused on the variation found among *Polistes* species. While their total-evidence tree yielded a monophyletic group of New World *Polistes*, the tree based on molecular data alone still found three Old World species nested in *P. (Epicnemius)*. However, this relationship disappeared when only protein-coding molecular data was considered, once again recovering the New World species as monophyletic. Hence, it is possible that the placement of *P. jokahamae* and related species in the New World clade may be an artifact generated by unalignable regions in ribosomal loci.

Our results also strongly support the validity of the five subgenera proposed by Richards (1973); for the total-evidence analyses, support for the monophyly of all subgenera represented by multiple species was almost always >0.90, and each subgenus was supported by at least one uniquely derived synapomorphy.

In a previous analysis based on morphological characters, Carpenter (1996b) had recovered *P.* (*Aphanilopterus*) and *P.* (*Epicnemius*) as paraphyletic and, largely based on that result, suggested synonymizing all New World genera with *Aphanilopterus*. Pickett and Wenzel (2004) added COI sequences to their phenotypic dataset and recovered a similar result, with species from several subgenera nested within a clade composed mostly by species of *P.* (*Aphanilopterus*). In the same year, however, Arévalo et al. (2004), found a different result combining COI sequences with microsatellite data and morphological characters. In their analyses, the New World species grouped in a five-clade polytomy, with each lineage corresponding to one of Richards's (1973) subgenera.

Later, Pickett et al. (2006) combined the nonoverlapping COI fragments used by Arévalo et al. (2004) and Pickett and Wenzel (2004) and a modified phenotypic character set. Their analyses recovered a topology consistent with five subgenera, but the authors preferred to continue to recognize a single New World subgenus "until anything resembling phylogenetic stability has been reached." Subsequent analyses incorporated further molecular data from ribosomal (Pickett and Carpenter, 2010) and nuclear protein-coding (Santos et al., 2015) loci; both studies recovered *P.* (*Onerarius*) nested within the *P.* (*Fuscopolistes*) clade, but it is hard to determine whether this was a result from the inclusion of more molecular data, since in both studies *P. carnifex* was represented only by COI sequences. At any rate, the coding of additional phenotypic characters for this study seems to have been instrumental in recovering *P.* (*Onerarius*) as distinct.

The relationship among subgenera has been unstable not only among our three analyses and datasets, but among previous works as well, with almost every possible combination of relationships found across various studies (fig. 4). So far, the only seemingly well-established

result, as shown by most total-evidence analyses, is the close relationship between *P*. (*Onerarius*) and *P*. (*Fuscopolistes*). Most recent studies have also shown *P*. (*Fuscopolistes*) and *P*. (*Aphanilopterus*) more closely related to each other than to *P*. (*Epicnemius*), with the placement for *P*. (*Palisotius*) the most unstable across various analyses.

Overall, studies since Pickett et al. (2006) have progressively increased the amount of data and the number of taxa used for inferring the phylogeny of New World species of *Polistes*. The results have supported the recognition of at least four of the five subgenera of Richards (1973), with support for *P*. (*Onerarius*) still equivocal in some of the past studies. Herein we have greatly expanded the phenotypic dataset, including almost every species occurring in the New World, and found stronger support for a classification into five subgenera. While additional data are needed to elucidate the relationships among subgenera and future studies may change the status of *P*. (*Onerarius*), we believe we have approached the semblance of phylogenetic stability required by Pickett et al. (2006) to make changes to the sugeneric classification. Hence, we propose the revalidation of the five subgenera proposed by Richard s (1973) as monophyletic and diagnosable groups, as follows.

SYSTEMATIC ACCOUNTS

Polistes (*Onerarius*) Richards, 1973, status rev.

Onerarius Richards, 1973: 94, 101. Type species: *Vespa camifex* Fabricius, 1775, by original designation.

Included species: *P. carnifex*.

Diagnosis (morphological synapomorphies in boldface):Body large, about 30 mm or more in length. Color light brown to yellowish. **Malar space longer than wide.** Clypeus distinctly separated from the eye, or when in contact, touching the lower edge of the eye. Pronotal fovea present. Epicnemial carina absent. Mesepisternal dorsal groove strong and complete. Propodeal striae strong, surpassing the metapleural border. Tergum I slightly wider than long, abruptly widened in lateral view. **Last sternum laterally with two tubercles.** Male genitalia with robust aedeagus, teeth on apical portion well developed and strong; penis valve dilated and nonbilobed; digitus with developed apical process and rounded anteroventral lobe.

Polistes (*Palisotius*) Richards, 1973, status rev.

Palisotius Richards, 1973: 95, 96, 100. Type species: *Polistes major* Palisot de Beauvois, 1818, by original designation.

Included species: *P. major*, *P. palmarum*, and *P. paraguayensis*.

Diagnosis: Body large, about 25 mm long. Color usually dark yellow with brown marks or completely brown. Tergum I slightly wider than long, abruptly widened in lateral view. Malar space as long as wide or weakly transverse. Clypeus in female touching eye for an extent smaller than diameter of antennal socket; in males, clypeus touching the ventral edge of the eye. Pronotal

fovea present. **Epicnemial carina, when present, incomplete.** Mesepisternal dorsal groove conspicuous, complete. Propodeal striae strong, developed at the most to propodeal margins. Posterior sternum laterally without tubercle. Male genitalia with aedeagus thin, teeth on apical portion intermediate; penis valve dilated, nonbilobed or weakly bilobed; digitus with developed apical process and rounded anteroventral lobe.

Polistes (*Fuscopolistes*) Richards, 1973, status rev.

Fuscopolistes Richards, 1973: 95, 96, 100. Type species: *Vespa fuscata* Fabricius, 1793, by original designation.

Included species: *P. apachus*, *P. aurifer*, *P. bellicosus*, *P. carolina*, *P. dorsalis*, *P. flavus*, *P. fuscatus*, *P. hirsuticornis*, *P. metricus*, *P. parametricus*, *P. poeyi*, *P. rossi*, and *P. rubiginosus.*

Diagnosis: Body large, about 25 mm in length, except for *P. poeyi* which is smaller, about 15 mm. Species with varying pigmentation: entirely brown or yellowish, or with extensive spots on mesosoma and metasoma. Malar space as long as wide. **Clypeus** in female touching eye for an extension shorter than diameter of antennal socket; **in male, strictly separated from eyes.** Pronotal fovea present. Epicnemial carina absent. Mesepisternal dorsal groove distinct, sometimes incomplete. Propodeal striae strongly marked on center, laterally weaker but reaching propodeal margin laterally. Tergum I slightly wider than long, abruptly widened in lateral view. Posterior sternum with tubercles. Male genitalia with aedeagus strong, teeth on the apical portion developed and prominent, generally with smaller teeth intercalated; **penis valve dilated and strongly bilobed, digitus with reduced apical process and pointed anteroventral lobe,** except in *P. poeyi*

Polistes (*Epicnemius*) Richards, 1973, status rev.

Epicnemius Richards, 1973: 96, 102. Type species: *Polistes bicolor* Lepeletier, 1836, by original designation.

Included species: *P. actaeon*, *P. angulinus*, *P. atrox*, *P. bequaertianus*, *P. bicolor*, *P. billardieri*, *P. boharti*, *P. candidoi*, *P. cinerascens*, *P. claripennis*, *P. davillae*, *P. deceptor*, *P. geminatus*, *P. melanosoma*, *P. moraballi*, *P. niger*, *P. obscurus*, *P. occipitalis*, *P. pacificus*, *P. rufiventris*, *P. subsericeus*, *P. testaceicolor*, *P. thoracicus*, and *P. torresae*.

Diagnosis: Body of moderate to large size, 10–25 mm in length. Species with varying pigmentation: black or yellowish, with extensive spots on mesosoma and metasoma. Malar space slightly wider than long. Clypeus in female touching eye for an extent equal or greater than diameter of antennal socket; in male usually touching eye except for *P. thoracicus*. Pronotal fovea present or absent. **Epicnemial carina complete and strongly distinct.** Mesepisternal dorsal groove usually present and complete, sometimes incomplete or absent. Propodeal striae weak, sometimes evanescent, rarely with stronger striae restricted to central concavity. Tergum I longer than wide, gradually widened in lateral view. Last sternum without tubercles. Male genitalia with

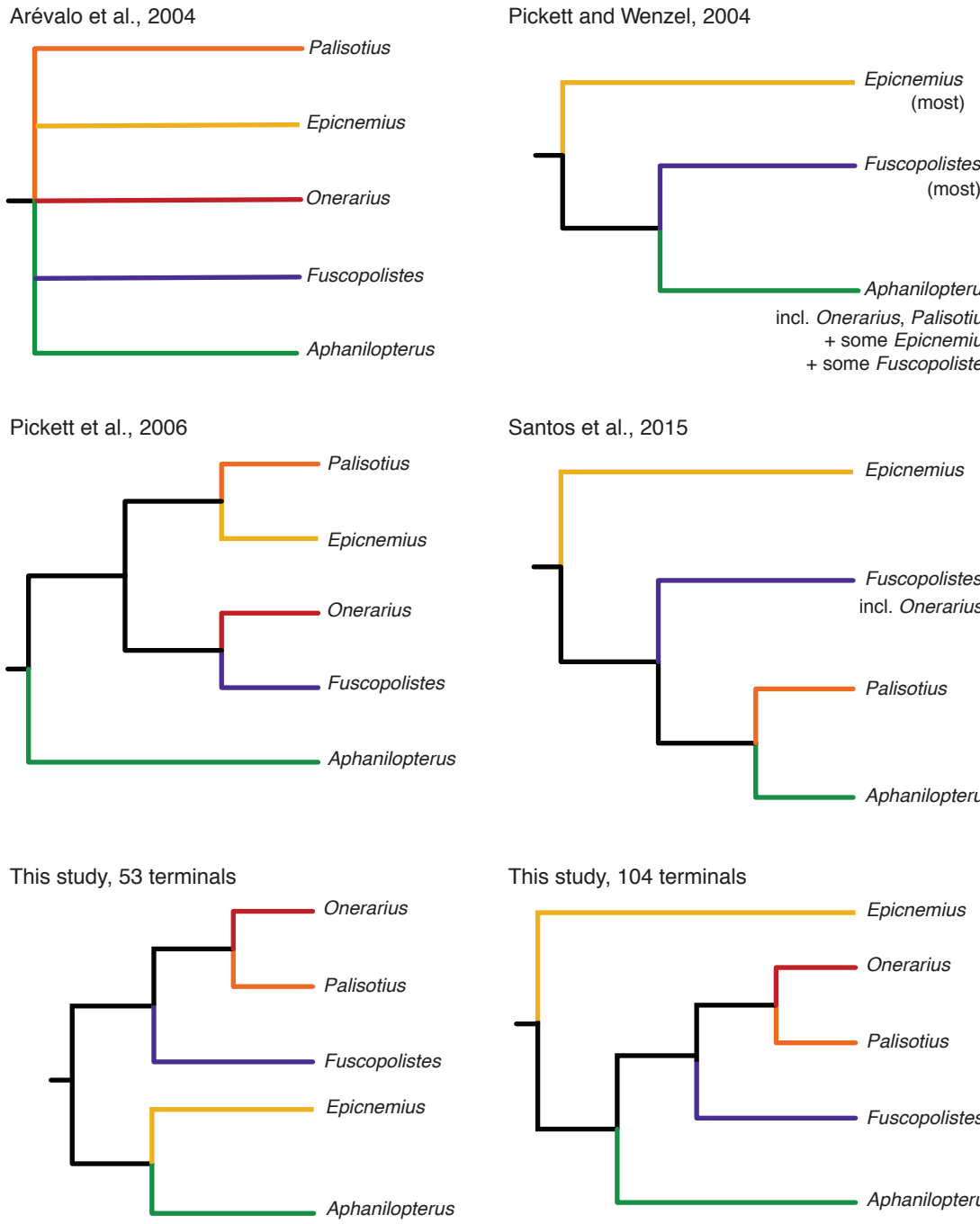


FIGURE 4. Summary subgenera relationships for New World *Polistes* obtained in our analyses compared to previous studies.

aedeagus slender, teeth on the apical portion reduced or evanescent, penis valve little dilated and not or only weakly bilobed, digitus with developed apical process and rounded anteroventral lobe.

Polistes (*Aphanilopterus*) Meunier, 1888

Aphanilopterus Meunier, 1888: 302. Type species: *Aphanilopterus vagabundus* Meunier, 1888 [= *Vespa lanio* Fabricius, 1775], by monotypy.

Polistarchus Richards, 1973: 94, 95, 101. Type species: *Vespa canadensis* Linnaeus, 1758, by original designation. Syn. n.

Included species: *P. adelphus*, *P. annularis*, *P. apicalis*, *P. arizonensis*, *P. aterrimus*, *P. bahamensis*, *P. bequaertellus, P. biguttatus*, *P. binotatus*, *P. brevifissus, P. buyssoni*, *P. canadensis*, *P. cavapyta, P. cavapytiformis*, *P. comanchus*, *P. consobrinus*, *P. crinitus*, *P. cubensis*, *P. dominicus*, *P. eburneus*, *P. erythrocephalus*, *P. exclamans*, *P. ferreri*, *P. franciscanus*, *P. goeldii*, *P. huacapistana*, *P. incertus*, *P. infuscatus*, *P. instabilis*, *P. kaiababensis*, *P. lanio*, *P. lineonotus*, *P. maranonensis*, *P. melanotus*, *P. mexicanus*, *P. minor*, *P. myersi*, *P. ninabamba*, *P. notatipes*, *P. oculatus*, *P. penai*, *P. peruvianus*, *P. pseudoculatus*, *P. ridleyi*, *P. rufidens*, *P. satan*, *P. simillimus*, *P. stabilinus*, *P. veracrucis*, *P. versicolor*, *P. weyrauchorum*, and *P. xanthogaster*.

Diagnosis: Body of moderate to large size, 10–25 mm in length, some species large, 30 mm in length. Species with varying pigmentation: totally dark brown or black to yellowish, or with extensive yellow or reddish spots. **Malar space transverse**. Clypeus in female touching eyes for an extent equal or greater than diameter of antennal socket; in males usually touching eyes. Pronotal fovea present but somewhat reduced in some species. Epicnemial carina completely absent. Mesepisternal dorsal groove conspicuous and complete, except for *P. penai* and *P. oculatus* in which is weak and incomplete. Propodeal striae varied, sometimes mostly weak, stronger only on central concavity, sometimes strong and extending to propodeal margin. Tergum I longer than wide, gradually widened in lateral view. Last sternum without tubercles. Male genitalia with aedeagus slender, teeth on the apical portion reduced, sometimes medium sized; penis valve dilated and nonbilobed or weakly bilobed, digitus with developed apical process and rounded anteroventral lobe.

Key to the New World *Polistes* Species

The dichotomous key is based on female morphological characters. Geographical distribution is summarized.

1. Metasoma tergum I more enlarged, wider than long or as wide as longe in dorsal view, dilated abruptly in lateral view ……..……. 2
– Metasoma tergum I not enlarged, longer than wide in dorsal view, dilated gradually in lateral view .....…….....19
2. Malar space longer than wide; clypeus narrowly separated from the eyes, or when in contact just by tapping on the margin of the eyes; color light brown to dark yellow; generally, more robust species, with 30 mm long or more …….....…….. *P.* (*Onerarius*) – *P. carnifex* (from southern United States to Argentina)

– Malar space as long as wide or weakly transverse; clypeus always in contact with the eyes, usually the part in contact with the eye is less than or equal to the diameter of the antenal socket size..... 3

3. Mesepisternum with epcinemial carina incomplete; last visible metasoma sternum without a tubercle.....*P.* (*Palisotius*) – 4

– Mesepisternum without an epcinemial carina, some species have a small groove but no carina; last visible metasoma sternum with a central tubercle.....*P.* (*Fuscopolistes*) – 6

4. Pronotum humeri projected laterally, in dorsal view; epicnemial groove absent; color dark brown with reddish aspect, with few yellow markings; scutum black with large brown spots; propodeum dark brown with two broad yellow stripes laterally ..... *P. paraguayensis*
(in central-south Brazil, Argentina and Paraguay)

– Pronotum humeri not projected laterally, pronotum rounded on the sides, in dorsal view; with a weak epicnemial groove; pigmentation light brown or yellowish without reddish aspect; propodeum with uniform color.....5

5. General color yellow or dark brown; when yellow, with some dark-brown spots on the base of tergum and legs; when brown, almost completely dark brown, without spots of other color; scutum completely dark brown in both forms; terga I–II with evident bristles; dark-brown wings.....*P. major*
(from the United States to central Brazil)

– General color light brown; without black spots and reduced yellow marks in pronotum; terga I–II without evident bristles; light-brown wings.....*P. palmarum*
(southwestern United States and Mexico)

6. Dorsal groove evanescent, present only in initial dorsal portion; generally small, 15 mm long .....*P. poeyi*
(Cuba, Haiti, and Dominican Republic)

– Dorsal groove developed, usually complete; usually more robust, larger than 20 mm long.....7

7. Color of metasoma entirely brown or black, without evident yellow marks but when present are reduced to an apical yellow band in tergum I.....8

– Color of metasoma entirely yellow or brown; when brown with large yellow marks and may have apical yellow band in the terga I–VI.....13

8. Mesosoma black or extensively dark brown; metasoma completely black, sometimes terga I–II with dark-brown aspect, and may or may not have apical yellow bands.....9

– Mesosoma brown; metasoma completely brown.....11

9. Scutum dark brown, with two black stripes in the sides; terga I–II black with dark-brown aspect, terga III–VI black.....*P. metricus*
(United States)

– Scutum completely black; terga I–VI black, usually tergum I with an apical yellow band.....10

10. Tergum I with a longer apical yellow band; punctation a little deeper and stronger with distinct punctures on mesosoma and clypeus.....*P. parametricus*
(United States)

– Tergum I with a narrow apical yellow band; punctation very small and shallow, without distinct punctures on mesosoma and clypeus.....*P. hirsuticornis*
(United States)

11. Propodeal striae strongly marked and extending to the metanotum border; clypeus punctation deep and spaced; usually more robust, about 25 mm long.....*P. rubiginosus*
(United States)

– Propodeal striae strong only on the center and weak on the sides, not extending to the metanotum border; clypeus with a small and shallow punctation; usually smaller species, less than 23 mm longer…….....2

12. General color brown, with a few black marks when they are present; dorsal groove weak…… …….....……*P. carolina* (United States)

– General color brown, with large black marks on the tergum and legs; sometimes general color dark-brown, almost black; dorsal groove strongly marked..….....*P. fuscatus* (in part) (southern Canada and the United States)

13. Metasoma yellow or brown with extensive, poorly defined yellow spots covering almost entirely...14

– Metasoma brown with well-defined apical yellow bands…….....…16

14. Color of the head and mesosoma dark-brown with some black marks on the vertex and scutum; terga I–III brown at the base and almost entirely colored with irregular yellow spots, terga IV–VI yellow……...…….....……..……*P. aurifer* (southern Canada, United States and Mexico)

– Color of the head and mesosoma yellow without black marks; tergum I completely yellow or with brown spots, terga II–VI entirely yellow…….....…...…15

15. Scutum with large light-brown marks; tergum I with brown base and apical region more yellow; wings hyaline to light brown…….....…...…*P. apachus* (United States and Mexico)

– Scutum completely yellow or yellow with one central brown mark; tergum I completely yellow; wings reddish black.....…….....……..…*P. flavus* (United States and Mexico)

16. Clypeus touching the eyes by a distance equal to the diameter of antennal socket..….....17

– Clypeus touching eyes by a distance shorter than the diameter of antennal socket.….....18

17. General color light brown with small black marks; scutum brown with a narrow central mark and two black side stripes; mesepisternum brown; vertex black only on the region of the ocelli; coxae brown……...…….....…*P. bellicosus* (United States)

– General color dark brown with large black marks; scutum completely black; mesepisternum black; vertex largely black; coxae black…….....…*P. fuscatus* (in part) (southern Canada and the United States)

18. General color dark brown, with larger yellow marks; usually a yellow mark on the region of the gena; scutellum and metanotum with yellow markings; propodeum with two yellow lateral stripes …….....…*P. dorsalis* (southern United States, Mexico to Costa Rica)

– General color light brown, appearance paler; yellow marks reduced; gena completely light brown; scutellum and metonotum brown; propodeum brown without two yellow lateral stripes……..….....*P. rossi* (southern United States and Mexico)

19. Mesepisternum with an epicnemial carina, sometimes incomplete and sometimes weak, but always present…….....…*P.* (*Epicnemius*) – 20

– Mesepisternum without an epicnemial carina.....……..…*P.* (*Aphanilopterus*) – 43

20. Mesepisternum with a dorsal groove, sometimes incomplete and sometimes weak, but always present…….....……..…21

– Mesepisternum without a dorsal groove ……26
21. Clypeus separated from the eyes; general color brown, mesepisternum largely black……*P. thoracicus*
(central Brazil, Argentina and Paraguay)
– Clypeus always in contact with the eye……22
22. Clypeus in contact with the eyes for a distance shorter than the diameter of the antennal socket; humeri weakly projected on the sides; pronotum more rounded……23
– Clypeus in contact with the eyes for a distance equal or larger than the diameter of antennal socket; humeri strongly projected on the sides; pronotum quadrate, with a central projection ……24
23. Scutum black; mesosoma with large yellow marks; terga I–VI with apical yellow bands; reduced pubescence, when present, whitish in appearance; wings hyaline to light brown……*P. billardieri*
(from northern Colombia to southern Brazil and Argentina)
– Scutum reddish brown with ferruginous aspect; mesosoma with reduced yellow marks; tergum I with apical yellow bands, terga II–VI color uniform black, without apical yellow bands; pubescence more evident and golden; wings dark brown……*P. subsericeus*
(from Venezuela to central Brazil)
24. General color light brown, mesosoma with large yellow marks; metasoma completely light brown without dark spots……*P. claripennis*
(Brazilian Amazon and Peru)
– General color yellow, mesosoma with brown marks; metasoma yellow with large black spots……25
25. Top region of the gena more enlarged, in dorsal view; tergum I slender and with black spots; tergum II yellow with black mark only at apex……*P. moraballi*
(Guyana)
– Top region of the gena narrower, in dorsal view; tergum I more robust and yellow and with reduced black spots, tergum II completely yellow, terga III–VI almost entirely black……*P. testaceicolor*
(from Costa Rica to the Brazilian Amazon)
26. Gena largely dilated on central region, genal width always wider than eye, in lateral view……27
– Genal width equal to or slightly wider than eye on central region in lateral view……29
27. Anterior margin of pronotum sinuous, with a strong central projection……*P. atrox*
(Brazil: Pará)
– Anterior margin of pronotum straighter, without a central projection……28
28. Metasoma dark brown; golden pubescence more evident……*P. rufiventris*
Colombia, Ecuador, Guyana, and the Brazilian Amazon)
– Metasoma light brown; golden pubescence not evident……*P. occiptalis*
(from Panama to central Brazil)
29. Clypeus in contact with the eyes for a distance shorter than the diameter of the antennal socket……30
– Clypeus in contact with the eyes for a distance equal to or larger than the diameter of antennal socket ……34
30. General color black, sometimes with small brown marks; metasoma completely black……31
– Head and mesosoma almost entirely black; metasoma completely brown……33
31. Color totally black, without brown spots; wings with blackish to dark brown; whitish pubescence around all over the body……*P. niger*
(Colombia and Brazil)

– General color black, with small brown marks; wings brown but never blackish; golden pubescence around the body…….....……..…32

32. Anterior margin of pronotum rounded; gena slightly dilated on central region, genal width wider than eye, in lateral view; generally more robust, about 20 mm long.....*P. deceptor*
(from Panama to central Brazil)

– Anterior margin of pronotum straighter, rounded only on humeral region; genal width equal to eye width on central region in lateral view; smaller, usually not exceeding 17 mm long.....*P. obscurus*
(Brazil, Argentina, and Paraguay)

33. Anterior margin of pronotum sinuous, with a weak central projection; humeri strongly projected; wings hyaline with dark-brown to black venation; more robust species, usually more than 20 mm long...*P. bicolor*
(from Costa Rica to central-south Brazil)

– Anterior margin of pronotum straight, humeri weakly projected; wings brown with light-brown venation; small species usually not exceeding 15 mm long…….*P. bequaertianus*
(Argentina: Misiones; Paraguay)

34. Anterior margin of pronotum sinuous, with a strongly central projection…….....……35

– Anterior margin of pronotum straighter or rounded, without a central projection.....…36

35. General color black, usually with small brown marks; anterior margin of pronotum with a weak central projection; larger species, usually more than 20 mm long …….…… *P. melanossoma*
(from Guiana to southern Brazil and Argentina)

– General color black with pronotum, scutum, and tegulae dark brown; anterior margin of pronotum with a very strong central projection; smaller species, usually not exceeding 17 mm long.....
.....*P. angulinus*
(Guyana and the Brazilian Amazon)

36. Species of small size, no more than 12 mm long…….....……..……...…37

– Species intermediate in size, generally larger than 15 mm long but not exceeding 20 mm…….38

37. General color black, with large brown marks on pronotum, mesepisternum, propodeum, and legs; narrow yellow bands on mesosoma; terga I–II with an apical yellow band; golden pubescence on the whole body.....*P. geminatus*
(from Guyana to central Brazil)

– General color black without large brown marks; larger yellow bands on mesosoma; terga I–VI with an apical yellow band; whitish pubescence on the whole body..... *P. davillae*
(Brazilian Amazon)

38. General color of metasoma brown, some specimens black with yellow marks…….....*P. pacificus*
(from southern United States to southern Brazil and Argentina)

– General color of metasoma black…….....……39

39. Terga black with apical yellow bands…….....……..……..…40

– Terga completely black without apical yellow bands…….....……..……...…42

40. Terga I–III with apical yellow bands, terga IV–VI black…….....……..…*P. boharti*
(Mexico)

– Terga I–VI with apical yellow bands…….…….....……..…41

41. Mesosoma with small yellow marks; propodeum completely black; punctation deep and bigger on clypeus and mesepisternum……..……..…*P. cinerascens*
(from Mexico to southern Brazil and Argentina)

– Mesosoma black with yellow marks on the pronotum, scutum with two yellow stripes on the sides, scutellum and metanotum almost entirely yellow; propodeum with two yellow stripes on the side; punctation evanescent and shallow on clypeus and mesepisternum……*P. torresae*
(Guyana, Suriname, and the Brazilian Amazon)

42. Mesosoma almost black with small yellow marks; propodeum with two narrow yellow stripes on the sides; tergum I completely black……*P. actaeon*
(Brazil, Argentina, and Paraguay)
– Mesosoma partially black with large yellow marks, scutum with two yellow stripes on the sides, scutellum and metanotum almost entirely yellow; propodeum with two larger yellow stripes on the sides; tergum I black with circular spots on the sides……*P. candidoi*
(Bolivia)
43. Mesepisternum with punctation small and shallow, without distinct, deep, and large punctures; propodeum with weak or moderately strong striae, usually concentrated on the center, not touching the lateral margin of propodeum, if touching the side, they are very weak; usually smaller species……44
– Mesepisternum with punctation bigger and deeper, with the presence of distinct, deep, and large punctures; propodeum with strong striae, developed to the lateral margin of propodeum; usually larger species……75
44. Pronotal carina strongly acuminate, sharp; general color black without pale marks; when these are present, extremely small; wings completely or partly black……45
– Pronotal carina weak, if higher then rounded and never acuminate; varied color, never completely black, with large yellow and ferruginous marks; wings hyaline to brown, but never black……47
45. General color black with metallic appearance; wings completely black; apex of clypeus and mandibles reddish; punctation very small and shallow……*P. goeldii*
(Bahamas, Dominican Republic, and from Costa Rica to central Brazil)
– General color black without metallic appearance; wings dark brown; clypeus and mandible totally black……46
46. Occipital carina developed at the end of the gena; general color black with dark-brown markings defined on pronotum, scutellum, tegulae, and legs; wings dark brown over their entire surface……*P. penai*
(Peru and Bolivia)
– Occipital carina developed at the middle of the eyes; color completely black, no brown marks; wings dark brown at the base and becoming hyaline halfway to apex……*P. apicalis*
(Mexico, Central America to Guyana and Ecuador)
47. Propodeum with weak striae only on middle of central concavity, not touching the lateral margin of propodeum; species usually with apical yellow bands on some terga……48
– Propodeum with moderately strong striae on the middle of central concavity, touching the sides weakly; species usually without apical yellow bands on terga, but with circular spots on tergum I and sometimes on tergum II……62
48. Pronotum rounded but humeri slightly projected on the sides……49
– Pronotum rounded to the fullest extent with the humeri not projected on the sides……56
49. Eyes with small bristles on their entire surface……50
– Eyes bare……52
50. Pronotum and scutum with black color, with large yellow marks; tergum black with brown and yellow apical bands; size large, ~20 mm long or longer……*P. cubensis*
(Bahamas and Cuba)
– Small species, not exceeding 18 mm long; color different from above……51
51. Golden pubescence on the whole body; scutum black with large brown marks and two yellow stripes on the sides; terga I–VI with narrow yellow apical bands……*P. incertus*
(Cuba, Haiti, and Dominican Republic)

– Whitish pubescence on the whole body; scutum light brown with two yellow stripes on the sides; terga I–VI with larger yellow apical bands…….....*P. minor*
(Mexico, Cuba, Haiti, Dominican Republic, and Puerto Rico)

52. Pronotal fovea reduced and shallow; very small species, not exceeding 13 mm long; scutum light brown; propodeum black with two yellow stripes on the sides.....…… *P. crinitus*
(Jamaica, Dominican Republic, Puerto Rico, and Peru)

– Pronotal fovea developed; species medium sized, about 15–20 mm long; scutum dark brown, sometimes with yellow markings; propodeum brown with two yellow stripes on the sides……53

53. Mesepisternum black with yellow markings; coxae and femur black, apical region of femur yellow...54

– Mesepisternum brown with yellow markings; coxae and femora brown, apical region of femur yellow...55

54. Pronotal carina higher; scutellum brown with a wide yellow mark; propodeum striae a little stronger on the center …….....…… *P. pseudoculatus*
(Mexico: Chihuahua)

– Pronotal carina lower; scutellum completely yellow; propodeum striae less developed and weakly marked on the center……...….....*P. instabilis*
(from Mexico to Costa Rica)

55. Scutum narrow and partially black with two yellow stripes on the sides; about 20 mm long…… …….……..……..….....*P. bequaertellus*
(El Salvador)

– Scutum wider and completely brown without yellow stripes on the sides; about 18 mm long… ……*P. stabilinus*
(from Mexico to Honduras)

56. Genal width at center less than eye width, in lateral view……...……57

– Genal width at center wider than eye width, in lateral view……....……58

57. Scutum, propodeum and tergum completely black; terga I–IV with yellow apical bands and terga V–VI with brown apical bands…….....……*P. franciscanus*
(Guatemala)

– Scutum and propodeum brown, scutum with two yellow stripes on the sides; terga partially brown, terga I–VI with yellow apical bands…….….....…*P. lineonotus*
(southwestern United States, Mexico, and Dominican Republic)

58. Scutum black, with small brown lateral marks; mesosoma with small yellow marks; terga I–IV brown with yellow apical bands; wing venation light-brown.....,*P. bahamensis*
(southern United States and Bahamas)

– Scutum brown; mesosoma with larger yellow marks; wing venation dark brown.....59

59. Terga dark brown, without yellow apical bands; mesepisternum black with a yellow mark.....*P. ridleyi*
(Brazil: Fernando de Noronha)

– Terga brown, with yellow apical bands; mesepisternum black or brown.....60

60. General color brown with extensive black marks; mesepisternum black with a yellow mark; propodeum black with two yellow stripes on the sides; legs largely black……*P. oculatus*
(from Mexico to Costa Rica)

– General color brown with reduced black marks; mesepisternum brown with yellow marks; propodeum brown with two yellow stripes on the sides; legs largely brown.....61

61. Terga brown, I–VI with larger yellow apical bands…….....……*P. exclamans*
(United States and Mexico)

– Terga brown, I–III with smaller yellow apical bands.....*P. arizonensis*
(southwestern United States and Mexico)

62. Pronotal carina a little higher and usually developed to the end of pronotum, exceeding the humeral region.....63
– Pronotal carina slightly lower and developed up to the humeri, but not extending into the humeri region of pronotum.....69
63. General color pale yellow.....*P. eburneus*
(Paraguay: Guaira)
– General color black or brown, with large yellow marks.....64
64. Scutum with general color black.....65
– Scutum with general color brown.....66
65. Scutum completely black; pronotum and propodeum yellow; terga I–II completely or mostly yellow; terga III–VI with reddish-brown color.....*P. maranonensis*
(Ecuador and Peru)
– Scutum mostly black, with reduced brown stripes on the sides; pronotum and propodeum brown with yellow markings; terga I–VI brown, with yellow marks.....*P. xanthogaster*
(Peru, Bolivia, and northern Argentina)
66. General color light brown; terga I–II with apical yellow bands and without spots on the side .....*P. veracrucis*
(Mexico)
– General color dark brown; terga I–II with yellow spots on the side.....67
67. Mesepisternum completely black; scutelum and metanotum dark-brown, without yellow marks; propodeum completely dark brown.....*P. myersi*
(Bahamas and from Costa Rica to Colombia)
– Mesepisternum black with yellow marks; scutelum and metanotum dark-brown, with yellow marks; propodeum completely brown with two yellow stripes on the sides.....68
68. Humeri weakly projected on the sides.....*P. ninabamba*
(Peru: Ayacucho)
– Humeri not projected on the sides; pronotum rounded.....*P. versicolor*
(Dominican Republic and from Costa Rica to southern Brazil and Argentina)
69. Scutum with general color black.....70
– Scutum with general color brown.....73
70. Extended yellow marks on the body; pronotum, scutellum, and metanotum with yellow markings; propodeum with two yellow stripes on the sides.....71
– General coloration brown or black, with rare yellow marks; pronotum, scutellum, and metanotum black; propodeum totally black.....72
71. Terga I–II and rarely III with yellow circular spots on the sides.....*P. weyrauchorum*
(Ecuador, Peru, and Chile)
– Terga I–IV with yellow circular spots on the sides well defined.....*P. peruvianus*
(Peru)
72. Integument with a shiny appearance and punctation generally stronger, with some clusters of punctures on mesepisternum; general color black with small brown marks on the face, pronotum, tegulae, and legs; terga I–VI black, II with two yellow circular spots on the sides.....*P. binotatus*
(Brazil: Rio de Janeiro)
– Integument dull, without a shiny appearance, and punctation generally thinner and shallower on mesepisternum; general color black with large brown marks on the face, pronotum, tegulae, and legs; terga I–VI brown, I with two yellow circular spots on the sides.....*P. biguttatus*
(Brazil)

73. General color dark brown, almost black, with small brown marks on pronotum, scutum, and scutellum; face dark brown; propodeum completely black; tergum dark brown, without the presence of yellow spots.....*P. consobrinus*
(southern Brazil, Paraguay, Argentina, and Uruguay)
– General color light brown, with larger yellow marks; face light brown; propodeum black or brown with two yellow stripes on the sides; terga light brown, with yellow spots.....74
74. Scutum distinctly longer than wide; propodeum black with two yellow stripes on the sides; tergum I with two well-defined circular spots on the sides.....*P. adelphus*
(Colombia, Ecuador, and Peru)
– Scutum as long as wide; propodeum brown with two yellow stripes on the sides; terga I–II with two well-defined circular spots on the sides.....*P. simillimus*
(Colombia, Peru, Bolivia, central-south Brazil, Paraguay, and Argentina)
75. Pronotal carina strongly elevated and acuminate, sharp; anterior margin of pronotum more straight, and rounding only on the humeral region; general color black, normally without marks on the body, but if so size extremely small.....76
– Pronotal carina weakly elevated, and if higher then rounded and never acuminate; anterior margin of pronotum more rounded; general color dark brown, never completely black.....79
76. Humeri strongly projected; wings blackened; general color of mesosoma black, no brown areas...77
– Humeri not projected; wings dark brown; general color of mesosoma black, but pronotum and scutellum brown.....78
77. Pronotal carina developed by the end of pronotum, going beyond the humeral region; clypeus apex and mandible reddish.....*P. rufidens*
(Colombia and Venezuela)
– Pronotal carina developed to the humeral region, not reaching the end of pronotum; clypeus apex and mandible black.....*P. aterrimus*
(from Costa Rica to northern Argentina)
78. Dorsal groove incomplete and weak; propodeum striae less developed and weakly marked on the sides.....*P. penai*
(Peru and Bolivia)
– Dorsal groove complete and strong; propodeum striae more developed and more marked on the sides.....*P. huacapistana*
(Peru: Junín)
79. General color light brown to pale yellow with some areas marked in black; terga completely pale yellow or, if brown, with large yellow spots.....80
– General color dark brown to black; terga dark brown, only tergum I partially yellow.....86
80. Scutum and propodeum black; terga black with large brown and yellow spots.....81
– Scutum and propodeum brown, sometimes with yellow markings; terga brown, sometimes with large yellow spots.....83
81. Pronotum and scutellum with large yellow marks; face and gena yellow; terga I–VI with basal part black, central part brown and with narrower, well-defined yellow apical bands.....*P. buyssoni*
(Bolivia, Argentina, and Chile)
– Pronotum and scutellum with large brown marks; face and gena yellow or brown; terga I–II with basal part black, central part brown and with larger yellow apical bands, terga III–VI completely pale yellow...82
82. Face and gena with brown color; clypeus brown.....*P. cavapytiformis*
(southeastern and southern Brazil)
– Face and gena with yellow color; clypeus yellow.....*P comanchus*
(southern United States and Mexico)

83. General color reddish brown; tergum I with very large yellow apical band covering almost tergum I; humeri projected; intermediate in size, not exceeding 20 mm long.....*P. dominicus* (Bahamas, Cuba, and Brazil)
– General color light brown; tergum I totally brown, sometimes with a very narrow yellow apical band; humeri not projected; larger species, usually more than 20 mm long.....84
84. Scutum brown, usually with yellow stripes on the sides; propodeal muscle orifice relatively short and wide; terga II–VI with large yellow spots on the entire length; large species, about 30 mm long.....*P. cavapyta* (Brazil to Argentina and Paraguay)
– Scutum completely brown; propodeal muscle orifice relatively long and slender; terga I–VI light brown and without large yellow spots; species about 25 mm long.....85
85. Face and gena brown; wings dark brown, with reddish appearance, venation dark brown, almost black; terga brown, I with a well-defined yellow apical band.....*P. mexicanus* (Mexico)
– Face and gena yellow; wings light brown, with hyaline appearance, venation light brown; terga brown without well-defined yellow apical bands.....*P. kaibabensis* (southwestern United States and Mexico)
86. Scutum, scutellum, and metanotum completely black or with small brown marks; metasoma black or brown.....87
– Scutum, scutellum, and metanotum brown; metasoma usually brown.....91
87. General color black, with brown or red spots on the face and legs; wings blackened; tergum completely black.....88
– General color brown, with yellow marks, sometimes on the face, legs, or terga; wings brown; terga brown.....89
88. Head with reddish appearance, color different from the rest of the body.....*P. erythrocephalus* (from Nicaragua to central Brazil)
– Head with black appearance, color similar to the rest of the body.....*P. satan* (southwestern Brazil)
89. Pronotum black; terga II–VI with extensive light-brown spots.....*P. brevifissus* (from Panama to southern Brazil and Argentina)
– Pronotum brown; terga II–VI brown or reddish spots.....90
90. Scutum black and usually with small brown marks; tergum I with a large yellow apical band, but sometimes without it; terga II–VI dark brown.....*P. lanio* (from Panama to southern Brazil and Argentina)
– Scutum completely black; terga I–VI brown with reddish appearance on apical region, but without yellow apical bands.....*P. melanotus* (Colombia and southeastern Brazil)
91. Propodeal muscle orifice short and wide, rounded at the top; general color brown with reddish appearance; femora with a yellow apical band; propodeum may or may not have two yellow stripes on the sides.....*P. ferreri* (Brazil, Bolivia, and Argentina)
– Propodeal muscle orifice long and slender, acuminate at the top; general color dark brown with reddish appearance; propodeum without two yellow stripes on the sides.....92
92. Tergum I with yellow apical band; terga II–VI completely black.....*P. annularis* (United States and Mexico)
– Terga usually black or brown; tergum I uniform in color, without the presence of a yellow apical band...93

93. Propodeum completely black.....*P. notatipes*
(southeastern and southern Brazil)
– Propodeum completely brown.....94
94. Head yellow or light brown, usually a little lighter than the rest of the body; black marks reduced or absent.....*P. infuscatus*
(from Honduras to the Brazilian Amazon)
– Head dark brown, usually same color as the rest of the body; black marks more evident, especially in mesosoma.....*P. canadensis*
(southern United States to southern Brazil and Argentina)

ACKNOWLEDGMENTS

This research was funded in part by a postdoctoal scholarship from FIXAM-FAPEAM (process number 062.01427/2018 – Taxonomia, Filogenia e Biogeografia do gênero de vespa social *Polistes* Latreille, 1802 (Vespidae: Polistinae)); financial support from FAPEAM (062.00661/2015 Universal Amazonas) and CNPq Universal (443213/2014-3); a PDSE scholarship grant from CAPES (process number 99999.003756/2015-07); and a grant from Deutscher Akademischer Austauschdienst Diens-DAAD, all to A.S. M.L.O to CNPq scholarship (process number 305150/2020-0). The authors express their thanks to Cassio van den Berg and Eddy Oliveira (UEFS) for manuscript support. Many thanks to all the curators and assistants for *Polistes* loan: C. LeBeau, G. Broad, C. Villemant, A. Touret-Alby, S. Brady, M. Ohl, F. Koch, S. Schmidt, M. Buck, L. Vilhelmsen, P.D. Perkins, B.R. Garcete-Barrett, C.R. Brandão, A. Kohler, F. Vivalo, and F. Limeira.

REFERENCES

Andena, S.R., and J.M. Carpenter. 2012. A phylogenetic analysis of the social wasp genus *Brachygastra* Perty, 1833, and description of a new species (Hymenoptera: Vespidae: Epiponini). American Museum Novitates 3753: 1–38.

Arévalo, F., Y. Zhu, J.M. Carpenter, and J.E. Strassmann. 2004. The phylogeny of the social wasp subfamily Polistinae: evidence from microsatellite flanking sequences, mitochondrial CO1 sequence, and morphological characters. BMC Evolutionary Biology 4: 1–8.

Buck, M., T.P. Cobb, J.K. Stahlhut, and R.H. Hanner. 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.

Carpenter, J.M. 1993. Biogeographic patterns in Vespidae (Hymenoptera): two views of Africa and South America. *In* P. Goldblatt (editor), Biological relationship between Africa and South America: 139–154. New Haven, CT: Yale University Press.

Carpenter, J.M. 1996a. Distributional checklist of species of the genus *Polistes* (Hymenoptera: Vespidae; Polistinae, Polistini). American Museum Novitates 3188: 1–39.

Carpenter, J.M. 1996b. 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.

Dias-Filho, M.M. 1975. Contribuição à morfologia de larvas de vespídeos sociais do Brasil (Hymenoptera, Vespidae). Revista Brasileira de Entomologia 19: 1–36.

Goloboff, P.A. 1993. NONA, Version 2.0. Published by the author. Tucumán, Argentina: NSUE, Fundacion y Instituto Miguel Lillo.

Goloboff, P.A. 1999. Analyzing large data sets in reasonable times: solutions for composite optima. Cladistics 15: 415–428.

Goloboff, P.A., J.S. Farris, and K.C. Nixon. 2003. TNT: tree analysis using new technology. Computer software and documentation. Online resource (https:// cladistics.org/tnt)..

Goloboff, P.A., J.S. Farris, and K.C. Nixon. 2008a. TNT, a free program for phylogenetic analysis. Cladistics 24: 774–786.

Goloboff, P.A., J.M. Carpenter, J.S. Arias, and D.R.M. Esquivel. 2008b. Weighting against homoplasy improves phylogenetic analysis of morphological data sets. Cladistics 24: 758–773.

Hermes, M.G., G.A.R. Melo, and J.M. Carpenter. 2014. The higher-level phylogenetic relationships of the Eumeninae (Insecta, Hymenoptera, Vespidae), with emphasis on *Eumenes* sensu lato. Cladistics 30: 453–484.

Katoh, M., K. Kuma, T. Miyata. 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. Nucleic Acids Research 30: 3059–3066.

Katoh, K., K. Kuma, H. Toh, and T. Miyata. 2005. MAFFT version 5: improvement in accuracy of multiple sequence alignment. Nucleic Acids Research 33: 511–518.

Kojima, J. 1987. Descriptions of mature larvae of 8 Australian Polistinae (Hymenoptera, Vespidae). Journal of Australian Entomology Socity 26: 141–148.

Kojima, J. 1998. Larvae of social wasps (Insecta: Hymenoptera; Vespidae). Natural History Bulletin of Ibaraki University 2: 7–227.

Kojima, J., and S. Yamane. 1984. Systematic study of the mature larvae of Oriental polistine wasps (Hymenoptera: Vespidae) (I) Species of *Ropalidia* and *Polistes* from Sumatra and Java islands. Reports of the Faculty of Science, Kagoshima University (Earth Sciences and Biology) 17: 103–127.

Nelson, J.M. 1982. External morphology of *Polistes* (paper wasp) larvae in the United States. Melanderia 38: 1–29.

Nguyen, T.P.L. 2017. Notes on the paper wasp genus *Polistes* (*Polistella*) (Hymenoptera: Vespidae: Polistinae) from the northern part of Vietnam with description of males and nests. Raffles Bulletin of Zoology 65: 220–225.

Nixon, K.C. 1999. The parsimony Ratchet, a new method for rapid parsimony analysis. Cladistics 15: 407–414.

Pardi, L. 1996. *Polistes*: analysis of a society. *In* S. Turillazzi and M.J. West-Eberhard (editors), Natural History and Evolution of Paper-Wasps, p. 1–17. Oxford University Press, Oxford, New York, Tokyo.

Pickett, K.M., and J.M. Carpenter. 2010. Simultaneous analysis and the origin of eusociality in the Vespidae (Insecta: Hymenoptera). Arthropod Systematics and Phylogeny 68: 3–33.

Pickett, K.M., and J. Wenzel. 2004. Phylogenetic analysis of the New World *Polistes* (Hymenoptera: Vespidae: Polistinae) using morphology and molecules. Journal of the Kansas Entomological Society 77: 742–760.

Pickett, K.M., J.M. Carpenter, and W.C. Wheeler. 2006. Systematics of *Polistes* (Hymenoptera: Vespidae), with a phylogenetic consideration of Hamilton's haplodiploidy hypothesis. Annales Zoologici Fennici 43: 390–406.

Richards, O.W. 1973. The subgenera of *Polistes* Latreille (Hymenoptera, Vespidae). Revista Brasileira de Entomologia 17: 85–104.

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

Santos, B.F., A. Payne, K.M. Pickett, and J.M. Carpenter. 2015. Phylogeny and historical biogeography of the paper wasp genus *Polistes* (Hymenoptera: Vespidae): implications for the overwintering hypothesis of social evolution. Cladistics 31: 535–549.

Silveira, O.T., S.R. Andena, A. Somavilla, and J.M., Carpenter. 2021. Phylogeny and classification of the Neotropical social wasps. *In* F. Prezoto, F.S. Nascimento, B.C. Barbosa, and A. Somavilla (editors), Neotropical social wasps: 267–291. Gewerbestrasse, Switzerland: Springer.

Somavilla, A., and J.M., Carpenter. 2021. Key to the genera of social wasps. (Polistinae) occurring in Neotropics. *In* F. Prezoto, F.S. Nascimento, B.C. Barbosa, and A. Somavilla (editors), Neotropical Social Wasps. p. 327–336. Gewerbestrasse, Switzerland: Springer.

Somavilla, A., M.L. Oliveira, S.R. Andena, and J.M. Carpenter. 2018. An illustrated atlas for male genitalia of the New World *Polistes* Latreille, 1802 (Vespidae: Polistinae). Zootaxa 4504 (3): 301–344.

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.

Wheeler, G.C., and J. Wheeler. 1979: Larvae of some eusocial bees and wasps. Contributions in Science 321: 1–19.

APPENDIX 1

List of Phenotypic Characters in This Work

Figures 5–16

Head (chars. 1–36)

1. Clypeus dimensions: **0,** as long as wide or wider than long; **1,** longer than wide.
2. Clypeal apex: **0,** strongly bidentate; **1,** pointed; **2,** rounded. [Additive.] Adapted from Carpenter (1996b).
3. Lateral lobe of clypeus, shape: **0,** forming an angle of 90°; **1,** forming an angle of less than 90°.
4. Lateral lobes of clypeus, projection: **0,** reduced; **1,** projecting; **2,** strongly projecting. [Additive]
5. Pubescence on clypeus: **0,** equal to or more than top half; **1,** equal to or less than top half or absent.
6. Bristles on clypeus, distribution: **0,** present all over; **1,** present only on apical region.
7. Bristles on clypeus, length: **0,** very long; **1,** long; **2,** short; **3,** short, becoming long toward the apex.
8. Punctures on clypeus, size: **0,** medium-sized, deep; **1,** large and deep; **2,** small, shallow.
9. Punctures on clypeus, density: **0,** separated from each other by distance equal to or less than their diameter; **1,** separated from each other by distance greater than their diamenter.
10. Punctures on clypeus, distribution: **0,** present all over; **1,** present only in basal third.
11. Clypeus-eye contact: **0,** touching for an extension equal to or greater than width of antennal socket; **1,** touching for an extension shorter than width of antennal socket; **2,** narrowly separated. [Additive.] Adapted from Carpenter (1996b).
12. Lateral margin of clypeus: **0,** sinuous; **1,** almost straight.
13. Clypeus shape in profile: **0,** convex; **1,** compressed.
14. Dorsal margin of clypeus: **0,** sinuous; **1,** almost straight.

15. Dorsal margin of clypeus: **0,** touching antennal socket; **1,** separated from antennal socket by distance shorter than width of antennal socket; **2,** separated from antennal socket by distance equal to or greater than width of antennal socket. [Additive.]
16. Clypeal dorsum in profile: **0,** straight; **1,** produced above tentorial pits.
17. Reddish spot on clypeus apex: **0,** absent; **1,** present.
18. Dimensions of malar space: **0,** distinctly wider than long; **1,** slightly wider than long, or about as wide as long; **2,** distinctly longer than wide; **3,** transverse. Adapted from Carpenter (1996b).
19. Mandible teeth: **0,** tridentate; **1,** quadridentate.
20. Mandible dimensions: **0,** less than three times as long as wide; **1,** three times as long as wide, or longer.
21. Bristles on eyes: **0,** long; **1,** short; **2,** absent.
22. Separation between ocelli: **0,** separated by less than twice their diameter; **1,** separated by more than twice their diameter. Adapted from Carpenter (1996b).
23. Interantennal area, sculpturing: **0,** with a marked furrow; **1,** with a raised line.
24. Interantennal area, projection: **0,** prominent; **1,** almost flat.
25. Interantennal carina, outline: **0,** blunt; **1,** toothed, serrated.
26. Punctures on frons and vertex, size: **0,** small, shallow; **1,** large to medium, deep.
27. Punctures on frons and vertex, density: **0,** separated by distance shorter than or equal to their one diameter; **1,** separated by distance greater than their diamenter.
28. Bristles on frons and vertex: **0,** very long; **1,** long; **2,** short.
29. Gena width at midlength, lateral view: **0,** narrower than eye; **1,** equal to or slightly wider than eye; **2,** distinctly wider than eye. [Additive.]
30. Pubescence on gena: **0,** present from dorsal end to the midlength; **1,** present from dorsal end to ventral margin of eye or almost so.
31. Posterior margin of gena: **0,** rounded; **1,** sinuous.
32. Punctures on middle region of gena: **0,** small and shallow; **1,** large and deep.
33. Bristles on margin of gena: **0,** very long; **1,** long; **2,** short.
34. Occipital carina: **0,** weak; **1,** strong.
35. Occipital carina: **0,** reaching middle of the head; **1,** extending to middle of the eye; **2,** extending to gena. [Additive.] Adapted from Carpenter (1996b).
36. Occiput, dorsal view: **0,** strongly convex; **1,** almost straight or weakly convex.

Mesosoma (chars. 37–75)

37: Pronotal carina: **0,** absent; **1,** extending to end of pronotum; **2,** extending to humeri. Adapted from Carpenter (1996b).
38. Pronotal carina, if present: **0,** blunt; **1,** sharp.
39. Humeri outline: **0,** not projecting; **1,** slightly projecting; **2,** strongly projecting. [Additive.]
40. Pronotal fovea: **0,** present; **1,** absent. Adapted from Carpenter (1996b).
41. Anterior region of pronotum, dorsal view: **0,** straight or rounded; **1,** with a central projection.
42: Bristles on anterior margin of pronotum: **0,** long; **1,** short; **2,** absent or evanescent.

43. Striation on pronotum, lateral view: **0,** absent; **1,** present.
44. Dorsal groove: **0,** absent; **1,** complete; **2,** incomplete. Adapted from Carpenter (1996b).
45. Epicnemial carina: **0,** absent; **1,** complete; **2,** incomplete. Adapted from Carpenter (1996b).
46. Mesepisternum punctation clathrate: **0,** absent; **1,** present. Adapted from Carpenter (1996b).
47. Mesepisternum punctation: **0,** medium, deep; **1,** large, deep; **2,** small, shallow.
48. Mesepisternum punctuation, density: **0,** separated by distance equal to or shorter than their diameter; **1,** separated by distance greater than their diamenter. Adapted from Carpenter (1996b).
49. Mesepisternum outline, lateral view: **0,** flat; **1,** concave.
50. Dimensions of scutum: **0,** as long as wide; **1,** longer than wide.
51. Center line in scutum: **0,** present; **1,** absent.
52. Dimensions of scutellum: **0,** wider than long; **1,** as long as wide.
53. Posterior region of scutellum: **0,** straight; **1,** with central emargination.
54: Center line on scutellum: **0,** absent; **1,** present, reaching the midlength; **2,** present, complete.
55. Posterior region at metanotum: **0,** with central emargination; **1,** straight.
56. Axillary fossa: **0,** narrow; **1,** broad.
57. Tegula, dorsal view: **0,** oval; **1,** D-shaped.
58. Bristles on tegula: **0,** long; **1,** short; **2,** absent or evanescent.
59. Metapleura: **0,** as long as wide; **1,** longer than wide; **2,** narrowed on anterior portion. [Additive.]
60. Propodeal angle: **0,** rounded; **1,** quadrate.
61. Propodeal concavity: **0,** absent; **1,** present only in the center; **2,** present beyond the center.
62. Propodeal striae: **0,** absent; **1,** present. Adapted from Carpenter (1996b).
63. Propodeal striae, if present: **0,** strong all over; **1,** weak all over; **2,** centrally strong, laterally evanescent. Adapted from Carpenter (1996b).
64. Carina on propodeal valve: **0,** incomplete; **1,** complete.
65. Propodeal muscle: **0,** rounded; **1,** elongate.
66. Central portion of propodeal valve, lateral view: **0,** broad, rounded; **1,** narrow, rounded; **2,** acuminate. Adapted from Carpenter (1996b).
67. Propodeal orifice, dorsally: **0,** rounded; **1,** acute; **2,** elongate.
68. Propodeal color: **0,** uniform; **1,** with a central spot; **2,** with lateral two strips; **3,** with a central spot and two lateral strips.
69. Bristles on propodeum: **0,** very long; **1,** long; **2,** short or evanescent.
70. Pubescence on propodeum: **0,** absent; **1,** present.
71. Pubescence on propodeum color, if present: **0,** whitish; **1,** golden.
72. Wings color: **0,** hyaline to fuscous; **1,** yellow to light brownish; **2,** reddish to brown; **3,** dark brown to blackish.
73. Wing veins color: **0,** dark brown to blackish; **1,** reddish to brown; **2,** yellow.
74. Pterostigma size: **0,** reduced; **1,** pronounced.
75. Trochanter: **0,** wide; **1,** compact.

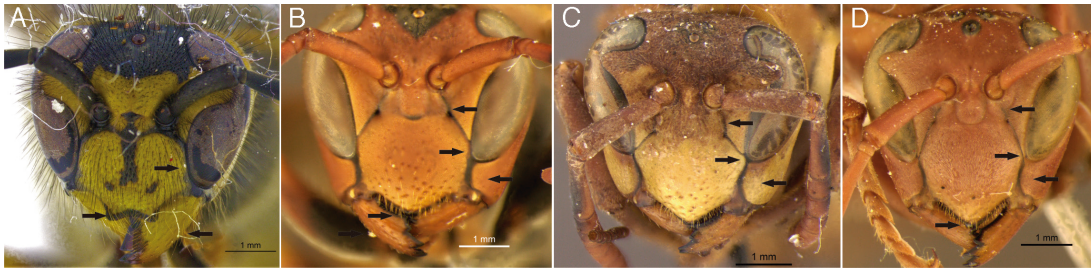


FIGURE 5. Face in front view: **A,** clypeus wider than long, clypeal apex strongly bidentate, clypeus touching for an extension greater than width of antennal socket the eye in *Vespula germanica* (outgroup); **B,** clypeus as long as wide, clypeal apex rounded, clypeus touching for an extension equal to width of antennal socket the eye *Polistes cavapytiformis*; **C,** clypeus as long as wide, clypeal apex pointed, clypeus touching for an extension shorter than width of antennal socket the eye in *Polistes carnifex*; and **D,** clypeus longer than wide, clypeal apex pointed, clypeus narrowly separated by eye in *Polistes thoracicus*. For all bristles length very long (A), long (B), short, becoming long toward the apex (D).

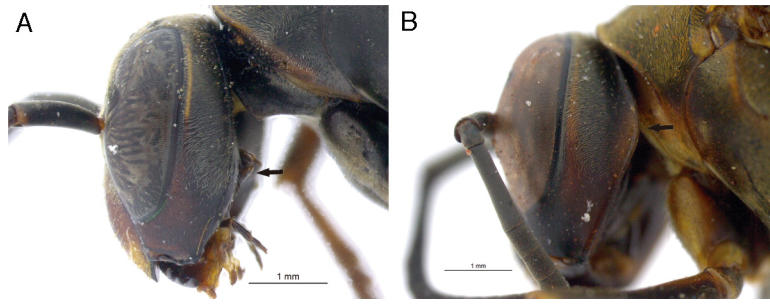


FIGURE 6. Gena width at midlength, lateral view: **A,** equal to or slightly wider than eye in *Polistes pacificus*; and **B,** distinctly wider than eye in *Polistes rufiventris*.

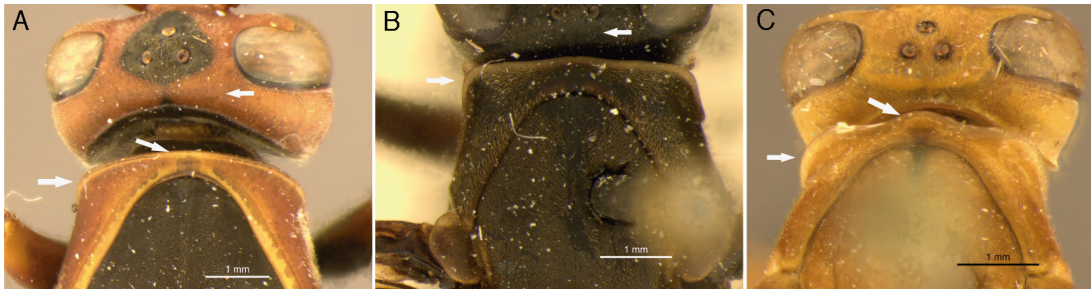


FIGURE 7. Head and pronotum, in dorsal view: **A,** occiput strongly convex, anterior region of pronotum rounded and humeri outline not projecting in *Polistes cavapytiformis*; **B,** occiput almost straight or weakly convex and humeri outline slightly projecting in *Polistes occipitalis*; **C,** anterior region of pronotum with a central projection and humeri outline strongly projecting in *Polistes testaceicolor*.

Metasoma (chars. 76–88)

76. Tergum I, dorsal view: **0,** truncate; **1,** conical, as wide or wider than long; **2,** conical, longer than wide. Adapted from Carpenter (1996b).
77. Tergum I anterior part, dorsal view: **0,** enlarged; **1,** not enlarged.
78. Tergum I shape, lateral view: **0,** abruptly widened; **1,** gradually widened.
79. Tergum I bristles, length: **0,** very long and sparse; **1,** short and dense; **2,** evanescent.
80. Tergum I punctures, size: **0,** weak, small and shallow; **1,** strong, medium sized, and deep.
81. Tergum I color: **0,** uniform; **1,** with apical band; **2,** with lateral spots.
82. Sternum I shape on posterior margin: **0,** straight; **1,** concave.
83. Sternum I anterior portion, dimensions: **0,** long and narrow; **1,** short and enlarged.
84. Sternum I lateral carena: **0,** absent; **1,** present.
85. Carina between sterna I and II: **0,** absent; **1,** incomplete; **2,** complete.
86. Tergum II dimensions, dorsal view: **0,** as wide as long or wider than long; **1,** longer than wide.
87. Tergum II, sculpturing: **0,** weakly punctate; **1,** strongly punctate; **2,** corrugated.
88. Tubercle on the VI sternum: **0,** absent; **1,** present.

Male Anatomy (chars. 89–98)

89. Antenna, segment 4: **0,** distinctly <2.0 times as long as wide; **1,** about 2.0 times as long as wide; **2,** distinctly >2.0 times as long as wide.
90. Antenna, segment 13: **0,** ≤2.0 as long as wide; **1,** about 3.0 times longer than wide; **2,** distinctly >3.0 times as long as wide.
91. Antenna: **0,** apically tapering; **1,** apically coiling; **2,** apically expanded. Adapted from Carpenter (1996b).
92. Clypeus-eye contact: **0,** touching for an extension equal to or greater than width of antennal socket; **1,** touching for an extension shorter than width of antennal socket; **2,** narrowly separated; **3,** widely separated. [Additive.] Adapted from Carpenter (1996b).
93. Clypeal apex outline: **0,** bidentate; **1,** pointed; **2,** rounded. [Additive.] Adapted from Carpenter (1996b).
94. Mandible dimensions: **0,** no more than 2.0 times as long as wide; **1,** 3.0 times as long as wide; **2,** as long as wide.
95. Mandible, number of teeth: **0,** quadridentate; **1,** tridentate. Adapted from Carpenter (1996b).
96. Lateral process of metasomal sternum VII: **0,** absent; **1,** present. Adapted from Carpenter (1996b).
97. Disc of metasomal sternum VII: **0,** medially slightly depressed; **1,** tuberculate. Adapted from Carpenter (1996b).
98. Base of metasomal sternum VII: **0,** without anterior lobes; **1,** lobed. Adapted from Carpenter (1996b).

Male Genitalia (chars. 99–120): see Somavilla et al. (2018).

99. Paramere dimensions: **0,** less than 2.0 as long as wide; **1,** 2.0–3.0 times as long as wide; **2,** >3.0 times longer than wide.
100. Paramere spine: **0,** very short; **1,** medium; **2,** long or very long.

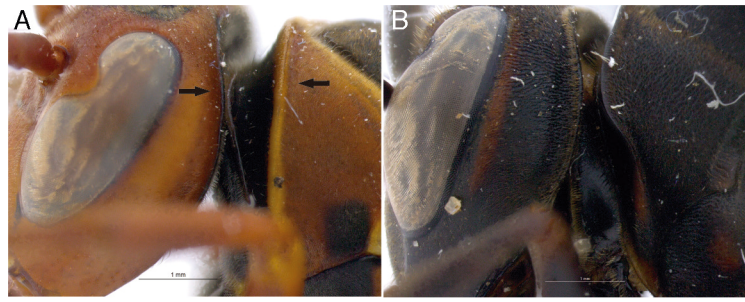


FIGURE 8. Occipital carina and pronotal carina of **A,** *Polistes cavapytiformes* and **B,** *Polistes penai*. Extension of occipital carina and shape and extension of pronotal carina.

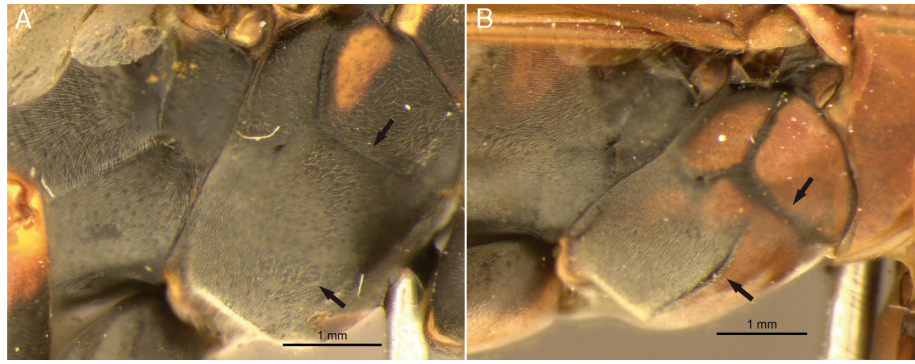


FIGURE 9. Mesepisternum: dorsal groove complete and epicnemial carina absent in **A,** *Polistes cavapytiformis*; and **B,** dorsal groove incomplete and epicnemial carina complete in *Polistes thoracicus*.

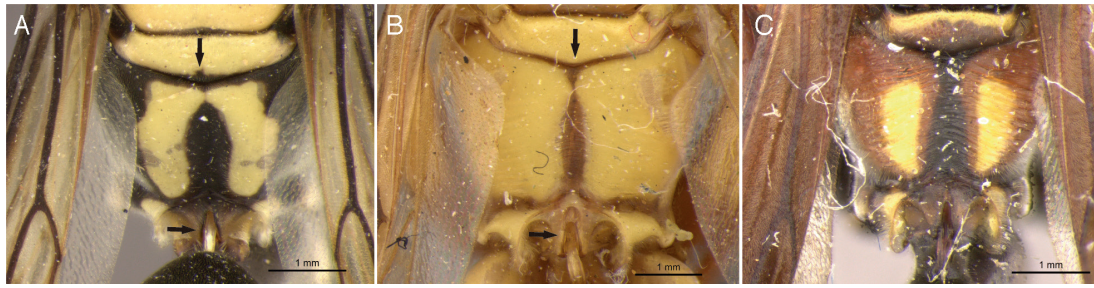


FIGURE 10. Propodeum and propodeal orifice: **A,** propodeal striae absent, and propodeal orifice rounded in *Polistes torresae*; **B,** propodeal striae weak all over and propodeal orifice rounded in *Polistes apachus*; and **C,** propodeal striae strong all over and propodeal orifice elongate in *Polistes versicolor*.

101. Paramere lateral groove: **0,** absent; **1,** shallow; **2,** deep.
102. Paramere, bristle on apical part: **0,** short; **1,** long.
103. Paramere, bristles on apical part: **0,** sparse; **1,** dense.
104. Digitus, apical process: **0,** developed; **1,** reduced.
105. Digitus, punctures: **0,** covering entire length; **1,** distributed only on strip in the central portion.
106. Digitus, bristles: **0,** very long; **1,** short; **2,** absent or evanescent.
107. Digitus, anteroventral lobe: **0,** rounded; **1,** pointed.
108. Cuspis size: **0,** robust; **1,** slender.
109. Cuspis, apex: **0,** tapering gradually; **1,** tapering abruptly.
110. Cuspis, bristles: **0,** short; **1,** long.
111. Aedeagus size: **0,** robust; **1,** slender.
112. Aedeagus, lateral view: **0,** distinctly curved; **1,** straight or weakly curved.
113. Aedeagus, penis valve dilation: **0,** very dilated; **1,** dilated; **2,** slightly dilated.
114. Aedeagus, penis valve lobes: **0,** not bilobed or weakly bilobed; **1,** distinctly bilobed.
115. Aedeagus, median expansion: **0,** absent; **1,** present on top; **2,** present on center.
116. Aedeagus, median expansion shape: **0,** rounded; **1,** acuminated.
117. Aedeagus, median portion surface: **0,** smooth; **1,** serrate or with small teeth; **2,** with moderately sized teeth; **3,** strongly denticulate.
118. Aedeagus, serrations on median portion, if present: **0,** teeth developed from penis valve to the end of median expansion; **1,** teeth reaching the median expansion; **2,** teeth only on median portion.
119. Aedeagus, median basal apodeme: **0,** short; **1,** long.
120. Aedeagus, lateral apodeme: **0,** shorter than median basal apodeme; **1,** equal or bigger than the median basal apodeme.

Larva (chars. 121–133)

121. Bristles on the head: **0,** absent; **1,** short; **2,** long.
122. Labrum papillae: **0,** absent; **1,** present.
123. Labrum bristles: **0,** absent; **1,** present. Adapted from Pickett and Carpenter (2010).
124. Mandible teeth**: 0,** three; **1,** two. Adapted from Carpenter (1996b).
125. Teeth dimensions: **0,** long and slender; **1,** short and stout.
126. Thoracic sterna, shape: **0,** without lobes; **1,** with two lobes.
127. Thoracic sterna bristles: **0,** absent or very short; **1,** present and conspicuous.
128. Abdominal sterna bristles: **0,** absent or very short; **1,** present and conspicuous.
129. Color of cuticle: **0,** dark; **1,** clear; **2,** mostly clear, with dark bands on the head.
130. Mandible teeth sclerotization: **0,** strong, well sclerotized; **1,** weak, sclerotized as strongly as in basal area of mandibula.
131. Maxilla: **0,** basally compressed; **1,** basally strongly swollen. Adapted from Pickett and Carpenter (2010).

FIGURE 11. Mesosoma, dimensions of scutum and scutellum: **A,** *Vespula squamosa* (outgroup); **B,** *Polistes apachus*; **C,** *Polistes fuscatus*; **D,** *Polistes versicolor*; **E,** *Polistes bicolor*; and **F,** *Polistes terresae*.

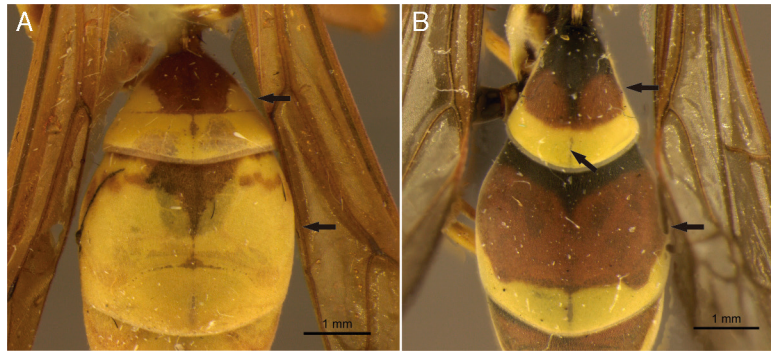


FIGURE 12. Terga I and II, dorsal view: **A,** tergum I conical, as wide as long, and tergum II as wide as long in *Polistes aurifer*; and **B,** tergum I conical, longer than wide and tergum II longer than wide in *Polistes exclamans*.

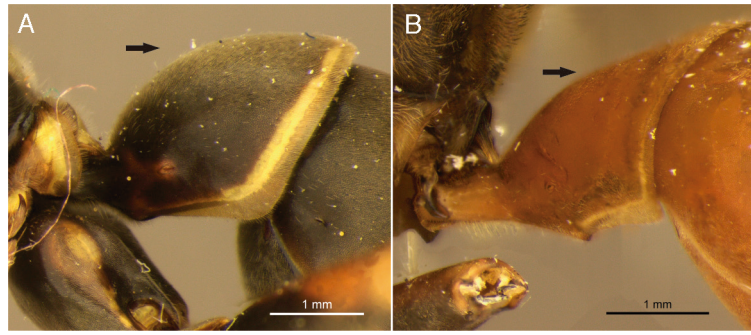


FIGURE 13. Tergum I shape, lateral view: **A,** abruptly widened in *Polistes huristicornis*, and **B,** gradually widened in *Polistes occipitalis*.

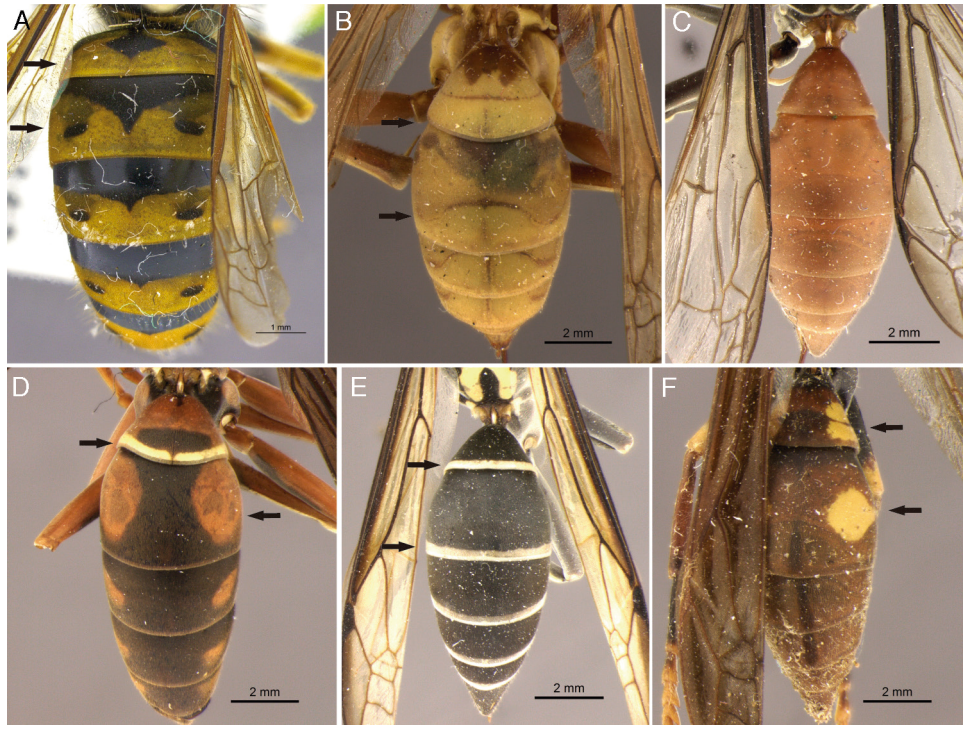


FIGURE 14. Mesosoma, terga I and II shape and dimensions: **A,** *Vespula squamosa* (outgroup); **B,** *Polistes apachus*; **C,** *Polistes bicolor*; **D,** *Polistes fuscatus*; **E,** *Polistes terresae*; and **F,** *Polistes versicolor*.

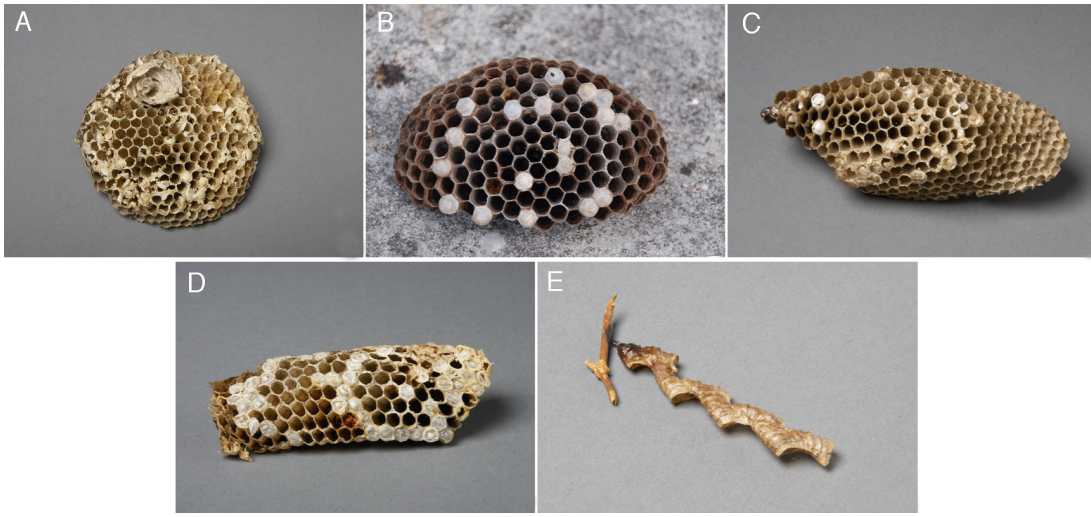


FIGURE 15. Comb shape: **A,** circular in *Polistes fuscatus*; **B,** subcircular in *Polistes instabilis*; **C,** leaf shaped in *Polistes versicolor*; **D,** narrow in *Polistes crinitus*; and **E,** long and vertical in *Polistes goeldii*.

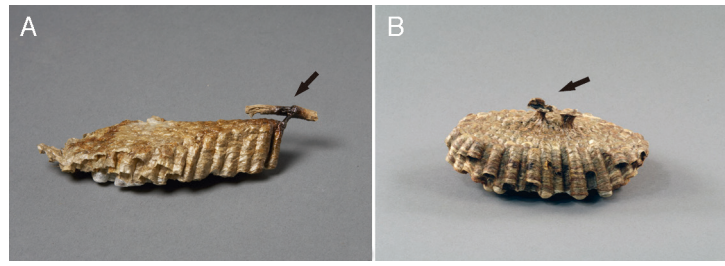


FIGURE 16. Peduncle: **A,** lateral peduncle in *Polistes instabilis*; **B,** central peduncle in *Polistes carolina*.

132. Cranial shape in frontal view: **0,** subcircular or suboval, with lateral sides uniformly curved; **1,** widest at or below level of line joining anterior tentorial pits. Adapted from Pickett and Carpenter (2010).
133. Galea: **0,** apically flat, without apical sensillae; **1,** bilobed, with two apical sensilla on one of lobes, or trilobed; **2,** complex, usually with more than two apical sensilla on each lobe.

Nest Architecture (chars. 134–140)

134. Envelope: **0,** present; **1,** absent.
135. Fiber length: **0,** long; **1,** short. From Pickett and Carpenter (2010).
136. Comb shape: **0,** circular; **1,** subcircular; **2,** leaf shaped; **3,** narrow; (4) long vertically.
137. Secondary combs: **0,** present; **1,** absent.
138. Comb cells shape: **0,** rectinidal; **1,** laterinidal. Adapted from Pickett and Carpenter (2010).
139. Peduncle: **0,** without a visible peduncle; **1,** with central peduncle; **2,** with lateral peduncle.
140. Color of peduncle: **0,** clear; **1,** brown and shiny; **2,** black and shiny.

All issues of *Novitates* and *Bulletin* are available on the web (http://digitallibrary.amnh.org/dspace). Order printed copies on the web from:
http://shop.amnh.org/a701/shop-by-category/books/scientific-publications.html

or via standard mail from:
American Museum of Natural History—Scientific Publications
Central Park West at 79th Street
New York, NY 10024

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