



A Phylogenetic Approach to the Neotropical Social Wasp Genus *Leipomeles* Möbius, 1856 (Vespidae: Epiponini), with a New Identification Key

Authors: Somavilla, Alexandre, Vieira, Gabriel Santos, Andena, Sérgio Ricardo, Noll, Fernando Barbosa, and Carpenter, James M.

Source: American Museum Novitates, 2023(4006) : 1-12

Published By: American Museum of Natural History

URL: <https://doi.org/10.1206/4006.1>

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.

A phylogenetic approach to the Neotropical social wasp genus *Leipomeles* Möbius, 1856 (Vespidae: Epiponini), with a new identification key

ALEXANDRE SOMAVILLA,¹ GABRIEL SANTOS VIEIRA,² SÉRGIO RICARDO ANDENA,³ FERNANDO BARBOSA NOLL,⁴ AND JAMES M. CARPENTER⁵

ABSTRACT

Leipomeles Möbius, 1856, is a neotropical genus of swarm-founding wasps extending from Costa Rica to the middle of Brazil, with four species described. A combined phylogenetic analysis using female and male morphology, and nest architecture was performed with the program TNT. *Leipomeles* is supported as monophyletic with the following relationships among species: (*L. pusilla* + *L. albogrisea*) + (*L. spilogaster* + *L. dorsata*). A new identification key for the genus is also presented.

INTRODUCTION

Leipomeles Möbius, 1856 (Vespidae: Epiponini), is a small neotropical genus of swarm-founding social wasps comprising four species: *Leipomeles dorsata* (Fabricius, 1804), *Leipomeles pusilla* (Ducke, 1904), *Leipomeles spilogastra* (Cameron, 1912), and *Leipomeles albogrisea* (Richards, 1978). The genus is widely distributed in the Neotropics, ranging from Costa Rica to Central Brazil. The species are found mostly in rainforests in Bolivia, Brazil, Colombia, Costa Rica, Ecuador, French Guiana, Guyana, Panama, Peru, and Suriname, (Richards, 1978; Somavilla et al., 2021a).

¹ Instituto Nacional de Pesquisas da Amazônia, Coordenação de Biodiversidade, Manaus, AM, Brazil.

² Universidade Federal da Bahia, Instituto de Biologia, Salvador, BA, Brazil.

³ Universidade Estadual de Feira de Santana, Feira de Santana, BA, Brazil.

⁴ Universidade Estadual Paulista, Instituto de Biociências Letras e Ciências Exatas, São José do Rio Preto, Brazil.

⁵ American Museum of Natural History, Division of Invertebrate Zoology, New York.

Despite being a small genus, the taxonomic background is troublesome. The genus was first described as monotypic by Möbius (1856) with the type species, *Leipomeles lamellaria*, later synonymized with *Leipomeles dorsata* [= *Polistes dorsata*, Fabricius, 1804] (Schulz, 1912). Richards (1978) recognized two species in *Leipomeles*, *L. dorsata* (Fabricius, 1804) and *L. nana* [misidentification; non *Polybia nana* de Saussure, 1863; = *Polybia spilogastra* Cameron, 1912]. In the same work, Richards (1978) also described the genus *Marimbonda* for two species, *M. albogrisea* as type species, and *M. pusilla* (Ducke, 1904), originally described in *Chartergus* by Ducke (1904).

In both genera a curved bristle on the third segment of the labial palp is present, a feature also shared by *Pseudopolybia*, *Parachartergus*, *Chartergellus*, and *Nectarinella* (Carpenter, 1991). In cladistic analyses (Carpenter, 1991; Wenzel and Carpenter, 1994) *Leipomeles* and *Marimbonda* were placed as sister groups. Later, Carpenter (2004) synonymized *Leipomeles* with *Marimbonda* based on morphological characteristics, like reduction in the palpal formula to 5:3, mesepisternum without dorsal groove and first metasomal segment conically petiolate, as well as nest architecture.

In this work we propose a phylogenetic analysis of the four species of the genus, a new identification key, and correction of the species epithet *Leipomeles spilogastra*.

MATERIAL AND METHODS

We analyzed specimens from the American Museum of Natural History (AMNH – New York), the Natural History Museum (NHM – London), the Zoology Museum of the Universidade de São Paulo (MZSP – São Paulo, Brazil), the invertebrates collection of the Instituto Nacional de Pesquisas da Amazônia (INPA – Amazonas, Brazil), Museu Paraense Emilio Goeldi (MPEG – Pará, Brazil), the Johann Becker entomological collection of Museu de Zoologia da Universidade de Feira de Santana (MZFS – Bahia, Brazil), and University of California Washington Center (UCDC – Washington DC).

For adult morphological structures and male genitalia, we employed the terminology following the original descriptions and Somavilla et al. (2018; 2021b). The procedure for extraction and clearing of male genitalia followed the protocol proposed by Somavilla et al. (2018).

We compiled 36 morphological characters (see supplementary material, available online: <https://doi.org/10.5531/sd.sp.64>), including 28 from females and eight from males (including male genitalia), and five behavioral characters related to nest architecture. All 41 characters were assembled in a data matrix using Winclada v. 1.00.08 (Nixon, 2002).

Morphological characters were studied under a Nikon SMZ1500 stereomicroscope with an accessory magnifying lens of Nikon G-AL 2x. Photos were taken with the aid of a Leica DMC4500 digital camera coupled to a Leica M205A stereomicroscope with a self-assembly system, using the Leica Application Suite v.4.10.0-Montage® software. The nest architecture characters were from Richards (1978), Wenzel (1998), and direct observations on nests deposited at AMNH. Nest images come from the AMNH database. We edited the images and assembled the plates using Adobe Photoshop® CS6 v.6.1 and Gimp v. 2.10.34. POL : OOL means ratio between postocellar distances and ocello-ocular.

Angiopolybia pallens (Lepeletier, 1836), *Agelaisia centralis* (Cameron, 1907), *Pseudopolybia vespiceps* (de Saussure, 1863), *Parachartergus fraternus* (Gribodo, 1892), *Chartergellus commu-*

nis Richards, 1978, and *Nectarinella xavantinensis* Mateus and Noll, 1998, were used as out-group taxa based on previous phylogenetic studies (Carpenter, 1991; Wenzel and Carpenter, 1994; Menezes et al., 2020; Noll et al., 2021). We performed a phylogenetic analysis using our morphological data employing Maximum Parsimony (MP) in TNT version 1.5 (Goloboff et al., 2008) and conducted tree search with Implicit Enumeration. Clade support was assessed using Symmetric Resampling with 1.000 replicates for MP (Goloboff et al., 2003).

RESULTS

TAXONOMY

Genus *Leipomeles* Möbius

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

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

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

Marimbonda Richards, 1978, Social Wasps of Americas: v, 10, 201, genus.

Type species: *Marimbonda albogrisea* Richards, 1978, by original designation.

Leipomeles albogrisea (Richards, 1978)

Figures 1A, 2A

Marimbonda albogrisea Richards, 1978, The Social Wasps of the Americas: 201 (key), 202, fig. 84, female, male – “BRAZIL: MT, base camp, 12°50’S, 51°47’W” (holotype female Rio de Janeiro). – Carpenter and Mateus, 2004, Revista Brasileira de Entomologia 48 (3): fig. 5 (male genitalia).

DISTRIBUTION: Brazil: Mato Grosso.

COMMENTS: According to Richards (1978) the holotype of this species is in the Museu Nacional of Rio de Janeiro (MNRJ, Rio de Janeiro, Brazil); this holotype was probably lost in the fire on September 2nd, 2018. Here we insert images of a paratype from the Natural History Museum (NHM, London), from the same location and same expedition.

Leipomeles dorsata (Fabricius, 1804)

Figures 1B, 2A, 3A

Polistes dorsata Fabricius, 1804, Systems Piez: 281 – “America meridionali” (Kobenhavn). – Dalla Torre, 1904, Gen. Ins. 19: 71, species dubiae.

Polybia dorsata; de Saussure, 1854, Ét. Famille Vespidae 2: 212, species dubiae. – Ducke, 1910, Annales historico-naturales Musei Nationalis Hungarici 8: 540, species dubiae.

Leipomeles lamellaria; Möbius, 1856: 26, 35 (key), pl. XVII, female, nest – “Brasilien” (? Hamburg); 1856, Archiv für Naturgeschichte 22: 330 (key), fig. 8. – Ducke, 1910, Annales historico-naturales Musei Nationalis Hungarici 8: 536, fig. 17 (syn.: *P. nana* de Saussure; male; Suriname; Brazil; Peru; Ecuador). – Overal, 1978, Boletim do Museu Goeldi (N. S.), Zool. 94: 9 (list).

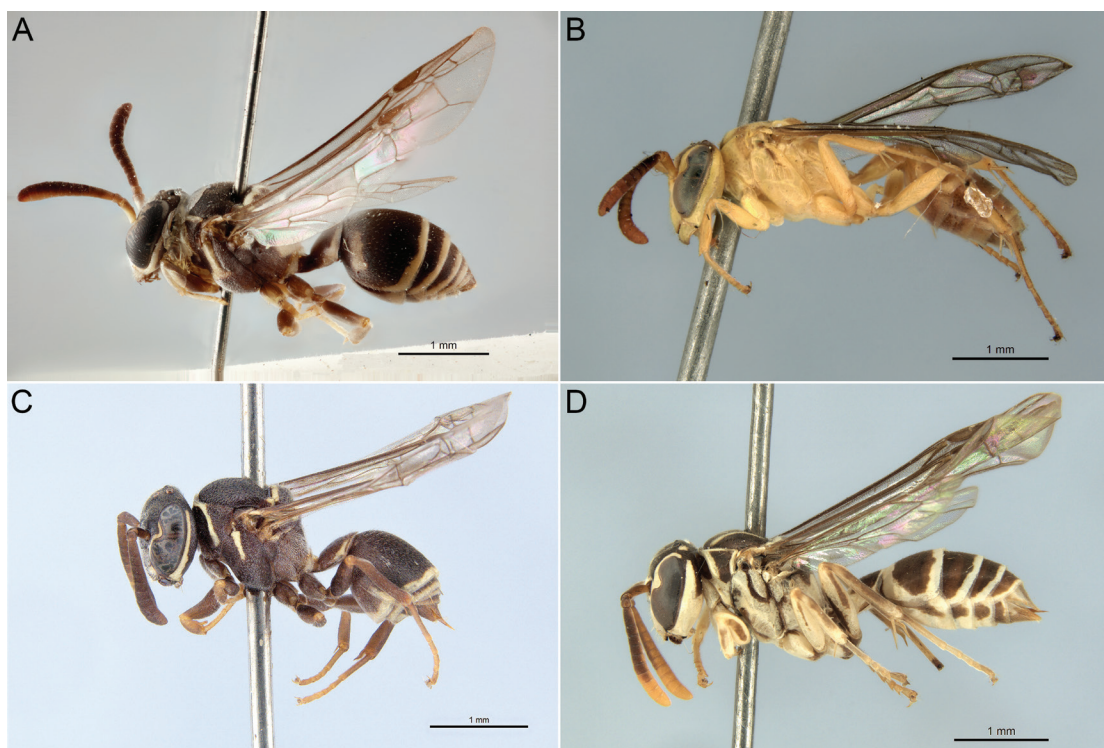


FIGURE 1. *Leipomeles* species, lateral view. **A.** *Leipomeles albogrisea* (Richards, 1978) paratype. **B.** *Leipomeles dorsata* (Fabricius, 1804). **C.** *Leipomeles pusilla* (Ducke, 1904). **D.** *Leipomeles spilogaster* (Cameron, 1912).

Polybia nana de Saussure, 1863, Memoires de la Société de physique et d'histoire naturelle de Genève 17: 240, pl. 2 fig. 28, female (in division *Alpha*) – “Brésil” (Frankfurt). – Dalla Torre, 1904, Genève Institute 19: 78 (cat.). – Ducke, 1904: 349. – Carpenter, 1999, American Museum Novitates 3259: 1, 9 (notes on types; syn. of *dorsata* Fabricius).

Lipomeles lamellaria; Dalla Torre, 1904, Genève Institute 19: 81, pl. 5 fig. 7 (cat.).

Polybia lamellaria; Ducke, 1904, Boletim do Museu Goeldi, Pará 4: 348 (key), 357 (Brazil).

Polybia sulciscutis Cameron, 1912, Timehri (3) 2: 208 (key), 215, female – locality not stated [Guyana] (lectotype London). – Richards, 1978, The Social Wasps of the Americas: 214 (designation of lectotype).

Lipomeles dorsata; Schulz, 1912, Berliner entomologische Zeitschrift 57: 87 (syn.: *lamellaria* Möbius).

Protopolybia sulciscutis; Bequaert, 1944, Revista Brasileira de Entomologia 15: 132 (unrecognized species); 1944, Bulletin of the Museum of Comparative Zoology at Harvard 94: 270 (unrecognized).

Leipomeles dorsata; Bequaert, 1944, Bulletin of the Museum of Comparative Zoology at Harvard 94: 304. – Richards, 1978, The Social Wasps of the Americas: 214, fig. 87. – Schremmer, 1983, Zool. Anz. 211: 95-107 (nest); 1986, Öko-L 8 (nest). – Almeida and Castro, 1991, Acta Biológica Paranaense, Curitiba 20: 48 (coll. list). – Sarmiento, 1994, Revista de Biología Tropical 42 (1/2): 359 (list). – West-Eberhard et al., 1995, Hymenoptera of Costa Rica: 586 (Costa Rica). – Strassmann et al., 1996, Molecular Ecology 5: 461 (genetics). – Carpenter, 1999, American Museum Novitates 3259: 9 (syn.: *Polybia nana* de Saussure). – Carpenter and Mateus, 2004: fig. 4 (male genitalia). – Valverde et al., 2019, Revista de Biología Tropical 67 (2), Suplemento: S176, S177

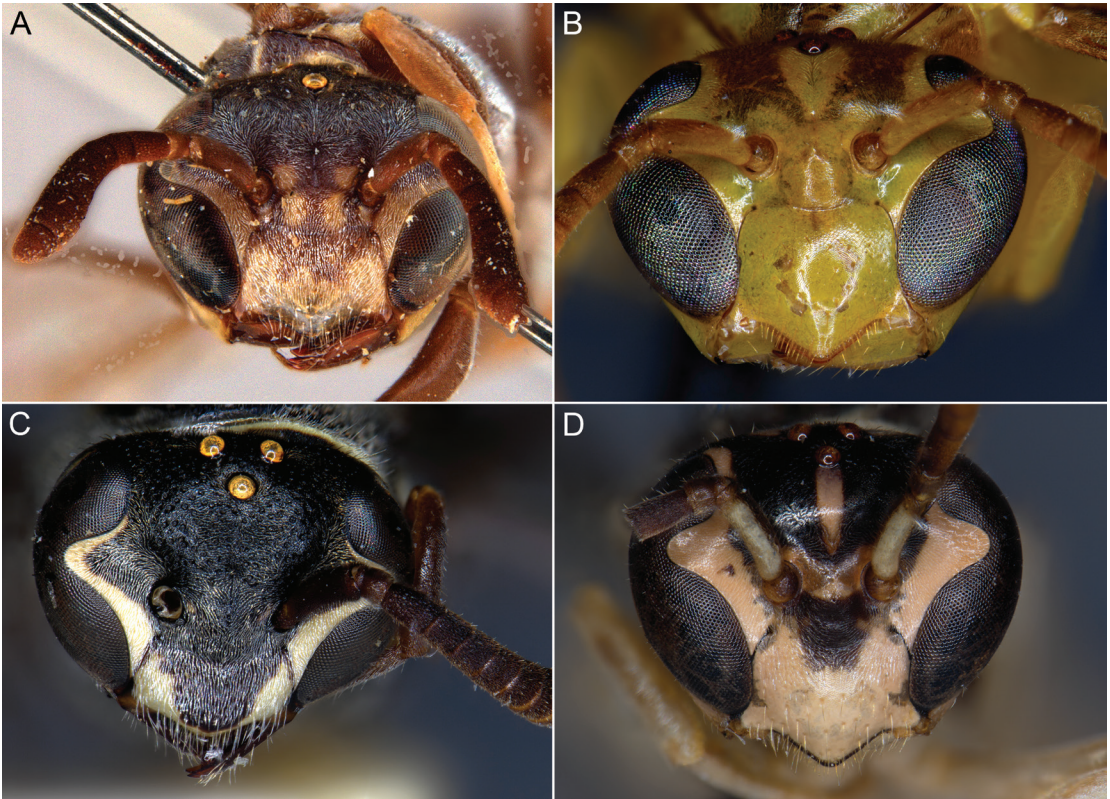


FIGURE 2. *Leipomeles* species, face, frontal view. **A.** *Leipomeles albogrisea* (Richards, 1978) paratype. **B.** *Leipomeles dorsata* (Fabricius, 1804). **C.** *Leipomeles pusilla* (Ducke, 1904). **D.** *Leipomeles spilogaster* (Cameron, 1912).

(key). – Menezes et al., 2020: Proceedings B of Royal Society 287 (4, 6) figures 1, 2 (phylogeny).

– Noll et al., 2021 Cladistics: (8, 10), figures 3, 4 (phylogeny).

DISTRIBUTION: Bolivia: Beni, Cochabamba, Pando; Brazil: Amapá, Amazonas, Bahia, Espírito Santo, Mato Grosso, Pará; Colombia: Amazonas, Meta, Nariño, Putumayo, Vaupés; Costa Rica; Ecuador: Napo; Panama; French Guiana; Guyana; Peru: Cuzco, Huánuco, Junín, Loreto, Madre de Dios; Suriname.

Leipomeles pusilla (Ducke, 1904)

Figures 1C, 2C

Chartergus pusillus Ducke, 1904, Boletim do Museu Goeldi, Pará 4: 325, 329 (key), 336, female – [Brazil] “Belem do Pará” (lectotype Paris); also from Oyapoc. – Richards, 1978, The Social Wasps of the Americas: 202 (designation of lectotype). – Nascimento and Overall, 1979, Boletim do Museu Goeldi (N. S.) 95: 9 (list). – Carpenter, 1999, American Museum Novitates. 3259: 10 (notes on types).

- Parachartergus pusillus*; Ducke, 1905, Annual Review of Entomology, Caen 24: 15; 1905, Boletim do Museu Goeldi, Pará 4: 667; 1907, Boletim do Museu Goeldi, Pará 5: 159 (key); 1910, Annales historico-naturales Musei Nationalis Hungarici 8: 528 (key), 530.
- Pseudopolybia pusilla*; Ducke, 1914, Zoologische Jahrbücher Abteilung für Systematik 36: 319, 327; 1918, Revista do Museu Paulista 10: 349. – Bequaert, 1938, Annual Review of Entomology, Rio de Janeiro 9: 113.
- Marimbonda pusilla*; Richards, 1978, The Social Wasps of the Americas: 201 (key), 202, fig. 84. – Overal, 1978, Boletim do Museu Goeldi (N.S.), Zool. 94: 9 (list).

DISTRIBUTION: Peru: Huánuco; Brazil: Amapá, Amazonas, Pará.

Leipomeles spilogastra (Cameron, 1912), specific epithet correction

Figures 1D, 2D, 3B

- Polybia spilogastra* Cameron, 1912, Timehri (3) 2: 208 (key), 213, female – locality not stated [Guyana] (lectotype London). – Richards, 1978, The Social Wasps of the Americas: 215 (syn. of *L. nana* [misidentification]).
- Pseudopolybia pusilla*; Bequaert, 1944, Bulletin of the Museum of Comparative Zoology at Harvard 94: 298 (key), 299. – Richards, 1951, in Richards and Richards, Transactions of the Entomological Society of London 102: 85. Misidentification.
- Leipomeles nana*; Richards, 1978, The Social Wasps of the Americas: 214 (key), 215 (syn.: *Polybia spilogastra* Cameron) [misidentification]. – Sarmiento, 1994, Revista de Biología Tropical 42 (1/2): 359 (list). – Carpenter, 1999, American Museum Novitates 3259: 1, 9 (*nana* sensu Richards a misidentification).
- Leipomeles spilogastra*; Carpenter, 1999, American Museum Novitates 3259: 1, 9. Menezes et al., 2020, Proceedings B of Royal Society 287: (4, 6) figures 1, 2 (phylogeny). – Noll et al., 2021, Cladistics: (8, 10), figures 3, 4 (phylogeny).
- Leipomeles spilogastra*; Somavilla et al., specific epithet correction.

DISTRIBUTION: Brazil: Amapá, Amazonas; Colombia: Nariño, Putumayo, Vaupés; Ecuador: Napo; French Guiana; Guyana; Panama; Peru: Huánuco, Junín, Loreto; Suriname.

COMMENTS: We propose a correction of the species epithet *Leipomeles spilogastra* to *Leipomeles spilogaster*. Cameron described *spilogastra* in the genus *Polybia*, evidently considering the epithet to be an adjective and incorrectly assuming it needed to be feminized to agree with the genus name, which is feminine. The word “gaster” is also feminine, hence agrees in gender with *Leipomeles*.

KEY TO THE SPECIES OF *LEIPOMELES* MÖBIUS

Adapted from Richards, 1978

1. Smooth and shining, less punctured (fig. 1B, D); first metasomal segment about twice as long as wide; hind wing with Cu1 shorter than Cu-a2
- 1'. Darker, more punctured—colors dark brown to black (fig. 1A, C); first metasomal segment slightly longer than wide; hind wing with Cu1 as long as Cu-a3



FIGURE 3. Nests of *Leipomeles* from AMNH nest database. A. *Leipomeles dorsata* (Fabricius, 1804). B. *Leipomeles spilogaster* (Cameron, 1912).

2. Pronotal carina stronger and straighter; clypeus a little wider than long (fig. 2D); coloration blackish and creamy white (fig. 1A); head with substantial blackish marking *L. spilogaster* (Cameron, 1912)
- 2'. Pronotal carina weak, more recurved laterally; clypeus a little longer than wide (fig. 2B); coloration yellow-brown and yellow or whitish-yellow (fig. 1B); head hardly with darker color..... *L. dorsata* (Fabricius, 1804)
3. Head and mesosoma very indistinctly punctured (figs. 1A, 2A); clypeus rounded below; POL : OOL = 2 : 3; metanotum with a slight dorsal area; propodeum yellow marked (fig. 1A) *L. albogrisea* (Richards, 1978)
- 3'. Head and mesosoma more shining, more distinctly punctured (fig. 1C, 2C); clypeus angled below; POL : OOL = 1 : 2.5; metanotum without dorsal area; propodeum black (fig. 1C) *L. pusilla* (Ducke, 1904)

PHYLOGENETIC ANALYSIS

Our phylogenetic analyses (fig. 4) resulted in a single cladogram of length 84, consistency index 0.58, and retention index 0.65. *Leipomeles* is supported as monophyletic, sister group of *Nectarinella*, and revealed the following relationships among the *Leipomeles* species: (*L. albogrisea* + *L. pusilla*) + (*L. spilogaster* + *L. dorsata*), with high support (Symmetric Resampling support = 73).

The genus was supported by three unique synapomorphies: the clypeus widely touching the eyes (char. 10: 2), the first metasomal segment conically petiolate (char. 24: 2), and nest with central furrow (char. 39: 1), which is exclusive to *Leipomeles* among all Epiponini. In addition, five homoplasies support *Leipomeles* related to mandible, clypeus apex and bristle distribution, propodeal concavity, propodeal valve, and digitus of the male genitalia.

Two clades, also strongly supported, were recovered within *Leipomeles*: the first, *L. albogrisea* + *L. pusilla*, with 65 symmetric resampling support, is formed by darker, more punctured species, and was supported by one synapomorphy, Cu1 vein of the hind wing as long as Cu-a (char. 28: 1). The second, *L. spilogaster* + *L. dorsata* with 96 symmetric resampling support, is formed by smooth and shining, less punctured species, and was supported by six homoplasies, related to pubescence and punctuations (chars. 8: 1, 18: 0, 19: 0), and distance between ocelli less than or equal to one ocellus (char. 14: 0), size of first metasomal segment equal or longer than tergum II (25: 0), and metasomal sternum VI not convex transversely (26: 0).

CONCLUDING REMARKS

The phylogenetic analysis based on morphological data, including females, males, and nest architecture, provided valuable insights into the phylogenetic relationships of *Leipomeles* species, and the recovered phylogeny supported a monophyletic genus. These findings contribute to our understanding of the morphological variation within *Leipomeles*. Lastly, we wish to reemphasize the importance of collection in social wasps as a source of data for elucidation of the evolution of this important group.

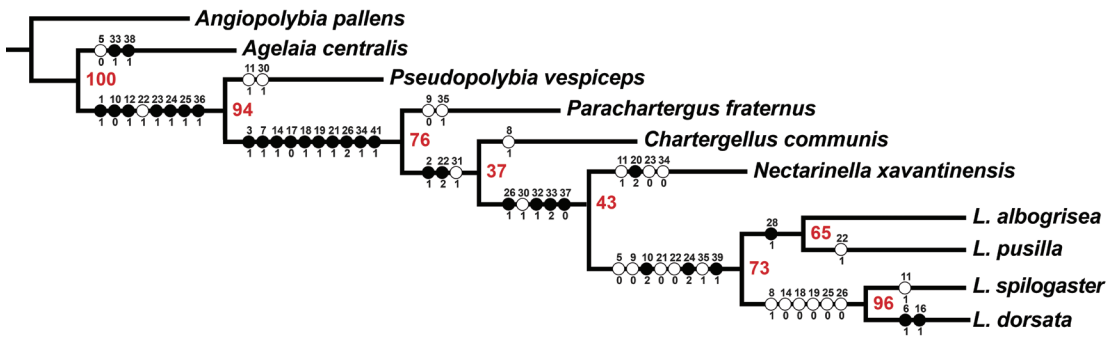


FIGURE 4. Phylogenetic relationships of *Leipomeles* species inferred by maximum parsimony analysis using morphological and nest architecture data. Values red at the nodes represent symmetric resampling support. Numbers above each circle represent character number, and below, character state. Black circles are unique synapomorphies. White circles are homoplasies.

ACKNOWLEDGMENTS

We are thankful to Gavin Broad and Jaswinder Boparai for support in the Natural History Museum (London), Carlos Roberto Brandão and Gabriela Camacho of the Museu de Zoologia of Universidade de São Paulo; Marcio Luiz Oliveira, José Albertino Rafael, and Raimundo N.M.M. Junior for material and support in the invertebrate collection of Instituto Nacional de Pesquisas da Amazônia; Felipe Vivalo and Museu Nacional–UFRJ for sharing the images of *L. albogrisea*; and the University of California Washington Center (UCDC) for the loan of specimens. A.S. is supported by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq–PDE scholarship, process number 200731/2022-0), G.S.V. by FAPESP (scholarship T.O.B, grant no. BOL0700/2022), and F.B.N. by FAPESP (grant no. 19/09215-6).

REFERENCES

- Carpenter, J.M. 1991. Phylogenetic relationships and the origin of social behavior in the Vespidae. *In* K.G. Ross and R.W. Matthews (editors), *The social biology of wasps*: 7–32. Ithaca, NY: Cornell University Press.
- Carpenter, J.M., 1999. Taxonomic notes on paper wasps (Hymenoptera, Vespidae, Polistinae). *American Museum Novitates* 3259: 1–44.
- 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 Mateus, S. 2004. Males of *Nectarinella* Bequaert (Hymenoptera, Vespidae, Polistinae). *Revista Brasileira de Entomologia* 48 (3): 297–302.
- Ducke, A. 1904. Sobre as vespidas sociaes do Pará. *Boletim do Museu Goeldi* 4: 317–374.
- Goloboff, P.A., et al. 2003. Improvements to resampling measures of group support. *Cladistics* 19: 324–332.

- Goloboff P.A., J.S. Farris, and K.C. Nixon. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24: 774–786.
- Menezes R.S.T., M.W.Lloyd, and S.G. Brady. 2020. Phylogenomics indicates Amazonia as the major source of Neotropical swarm-founding social wasp diversity. *Proceedings of the Royal Society of London B, Biological Sciences* 287 (1928): 20200480.
- Möbius, K.A. 1856. Die Nester der geselligen Wespen. Beschreibungen neuer Nester-und einigerneuen Wespen-arten des naturhistorischen Museums zu Hamburg nebst Betrachtungen über den Nesterbau im Allgemeinen. *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg* 3: 117–171, 19 pls.
- Nixon, K.C. 2002. Winclada, version 1.00.08. Ithaca, NY: Published by the author.
- Noll, F.B., et al. 2021. Marimbondos: systematics, biogeography, and evolution of social behaviour of neotropical swarm-founding wasps (Hymenoptera: Vespidae: Epiponini). *Cladistics* 37: 423–441.
- Richards, O.W. 1978. The social wasps of the Americas (excluding the Vespinae). London: British Museum of Natural History.
- Schulz, W. A. 1912. Aelteste und alte Hymenopteren skandinavischer Autoren. *Berliner Entomologische Zeitschrift* 57: 52–102.
- 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.
- Somavilla A., B.C. Barbosa, M.M. Souza, and F. Prezoto. 2021a. List of species of social wasps from Brazil. *In* F. Prezoto, F.S. Nascimento, B.C. Barbosa, and A Somavilla (editors), *Neotropical social wasps*: 293–316. Cham, Switzerland: Springer Nature Switzerland AG.
- Somavilla A., P.C.S. Barroso, M. Aragão, S. Mateus, and R.S.T. Menezes. 2021b. An integrative taxonomic and phylogenetic approach reveals a new Neotropical swarm-founding social wasp, *Pseudopolybia cryptica* sp. n. (Vespidae: Polistinae: Epiponini). *Arthropod Systematics and Phylogeny* 79: 25–35.
- Wenzel, J.W. 1998. A generic key to the nests of hornets, yellowjackets, and paper wasps worldwide (Vespidae: Vespinae, Polistinae). *American Museum Novitates* 3224: 1–39.
- Wenzel J.W., and J.M. Carpenter. 1994. Comparing methods: adaptive traits and tests of adaptation. *In* P. Eggleton and R.I. Vane-Wright (editors), *Phylogenetics and ecology*: 79–101. London: Academic Press.

APPENDIX 1

LIST OF MORPHOLOGICAL AND NEST ARCHITECTURE CHARACTERS

1. Third labial palpomere: **0**, without curved bristle; **1**, with curved bristle.
2. Number of segments of maxillary palpi: **0**, 6 segments; **1**, 5 segments.
3. Number of segments of labial palpi: **0**, 4 segments; **1**, 3 segments.
4. Eye bristles: **0**, present; **1**, absent.
5. Mandible, inferior line: **0**, straight; **1**, curved.
6. Proportion of clypeus: **0**, equal to or wider than long; **1**, longer than wide.
7. Clypeus profile: **0**, concave; **1**, flattened.
8. Pubescence on clypeus: **0**, top half or more; **1**, less than top half.
9. Clypeus bristle distribution: **0**, all over; **1**, first third.
10. Clypeus-eye contact: **0**, clypeus separated from eyes; **1**, clypeus touching eyes for a short distance; **2**, clypeus touching eyes for a wide distance.
11. Bristles on front: **0**, absent or very short; **1**, long.
12. Size of the gena: **0**, narrower than the eye; **1**, equal to or larger than eye.

13. Gena pubescence distribution: **0**, extending from top down to middle of gena; **1**, extending from top to lower than middle of gena.
14. Distance between ocelli: **0**, less than or equal to one ocellus; **1**, greater than one ocellus.
15. Occipital carina: **0**, present; **1**, absent.
16. Pronotal carina: **0**, absent; **1**, a trace; **2**, present, evident.
17. Dorsal groove: **0**, absent; **1**, present, evident.
18. Scutum punctuations: **0**, absent; **1**, present.
19. Mesopleura punctuations: **0**, absent or evanescent; **1**, present, evident.
20. Form of metanotum in lateral view: **0**, curved; **1**, compressed; **2**, vertical.
21. Form of propodeal valve: **0**, rounded; **1**, truncated;
22. Propodeal concavity: **0**, narrow; **1**, broad; **2**, propodeum nearly flat.
23. Dorsolateral bristles on propodeum: **0**, absent or evanescent; **1**, present.
24. Form of the first metasomal segment: **0**, elongated; **1**, conically sessile; **2**, conically petiolate.
25. Size of first metasomal segment: **0**, equal to or longer than tergum II; **1**, shorter than tergum II.
26. Form of metasomal sternum VI: **0**, not convex transversely; **1**, fairly convex transversely; **2**, strongly convex transversely.
27. Size of prestigma: **0**, as long as wide; **1**, longer than wide.
28. Size of Cu1 vein of the hind wing: **0**, shorter than Cu-a; **1**, about as long as Cu-a.
29. Basal angle of paramere: **0**, obtuse; **1**, acute.
30. Apical angle of paramere: **0**, rounded; **1**, truncated.
31. Bristles on the paramere spine: **0**, present; **1**, absent.
32. Shape of ventral process of the aedeagus: **0**, short and straight; **1**, long and straight; **2**, long and curved.
33. Aedeagus serrated: **0**, short apically, long in basal region; **1**, short in entire extension; **2**, very long.
34. Bristles on cuspis: **0**, short or absent; **1**, long.
35. Shape of digitus: **0**, apically pointed; **1**, rounded.
36. Digitus, basal process: **0**, absent; **1**, present.
37. Comb: **0**, sessile; **1**, pedicellate.
38. Nest envelope: **0**, absent; **1**, present.
39. Central furrow of the nest: **0**, absent; **1**, present.
40. Ridges parallel to lines of construction: **0**, absent; **1**, present.
41. Blots of colored pulp: **0**, absent; **1**, present.

APPENDIX 2

LIST OF *LEIPOMELES* SPECIMENS ANALYZED

- L. albogrisea*: BRAZIL: Mato Grosso, Nova Xavantina (1 ♀, NHM; 1 ♀, AMNH; 1 ♀, MNRJ).
L. dorsata: COSTA RICA: Heredia, La Selva (4 ♀, AMNH); PANAMA: Canal Zone (2 ♀, UCDC), Colorado (1 ♀, AMNH), El Liano (4 ♀, AMNH); BRAZIL: Acre, Reserva Catuaba (9 ♀, AMNH), Bujari (9 ♀, INPA), Senador Guiomard (13 ♀, INPA); Amazonas, Manaus (16 ♀, INPA), Reserva Ducke (3 ♀, INPA), Reserva Campina (7 ♀, INPA), Careiro Castanho (8 ♀, INPA), Canutama (7 ♀, INPA),

Ipixuna (1 ♀, INPA), Rio Aracá (10 ♀, INPA), São Gabriel da Cachoeira (2 ♀, INPA); Pará, Anajás (1 ♀, MPEG), Belterra FLONA Tapajós (1 ♀, INPA), Juruti (1 ♀, MPEG), Melaço Caxiuanã – ECFPn (1 ♀, MPEG), Marituba (1 ♀, MPEG), Morro do Senador (4 ♀, INPA), Paragominas (1 ♀, MPEG); Rondônia: Ariquemes (2 ♀, UCDC), Itapuã do Oeste (8 ♀, INPA); Mato Grosso, Aripuanã Resv. Humbolt (1 ♀, MPEG); ECUADOR: Napo (20 ♀, AMNH); Sucumbios, Limonococha (115 ♀, AMNH); Pastaza (12 ♀, AMNH); Anangu (4 ♀, AMNH); Coca (1 ♀, AMNH); Pichincha (1 ♀, AMNH; 1 ♀, UCDC); Morona Santiago (1 ♀, UCDC); Tena (1 ♀, UCDC); PERU: Huanuco (1 ♀, UCDC), Loreto, Iquitos (245 ♀, AMNH), Rio Sucussari (1 ♀, AMNH); Madre de Dios (1 ♀ 1 ♂, AMNH); Valle Chanchamayo (1 ♀, AMNH; 1 ♀, UCDC); GUIANA: Rio Essequibo (1 ♀, AMNH); FRENCH GUIANA: Cyenne, Petit Saul (10 ♀, AMNH).

L. pusilla: BRAZIL: Amazonas, Manaus, Reserva Ducke (1 ♀, INPA), Reserva Campina (1 ♀, INPA); PERU: Tingo Maria (1 ♀, AMNH).

L. spilogaster: BRAZIL: Roraima, Rorainópolis (10 ♀, INPA), Tepequém (1 ♀, INPA); Amapá, Serra do Navio (1 ♀, INPA); Acre, Bujari (2 ♀, INPA); Amazonas, Manaus (12 ♀, AMNH), Reserva Ducke (18 ♀, INPA), Reserva ZF2 (3 ♀, INPA), Careiro Castanho (18 ♀, INPA), *Ipixuna* (2 ♀, INPA), Novo Aripuanã (6 ♀, INPA), Parque Nacional do Jaú (2 ♀, INPA), Rio Preto da Eva (5 ♀, INPA), Santa Izabel do Rio Negro (1 ♀, INPA), Tefé (1 ♀, INPA); Pará, Juruti (1 ♀, MPEG); Mato Grosso (1 ♀, MPEG), Rondônia, Nova Mamoré (1 ♀, INPA), Itapuã do Oeste (2 ♀, INPA); ECUADOR: Napo, Tena (10 ♀, AMNH), Rio Misahualli (1 ♀, AMNH); Morona Santiago (1 ♀, UCDC); PERU: Loreto, Iquitos (102 ♀ 1 ♂, AMNH); Tingo Maria (1 ♀, AMNH); GUIANA: Coppename River (1 ♀, AMNH); Kalacoon Bartica (1 ♀, UCDC); SURINAME: Raleigh, Vallen Voltzberg Res. (1 ♀, AMNH); FRENCH GUIANA: Cayenne, Petit Saul (5 ♀, AMNH).

All issues of *Novitates* and *Bulletin* are available on the web (<https://digitallibrary.amnh.org/handle/2246/5>). Order printed copies on the web from:
<https://shop.amnh.org/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).