

A Phylogenetic Analysis of the Social Wasp GenusBrachygastra Perty, 1833, and Description of a NewSpecies (Hymenoptera: Vespidae: Epiponini)

Authors: Andena, Sergio R., and Carpenter, James M.

Source: American Museum Novitates, 2012(3753): 1-38

Published By: American Museum of Natural History

URL: https://doi.org/10.1206/3753.2

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

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

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

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

AMERICAN MUSEUM NOVITATES

Number 3753, 38 pp.

July 26, 2012

A phylogenetic analysis of the social wasp genus *Brachygastra* Perty, 1833, and description of a new species (Hymenoptera: Vespidae: Epiponini)

SERGIO R. ANDENA¹ AND JAMES M. CARPENTER²

ABSTRACT

Phylogenetic relationships among the species of the genus *Brachygastra* Perty, 1883, are analyzed based on characters of female morphology, male genitalia, and nest architecture. Analysis of the data matrix with equal weights results in one tree, which is also obtained under implied weighting. A new species is described and an identification key is presented. The males of *B. borellii* and *B. scutellaris* are described.

KEY WORDS: social wasps, phylogenetic analysis, Epiponini, Brachygastra.

INTRODUCTION

The species of the genus *Brachygastra* form one of the common elements of the neotropical social wasp fauna (Naumann, 1968; Jeanne, 1991: table 6.4). The genus is widely distributed in Central and South America (Mexico to Argentina), and one species, *Brachygastra mellifica*, occurs in the southwestern United States, in Texas and Arizona (Naumann, 1968; Richards, 1978; West-Eberhard et al., 2006). Hitherto 16 species were known for the genus, which are easily recognized by the very high scutellum that often projects over the metanotum, and that together with the metanotum and propodeum forms a flat, vertical posterior surface of the

Copyright © American Museum of Natural History 2012

ISSN 0003-0082

¹Universidade Estadual de Feira de Santana, Dept. Ciências Biológicas, Lab. Sistemática de Insetos, Av. Transnordestina, s/n, Feira de Santana, BA, 44.036-900, Brazil.

²Division of Invertebrate Zoology, American Museum of Natural History.

mesosoma, and by the truncate abdomen, which is wider than long (du Buysson, 1905; Ducke, 1905, 1910; Naumann, 1968; Richards, 1978; Carpenter, 2004).

Studies on morphological caste differences have been reported for *B. augusti* (Richards, 1978; Baio et al., 2004), *B. bilineolata* (Richards, 1978), *B. lecheguana* (Shima et al., 2000), *B. moebiana* (Richards, 1978), *B. myersi* (Richards and Richards, 1951) and *B. scutellaris* (Richards, 1978; Carpenter and Ross, 1984), which have tended to show queens to be larger than workers.

Bequaert (1933: 100) considered that early historical accounts of honey-storing insects in tropical America referred in part to species of the genus Brachygastra ("honey wasps"), because these wasps are often numerous and their nests more conspicuous than those of the native stingless bees. Two species, Brachygastra mellifica and B. lecheguana, store large amounts of nectar (Richards, 1978), and they are very similar morphologically, but differ in distribution, and in features of the male genitalia (see discussion below). Brachygastra azteca also stores nectar, but less than B. mellifica and B. lecheguana (Richards, 1978). Hermes and Köhler (2006) reported that B. lecheguana is an abundant floral visitor in southern Brazil, storing nectar for the brood in addition to animal food. Besides nectar, B. mellifica also collects honeydew as a carbohydrate source (Sugden and McAllen, 1994). These wasps have been observed attending honeydew-secreting cercopids and nymphal membracids (Belt, 1874). Despite some imprecision, Bequaert (1933) reported records of several authors about the use of the honey of Brachygastra lecheguana by natives in Mexico; however, it was not a practice by natives of South America. Pison (1648 in Bequaert, 1933: 100) mentioned "bees" called "eixy" and "copij" in Brazil, which produce small amounts of honey, yet were neglected by the natives because of their fierce sting. Saint-Hilaire (1822 and 1825, in Bequaert, 1933: 102 [we have seen the 1825] paper]), in his travel in the provinces of Rio de Janeiro and Minas Gerais, described how he was poisoned by eating honey from a nest of B. lecheguana, and stated that the inhabitants of that part of South America were perfectly aware that the honey stored by this wasp could be poisonous, and even claimed to know the plant that was the source of the poisonous honey. Say (1837, in Bequaert, 1933: 102 [seen]) concluded the description of B. mellifica with an account of tasting the honey of the wasp in Mexico. Bequaert (1933: 106-107) also described regular harvesting of the honey of these wasps in Jalisco, with the honey even sold in the market, but added that it might be toxic "when the Daturas are in bloom." A nest of B. azteca from Jalisco, number 753, apparently studied by Buysson, has a string included in the nest indicating that this species is sometimes managed for honey (Wenzel, 1992).

Nests are quite variable, but are always arboreal and of sessile initiation (Wenzel, 1998). The carton is brown, brittle, and composed of short chips or gray, supple, long fibers, without obvious secretion (Wenzel, 1998). The entrance is simple, sometimes aligned to form an internal passage between stories, or sometimes a peripheral, long, and vertical slit, or there are multiple entrances arranged chaotically (Richards, 1978; Wenzel, 1998). The primary comb is built rapidly to full size, and is entirely sessile on a broad substrate or grows off a narrow or upright surface; it may be planar or spherical (Wenzel, 1998). Secondary combs are sessile on the preceding envelope, and are sometimes chaotic and start at several places in gray nests while being orderly in brown nests (Wenzel, 1998).

TAXONOMIC BACKGROUND

Perty (1833) proposed the name *Brachygastra* for two species, the newly described *B. analis* (= *Polistes lecheguana* Latreille), and *B. scutellaris* (Fabricius). *Brachygastra* was erroneously considered a homonym of *Brachygaster* Leach, 1817, a genus of Evaniidae, by Swainson and Shuckard (1840), who replaced it with *Nectarina*. *Nectarina* was in turn erroneously thought to be a homonym of *Nectarinia* Illiger, 1811, a genus of birds (Nectariniidae), by Shuckard (1841). Shuckard replaced *Nectarina* with *Melissaia*, but this name was never widely used.

To complicate matters further, de Saussure (1853–1858), in his monograph published over the course of several years, first used the name *Brachygaster* (a misspelling of *Brachygastra* Perty) and then the name *Nectarinia* (a misspelling of *Nectarina* Swainson and Shuckard). Smith (1857) used *Nectarina*, thus both names (*Nectarinia* and *Nectarina*) were used at the same time.

Still later, von Ihering (1904) proposed the name *Caba* to replace *Nectarina* Shuckard, overlooking Shuckard (1841); however, this new name was also not widely used. Bequaert (1933) recognized *Brachygastra* as the senior synonym, but he did not use this name in publication until 1943.

As pointed out by Naumann (1968), many of the species that have been assigned to the genus were first described as color forms or varieties. In his revision Naumann (1968) reevaluated various forms and recognized 12 species, describing a new one (*B. fistulosa*) and elevating four taxa to species status. Richards (1978) considered some characters not used by Naumann (1968) and recognized 16 species, describing two (*B. mouleae* and *B. albula*) as new.

Systematic Placement

In Carpenter's (1991) cladogram of Polistinae, based on morphological data, *Brachygastra* was sister group of *Chartergus*. This clade was part of a polytomy, termed the *Polybia* component, which included six clades. Wenzel (1993), using nest architecture characters, placed *Brachygastra* as sister of *Protonectarina* + *Polybia*. In a combined analysis of Carpenter's (1991) and Wenzel's (1993) characters, plus morphology of larva, presented by Wenzel and Carpenter (1994), the *Polybia* component was fully resolved and *Brachygastra*, again, was sister of *Chartergus*. Noll et al. (2004), in their phylogeny for the Epiponini included discretized morphometric measurements of caste differentiation in the matrix of Wenzel and Carpenter (1994), and also found a sister-group relationship between *Chartergus* and *Brachygastra*. Arévalo et al. (2004) analyzed a combination of molecular, morphological, and behavioral data and placed *Brachygastra* as sister of *Protonectarina*; however, they did not include *Chartergus*. This was the same result obtained by Pickett and Carpenter (2010) in their extensive combined analysis, but they also did not include *Chartergus*.

Materials and Methods

A total of 1120 specimens was studied at the American Museum of Natural History (AMNH) and University of Vermont (UVM), and borrowed from the Bohart Museum of Entomology (UCDC), Snow Entomological Museum–University of Kansas (SEMC), Field Museum of Natural History (FMNH), British Museum of Natural History (BMNH, United Kingdom), Universidade Federal do Paraná (UFPR, Brazil), Cornell University Insect Collection (CUIC),

Museum of Zoology–University of Michigan (UMMZ), Museum für Tierkunde, Dresden, (MTKD, Germany) and Muséum National d'Histoire Naturelle (MNHN, France). A complete list of the specimens studied can be found in appendix 1.

Male genitalia of the species, depicted in figures 2, 3, and 5, were cleared in lactophenol and examined under glycerin. The drawings of male genitalia in figure 4 were part of an unpublished parcel of van der Vecht given to the second author. Despite the fact that the male genitalia of *B. augusti, B. azteca, B. bilineolata, B. lecheguana, B. mellifica,* and *B. smithii* have been already described and depicted in Naumann (1968), new drawings were included in this work to aid in elucidating these structure; however, they were not redescribed.

Forty-nine morphological characters of the female, five of male genitalia, and six nest characters were assembled in a data matrix for the phylogenetic analysis (table 1), using Winclada ver. 1.00.08 (Nixon, 2002). The characters of nests and part of the male genitalia data were based on the papers published by du Buysson (1905), Naumann (1968), Richards (1978), Wenzel (1998), and Andena and Mateus (2011).

The characters were treated as additive (Farris, 1970), except for some of the multistate characters (3, 7, 10, 20, 25–27, 43, 45, 48, 55, 57–58 and 60), which were treated as nonadditive (Fitch, 1971), because nested homology was not observed in the character states. The characters and their respective states are listed in table 2 and partially illustrated in figures 2–11. Outgroup rooting (Nixon and Carpenter, 1993) was implemented with the following taxa: *Angiopolybia pallens, Pseudopolybia difficilis, Protopolybia bituberculata, Charterginus xanthura, Chartergus artifex, Protonectarina sylveirae, Polybia jurinei*, and *Epipona guerini*.

Search for the most parsimonious trees was undertaken using the program TNT (Goloboff et al., 2008), with equal weights of the characters (commands hold 10000; xmult = level 10 rep 1000). Implied weighting (k = 3) was also applied to characters, using the same search parameters.

RESULTS

The analysis with equal weights resulted in one tree (fig. 12), with length 178, consistency index (CI) 0.57, and retention index (RI) 0.80. Implied weighting resulted in the same tree, with score 14.73929. *Brachygastra* is supported as monophyletic, with *B. azteca* the most basal species, and then three main clades, called here *lecheguana*, *scutellaris*, and *smithii* groups.

DESCRIPTIONS

Brachygastra cooperi, new species

Specimens of this species were deposited in the BMNH, and were kindly sent to us by Gavin Broad. The species was labeled as "*Brachygastra cooperi* Richards ms."

DIAGNOSIS: In general aspects like *B. fistulosa*, but with denser punctures on scutum and metasomal tergum II, surface dull, frons and vertex without hairs, eyes with scattered short hairs, width of the medial region of gena less than that of the eyes, and pronotal carina weakly lamellate, not reaching the ventral corner.

FEMALE (fig. 1A, B): Length 6.5 mm.





FIGURE 1. Female of *Brachygastra cooperi*, sp. n. A, lateral view; B, dorsal view. Scale bars = 1.0 mm.

TABLE 1. Character matrix for Brachygastra. The following symbols are used: ? = not seen; - = inapplicable.

	-	7	3	4	5	9	^	∞	6	_	1		1	1	1	-	1	_	7	7	7	7	7	7	7	7	7	2 3	Ι.
										0	-	3	3 4	ī.	9	^	∞	6	0	1	7	3	4	r	9	 	»	0 6	_
Angiopolybia pallens	0	0	0	0	0	0	0	1	0	0	0	0	0 0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0 0	1
Pseudopolybia vespiceps	0	1	0	0	1	0	0	0	0	0	0	0	0 1	1	0	0	0	0	7	1	1	0	0	2	0	0	0	0 0	
Protopolybia bituberculata	0	0	1	1	7	0	0	1	0	_	0	0	0 1	0	0	0	0	0	0	0	0	0	0	7	0	1	1	0 0	
Charterginus xanthura	0	0	2	П	7	0	1	1	П	2	0	1	1 1	0	0	0	0	0	0	0	0	П	0	7	2	1	1	0 0	
Chartergus artifex	0	2	1	П	7	0	1	0	1	2	1	1 (0 1	0	0	1	1	-	П	0	0	0	1	3	3	2	1	0 0	
Protonectarina sylveirae	0	7	1	П	0	0	1	0	0	0	0	1	1 1	0	0	0	1	0	0	0	0	0	0	7	7	0	1	0 0	_
Polybia jurinei	0	1	1	П	2	0	1	1	0	П	0	0	0 0	0	0	0	0	0	0	0	0	0	0	7	0	1	1	0 0	_
Epipona guerini	0	2	3	П	0	0	П	П	1	П	0	0	0 0		0	0	0	0	7	1	0	0	1	0	1	0	1	0 0	_
Brachygastra albula	0	2	1	П	П	0	П	0	1	3	П	2	1 1	1	0	1	1	7	1	П	П	1	1	2	7	4	П	1	
Brachygastra augusti	П	7	1	П	П	0	П	1	П	3	П	2	1 1	0	1	1	1	1	1	0	0	1	1	4	4	3	П	1	
Brachygastra azteca	П	2	1	П	2	0	П	0	П	3	П	2	1 1	0	0	1	0	1	0	0	0	1	1	4	2	3	_	_	
Brachygastra baccalaurea	0	2	1	П	П	0	П	0	П	3	1	3 1	1 1	1	0	1	1	2	П	-	1	1	1	2	2	4	_	_	
Brachygastra bilineolata	0	7	1	П	-	0	_	0	_	3		2 1	1 1	0	1	_	1	П	П	0	0	1	_	5	7	4	_	_	
Brachygastra moebiana	0	7	1	П	_	0	1	1	П	3	1	2 1	1 1	0	1	1	0	П	П	1	0	1	1	5	7	4	_	_ 1	
Brachygastra borellii	0	7	1	1	7	1	7	0	1	3	1	3 1	1 1	0	0	1	1	0	1	0	1	1	1	4	2	3	-	_ 1	
Brachygastra buyssoni	0	7	1	П	1	0	1	0	П	3	1	2 1	1 1	0	1	_	П	2	П	1	1	1	1	5	4	4	_	_	
Brachygastra cooperi	П	2	1	П	1	0	1	1	1	3	-	0	1 1	1	0	_	0	П	П	0	0	1	1	4	4	4	_	_	
Brachygastra fistulosa	П	7	1	П	1	0	П	П	П	3	1	2	1 1	1	0	1	1	П	П	0	0	П	П	4	4	3	_	_	
Brachygastra lecheguana	0	2	1	_	7	_	_	0	_	3	_	2	1 1	0	0	1	1	0	П	0	0	П	1	4	4	3	_	_	
Brachygastra mellifica	0	2	1	П	2	П	П	0	1	3		2	1 1	0	0	1	1	0	1	0	0	П	1	4	4	3	_		
Brachygastra mouleae	П	2	1	П	П	0	П	П	1	3		7	1 1	0	1	1	1	1	1	0	0	П	1	4	4	3	_		
Brachygastra myersi	П	7	1	П	1, 2	0	П	П	П	3	П	-	1 1	0	2	1	0	П	1	0	0	П	П	5	4	4	_	_	
Brachygastra propodealis	0	7	1	П	1	0	П	1	П	3	_	2	1 1	0	1	1	1	7	1	П	П	П	П	2	4	4	_	_	
Brachygastra scutellaris	П	7	1	П	1, 2	0	_	0, 1	_	3	_	_	1 1	0	2	П	0	1	1	0	0	_	П	5	4	4	_	_	
Brachygastra smithii	0	2		-	_	0	-	0	-	3	-	2		0	-	-	-	7	-	-	0	_	_	5	7	4			- 1

	c	3	3	3	3	3	3	3	3	4	4	4	4	4 4	4 4	1 4	4	4	ıc	5	5	5	5	5	5	5	5	5	9
	-	7	3	4	rv	9	^	∞	6	0	1	7	Ю	4	5 6	7	∞	6	0	1	7	3	4	rc	9	^	∞	6	0
Angiopolybia pallens	0	0	0	0	0	0	0	0	0	0	0	0					0	0	0	0	0	0	0	0	0	0	0	0	0
Pseudopolybia vespiceps	0	0	0	0	0	0	0	0	0	0	0	0	_	0 3		0 0	0	1	0	0	0	0	0	0	0	0	0	0	0
Protopolybia bituberculata	0	0	0	0	0	0	0	0	1	0	0	0			0		0	1	0	0	0	0	0	0	0	0	3	0	0
Charterginus xanthura	0	0	0	0	1	П	1	0	0	0	0	0				0 (1	0	0	0	0	0	1	1	7	1	0	1
Chartergus artifex	1	0	0	0	П	П	П	0	0	П	0	П				0 0	2	1	0	0	0	0	0	7	0	П	0	1	7
Protonectarina sylveirae	0	0	0	0	0	0	0	0	П	0	0	0					4	1	0	0	0	0	0	7	0	П	0	1	2
Polybia jurinei	0	0	0	0	0	0	0	0	0	0	0	0	3	0	2 (0 (1	0	0	0	0	0	7	0	_	0	1	7
Epipona guerini	0	0	0	0	0	0	0	0	0	0	0	0				0 0	0	1	0	0	0	0	0	7	0	П	0	1	7
Brachygastra albula	7	0	1	П	7	0	П	0	0	-	7	1				_ 1		1	۸.	٨.	٨.	٨.	٨.	٨.	٨.	٨.	٨.	٨.	۵.
Brachygastra augusti	7	0	1	П	7	0	П	0	П	-	7	1				1 1		-	1	1	0	1	П	7	0	1	7	1	2
Brachygastra azteca	0	0	0	0	7	0	П	0	0	1	7	1				1		1	1	0	0	1	П	7	0	1	3	1	2
Brachygastra baccalaurea	0	0	0	0	2	1	1	0	0	1	2	1						1	۸.	۸.	1	П	1	۸.	٨.	۸.	۸.	۸.	۵.
Brachygastra bilineolata	2	0	1	1	7	0	1	0	0	1	2	П	4		5	2 1	2	1	1	1	1	П	1	2	0	П	2	1	2
Brachygastra moebiana	2	0	1	1	7	0	1	0	1	П	7	П	4			2 1		1	1	1	1	П	1	2	0	П	П	П	2
Brachygastra borelli	2	П	1	1	7	0	0	0	0	П	3	П						1	0	0	1	П	1	٨.	٨.	۸.	٨.	۸.	۵.
Brachygastra buyssoni	2	0	1	П	7	0	1	П	0	П	2	П	4			2 1		1	۸.	٨.	٨.	٨.	٨.	٨.	٨.	٨.	۸.	۸.	۵.
Brachygastra cooperi	2	0	1	П	7	0	1	0	П	П	2	П	4		5 1	1 1	1	1	1	1	0	1	1	٨.	٨.	٨.	۸.	۸.	۵.
Brachygastra fistulosa	7	0	1	П	7	0	П	0	П	П	7	_	4	0		1 1	1	1	۸.	٨.	٨.	٨.	٨.	٨.	٨.	٨.	٨.	۸.	۸.
Brachygastra lecheguana	7	П	1	П	7	0	0	0	0	П	3	_			5]	1	3	1	0	0	П	П	П	7	0	_	3	1	7
Brachygastra mellifica	7	_	1	_	7	0	0	0	0	_	3	_			5]		3	1	0	0	0	_	П	7	0	_	3	П	2
Brachygastra mouleae	7	0	1	П	7	0	П	0	П	П	1	_			5]	1	2	1	۸.	٨.	٨.	٨.	٨.	7	0	П	0	1	2
Brachygastra myersi	1	0	1	_	7	0	_	_	0	_	1	_	4	0		1	1	1	٨.	~٠	٨.	٨.	٨.	7	0	1	7	1	7
Brachygastra propodealis	2	0	0	_	7	0	П	П	0	П	7	_	4		5]	1	7		۸.	٨.	۸.	٨.	٨.	٨.	٨.	٨.	٨.	۸.	۸.
Brachygastra scutellaris	1	0	0, 1	$\overline{}$	7	0	_	1	0	П	1	1	4		5		_	П	_	П	0	0	П	7	0	_	7	1	7
Brachygastra smithii	7	0	_	-	7	0	-	0	0	_	7	_	4		5 2	-	2	-	-	-	-	-	-	7	0	-	7	_	7

TABLE 2. List of characters for *Brachygastra*.

Numerical scores for each state follow equals sign (=).

- 1. Eighth flagellomere: less than twice as wide as long = 0; equal to or more than twice as wide as long = 1.
- 2. Shape of clypeus: longer than wide = 0; as long as wide = 1; wider than long = 2.
- 3. *Apex of clypeus*: sharply pointed = 0; rounded = 1; truncate = 2; bidentate = 3.
- 4. $Clypeal\ lateral\ lobes$: developed = 0; reduced = 1.
- 5. Pubescence on clypeus: absent = 0; covering top third =1 (fig. 6A); covering top half or more = 2 (fig. 6B).
- 6. Bristles on clypeus: present on ventral third, absent medially = 0; present all over = 1.
- 7. Punctures on clypeus: absent = 0; present, very small, scattered = 1; present, small, separated by 1–2 diameters = 2.
- 8. Contact between clypeus and eyes: not touching or touching less than width of antennal socket = 0; touching equal to width of antennal socket = 1.
- 9. Tentorial pit: not touching the antennal socket = 0; touching the antennal socket = 1.
- 10. Interantennal prominence: raised, acute = 0; flat = 1; little raised = 2; wide, rounded = 3.
- 11. *Interantennal furrow*: marked, deep = 0; shallow or evanescent = 1.
- 12. *Hairs on frons and vertex:* absent or very sparse and short = 0; present, long and sparse = 1; present, long and dense = 2; present, extremely long and dense = 3.
- 13. Hairs on eyes: absent or very sparse and short = 0; long, moderate to dense = 1.
- 14. Ocelli: separated by less than ocellar diameter = 0; separated by more than ocellar diameter = 1.
- 15. Lateral ocellus separation from eyes: equal to or less than 1.5 ocellar diameters = 0; more than 1.5 ocellar diameters.
- 16. Vertex: strongly convex = 0; moderately convex = 1; flat = 2.
- 17. Gena: curved = 0; sinuous = 1.
- 18. Middle region of gena: width less than that of eyes = 0; width about equal to or more than that of eyes = 1.
- 19. Lower region of gena (postgenal convexity): absent = 0; slightly developed = 1; very well developed = 2.
- 20. Occipital carina: present, not reaching the mandibular condyle = 0; present, extending to mandibular condyle = 1; absent = 2.
- 21. Height of occipital carina below: equal to or lower than medial region = 0; higher than medial region = 1.
- 22. Malar space: equal to or less than half diameter of antennal socket = 0; more than half diameter of antennal socket = 1.
- 23. $Pretegular\ carina:\ present=0;\ absent=1.$
- 24. Pronotal fovea: present = 0; absent = 1.
- 25. *Pronotal carina*: absent = 0; dorsal trace = 1; extending to pronotal lobe = 2; medially weak, laterally produced = 3; extending beyond pronotal lobe, not reaching ventral corner (fig. 4A); extending to ventral corner = 5.
- 26. *Humeri*: rounded, not projecting = 0; very slightly projecting in dorsal view = 1; projecting = 2; acute = 3; projecting, produced forward = 4.
- 27. Secondary spiracular entrance: long flange = 0; narrow tubercle = 1; wide tubercle = 2; wide arch = 3; arching, edge bent down = 4.
- 28. $Dorsal\ groove:$ present = 0; absent = 1.
- 29. Scrobal sulcus: present = 0; absent = 1.
- 30. *Scutum:* longer than wide = 0; wider than long = 1.
- 31. Scutellum in profile: rounded = 0; angular, dorsal and ventral surface distinct = 1; strongly angular = 2.
- 32. Lateral angle of scutellum: rounded = 0 (fig. 6D); markedly angled = 1 (fig. 6C).

- 33. Scutellum: not projecting over metanotum = 0; projecting over metanotum = 1.
- 34. Emargination on scutellum: absent = 0; present medially, V-shaped = 1 (fig. 6C).
- 35. Metanotum: rounded = 0; compressed = 1; flat = 2 (fig. 6E and F).
- 36. Dorsal tubercle on metanotum: absent = 0; present = 1.
- 37. Mesopleuron: rounded to moderately convex = 0; strongly convex = 1.
- 38. Dorsal sclerite of metapleuron: less than 3 times as long as wide = 0; equal to or more than 3 times as long as wide = 1.
- 39. Metapleural-propodeal suture: marked, evident = 0; weak, not evident = 1.
- 40. *Propodeum*: sloping = 0; vertical = 1.
- 41. *Propodeal angle*: not developed = 0; slightly produced = 1; strongly produced = 2; toothlike = 3.
- 42. Propodeal lateral ridge: absent = 0; present = 1.
- 43. *Propodeal concavity*: narrow = 0; broad = 1; posterior, deep = 2; very broad, shallow = 3; almost flat = 4; narrow, ventrally deep, propodeum forming large lateral lobes = 5.
- 44. *Propodeal valve*: triangular = 0; linear = 1.
- 45. *Metasomal segment I:* longer than wide = 0; filiform, long, not dilated at sides = 1; flask-shaped = 2; wider than long = 3; petiolate, transversely widened porsteriorly = 4; wider than long, cap-shaped = 5.
- 46. *Metasomal sternum I*: smooth = 0; rugose = 1; rugose, with a transverse medial ridge = 2.
- 47. *Metasomal tergum II in profile*: rounded = 0; convex = 1.
- 48. *Metasomal tergum II punctation:* little evident = 0; coarse, dense = 1; medium, dense = 2; fine, not dense = 3; large, superficial punctures anteriorly = 4.
- 49. Van der Vecht's gland: external modified area present = 0; externally absent = 1.
- 50. Lateral margin of aedeagus in ventral view: not prominent = 0; prominent = 1.
- 51. Lateral ridge of aedeagus: absent = 0; present = 1.
- 52. Digitus: long apically = 0; wide apically = 1.
- 53. Notch on digitus: absent = 0; present = 1.
- 54. Ventral process of aedeagus: short, angular = 0; long, attenuate = 1.
- 55. *Comb pedicel*: rodlike pedicel = 0; basally sessile, resembling stout pedicel = 1; absent = 2.
- 56. Combs: multiple = 0; single = 1.
- 57. Comb expansion: gradual = 0; absent = 1; contiguous blocks = 2.
- 58. Envelope entrance: ventral = 0; dorsal = 1; lateral = 2; multiple = 3.
- 59. Secondary envelopes: absent = 0; present = 1.
- 60. *Envelope*: built from substrate, not contacting combs = 0; built from edge of comb = 1; secondary combs built on envelopes = 2.

Color and vestiture: Black species with yellowish bands on upper region of metanotum, metasomal tergum I, and terga and sterna II–V; surface dull, punctures coarse; legs blackish, femora, tibiae, and tarsi dark yellow to brown, covered with appressed pubescence; forewings infuscate, veins dark brown, costal region blackish.

HEAD: (1) Clypeus about 1.8 times wider than long with pubescence on top third and very fine punctures, lateral margins touching the eyes with length equal to width of the antennal socket; lateral projections touching the eyes below; epistomal suture marked, touching the

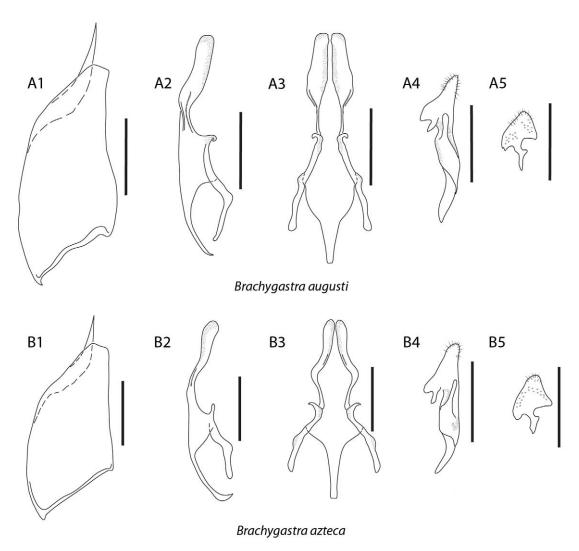


FIGURE 2. Male genitalia of (**A**) *Brachygastra augusti* and (**B**) *Brachygastra azteca*: A1, B1 = paramere, lateral view; A2, B2 = aedeagus, lateral view; A3, B3 = aedeagus, ventral view; A4, B4 = cuspis, lateral view; A5, B5 = digitus, lateral view. Scale bars = 0.5 mm.

antennal socket; apex rounded; (2) interantennal prominence slightly compressed; (3) frons and vertex with medium to large punctures, separated by 1–2 diameters, surface dull; hairs absent (fig. 8B); (4) vertex convex, posterior surface sloping ventrad in profile; (5) hairs on eyes short and sparse; (6) gena sinuous, width of the middle region 0.85 that of the eyes, with the same pattern of punctation as that found in frons and vertex, becoming sparser and smaller on lower region; postgenal convexity slightly produced; (7) malar space small, about 0.4 of the 4th antennal article; (8) occipital carina extending to mandibular condyle, uniform; (9) posterior region of the head slightly curved; (10) ocelli separated by more than 1 ocellar diameter, with a shining central area (= ocellar area) unpunctured.

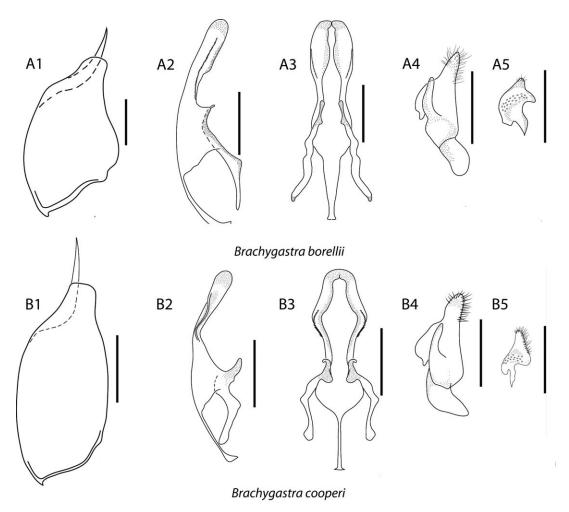


FIGURE 3. Male genitalia of (**A**) *Brachygastra borellii* and (**B**) *Brachygastra cooperi*: A1, B1 = paramere, lateral view; A2, B2 = aedeagus, lateral view; A3, B3 = aedeagus, ventral view; A4, B4 = cuspis, lateral view; A5, B5 = digitus, lateral view. Scale bars = 0.5 mm.

MESOSOMA: (1) Pronotal carina slightly lamellate, extending beyond the pronotal lobe, but not reaching the ventral corner, separating the pronotum into dorsolateral and anterior regions; punctures on dorsolateral region large and contiguous, on anterior region small and scattered; humeri projecting; (2) scutum 1.2 times wider than long, punctures large and deep, separated by less than 1 diameter; on central and posterior regions the punctures become smaller and sparser, surface dull (fig. 8D); (3) scutellum projecting over metanotum, distinctly separated into dorsal and ventral surfaces, slightly emarginate and rounded; punctures on dorsal surface large, moderately deep, separated by less than 1 diameter; punctures on ventral surface smaller and scattered, mostly on upper region; (4) metanotum vertical, slightly convex, with a yellow band on superior region, punctures scattered and very small; (5) mesopleuron strongly convex, with large and deep punctures on upper region separated by less than 1 diameter, becoming

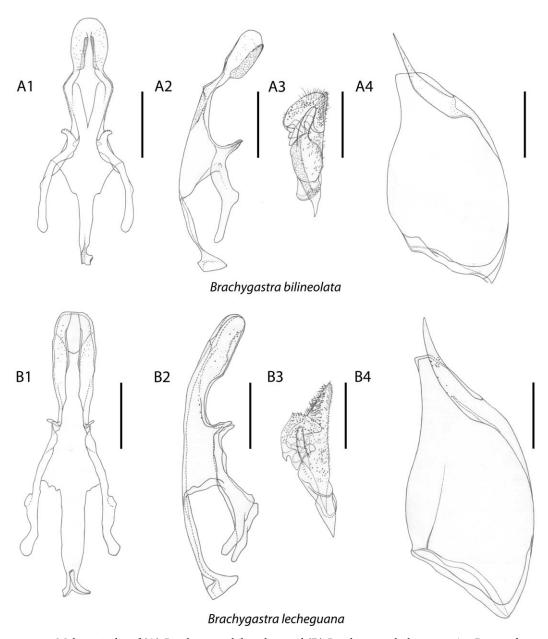


FIGURE 4. Male genitalia of (A) *Brachygastra bilineolata* and (B) *Brachygastra lecheguana*: A1, B1 = aedeagus, ventral view; A2, B2 = aedeagus, lateral view; A3, B3 = volsella, lateral view; A4, B4 = paramere, lateral view. Scale bars = 0.5 mm

smaller and sparse (separated by 1–2 diameters) on central and lower region; anterior and posterior region with smaller and scattered punctures, with some areas completely unpunctured; (6) upper plate of metapleura 2.5 times longer than wide at middle, punctures large and deep, contiguous, separated by less than 1 diameter, giving a rugose aspect; metapleural furrow deep, rounded, suture not evident; lower plate with very small, scattered punctures; metapleu-

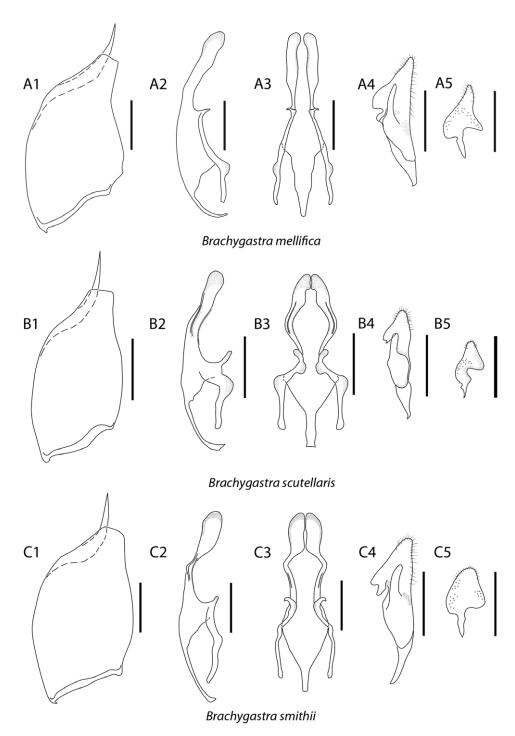


FIGURE 5. Male genitalia of (**A**) *Brachygastra mellifica*, (**B**) *Brachygastra scutellaris*, and (**C**) *Brachygastra smithii*: A1, B1, C1 = paramere, lateral view; A2, B2, C2 = aedeagus, lateral view; A3, B3, C3 = aedeagus, ventral view; A4, B4, C4 = cuspis, lateral view; A5, B5, C5 = digitus, lateral view. Scale bars = 0.5 mm.

ral-propodeal suture weak; (7) dorsolateral region of propodeum with large and deep punctures, separated by less than 1 diameter, becoming smaller and sparser laterally; propodeal lobe slightly produced; propodeal angle obtuse; propodeal concavity wide, shallow, weakly striate on lower and central region covered by short and dense pubescence; propodeal valve wide, narrowly triangular; (8) forewing length 6.5 mm.

METASOMA: (1) Tergum I wider than long, cap shaped with a narrow pale yellowish band on posterior region; punctures small and scattered, separated by about 2 diameters, dense and short hairs present; (2) sternum I rugose, with few scattered punctures; (3) tergum II about 1.2 times wider than long, strongly convex dorsally, parallel sided in dorsal view, in lateral view anteriorly vertical, almost flat; punctures medium to large, contiguous, separated by less than 1 diameter on medial and lateral region, becoming sparser and smaller anteriorly; pale yellowish band posteriorly (fig. 8F); (4) sternum II with the same pattern of color and punctation as on tergum II; (5) terga and sterna III–V with punctation smaller and sparser than that on tergum II, but with the same pattern of color.

MALE: In general aspects like female, but surface duller; more hairy than females; clypeus narrower than in females, with a yellow spot; two yellow spots on orbits; antenna brownish, scape yellow beneath, brownish above; gena narrower; interocellar area with punctures like those on frons and vertex; pronotum brownish-blackish; punctures on scutum even; scutellum and metanotum yellowish; punctation on mesopleura stronger, forming strips; metasomal tergum I–V brownish, with yellow bands posteriorly.

MALE GENITALIA: (1) Paramere about twice as long as wide at the middle, basal angle obtuse, apical angle broad and truncate, spine of paramere long, pointed apically (fig. 3 B1); (2) aedeagus slightly curved, lobe stout and rounded, lateral margin prominent, widening gradually on the middle; lateral ridge present with a row of small teeth extending ventrolaterally, the ventral process of aedeagus is long and curved apically, angular (figs. 3 B2, B3); (3) cuspis long and pointed apically, with short and sparse hairs, blackish on inferior region (fig. 3 B4); (4) digitus long apically, stout and acute, with short hairs, mesal surface with scattered punctures (fig. 3 B6).

NEST: Unknown.

Distribution: Colombia, Caquetá, Yuruyaco.

HOLOTYPE: Female, Colombia, Caquetá, Yuruyaco, 73km SW Florencia; 23.i.1979; М. Cooper (ВМNН), 1270 m elev.

Paratypes: 1 female, same locality and date as the holotype; 1 male, Colombia, Caquetá, Yuruyaco, 73km SW Florencia; 07.ii.1979; M. Cooper (BMNH).

ETYMOLOGY: The specific name is a reference to Martin Cooper, who collected this species.

Male Genitalia

Naumann (1968: 934) stated "the best characters are found in the male genitalia, but unfortunately the males are seldom collected and in some species are entirely unknown." Hitherto, males of only eight species of *Brachygastra* were known. Du Buysson (1905) depicted the male

genitalia of *B. azteca, B. baccalaura, B. lecheguana* (actually, *B. mellifica*; see below), and *B. smithii*, Naumann (1968) redescribed the male genitalia previously described by du Buysson (1905), plus *B. augusti, B. bilineolata*, and *B. mellifica*, and Andena and Mateus (2011) described the male genitalia of *B. moebiana*. Additionally, in this work, drawings and descriptions of the male genitalia of *B. borellii* and *B. scutellaris* are also provided.

Male of Brachygastra Borellii

Brachygastra borellii males are like females, but more hairy, especially on head; clypeus narrower and slightly more convex; scape yellow beneath, brownish above; gena much narrower and more punctured; upper plate of metapleuron with denser punctation, rugose.

MALE GENITALIA: (1) Paramere about 1.5 times longer than wide at the middle, basal angle obtuse, apical angle broad and truncate, spine of paramere long, pointed apically (fig. 3 A1). (2) aedeagus slightly curved, lobe broad and rounded, lateral margin rounded, not prominent, lateral ridge absent, a row of small teeth extending ventrolaterally, the ventral process of aedeagus long and pointed apically, (fig. 3 A2 and A3); (3) cuspis long and acute apically, with fine and long hairs (fig. 3 A4); (4) digitus wide apically, with few and scattered short hairs, mesal surface with scattered punctures (fig. 3 A5).

Male of Brachygastra scutellaris

Brachygastra scutellaris males are like females, but the clypeus is narrower and slightly more convex; scape yellow beneath, brownish above; gena much narrower and more punctured; scutellum and metanotum pale; sometimes a yellow spot on superior region of propodeum.

MALE GENITALIA: (1) Paramere about 1.7 times longer than wide at the middle, basal angle obtuse, apical angle truncate, spine of paramere long, pointed apically (fig. 5 B1); (2) aedeagus slightly curved, lobe stout and rounded, lateral margin prominent, widening gradually at the middle; lateral ridge present with a row of small teeth ventrally, extending little toward lateral region, ventral process of aedeagus long apically, angular (fig. 5 B2, B3); (3) cuspis long and pointed apically, with fine and short hairs, (fig. 5 B4); (4) digitus wide apically, broad, with few short hairs, mesal surface with scattered punctures, notch absent (fig. 5 B5).

DISCUSSION

THE MONOPHYLY OF BRACHYGASTRA

In this work *Brachygastra* is supported as monophyletic, traditionally diagnosed by the prominent projecting scutellum, which with the metanotum and propodeum forms a flat, vertical surface (du Buysson, 1905; Ducke, 1905, 1910; Naumann, 1968; Richards, 1978; Carpenter, 2004). Despite their utility in recognizing the genus, these features are not synapomorphies in figure 12. The scutellum is a prominent structure for most species of *Brachygastra*, but may or may not project over the metanotum. Among the species that have the projecting scutellum (char. 33-1) variation ranging from slightly to strongly projecting was seen. Due to such variation we coded only two states for this character (see table 2: char. 33). Naumann (1968)

described the scutellum not projecting over the metanotum for *B. scutellaris*, but instead we verified that it is slightly projecting in some specimens, hence it was coded as polymorphic. *Brachygastra azteca, B. propodealis*, and *B. baccalaurea* have the scutellum not projecting over the metanotum (char. 33-0). The propodeum vertical (char. 40-1), the propodeal lateral ridge present (char. 42-1), and the propodeal concavity almost flat (char. 43-4) are features shared with *Chartergus* that also are not synapomorphic in figure 12.

We list here the synapomorphies for Brachygastra in figure 12. The interantennal prominence wide and rounded (char. 10-3) was not cited by Naumman (1968) or Richards (1978), but, despite some small variation among the species, proved to be a synapomorphy for the genus. The hairs on frons and vertex are long and dense (char. 12-2), although they are extremely long and dense for B. borellii and B. baccalaurea (char. 12-3), both widely distributed in Andean region. As pointed out by Naumann (1968) for B. baccalaurea, this is often a characteristic of species from Andean regions of South America. The new species, B. cooperi, was collected in Colombia, 1270 m elev., not showing hairs on the frons and vertex, a reversal to a plesiomorphic condition. Brachygastra myersi and B. scutellaris show long hair, as in the other species within Brachygastra, but sparser. The scrobal sulcus absent (char. 29-1) and the scutum wider than long (char. 30-1) are features also cited by Carpenter (1991). Carpenter (1991), whose focus was the phylogeny of the genera of Polistinae, coded the metanotum as compressed for Charterginus, Chartergus, and Brachygastra. As the species of Brachygastra have the metanotum more vertical than those of other genera, we included another state, flat (char. 35-2). The metasomal tergum I is wider than long and cap shaped (char. 45-5). The metasomal tergum II is convex in profile (char. 47-1), and compressed at the frontal region. The propodeal angle is strongly produced (char. 41-2); however, it is less developed in B. mouleae and in B. myersi + B. scutellaris. Male genitalia characters that are also synapomorphies in figure 12 include the notch on digitus present (char. 53-1) and ventral process of aedeagus long and attenuate (char. 54-1). However, they may not be synapomorphies for the entire genus, because the males are still unknown for B. mouleae, B. fistulosa, B. myersi, B. buyssoni, B. propodealis, and B. albula, and the absence of the notch on the digitus is a reversal in B. scutellaris.

The punctation on different parts of the body has been used for description and identification of the species, subspecies, and forms of the genus (du Buysson, 1905; Ducke, 1905, 1907, 1910; Naumann, 1968; Richards, 1978). Naumann (1968) cited variation in the size and density of punctures, which sometimes forms long strips on the scutum. Here we used only the punctures on clypeus and tergum II, which are more stable (see table 2: chars. 7 and 48, respectively).

THE GROUPS WITHIN BRACHYGASTRA

Naumann (1868) divided the genus into two groups: (1) the *lecheguana* group, comprising *B. mellifica*, *B. lecheguana*, and *B. borellii*; and (2) the *smithii* group comprising *B. baccalaurea*, *B. bilineolata*, *B. smithii*, *B. propodealis*, and *B. buyssoni*. According to Naumann (1968) the remaining species are not closely related and could not be included within either group. In this work, these species are included in a third clade, called here *scutellaris* group, except *B. azteca*, which is the basalmost species. These three groups are supported as a clade, in contrast to *B. azteca*, by

features of the scutellum: being strongly angular (char. 31-2), projecting over the metanotum (char. 33-1) and medially emarginate, usually in a V-shape (char. 34-1). Nest characters based on size and season, proposed by Naumann (1968), are not enough to separate these groups.

Naumann (1968) described a pronotal carina (= pronotal keel) absent for *B. azteca*, but the pronotal carina for this species is, sometimes, weakly lamellate (Richards, 1978). In fact, *B. azteca* has the pronotal carina straighter than the species of the groups within *Brachygastra* and the humeri are also less projecting.

THE LECHEGUANA GROUP

As pointed out by Naumann (1968), the three species of the lecheguana group were previously grouped under one species, B. lecheguana. Naumann (1968), based on male features, raised the status of B. borellii and B. mellifica to species level. In fact, this group's species are similar, especially B. lecheguana and B. mellifica, which can be separated only by male genitalia features. The features shared by the lecheguana group cited by Naumann (1968) are: (1) occipital carina not well developed on ventral half of gena, in table 2 coded as height of occipital carina below (char. 21-0); (2) the postgenal convexity absent or very weak (char. 19-0), homoplastic in figure 12 because this feature is also found in the outgroups; (3) the pronotal keel low, not projecting cephalad on the humeral angle. This feature was divided and described as pronotal carina (char. 25), which, in the case of lecheguana group, is weakly lamellate and not extending to the ventral corner (state 4), also shared by B. azteca, B. augusti, B. mouleae, B. fistulosa, and B. cooperi, and the humeri (char. 26). The humeri of B. lecheguana and B. mellifica project and are produced forward (char. 26-4). Naumann (1968) stated "not produced cephalad on humeral angle" for the whole lecheguana group; however, this is a feature that might be referred to B. borellii, which has the humeri slightly more projecting than in B. azteca; (4) scutellum angular, described in this work as lateral angle of scutellum (char. 32-1), which is markedly angled and a remarkable feature for the lecheguana group. Richards (1978) in his identification key to the genus (couplet 3) cited the angles of propodeum distinctly lamellately produced (= propodel angle toothlike in table 2: char. 41-3). Additionally, we cite here another two features supporting the group: the mesopleura rounded (char. 37-0) and the bristles on clypeus present all over (char. 6-1).

Despite the similarities to *B. lecheguana*, *B. borellii* has distinct long hairs and deep punctation on the head and on the mesosoma (Ducke, 1910; Bequaert 1943; Naumann, 1968; Richards, 1978). Punctures on the clypeus of *B. borellii* are denser, separated by more than one diameter (char. 7-2) (Naumann, 1968), an autapomorphy for this species. Naumann (1968) and Richards (1978) cited the similarities of *B. mellifica* and *B. lecheguana*. In fact, these species are extremely similar and the identification is difficult, based only on female characters. In figure 12 they are supported by the punctation on metasomal tergum II, which is fine and sparse (char. 48-3). Naumann (1968) and Richards (1978) pointed out that the emargination on the scutellum is deeper in *B. lecheguana* than in *B. mellifica*, but in fact we have seen variation on this feature. Specimens of *B. lecheguana* from several localities in Argentina, Brazil, and Ecuador have the emargination as deep as the specimens of *B. mellifica* from Texas and Arizona, so this feature, alone, cannot be used for identification of the species. Naumann (1968), in his

identification key (couplet 17), used only geographic distribution, but as they overlap at the borders of South and Central America the females cannot be separated (Richards, 1978). The male genitalia, described by Naumann (1968), were used in the Richards's key (1978), as an additional feature for separating these two species, and also in this work. In *B. lecheguana* the digitus is wide apically vs. long in *B. mellifica* (see identification key and figs. 4 B3, 5 A5).

THE SMITHII AND SCUTELLARIS GROUPS

Within *Brachygastra*, the *smithii* group and the *scutellaris* group are supported as a clade by the pubescence on the clypeus covering the top third (char. 5-1), as also cited by Richards (1978). However, this is homoplastic in figure 12, because it is shared with the outrgroup *Pseudopolybia vespiceps*. Synapomorphies in figure 12 for this clade are the vertex moderately convex (char. 16-1), lateral ridge of the aedeagus present (char. 51-1) and the envelope entrance lateral (char. 58-2). We must take into account that the male and nest are still unknown for some species of these groups.

THE SMITHII GROUP

Besides the species comprising the smithii group proposed by Naumann (1968), our phylogenetic analysis shows B. albula, described after Naumann's revision by Richards (1978), within the smithii group. The features cited by Naumann for his smithii group are exactly the opposite of those for the lecheguana group: (1) The height of occipital carina below is higher than the medial region (char. 21-1) (= occipital carina well developed on ventral half of gena), not shared with B. bilineolata, which has this feature equal to medial region. (2) Postgenal convexity (= lower region of gena) more or less well developed (char. 19). The lower region of gena of the smithii group is easily recognized; however, it is slightly developed (state 1) in B. bilineolata and B. moebiana, sharing it with the scutellaris group and B. azteca. The remaining species of the *smithii* group have the lower region very well developed (state 2), with that of B. albula the most prominent of the genus. (3) The pronotal carina extends to the ventral corner (char. 25-5), a feature shared with B. myersi and B. scutellaris, and the humeri projects, produced forward only for B. buyssoni + B. propodealis (char. 26-4), not for all species of the smithii group as cited by Naumann (1968). Two other features are shared by the smithii group: the entrance of secondary spiracle arching, edge bent down (char. 27-4), shared with B. cooperi + (B. myersi + B. scutellaris); and the metasomal sternum I rugose with a transverse medial ridge (char. 46-2), the medial ridge being absent in B. albula, B. baccalaurea, and B. propodealis.

The three basal most species of the *smithii* group, *B. bilineolata*, *B. moebiana*, and *B. smithii* have a complex taxonomic history. *Brachygastra smithii* and *B. moebiana* were considered varieties of *B. bilineolata* by Buysson (1905) and Ducke (1907), with most of the characters based on color pattern alone. Naumann (1968) raised *B. bilineolata* and *B. smithii* to species status, but he still considered *B. moebiana* as a variety of *B. bilineolata*. Richards (1978) raised the status of *B. moebiana* to species. In fact these three species are similar morphologically, but with wide variation in color pattern, which has caused confusion. One of the features for separating *B. smithii* and *B. bilineolata* is the occipital carina and Naumann (1968: 963) said, "In northern South America it is separable on the basis of the occipital carina which is low or absent on the ventral

half of the gena. *Brachygastra smithii* in the same region has a well-developed carina. In the southern part of its range, i.e., south of the Amazon, the occipital carina becomes very high but that of *smithii* is, in contrast, much reduced. This character, then, is inversely related in these two species." *Brachygastra bilineolata* is the most basal species of the *smithii* group, having the height of the occipital carina below equal to or lower than the medial region (char. 21-0), which in some specimens is very weak but not absent as stated by Naumann (1968). *Brachygastra moebiana* and *B. smithii* have the height of occipital carina below higher than the medial region. Probably the variation described by Naumman (1968: 963) for *B. bilineolata* pertains to *B. moebiana*, which, as cited above, was treated as a variety of *B. bilineolata*. On the other hand, in the specimens of *B. smithii* seen in this work there is not a reduction in the height of the occipital carina below.

Brachygastra moebiana and B. albula are the two species within Brachygastra that have the propodeal valve linear. Richards (1978: 177) described the similarities between these species based mainly on punctures. Brachygastra albula has denser punctures on the scutellum and humeri, making it easily distinguished. Richards (1978) designated as paratypes of B. albula specimens from "Aldeia Juruna, Rio Xingú, Mato Grosso, Brazil," which had previously been identified by Naumann (1968) as B. buyssoni. Brachygastra buyssoni shows the propodeal valve almost triangular, but Richards (1978: 177) stated that the propodeal valve is linear; however, in his identification key (couplet 10) he characterized the propodeal valve as "at least somewhat, often widely, triangularly expanded" in B. buyssoni, clearly a typographical error.

The clade *B. baccalaurea* + *B. albula* differs from the clade *B. buyssoni* + *B. propodealis* by the lateral ocellus separated from the eye by more than 1.5 ocellar diameters (char. 15-1) and by the vertex strongly convex (char. 16-0), both homoplastic in figure 12.

THE SCUTELLARIS GROUP

Finally, the scutellaris group comprises the remaining species of Brachygastra. Although the species of this clade are supported by homoplasies in figure 12, two features are useful to recognize them. First, the eighth flagellomere is more than two times as wide as long (char. 1-1), a feature shared with B. azteca and one that was totally ignored by Richards (1978). On the other hand, Naumann (1968) recognized this feature in his revision but did not use it to recognize these species as a group. Second, the clypeus touches the eyes by a distance equal to or more than the width of the antennal socket (char. 8-1); however, it is polymorphic in B. scutellaris. Naumann (1968: 940) stated that B. augusti is similar to the lecheguana group in color pattern, but has a large pronotal keel like B. scutellaris. The close relationship of B. augusti and B. mouleae is unsurprising. As cited by Richards (1978), B. mouleae is structurally extremely similar to B. augusti, but B. augusti has an area without punctures between the ocelli and a stronger triangular process from the angles of propodeum. Besides these features, the occipital carina and the metapleural-propodeal suture are weaker in B. mouleae, but not enough to be coded as another state. The entrance of the nest is also different between these species, lateral in B. augusti vs. multiple in B. mouleae. Richards (1978) pointed out a straight pronotal carina in B. mouleae vs. bisinuate in B. augusti, but, again, such variation is not enough to be coded differently, as in both species the carina does not reach the ventral corner.

The remaining species of the *scutellaris* group are supported by the coarse and dense punctation on metasomal tergum II (char. 48-1). Within *Brachygastra* this feature is shared only by these species; however, it is homoplastic in figure 12, because it is also shared with the outgroup *Charterginus xanthura*.

The new species *B. cooperi* resembles *B. fistulosa* in general aspects, as described above, and both are intermediate between the *B. augusti* and *B. mouleae* and the *B. scutellaris* + *B. myersi* clade. This intermediate position had been cited by Naumann (1968), referring to *B. fistulosa*. Within the *scutellaris* group these species have the vertex strongly convex (char. 16-0) and the lateral ocellus separated by more than 1.5 times its diameter from the eyes (char. 15-1). As described above *B. cooperi* lacks hairs on frons and vertex, an autapomomorphy for this species. Other remarkable features are the secondary spiracular entrance arching with the edge bent down, and the width of the middle region of the gena less than that of the eye for *B. cooperi*, vs. secondary spiracular entrance wide and arching, and the width of the middle region of the gena more than that of the eye for *B. fistulosa*.

Brachygastra myersi was described as a variety of B. scutellaris and Richards and Richards (1951), Naumann (1968), and Richards (1978) pointed out the variation in color in different localities for these species. The most common form of B. scutellaris shows a yellow scutellum; however, dark forms, in which the yellow maculation is reduced or absent, have also been observed (Naumann, 1968). Brachygastra myersi shows a reduction in the yellow maculation on the scutellum or it is even black, beyond the longer hairs on the eyes that differentiate the two species. Brachygastra myersi and B. scutellaris are supported as sisters by the vertex flat (char. 16-2), and also by the scutellum angular, with the dorsal and ventral surface distinctly separated (char. 31-1), homoplastic in figure 12.

Male Genitalia Remarks

Characters of the male genitalia of *Brachygastra* merit special remarks. The lateral margin of the aedeagus is prominent in all species of the *smithii* and *scutellaris* groups plus *B. azteca*, and is not prominent in the species of the *lecheguana* group. A lateral ridge is absent in *B. azteca* and the *lecheguana* group, so the presence of such a structure is probably a synapomorphy for the *smithii* and *scutellaris* groups.

Brachygastra borellii is the only species within the genus that has a remarkable paramere, which is as wide as it is long (vs. longer than wide in the remaining species). The apex of the paramere is truncate, although more rounded than in other species (fig. 2 A1). Despite Naumman (1968), who described small differences in the apical angle of the paramere for B. azteca, B. augusti, B. bilineolata, B. smithii, B. mellifica, and B. lecheguana, all of these have the apex truncate as does B. cooperi, B. scutellaris, and B. borellii, described here, as well as B. moebiana (Andena and Mateus, 2011: fig. 1). Naumann (1968) pointed out that the apex of the paramere of B. baccalaurea is blunt, not truncate; however, we did not have this species on hand to confirm it. Carpenter and Mateus (2004) and Andena et al. (2007) studied some species of basal clades of Epiponini and pointed out that the apical angle is homoplastic at the generic level.

Hairs are absent on the paramere spine in the species of *Brachygastra*; in fact, hairs are known only for the species of *Apoica*, *Pseudopolybia*, and *Parachartergus*; hence, the state "hairs absent" is general for Epiponini (Andena et al., 2007). Pickett and Wenzel (2007; figs. 12, 13) in their phylogeny coded the paramere spine with setae absent for only two species (*Apoica pallida* and *A. strigata*); however, their state "setae present" seems to refer to setae that are short and sparse, as also found in *Parachartergus* (see Carpenter and Mateus, 2004; Andena et al., 2007). The known males of *Pseudopolybia* (*P. difficilis*, *P. compressa*, and *P. vespiceps*) show long and dense hairs that are, probably, a synapomorphy of the genus.

One of the features cited by Richards (1978) for separating genera into two groups, based on male genitalia, is the aedeagus serrate beneath. As the species of *Brachygastra* lack this feature this genus would fall into group 1, but as already pointed out by Carpenter and Mateus (2004) and Andena et al. (2007) these groups should be abandoned, because they are unnatural. The character "aedeagus serrate beneath" is found in the basal groups of Epiponini; therefore, the state "not serrate beneath" is a derived condition.

Although Naumann (1968) did not mention hairs on the cuspis and digitus except for *B. azteca*, the hairs in the figures depicted here and by Andena and Mateus (2011: fig. 1) are short and sparse on both structures. In du Buysson (1905; pl. 12, figs. 9–12), the hairs look longer and denser for *B. azteca*, *B. baccalaurea*, *B. lecheguana*, and *B. smithii*. Also, du Buysson's figure 10 (1905: pl. 12: fig. 10) actually refers to *B. mellifica*, which has the digitus pointed, not *B. lecheguana* as cited.

Naumann (1968: 958) studied only four males of *B. augusti* and pointed out variation in male genitalia: "two from Jaén, Dept. Cajamarca, Perú, and Trinidad, Dept. Beni, Bolivia, had elongate volsellar lobes and angular digital lobes, and two from Rio Juruá Est. Amazonas, Brazil, and Muzo, Dept. Boyaca, Colombia, had the shorter tapered volsellar lobes and the rounded digital lobes as described above." Richards (1978) stated that two specimens from the series from Rio Juruá were somewhat intermediate to *B. mouleae*. Naumann (1968: 957) stated that the specimens of this series were more heavily punctured, also seen by us. Brandão (personal commun.) gave us information about the Rio Juruá series deposited in MZUSP:

Six exemplars are at Museu de Zoologia da Universidade de São Paulo (MZUSP), being one of them the lectotype [Richards handwriting], the other five exemplars were identified by Naumann and Ducke. Some labels of the specimens seem to be a problem. One of the exemplars with the number 1620 on the label belongs to Rio Juruá, however this number [1620] belongs to other locality in the record book of the old collection of the Museu de Zoologia. The male was not located in the collection.

Naumann's description of the male genitalia of *B. augusti* matches figure 2A, a specimen collected in Mato Grosso, Brazil. Variation in the genitalia of the species from Rio Juruá, Amazonas, Brazil, and Muzo, Dept. Boyaca, Colombia, cited by Naumann (1968) may refer to *B. mouleae*. We defer further discussion of the male of *B. mouleae*, as we did not have males of this species in hand.

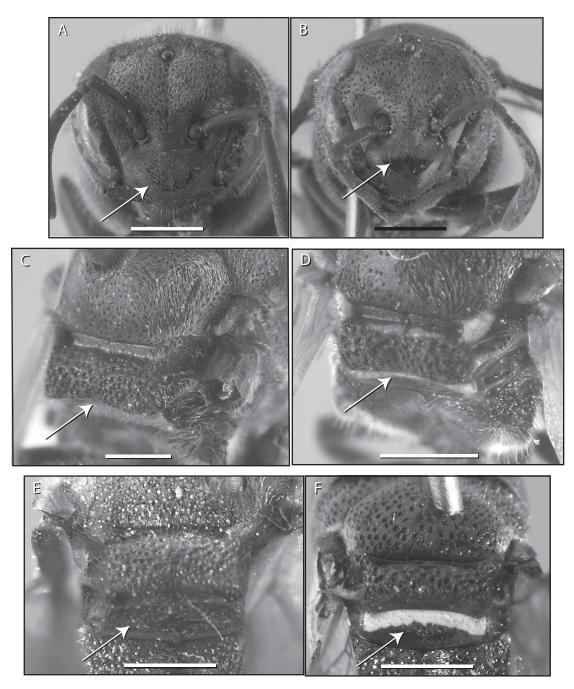
We hope that the males of the remaining species of *Brachygastra* will be examined, to help elucidate the phylogenetic relationship of the species of this genus.

IDENTIFICATION KEY FOR BRACHYGASTRA

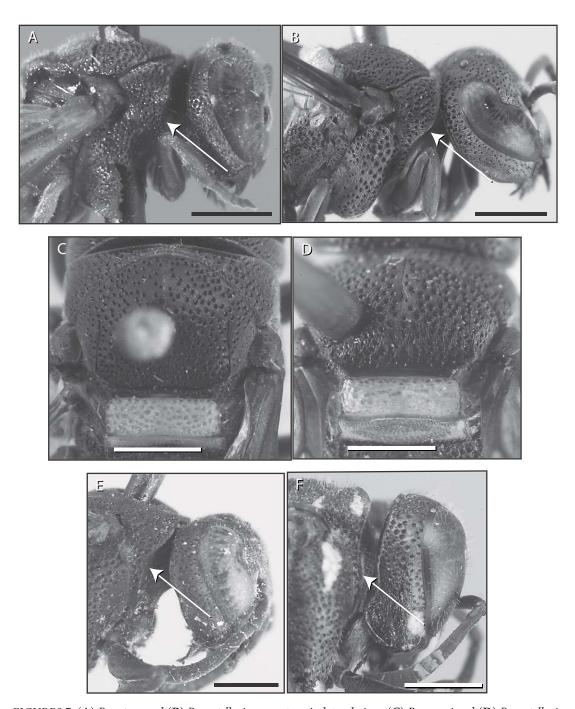
The	e identification key presented here is a revision of Richards's (1978) key, including the new
	species and new characters, some of which were also used in the phylogenetic analysis.
1.	Top half or more of clypeus covered with pubescence (fig. 6A); if somewhat less (B. scu-
	tellaris and B. myersi), then metasomal tergum II with medium to large punctures2
_	Only the top third or less of clypeus covered with pubescence (fig. 6B); if metasomal ter-
	gum II strongly punctured (B. fistulosa and B. cooperi), pronotal carina rounded medi-
	ally, occipital carina often higher below than above
2.	Scutellum with a marked angle between dorsal and posterior surfaces (fig. 6C); bristles
	on clypeus present all over; postgenal convexity absent; pronotal carina extending
	beyond pronotal lobe, weakly lamellate; mesopleuron rounded to moderately convex;
	angles of propodeum toothlike; metasomal tergum II with punctures fine to medium;
	lateral margin of aedeagus not prominent in ventral view (figs. 3 A2, 4 B2, 5 A2)
_	Scutellum with junction of dorsal and posterior surfaces rounded (fig. 6D); bristles on
	clypeus present on first third; postgenal convexity slightly developed; pronotal carina
	extending to ventral corner; mesopleuron strongly convex; angles of propodeum
	distinctly produced; metasomal tergum II coarsely punctured5
3	Metanotum with large punctures, separated by less than 1 diameter (fig. 6E); hair on
٥.	vertex, front and eyes long, dense; yellow markings reduced; metasomal tergum II with
	small punctures, separated by about 2 diamenters; metasoma with only rudimentary
	narrow bands on some terga, or sometimes absent
	Metanotum, if punctured, with punctures fine, separated by 2 diameters near dorsal margin
	(fig. 6F); hairs on vertex, front and eyes short and sparce; metasomal tergum II with small
	punctures, separated by at least 2 diameters, becoming larger and sparser laterally. Yellow
	markings always present; terga II–IV of metasoma with wide yellow bands
1	Male digitus distally blunt in lateral view (fig. 4 B3)
-T.	Male digitus pointed in lateral view (fig. 5 A5)
5	Vertex strongly convex; hairs on frons and vertex long and dense; pronotal carina extend-
٥.	ing to around middle of pronotum, weakly lamellate or lamella absent (fig. 7A); angles of
	propodeum rounded; metasomal tergum II with medium to large punctures, shallow, sepa-
	rated by less than 2 diameters; head and mesosoma black
_	Vertex flat; hairs on frons and vertex long and sparse; pronotal carina extending to ven-
	tral corner, lamellate (fig. 7B); angles of propodeum sharp, slightly produced; punctures
	on metasomal tergum II medium to large, becoming larger laterally, separated by 1
	diameter or less
6	Punctures of scutum medium, shallow, separated by about 2 diameters, surface shining
0.	fig. 7C).
_	Punctures of scutum large, deep, separated by about 1 diameter; surface reticulate (fig.
	7D). Scutellum and metanotum usually yellow
7	Pronotal carina extending beyond pronotal lobe, but not reaching the ventral corner, not
/ •	lamellate (fig. 7E); occipital carina not or weakly wider below gena; eighth flagellomere
	infinite (115. 71), decipital carilla not of weakly wider below gend, eighth hagehomere

	equal to or more than twice as long as wide; head and mesosoma black; metasomal ter-
	gum II with medium to large punctures, deep, separated by 1-2 diameters8
_	Pronotal carina reaching the ventral corner, lamellate (fig. 7F); occipital carina wider
	below on gena; eighth flagellomere less than twice as long as wide; head and mesosoma
	pale marked, inconspicuously so in B. baccalaurea; metasomal tergum II with small
	punctures, usually shallow11
8.	Lateral ocellus separated by a distance more than 1.5 times its diameter from eye;
	metasomal tergum II with large punctures9
_	Lateral ocellus separated by a distance equal to or less than 1.5 times its diameter from
	eye; metasomal tergum II with medium punctures10
9.	Frons and vertex with long and dense hairs (fig. 8A); punctures on scutum medium,
	separated by about 1 diameter or more, surface shiny (fig. 8C); metanotum black; metasoma
	brownish with evanescent yellow bands on terga I-III; metasomal tergum II with large
	punctation deep anteriorly, separated by about 1 diameter, becoming shallower and sparser
	posteriorly (fig. 8E), surface shiny with scattered short hairs
_	Frons and vertex without hairs (fig. 8B); punctures on scutum large, separated by less
	than 1 diameter, surface dull (fig. 8D); metanotum black with anterior yellow band;
	metasoma black, with marked yellow bands on terga I-III; metasomal tergum II with
	large punctures separated by less than 1 diameter (fig. 8F), surface dull, without hairs or
	hairs very short and sparse
10.	Area between the ocelli with a clearly marked, elongate oval area, shiny, without
	punctures; triangular process from the angles of the propodeum produced, pointed
-	Area between ocelli with punctures like those on frons; triangular process from angles of
	propodeum moderately produced, rounded
	Propodeal valve linear (fig. 9A),
	Propodeal valves at least somewhat, often widely, triangularly expanded (fig. 9B)13
12.	Clypeus equal to or less than 1.7 as long as wide; punctures on scutum medium, shallow,
	separated by equal to or more than 1 diameter, pubescence dense and long (fig. 9C);
	sternum I with a transverse medial ridge; punctures on metasomal tergum II fine,
	shallow, separated by 2 diameters, hair on metasoma long and dense (fig. 9E); pale
	markings bright yellow
-	Clypeus more than 1.7 as long as wide; punctures on scutum large, deep, separated by
	less than 1 diameter, usually more spaced laterally; pubescence very short and spaced
	(fig. 9D); sternum I without a transverse medial ridge; punctures on metasomal tergum
	II small, deep, separated by less than 1 diameter, hair on metasoma short and scattered,
	sometimes longer laterally (fig. 9F); pale markings white
13.	Large species (8.0-8.3 mm in body length) with numerous long hairs; humeri projecting
	(fig. 10B), acute; scutum with deep punctures separated by 2 diameters (fig. 10B); scutel-
	lum rounded, not bilobed, not projecting over the metanotum (fig. 10A); metanotum
	with dorsal tubercle; projecting angles of propodeum very small, punctures on meta-

	somal tergum II small, shallow, separated by 2 diameters or more (fig. 10C)
-	Small species (7.5–7.8 mm in body length) with sparse short hairs; humeri not or slightly
	projecting, usually rounded; scutum with punctures separated by equal to or less than
	1.5 diameters; scutellum angular in profile with a separate posterior surface; metanotum
	without dorsal tubercle; angles of propodeum projecting, punctures on metasomal
	tergum II small, usually deep, normally separated by around 1-2 diameters, sometimes
	less than 1 diameter14
14.	Angles of propodeum strongly projecting, so the tip is equidistant between propodeal
	spiracle and the valves; body without tomentum, except some fine on metasoma;
	punctures on scutum large, deep, separated by less than one diameter (fig. 10F); punctures
	of metasomal tergum II small, deep, separated by one or less than 1 diameter (fig. 10D)
_	Angles of propodeum less projecting (fig. 10E), only mesosoma with tomentum;
	punctures on scutum large, shallow, separated by about 1.5 diameters, sparser laterally;
	punctures on metasomal tergum II, small, separated by 1-2 diameters15
15.	Scutellum short and wide, not or slightly projecting over metanotum (fig. 11A); propodeum
	often with large yellow marks; yellow stripes on scutum interrupted or narrowed
	B. propodealis Bequaert
_	Scutellum longer and less wide, clearly projecting over metanotum (fig. 11B);
	propodeum black; scutal strips usually not centrally narrowed or interrupted, although
	sometimes absent16
16.	Scutellum more horizontal, less sloping up from scutal furrow, less raised above scutum
	(fig. 11C); axillary plates narrower; scutum slightly less closely punctured (fig. 11E),
	yellow stripes not extending to anterior region or often absent; punctures on metasomal
	tergum II small, shallow, separated by about 2 diameters; process of digitus about 2.4
	times as long as width at base (fig. 4 A3)
_	Scutellum less horizontal, more sloping up from mesoscutal furrow, posterior edge more
	raised above scutum (fig. 11D); axillary plates wider; scutum slightly more closely
	punctured (fig. 11F), yellow stripes always present; punctures on metasomal tergum II
	small, deep, separated by about 1 diameter or less; process of digitus about 2 times as
	long as width at base (fig. 5 C4)



FIGURES 6. (A) *B. mellifica* and (B) *B. augusti*, head in frontal view; (C) *B. mellifica* and (D) *B. moebiana*, scutellum in dorsolateral view; (E) *B. borellii* and (F) *B. albula*, metanotum in frontal view. Scale bars = 1.0 mm.



FIGURES 7. (**A**) *B. azteca* and (**B**) *B. scutellaris*, pronotum in lateral view; (**C**) *B. myersi* and (**D**) *B. scutellaris*, scutum in dorsal view; (**E**) *B. moulae* and (**F**) *B. buyssoni*, pronotum in lateral view. Scale bars = 1.0 mm.

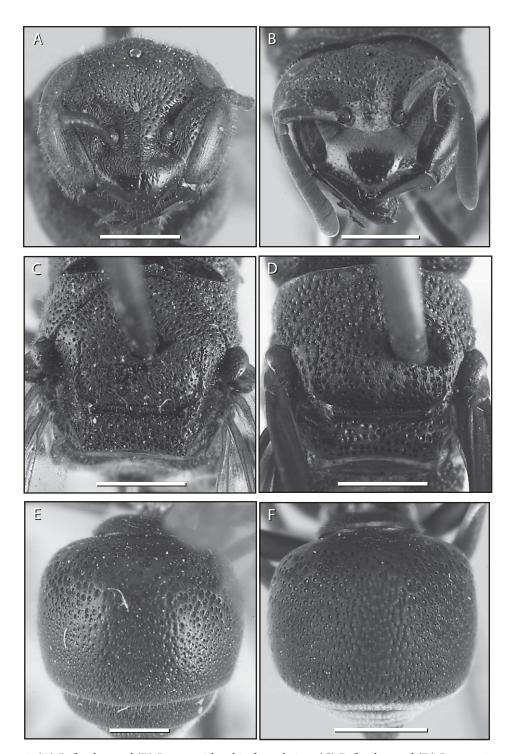


FIGURE 8. (A) *B. fistulosa* and (B) *B. cooperi*, head in frontal view; (C) *B. fistulosa* and (D) *B. cooperi*, scutum in dorsal view; (E) *B. fistulosa* and (F) *B. cooperi*, metasomal tergum II in dorsal view. Scale bars = 1.0 mm.

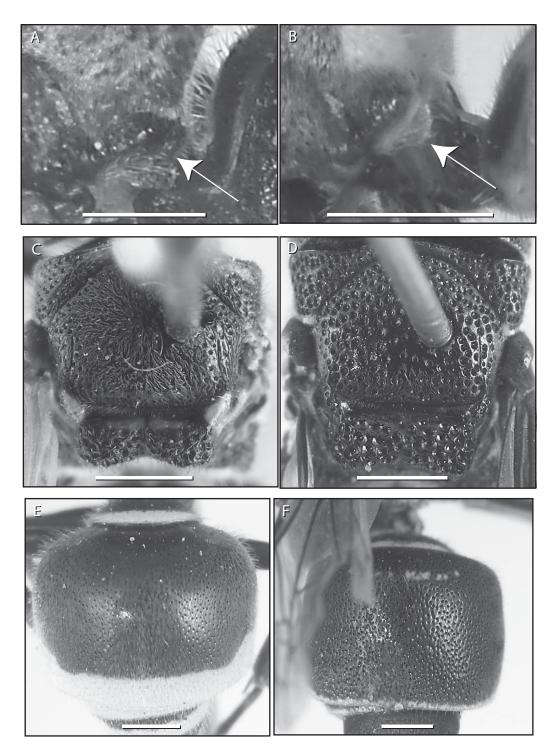


FIGURE 9. (A) *B. albula* and (B) *B. propodealis*, propodeal valve in lateral view; (C) *B. moebiana* and (D) *B. albula*, scutum in dorsal view; (E) *B. moebiana* and (F) *B. albula*, metasomal tergum II in dorsal view. Scale bars = 1.0 mm.

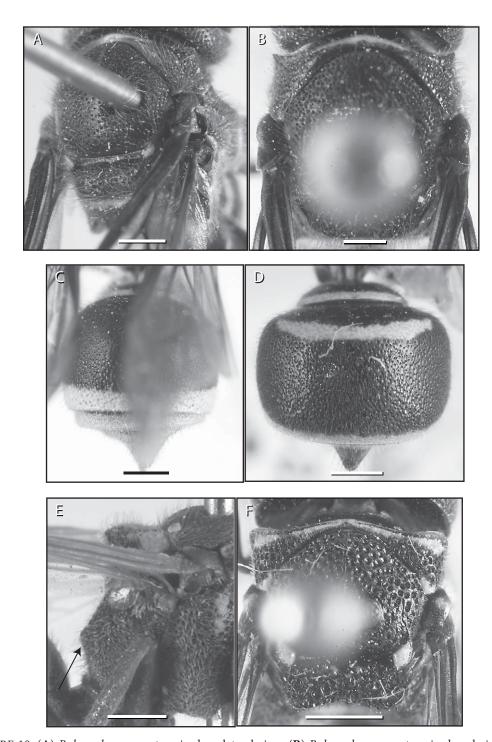


FIGURE 10. (A) *B. baccalaurea*, scutum in dorsolateral view; (B) *B. baccalaurea*, scutum in dorsal view; (C) *B. baccalaurea*, metasomal tergum II in dorsal view; (E) *B. smithii*, propodeum in lateral view; (F) *B. buyssoni*, scutum in dorsal view. Scale bars = 1.0 mm.

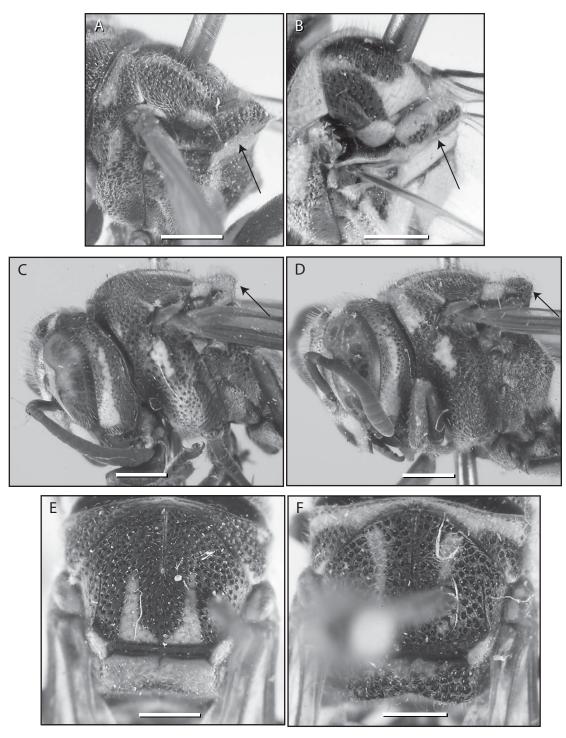


FIGURE 11. (**A**) *B. propodealis* and (**B**) *B. bilineolata*, scutellum in dorsolateral view; (**C**) *B. bilineolata* and (**D**) *B. smithii*, scutellum in lateral view; (**E**) *B. bilineolata* and (**F**) *B. smithii*, scutum in dorsal view. Scale bars = 1.0 mm.

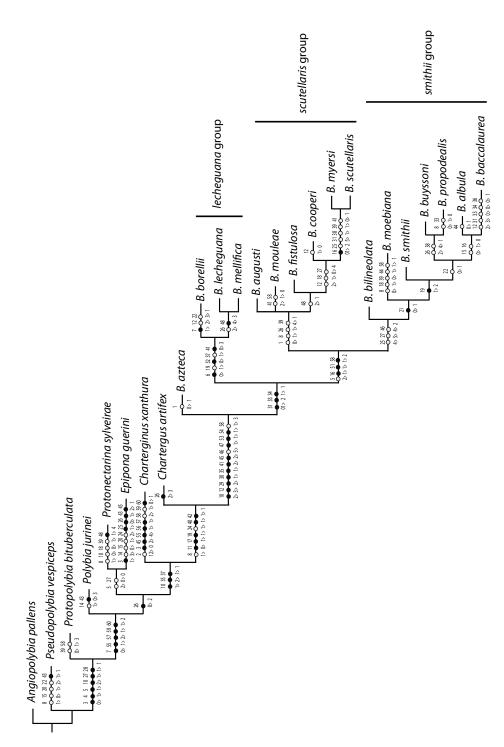


FIGURE 12. The single cladogram for species of Brachygastra, with a length of 178, consistency index of 0.57 and retention index of 0.80; based on the data matrix from table 1. Characters numbers are placed above circles, with state numbers below; filled circles denote an uncontroverted step, while open circles indicate reversals and convergences.

ACKNOWLEDGMENTS

We wish to thank Michael Engel and Jennifer C. Thomas (SEMC), Mark F. O'Brien (UMMZ), E. Richard Hoebeke (CUIC), Steve Heydon (UCDC), Gavin Broad (BMNH), Claire Villemant (MNHN), James H. Boone (FMNH), Bjoem Rulik (MTKD) for loans and Gabriel Melo and Marcel Hermes (UFPR) for assistance during S.R.A.'s visit to the Universidade Federal do Paraná. This work was supported by NSF award number DEB 0634748. We dedicate this work to late Kurt M. Pickett, coauthor and friend. TNT was made available with the sponsorship of the Willi Hennig Society.

REFERENCES

- Andena, S.R., and S. Mateus. 2011. Description of the male of *Brachygastra moebiana* Saussure, 1867 (Hymenoptera: Vespidae; Epiponini). Entomobrasilis 4 (2): 75–77.
- Andena, S.R., F.B. Noll, J.M. Carpenter, and R. Zucchi. 2007. Phylogenetic analysis of the neotropical *Pseudopolybia* de Saussure, 1863, with description of the male genitalia of *Pseudopolybia vespiceps* (Hymenoptera, Vespidae, Epiponini). American Museum Novitates 3586: 1–11.
- Arévalo E., Y. Zhu, J.M. Carpenter, and J.E. Strassmann. 2004. The phylogeny of the social wasp subfamily Polistinae: evidence from microsatellite flanking sequences, mitochondrial COI sequence, and morphological characters. BioMed Central Evolutionary Biology 4: 8.
- Baio, M.V., F.B. Noll, and R. Zucchi. 2004. Morphological caste differences and non-sterility of workers in *Brachygastra augusti* (Hymenoptera, Vespidae, Epiponini), a neotropical swarm-founding wasp. Journal of New York Entomological Society 111 (4): 242–252.
- Belt, T. 1874. The naturalist in Nicaragua. London: John Murray.
- Bequaert, J.C. 1933. The nearctic social wasps of the subfamily Polybiinae (Hymenoptera, Vespidae). Entomologica Americana (new series) 13: 87–150.
- Bequaert, J.C. 1943 (1942). New and imperfectly known neotropical Polybiinae (Hymenoptera, Vespidae). Journal of New York Entomological Society 50: 295–308.
- Buysson, R. du. 1905. Monographie des Vespides du genre *Nectarina*. Annales de la Société Entomologique de France 74: 537–564.
- Carpenter, J.M. 1991. Phylogenetic relationships and the origin of social behavior in the Vespidae. *In* K.G. Ross and R.W. Matthew (editors), The social biology of wasps: 7–32. Ithaca, NY: Cornell University Press.
- Carpenter, J.M. 2004. Synonymy of the genus *Marimbonda* Richards, 1978, with *Leipomeles* Möbius, 1856 (Hymenoptera: Vespidae; Polistinae), and a new key to the genera of paper wasps of the New World. American Museum Novitates 3465: 1–16.
- Carpenter, J.M., and S. Mateus. 2004. Males of *Nectarinella* Bequaert (Hymenoptera, Vespidae, Polistinae). Revista Brasileira de Entomologia 48 (3): 297–302.
- Carpenter, J.M., and K.G. Ross. 1984. Colony composition in four species of Polistinae from Suriname, with a description of the larva of *Brachygastra scutellaris* (Hymenoptera, Vespidae). Psyche 91: 237–250.
- Ducke, A. 1905. Nouvelles contributions à la connaissance des vespides sociaux de l'Amérique du sud. Revue d'Entomologie 24: 5–24.

- Ducke, A. 1907. Novas contribuições para o conhecimento das vespas sociaes (Vespidae sociales) da região neotropical. Boletim do Museu Paraense Emílio Goeldi 5: 152-199.
- Ducke, A. 1910. Revision des guêpes sociales polygames d'Amerique. Annales Historico-Naturales Musei Nationalis Hungarici 8: 449–544.
- Farris, J.S. 1970. Methods for computing Wagner trees. Systematic Zoology 19: 83-92.
- Fitch, W.M. 1971. Toward defining the course of evolution: minimum change for a specific tree topology. Systematic Zoology 20: 406–416.
- Goloboff, P., J.S. Farris, and K. Nixon. 2008. TNT, a free program for phylogenetic analysis. Cladistics 24: 774–786
- Hermes, M.G., and A. Köhler. 2006. The flower-visiting social wasps (Hymenoptera, Vespidae, Polistinae) in two areas of Rio Grande do Sul State, southern Brazil. Revista Brasileira de Entomologia 50 (2): 268–274.
- Ihering, R. von. 1904. As vespas sociaes do Brasil. Revista do Museu Paulista 6: 97-309.
- Jeanne, R.L. 1991. The swarm-founding Polistinae. In K.G. Ross and R.W. Matthews (editors), The social biology of wasps: 191–231. Ithaca, NY: Cornell University Press.
- Naumann, M.G. 1968. A revision of the genus Brachygastra (Hymenoptera: Vespidae). University of Kansas Science Bulletin 17: 929–1003.
- Nixon, K.C. 2002. Winclada, version 1.0000. Ithaca, NY: Published by the author.
- Nixon K.C. and J.M. Carpenter. 1993. On outgroups. Cladistics 9: 413-426.
- Noll, F.B., J.W. Wenzel, and R. Zucchi. 2004. Evolution of caste in neotropical swarm-founding wasps (Hymenoptera: Vespidae; Epiponini). American Museum Novitates 3467: 1–24.
- Perty, M. 1833. Delectus animalium articulatorum quae itinere per Brasiliam collegerunt Dr. J. de Spix et Dr. C. F. Ph. de Martius, fasc. 3. München.
- Pickett, K.M. and Carpenter, J.M. 2010. Simultaneous analysis and the origin of eusociality in the Vespidae (Insecta: Hymenoptera). Arthropod Systematics and Phylogeny 68 (1): 3–33.
- Pickett, K.M., and J.W. Wenzel. 2007. Revision and cladistic analysis of the nocturnal social wasp genus Apoica Lepeletier (Hymenoptera: Vespidae, Polistinae, Epiponini). American Museum Novitates 3562: 1–30.
- Richards, O.W. 1978. The social wasps of the Americas excluding the Vespinae. London: British Museum (Natural History).
- Richards O.W., and M.J. Richards. 1951. Observations on the social wasps of South America (Hymenoptera, Vespidae). Transactions of the Royal Entomological Society of London 102: 1–170.
- Saussure, H. de. 1853–58. Monographie des guêpes sociales ou de la tribu des vespiens. Paris: Masson. [1–96, 1853; 97–256, 1854]
- Shima, N.S., F.B. Noll, and R. Zucchi. 2000. Morphological caste differences in the neotropical swarm-founding Polistine wasps, *Brachygastra lecheguana* (Hymenoptera, Vespidae, Polistinae, Epiponini). Sociobiology 36 (1): 41–52.
- Shuckard, W.E. 1841. *In* A. White. Description of a South American wasp which collects honey. Annals and Magazine of Natural History 7: 315–322.
- Smith, F. 1857. Catalogue of hymenopterous insects in the collection of the British Museum. 5. Vespidae. London: Printed by order of the Trustees.
- Sugden, E.A., and R.L. McAllen. 1994. Observations on foraging, population and nest biology of the Mexican honey wasp, *Brachygastra mellifica* (Say) in Texas (Vespidae: Polybiinae). Journal of Kansas Entomological Society 67 (2): 141–155.
- Swainson, W., and W.E. Shuckard. 1840. On the history and natural arrangement of insects. Vol. 129.

London: Cabinet Cyclopaedia.

- Wenzel, J. W. 1992. Les nid de guêpes sociales d'intérêt historique conservés au MNHN, à Paris [Hymenoptera, Vespidae]. Revue française Entomologique (N.S.) 14: 1–11.
- Wenzel, J.W. 1993. Application of the biogenetic law to behavioral ontogeny: a test using nest architecture in paper wasps. Journal of Evolutionary Biology 6: 229–247.
- Wenzel, J.W. 1998. A generic key to the nests of hornets, yellowjackets, and paper wasps worldwide (Vespidade: Vespinae, Polistinae). American Museum Novitates 3224: 1–39.
- Wenzel, J.W., and J.M. Carpenter. 1994. Comparing methods: adaptative traits and tests of adaptation. *In* P. Eggleton and R. Vane-Wright (editors), Phylogenetics and ecology: 79–101. London: Academic Press.
- West-Eberhard, M.J., J.M. Carpenter, and P.E. Hanson. 2006. Familia Vespidae. *In P.E.* Hanson and I.D. Gauld, Hymenoptera de la región neotropical. Memoirs of the American Entomological Institute 77: 617–644.

APPENDIX 1

List of specimens of *Brachygastra* examined. Female = \Im ; male = \Im ; * = males whose genitalia were dissected.

Brachygastra albula: **Colombia**: Yuruyaco, $1 \$ (BMNH).**Costa Rica**: Heredia Puerto Viejo, $2 \$ (FMNH). **Brazil**: Pimenta Bueno, Rondônia State, $1 \$ [paratype] (BMNH), $01 \$ (UFPR). **Peru**: Cadena, $1 \$ (FMNH). Total = 6 specimens.

Brachygastra augusti: Argentina: Iguassu Falls, $1 \circ (BMNH)$; Missiones, $1 \circ (AMNH)$; **Bolivia:** Beni, 2° (AMNH); Coroico, 2° (MTKD); Mapiri, 4° (MTKD); Yungas, 2° (MTKD). **Brazil:** locality not specified, 1 \((MNHN); Brazopolis, Minas Gerais State, 1 \((UFPR); \) Caviuna, Paraná State, 1♀ (AMNH); Corumbá, Mato Grosso do Sul State, 26♀ (MTKD); Cuiabá, Mato Grosso State, 1♀ (MTKD); Curitiba, Paraná State, 1♀ (AMNH); Faz. Rancho Grande, Rondônia State, 1♀ (UCDC); Lussanvira, São Paulo State, 1♀ (CUIC); Miranda, Mato Grosso State, 1♀ (UMMZ); Espirito Santo State, locality not specified, 2♀ (MTKD); Guaira, Paraná State, 2♀ (UFPR); Itapeva, São Paulo State, 1♀ (AMNH); Itapura, Mato Grosso State, 2♀ (CUIC); Jaraguá, Sta Catarina State, 1♀ (MNHN); Mogi Guaçu, São Paulo State, 1♀ (AMNH); Pará State, locality not specified, 1 9 (MTKD), 3 9 (CUIC); Rio Saia Missa, Mato Grosso State, 1♂* (BMNH); Rio Juruá, Amazonas State, 3♀ and 1♀ [lectotype] São Paulo State, locality not specified, 1♀ (MTKD), 1♀ (CUIC); São José Petrópolis, Espirito Santo State, 1♀ (UFPR); Santa Tereza, Espírito Santo State, 1♀ (UFPR); Colombia: Cauca Valley, 4♀ (AMNH); Santa Rosa, San Miguel River, 7♀ (FMNH). Costa Rica: Colina, 1♀ (AMNH); Torrialba, 2♀ (SEMC); locality not specified, 7♀ (AMNH). **Ecuador:** Pastaza, Cusuimi River, 1♀ (FMNH); Pastaza, Morona River, 3♀ (FMNH); Pastaza, 1♀ (AMNH); Prov. Mor. Santiago, Miazel, 10 ? (UCDC); Puyo, 1 ? (CUIC). French Guiana: locality not specified, 2 ? (MNHN); St. Laurent, 3 \circlearrowleft (SEMC). **Panama**: Balboa, 1 \circlearrowleft (AMNH); Canal Zone, 2 \circlearrowleft (AMNH), 4 \circlearrowleft (SEMC); Canal Biological Station, 4♀ (SEMC); Sabanas, 1♀ (AMNH). Peru: Cadena, 42♀ (FMNH); Callanga, 7 $^{\circ}$ (MTKD); Cotube River, 2 $^{\circ}$ (CUIC); Loreto, 6 $^{\circ}$ (FMNH), 4 $^{\circ}$ (AMNH); Madre de Brachygastra azteca: Mexico: locality not specified, 17♀ (MTKD), 35♀ (CUIC); Acapulco, 1♀ (AMNH), 2♀ (CUIC); Alpuyeca, 26♀ (CUIC); Cacalopan, 1♂ (UCDC); Caxaca, Juchitan, 1 ♀ (UMMZ); Canyon del Lobos, 2 ♀ (CUIC); Cintalapa, 1 ♀ (UCDC); Colima, 6 ♀ (FMNH), 3 \circ (UMMZ), 1 \circ (BMNH), 20 \circ (SEMC); Chiapas, 1 \circ (SEMC); Chimpanchingo, 1 \circ (CUIC); Chivela, 6♀ (UCDC); Choix Sin, 4♀ (UCDC); Cocorit, 20♀ (UCDC); Cuernavaca, 23♀ (CUIC); Culiacan, 3♀ (AMNH), 2♀ (UCDC); El Chapulin, Oaxaca, 1♀ (SEMC); Elota, 26♀ and 1♂ (UCDC); Guanajuato, 1♀ (AMNH); Guaiamuchil, 4♀ (UCDC); Guerrero, 21♀ (SEMC); Huajintlan, 3♀ (CUIC); Jalisco, 20♀ (SEMC); Jiquilpan, 1♀ (UCDC); Lake Tequesquitengo, 2♀ (CUIC); La Aduana, 3♀ (UCDC); Matias Romero, 1♀ (UCDC); Michoaca, 1♀ (SEMC); Morelos, 1♀ (SEMC); Oaxaca, 2♀ (SEMC); San Bernardo, Rio Mayo, 1♀ (UCDC); Pentlalcingo, 50♀ and 1♂ (UCDC); Puebla, 2♀ (SEMC); Puerto Escondido, Sonora, La Aduana, 34 ♀ (UCDC); Sonora, Cocorit, 22 ♀ (UCDC); Sonora, Rio Mayo, 1 ♀ (UCDC); Tehuantepec, 7 \circlearrowleft (UCDC); Tehuacan, 23 \circlearrowleft (MTKD), 1 \circlearrowleft (MNHN), 1 \circlearrowleft (CUIC); Tenancinge, 18 \circlearrowleft (SEMC); Tetecala, 2♀ (CUIC); Tepic, 4♀ (UCDC); Salina Cruz, 1♀ (AMNH); San Blas Nay, 2♀ (UCDC); Sierra Del Alo, Jalisco, 1♀ (MNHN); Sierra de Pluma, 1♀ (MNHN); Xalitla, 1♀ (CUIC); Zanatepec, 1 \circlearrowleft (UCDC); Xucumanatlan, Guerrero, 1 \circlearrowleft and 1 \circlearrowleft * (BMNH). Total = 440 specimens.

Brachygastra baccalaurea: **Bolivia:** La Paz, Chulumani, $1 \$ (BMNH); Yungas, $1 \$ (MTKD); **Ecuador:** Tungurahua, $1 \$ (BMNH). **Peru:** Huacapistana, $2 \$ (CUIC); $1 \$ locality not specified, labelled as "Peru, 1892, R. V. Ihering type" is probably the paralectotype, as cited by Richards, 1978). Total = 6 specimens.

Brachygastra bilineolata: **Bolivia:** Beni Prov., 24 $^{\circ}$ (FMNH). **Brazil:** Mato Grosso State, locality not specified, 2 $^{\circ}$ (BMNH), Pimenta Bueno, Rondônia State, 1 $^{\circ}$ (UFPR); Rio Verde, Mato Grosso State, 1 $^{\circ}$ (UFPR); Caraquata River, Mato Grosso State, 3 $^{\circ}$ (SEMC); Chapada, Mato Grosso State, 3 $^{\circ}$ (SEMC); Corumbá, Mato Grosso do Sul State, 1 $^{\circ}$ (MTKD); Gloria, Minas Gerais State, 1 $^{\circ}$ (SEMC); Óbidos, Pará State, 1 $^{\circ}$ (MTKD); Sta. Catarina State, locality not specified, 2 $^{\circ}$ (CUIC). **French Guiana:** Cayenne, 1 $^{\circ}$ (MNHN); Kourou, 1 $^{\circ}$ (SEMC), 1 $^{\circ}$ (MNHN); St. Jean Du Morone, 2 $^{\circ}$ (MNHN). **Guyana:** Demerara, 3 $^{\circ}$ (FMNH), 2 $^{\circ}$ (SEMC). **Colombia:** locality not specified, 1 $^{\circ}$ (MNHN). **Peru:** Dos de Mayo, 1 $^{\circ}$ (CUIC); Cadena, 3 $^{\circ}$ (FMNH), Loreto, 3 $^{\circ}$ (FMNH). **Suriname:** locality not specified, 1 $^{\circ}$ (MNHN); Paramaribo, 2 $^{\circ}$ (CUIC); Zanderij, 1 $^{\circ}$ (CUIC). **Trinidad:** locality not specified, 1 $^{\circ}$ (AMNH); Nariva, 1 $^{\circ}$ (AMNH); Piarco, 1 $^{\circ}$ (AMNH). **Venezuela:** Ciudad Bolívar, 4 $^{\circ}$ (SEMC), 1 $^{\circ}$ (CUIC). Total = 110 specimens.

Brachygastra borellii: Argentina: Posta de Lozano, 2 ? (AMNH). Bolivia: Cochabamba, 1 ? and 1 ? (BMNH), 1 ? (AMNH), 3 ? (SEMC); Santa Cruz, Comarapa, 1 ? (SEMC). Total = 9 specimens.

Brachygastra buyssoni: Locality not specified, $1 \$ (MNHN). **Brazil:** Nhambiquara, Mato Grosso State, $1 \$ (UFPR); Tefé, Amazonas State, $1 \$ (UFPR). Total = 3 specimens.

Brachygastra cooperi: Colombia: Caquetá Yuruyaco, 1° [holotype], 1° [paratype], 1° [paratype] (BMNH). Total = 3 specimens.

Brachygastra fistulosa: **Brazil**: Hansa Humbolt, Sta Catarina State, 1° [holotype] (AMNH). Total = 1 specimen.

Brachygastra lecheguana: Argentina: locality not specified, 1♀ (MTKD); Alta Gracia, Córdoba, 11 \, (UCDC); Buenos Aires, 2 \, (AMNH), 2 \, (UCDC); Cata Marca, El Cavillo, 1 \, (UCDC); Corrientes, 3♀ (MTKD); E. Rios, 2♀ (AMNH); Formosa, 1♀ (SEMC); Lãs Termas, S. D. Estero Prov. 1♀ (UCDC); Missiones, 2♀ (AMNH); Paso de La Pátria, 1♀ (SEMC); Rosacio de La Fronteira, 1º (UCDC); Salta, 4º (AMNH); San Luis, 3º (AMNH); San Pedro de Catalao, Prov. Tucuman, 5♀ and 1♂* (UCDC); Sierra de Cordoba, 5♀ (CUIC) Tucuman, 3♀ (AMNH) **Bolivia:** Beni Prov., 3♀ (FMNH), 10♀ (SEMC); Corpico, 3♀ (MTKD); Itenez River, 1♀ (AMNH); Madri, 1♀ (MTKD); Paila, 1♀ (AMNH). Brazil: Holotype, locality not specified, mislabed as Perou, 1♀ (see Richards, 1978: 165) (MNHN); locality not specified, Pernanbuco State, 1♀ (UCDC); Aldeia Juruna, Mato Grosso State, 10♀ (SEMC); Belém, Pará State, 4♀ (MTKD); Cauna, Santa Catarina State, 1♀ (AMNH); confluence of Tapirape River and Araguaia River, Mato Grosso State, 19 (FMNH); Corumbá, Mato Grosso do Sul State, 149 (MTKD); Curitiba, Paraná State, 2♀ (UFPR); Crato, Ceará State, 1♀ (AMNH); Curralinho, Minas Gerais State, 1♀ (CUIC); Diamantino, Mato Grosso State, 1♀ (UFPR); Espirito Santo State, locality not specified, 22 ♀ (MTKD); Jataí, Goiás State, 1♀ (UCDC); Jacaré, Xingu, Mato Grosso State, 2♀ (UFPR); Lassanoe, Minas Gerais State, 20♀ (CUIC); Mato Grosso State, locality not specified, 1♀ (BMNH); Nova Teutonia, Santa Catarina State, 1♀ (AMNH); Pelotas, Rio Grande do Sul State, 1♀ (AMNH), 39♀ (MTKD); Perdizes, Minas Gerais State, 1♀ (UFPR); Piracicaba, São Paulo State, 1♀ (UCDC); Santa Cruz, 1♀ (MTKD); São Paulo State, locality not specified, 1♀ (MTKD); Sta Tereza, Espirito Santo State, 1♀ (UFPR); Silva Jardim, Rio de Janeiro, 2♀ (UCDC); Sinop, Mato Grosso State, 1♀ (AMNH); Tapirape Indian Village, Mato Grosso State, 6♀ (FMNH); Nhambiquara, Mato Grosso State, 2♀ (UFPR); Vale dos Sonhos, Mato Grosso State, 1♀ (BMNH); Vilhena, Rondônia State, 1♀ (UFPR); Vila Velha, Paraná State, 2♀ (AMNH). Colombia: El Roncador, 1♀ (AMNH); Sta Marta, 2♀ (AMNH); Restrepo, 1 ? (UCDC); Tocoto, 1 ? (MTKD). Costa Rica: Guanacaste, 11 ? (SEMC). Guyana: St. Laurent, 5 \circlearrowleft (MTKD). **Ecuador:** Carchi Chical, 1 \circlearrowleft (AMNH); Namabi, 1 \circlearrowleft (AMNH); Pastaza, $1 \circ (AMNH)$]. French Guiana: Degrad dês Cannes, $1 \circ (SEMC)$; Kourou, $1 \circ (SEMC)$. **Panama:** Barro Colorado, 12♀ (SEMC); Canal Zone, 1♀ (AMNH); Corundu, 1♀ (SEMC); Panama City, 1♀ (AMNH); Sta Rosa, 3♀ (SEMC). Paraguay: locality not specified, 1♀ (MTKD); Asuncion, 1 ? (MTKD); Hobenau, 2 ? (MTKD). **Peru:** Callanga, 1 ? (MTKD); Catune River, 2♀ (CUIC); Jequetepeque, 1♀ (AMNH); Loreto, 19♀ (FMNH); Santiago, Miazal, 1♀ (UCDC); middle Ucayali River, 1♀ (AMNH). **Suriname:** locality not specified, 1♀ (MTKD); Kwokoegron, 4♀ (CUIC); Moengo, 1♀ (CUIC); Paramaribo, 1♀ (CUIC). **Venezu**ela: Bolívar, 1♀ (CUIC); Catia La Mar, 5♀ (SEMC); Guaricos, 1♀ (AMNH); Lãs Nieves, 1♀

(SEMC); La Pica, 1 \circlearrowleft (SEMC); Monagas, Laguan Grande, 1 \circlearrowleft (AMNH); Paraitepuy, 1 \circlearrowleft (CUIC). Total = 303 specimens.

Brachygastra mellifica: Belize: Corozal, 2♀ (SEMC), locality not specified, 3♀ (CUIC). Costa Rica: Guanacaste Prov., 1 \(\text{(BMNH)}, 22 \(\text{(SEMC)}, 22 \(\text{(CUIC)}, 1 \(\text{(UCDC)}; \) Barranca, 1 \circlearrowleft (UCDC); Junquilall, 1 \circlearrowleft (UCDC) Palo Verde, 1 \circlearrowleft (CUIC); Puntarenas, 1 \circlearrowleft (CUIC). El Salvador: Quezalbeteque, 36 % (UCDC). Guatemala: Nuevo Concepcion, 2 % (UCDC); Tiucal 1 \circ (UCDC); Yepocapa, Chimal, 1 \circ (FMNH); locality not specified, 3 \circ (AMNH). **Honduras:** Tegucigalpa, 1 ? (AMNH). **Mexico:** locality not specified, 1 ? (MTKD), 2 ? (CUIC); Acayucan, 2 ? (UCDC); Ajacuba, 1 ? (UCDC); Alamos, 1 ? (UCDC); Alpuyeca, 8 ? (CUIC); Atlixco, 19 (UCDC); Bio Res. Sta. Catamaco, Veracruz, 19 (UCDC) Cacaloapan, 229 (UCDC); Cintalapa, 2♀ (UCDC); Chaco de Santa-Fe, 4♀ (MNHN); Choix Sim, 129♀ (UCDC); Coahuila, 7♀ (SEMC); Cuernavaca, 23♀ (CUIC); Chiapas, Yaxoquintela, 1♀ (AMNH), Chiapas, 6♀ (SEMC); Chichen Itza, Yucatan, 7♀ (FMNH); Chimpancingo, 3♀ (CUIC); Chupaderos, 1♀ (UCDC); Colima, 2♀ (MTKD); Culiacan, 3♀ (AMNH), 6♀ (UCDC); Cuernavaca, 4 % (UCDC); Dindad de Maiz, 1 % (SEMC); El Salto, 5 % (SEMC); Elota, 2♀ (UCDC); Guaiamuchil, 7♀ and 1♂ (UCDC); Guaiahas, 1♀ and 1♂ (UCDC); Guasave, 2♀ (AMNH); Guerrero, 6♀ (SEMC), 1♀ (CUIC); Hidalgo, 12♀ (SEMC); Hopelchen, 1♀ (UCDC); Isla Piedras, Sinalos, 2♀ (UCDC); Jalapa, 4♀ (MTKD); Jacala, 2♀ (SEMC); Jimenez, 3 \circlearrowleft (SEMC); Mazatilan, 1 \circlearrowleft (AMNH), 3 \circlearrowleft (UCDC); Montezima, 1 \circlearrowleft (UCDC); Morelos, 6 \circlearrowleft (SEMC); Michoacan, 1♀ (SEMC); Monte Alban, Oaxaca, 1♀ (AMNH), 1♀ (SEMC); La Assuncion, 1♀ (SEMC); Lera Tamps, 1♀ (SEMC); Luis Potosi, 2♀ (SEMC); Quintana Roo, 10♀ (SEMC); Rancho El Bejuco, Ozuluama, 1♀ (UCDC); Santo Nino, Chin., 1♀ (UCDC); Sinaloa, Topolobampo, 1♂* (UCDC); Sonora, Yecora, 1♀ (AMNH); Sonora, El Gavilan, 1♀ (AMNH); Sonora, Cocorit, 36♀ (UCDC); Sonora, La Aduana, 29♀ (UCDC); Sonora, Quinta, Porto Morales, 2♀ (AMNH); Sonora, San Carlos, 23♀ (SEMC); Oaxaca, 7♀ (UCDC), 1♀ (CUIC); Plan de Barrancas, 3♀ (UCDC); Puebla, 2♀ (UCDC), 1♀ (SEMC); Panuco, 1♀ (UCDC); Petlacingo, 17 ♀ (UCDC); Quintana, 1 ♀ (SEMC); San Blas Ney, 3 ♀ (UCDC); San Bernardo, 4 (UCDC); San Luis, 1 (SEMC); Tamazunchale, 2 (CUIC); Tampico, 4(UCDC), 2♀ (CUIC); Tamaulipas, 2♀ (UMMZ), 2♀ (SEMC); Tapic, 1♀ (UCDC); Teapa, Tabanco, 1♀ (BMNH); Tehuacan, 1♀ (UCDC); Temixco, 1♀ (UCDC); Veracruz, 3♀ (UCDC), 17 $\$ (SEMC); Tequesquitengo, 1 $\$ (CUIC); Tetecala, 1 $\$ (CUIC); Villa Guadalupe, 1 $\$ (UCDC); Zacatecas, Nochistlan, 1 \, (UCDCC); Yucatán, 5 \, (SEMC); locality not specified, 1 \, (UCDC); Veracruz, 7♀ (CUIC); Xilitla, 4♀ (SEMC). **Panama:** Chirigui, Finca Suiza, 1♀ (UCDC); Such. Guate., 1 \circlearrowleft (AMNH). **United States:** Falcon State Park, Texas State, 1 \circlearrowleft (SEMC); Rio Grande, Texas State, 1♀ (UCDC); Hidalgo, Texas State, 2♀ (UMMZ); Texas State, locality not specified, 17 (FMNH); Browsville, Texas State, 3 (AMNH), 10 (CUIC); Edinburg, Texas State, 3 \circ (AMNH); Mission, Texas State, 1 \circlearrowleft (AMNH); Nogales, Texas State, 1 \circlearrowleft [paratype] (CUIC). Total = 649 specimens.

Brachygastra moebiana: Locality not specified, 1 \circlearrowleft (MNHM). **Brazil:** Vale dos Sonhos, Mato Grosso State, 1 \circlearrowleft (BMNH). Total = 2 specimens.

Brachygastra mouleae: Brazil: Rio Claro, São Paulo State, 1 ? [paratype] (BMNH). Total = 1 specimen.

Brachygastra myersi: **Guyana**: Kareteuz, 1 \bigcirc (BMNH). Total = 1 specimen.

Brachygastra propodealis: Locality not specified, 1 \circlearrowleft (MNHN). **Brazil**: Pimenta Bueno, Rondônia State, 2 \circlearrowleft (UFPR). **Colombia**: Caquetá, Yuruyaco, 1 \circlearrowleft (BMNH). **Peru:** Cadena, 3 \circlearrowleft (FMNH). Total = 7 specimens.

Complete lists of all issues of *Novitates* and *Bulletin* are available on the web (http://digitallibrary.amnh.org/dspace). Order printed copies on the web from http://www.amnhshop.com 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).