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Phylogeny of the Neotropical genus *Stenosigma* Giordani Soika, 1978 (Hymenoptera, Vespidae, Eumeninae) based on morphological data

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Abstract. *Stenosigma* Giordani Soika, 1990 is a small Neotropical genus of potter wasps (Hymenoptera, Vespidae, Eumeninae), with an interesting distributional pattern and a recent revision published. Unfortunately, the genus lacks a phylogenetic hypothesis with all species included — one major impediment for future biogeographic studies and hypotheses for evolutionary scenarios. Therefore, a phylogenetic treatment would help enlighten the history of this Neotropical wasp genus. We present the first phylogeny of *Stenosigma* based on cladistic methods using morphological data including all seven currently recognized species. We also give an overview of the distribution of the *Stenosigma* species and correlate the distribution pattern with the two major clades identified in the phylogeny.

Key words. Cladistics, evolutionary scenario, potter wasps.

1. Introduction

The systematics of potter wasps (Hymenoptera, Vespidae, Eumeninae) experienced an increase in the number of published studies in the last decade, both in traditional taxonomy (Ferreira et al. 2015, 2017, 2018, 2019; Hermes & Ferreira 2016; Oliveira et al. 2017) and phylogeny (Hermes & Melo 2008; Hermes & Carpenter 2012; Hermes et al. 2014; Grandinete et al. 2015; Hermes & Oliveira 2016; Oliveira et al. 2019). This recent interest in potter wasp classification and evolutionary history is important given the key position of this group in the evolutionary scenarios proposed about the origins of eusociality and the disputed relationships among Vespidae subfamilies (Hines et al. 2007; Bank et al. 2017; Piekarski et al. 2018).

Besides that, several shortfalls remain regarding our knowledge about potter wasps, especially in little-known regions like the Neotropics. The Neotropical potter wasp fauna is diverse (about 600 described species) but suffers from poor taxonomical practices of the past and a lack of updated revisions for most of the genera (Hermes et al. 2014; see an example in Hermes & Ferreira 2016). The proliferation of generic names and the designation of subspecies that resulted in recent synonymies (Grandinete et al. 2016; Hermes & Oliveira 2016; Ferreira et al. 2019) are two recognized problems in the taxonomy of the group (Carpenter & Garcete-Barrett 2003; Hermes et al. 2014).

Taxonomic reviews are the first step to solve such problems and reduces the gaps in the knowledge of Eumeninae Neotropical fauna, with the possibility of descriptions of new species and presentation of unpublished collection records. Therefore, in a previous contribution, we revised the genus *Stenosigma* Giordani Soika, 1978 (Ferreira et al. 2018), which is restricted to the Neotropical region. Even though we described three new species (Hermes & Ferreira 2016; Ferreira et al. 2018) and published new collecting data (Ferreira et al. 2018), the phylogenetic relationships among the species of *Stenosigma* have not been investigated so far.

Stenosigma comprises seven recognized species: *S. allegrum* (Zavattari, 1912), *S. humerale* Giordani Soika, 1990, *S. imitans* (Ducke, 1911), *S. mariae* Ferreira &

Hermes, 2018, *S. panamensis* Ferreira & Hermes, 2018, *S. quechua* Hermes & Ferreira, 2016, and *S. testaceum* (Fox, 1899). *Stenosigma allegrum* is the only species occurring further South in the Neotropical region, while the remaining of the species have a distribution associated with the Amazon rainforest. There is a great gap in the distribution records of the genus, especially in the central area of Brazil (colleting records in Giordani Soika 1990 and Ferreira et al. 2018).

The only attempt to investigate the phylogenetic position of *Stenosigma* species was presented by Hermes et al. (2014). These authors recovered *Stenosigma* as monophyletic and proximally related to the genus *Pararhaphidoglossa* von Schulthess, 1910 though only *S. testaceum* and *S. allegrum* were included in those analyses. We present the first phylogeny for the genus *Stenosigma* including all the seven recognized species, based upon morphological data and using a cladistic approach.

2. Material and methods

2.1. Material

The study of external morphology involved pinned specimens of both sexes, borrowed from the institutions listed in the section "Depositories". The holding institution acronyms follow Evenhuis (2018) or were provided by the curators. The complete list of material examined are presented in the Electronic Supplement S1.

Specimens from all species of the genus *Stenosigma* were available for study. The type material of *S. allegrum*, *S. testaceum*, *S. mariae*, *S. panamensis*, *S. humerale* and *S. quechua* were examined. We did not have access to the type material of *S. imitans*, but photographs were provided by Dr. Orlando T. Silveira (MPEG).

2.2. Methods

2.2.1. Microscopy

The analysis of the external morphology was performed using a Leica S8 APO stereomicroscope. Photographs of structures of interest were obtained with a Canon EOS Rebel T6 digital camera coupled to the stereomicroscope. When possible, the male genitalia was removed, cleared and examined (following Hermes & Melo 2008). General external morphology terminology follows Carpenter & Garcete-Barrett (2003) and for the male genitalia Bitsch (2012). Some terms for the mesepisternum were adapted from Richards (1978). For characters involving integument punctation, the term "sparse" is applied when the distance between punctures on the body surface of the same individual is greater than the size of a puncture (Fig. 12) and the term "dense" for the opposite condition (Fig. 11).

2.2.2. Analysis

The character matrix based on the observation of external morphological structures was assembled using Winclada v. 1.000.08 (Nixon 1999–2002). Females were used for comparisons, except for the characters related with the male genitalia and antennae. Two multi-state characters (i.e., char. 1, char. 20) used in this study were treated as non-additive.

All the seven recognized *Stenosigma* species were included as ingroup. Species belonging to the closely related genera *Pararhaphidoglossa* and *Alphamenes* Van der Vecht, 1977 were additionally included to test the monophyly of *Stenosigma*. The species *Monobia angulosa* Saussure, 1852 was selected as outgroup to root the tree (Nixon & Carpenter 1993).

Heuristic searches for the most parsimonious trees were conducted with TNT v. 1.5 (Goloboff & Catalano 2015), using equal character weighing. In TNT (Goloboff et al. 2008) the "New Technology Search" option was performed following Hermes et al. (2014) and Hermes & Oliveira (2016). Support for the branches was estimated through symmetric re-sampling (Goloboff et al. 2003) also with TNT 1.5 (traditional tree search – TBR = 1000 replications; 10000 re-sampling replications). Both the optimization of the characters and the visualization of the cladograms were performed in Winclada, with only unambiguous changes shown.

2.3. Abbreviations

Morphology. F1–F11 – antennal flagellomeres; **S1–S7** – metasomal sterna; **T1–T7** – metasomal terga.

Depositories. AMNH – American Museum of Natural History, New York, USA; **CMNH** – Carnegie Museum of Natural History, Pittsburgh, USA; **CEUFLA** – Coleção Entomológica da Universidade Federal de Lavras, Lavras, Brazil; **IBILCE-UNESP** – Instituto de Biociências, Letras e Ciências Exatas, Universidade Paulista "Júlio de Mesquita Filho", São José do Rio Preto, Brazil; **INPA** – Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil; **MIUP** – Museo de Invertebrados "G.B. Fairchild", Panama City, Panama; **MNHN** – Muséum National d'Histoire Naturelle, Paris, France; **MNHNPY** – Museo Nacional de Historia Natural del Paraguay, San Lorenzo, Paraguay; **MPEG** – Museu Paraense Emílio Goeldi, Belém, Brazil; **MSNVE** – Museo di Storia Naturale di Venezia, Venice, Italy; **NHMUK** – Natural History Museum, London, England; **UFES** – Universidade Federal do Espírito Santo, Vitória, Brazil; **ZMHB** – Museum für Naturkunde, Berlin, Germany.

3. Results

3.1. List of characters and character states

Head

1. Labrum, apex: **(0)** truncate (Fig. 1); **(1)** rounded (Fig. 2); **(2)** weakly emarginate (Fig. 3).

2. Clypeal dimensions: **(0)** longer than wide (Fig. 1, 2; Ferreira et al. 2018: pp. 5, 8, figs. 8, 9, 11–14); **(1)** wider than long (Fig. 3; Ferreira et al. 2018: p. 5, fig. 10).

3. Clypeal apex: **(0)** weakly emarginate (Fig. 2); **(1)** strongly emarginate (Fig. 1).

4. Clypeal apical carina: **(0)** absent (Fig. 3); **(1)** present (Fig. 1).

5. Clypeal lateral lamella: **(0)** absent (Fig. 2); **(1)** present (Fig. 4).

6. Frons, interantennal region: **(0)** not cariniform (Fig. 3); **(1)** cariniform (Fig. 2).

7. Vertex, lateral ocelli: **(0)** closer to each other than to the compound eye (Fig. 5); **(1)** more distant to each other than to the compound eye (Fig. 6).

8. Occipital carina: **(0)** dorsally sinuous (Fig. 7); **(1)** not dorsally sinuous (Fig. 8).

9. Antenna, form of male F11: **(0)** hook-shaped, thick and flat (Fig. 9); **(1)** hook-shaped, thick and pointed (Fig. 10).

Mesosoma

10. Pronotum, punctuation dorsally: **(0)** dense (Fig. 11, adapted from Ferreira et al. 2018: p. 8, fig. 15); **(1)** sparse (Fig. 12, adapted from Ferreira et al. 2018: p. 8, fig. 18).

11. Pronotum, pronotal carinae laterally: **(0)** continuous, not very sinuous (Fig. 13, adapted from Ferreira et al., 2018: p. 8, fig. 16); **(1)** continuous, very sinuous (Fig. 14).

12. Pronotum, pronotal carinae dorsally: **(0)** completely developed (Fig. 16, adapted from Ferreira et al., 2018: p. 10, fig. 26); **(1)** underdeveloped (Fig. 15, adapted from Ferreira et al. 2018: p. 10, fig. 25).

13. Pronotum, lamella on the dorsolateral margin of the pronotal carina: **(0)** absent (Fig. 12, adapted from Ferreira et al., 2018: p. 8, fig. 18); **(1)** present (Fig. 13, adapted from Ferreira et al. 2018: p. 8, fig. 16).

14. Pronotum, distance between the pronotal fovea and mesepisternum: **(0)** long (Fig. 17); **(1)** short (Fig. 18).

15. Pronotum, humeral projection: **(0)** absent (Fig 11, adapted from Ferreira et al. 2018: p. 8, fig. 15); **(1)** present (Fig 12, adapted from Ferreira et al. 2018: p. 8, fig. 18).

16. Mesonotum, medial margin of tegulae: **(0)** little depressed (Fig. 19); **(1)** very depressed (Fig. 20).

17. Mesepisternum, sternopleural carina: **(0)** undeveloped (Fig. 21); **(1)** well developed (Fig. 22).

18. Mesepisternum, epicnemial carina: **(0)** absent (Fig. 23); **(1)** present (Fig. 24).

19. Mesepisternum, punctuation: **(0)** dense (Fig. 25); **(1)** sparse (Fig. 26).

20 Mesepisternum, dorsal sulcus: **(0)** slightly demarcated (Fig. 24); **(1)** cariniform (Fig. 23); **(2)** punctuated (Fig. 25).

21. Mesepisternum, posterior projection: **(0)** well developed (Fig. 24); **(1)** undeveloped (Fig. 23).

22. Metapleura, striation: **(0)** present (Fig. 24); **(1)** absent (Fig. 23).

23. Propodeum, posterior surface: **(0)** without carina (Fig. 27); **(1)** carinate (Fig. 28–29).

24. Propodeum, carina: **(0)** not projected (Fig. 28); **(1)** projected (Fig. 29). Not applicable to taxa with state (0) in character 23.

25. Propodeum, postero-inferior surface: **(0)** posteriorly projected, fused to the submarginal carina (Hermes et al. 2014: p. 13, fig. 47); **(1)** not posteriorly projected, not fused to the submarginal carina (Hermes et al. 2014: p. 13, fig. 46).

26. Propodeum, postero-lateral surface: **(0)** with evident cavity (Hermes et al. 2014: p. 13, fig. 45); **(1)** without evident cavity (Hermes et al. 2014: p. 13, fig. 46).

27. Propodeum, medium posterior striation: **(0)** absent (Fig. 28); **(1)** present (Fig. 29).

Metasoma

28. T1, dimensions: **(0)** basal portion shorter than or as long as the apex (Fig. 30); **(1)** basal portion longer than the apex (Fig. 31).

29. T1, punctuation: **(0)** present, with deep punctures (Figs. 30, 34); **(1)** absent (Figs. 31, 35).

30 T1, preapical fossa: **(0)** absent (Fig. 31, 32); **(1)** present (Fig. 30, 33).

31 T1, apex: **(0)** with preapical transversal sulcus (Fig. 32); **(1)** without preapical transversal sulcus (Fig. 33).

32. T1, lateral margins: **(0)** touching ventrally (Fig. 36); **(1)** not touching ventrally (Fig. 37).

33. T2, apex: **(0)** lamellate (Fig. 34); **(1)** not lamellate (Fig. 35).

34. Male S7, lateral cristae: **(0)** absent (Fig. 38); **(1)** present (Fig. 39).

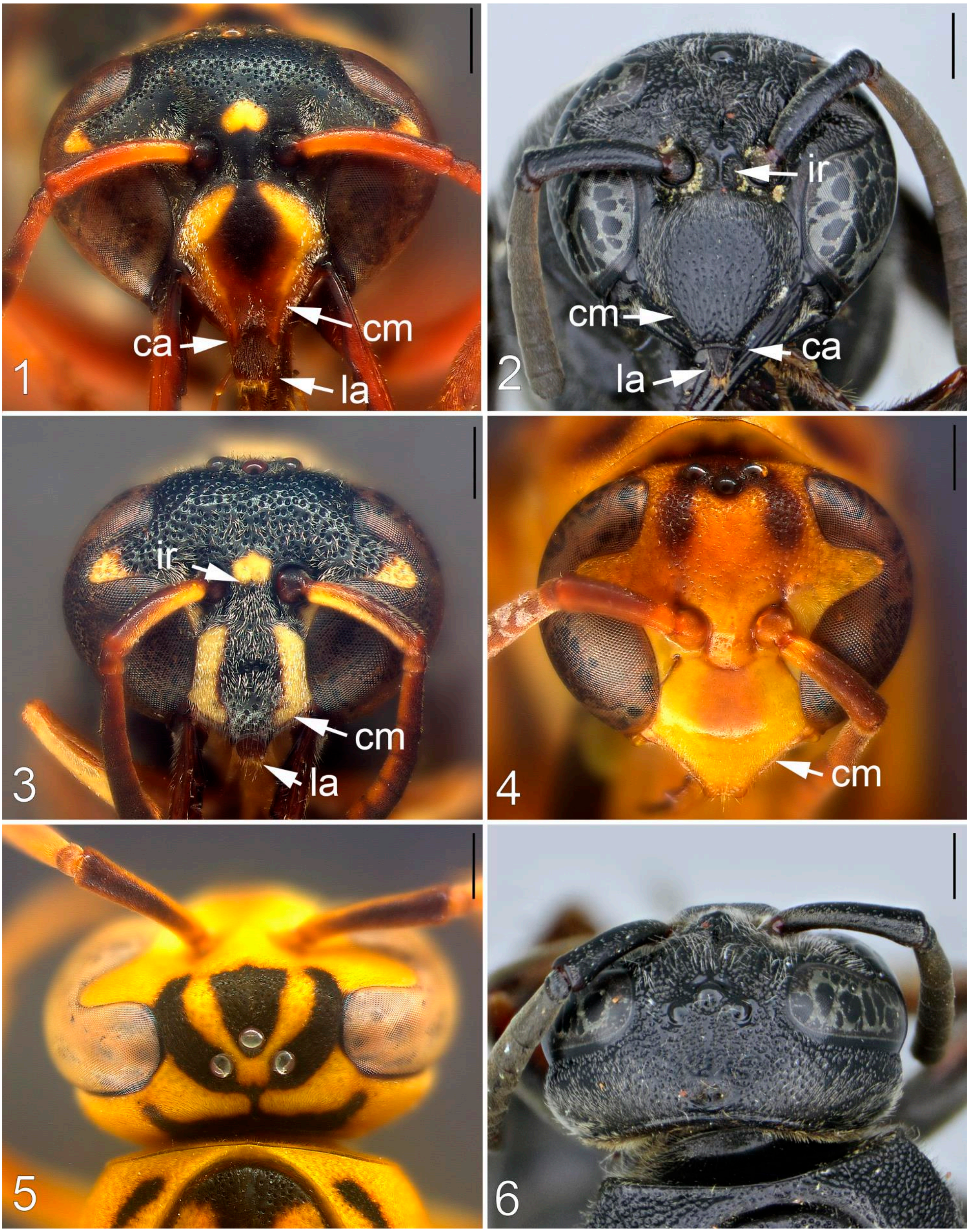
Male genitalia

35. Ventral margin of aedeagus I: **(0)** smooth (Hermes & Oliveira 2016: p. 193, fig. 32); **(1)** serrated, with medial enlargement (Oliveira et al. 2019: p. 78, fig. 9d).

36. Ventral margin of aedeagus II: **(0)** with basal projections along the medium enlargement (Oliveira et al. 2019: p. 78, fig. 9e); **(1)** without basal projections along the medium enlargement (Hermes & Oliveira 2016: p. 193, fig. 32).

37. Aedeagus, medium basal apodema: **(0)** short (Oliveira et al. 2019: p. 78, figs. 9–15); **(1)** elongated (Hermes & Oliveira 2019: p. 193, fig. 32).

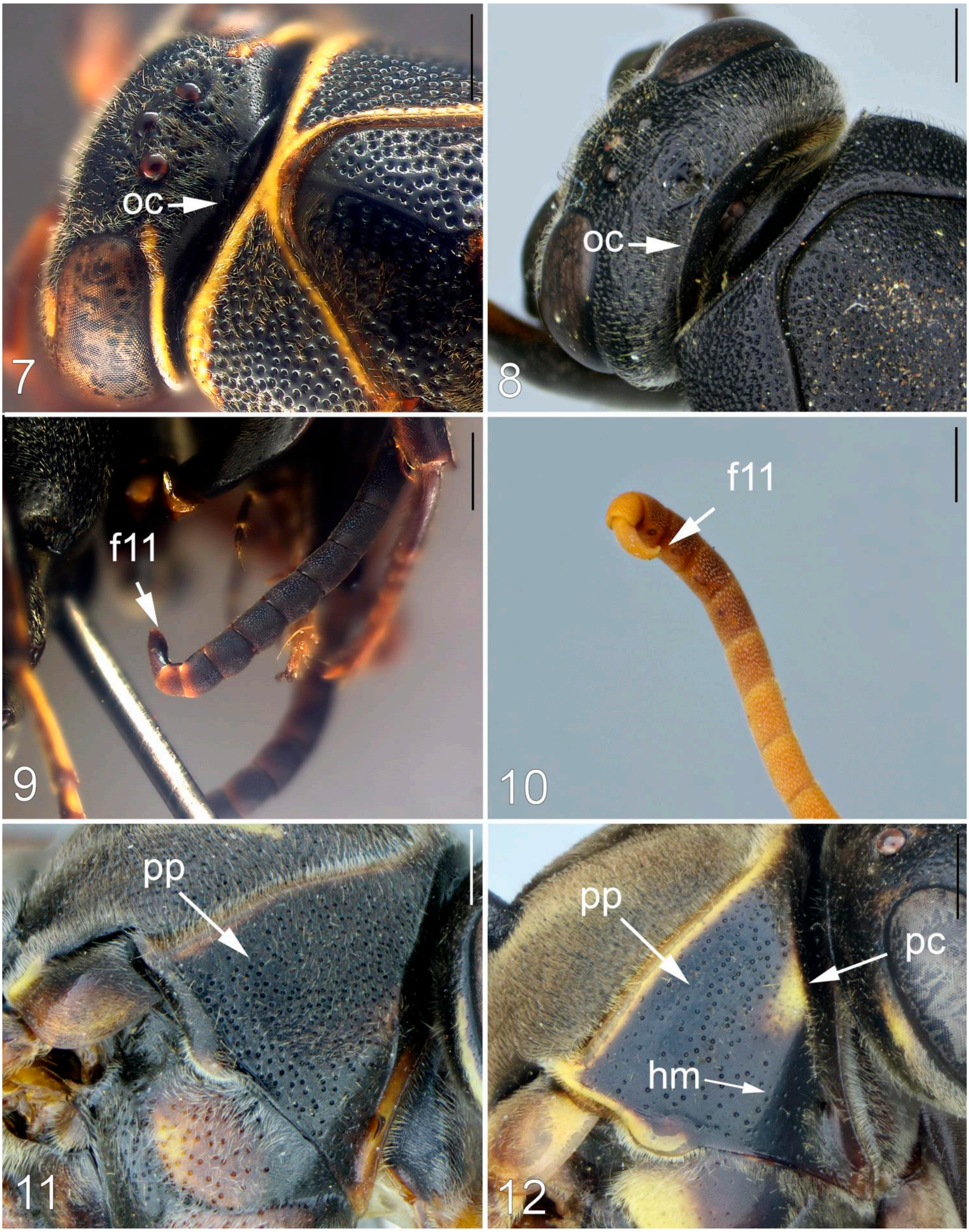
38. Digitus: **(0)** without median projection adjacent to lamella (Hermes & Oliveira 2016: p. 193, fig. 39); **(1)** with median projection adjacent to lamella (Oliveira et al. 2019: p. 78, fig. 8a).



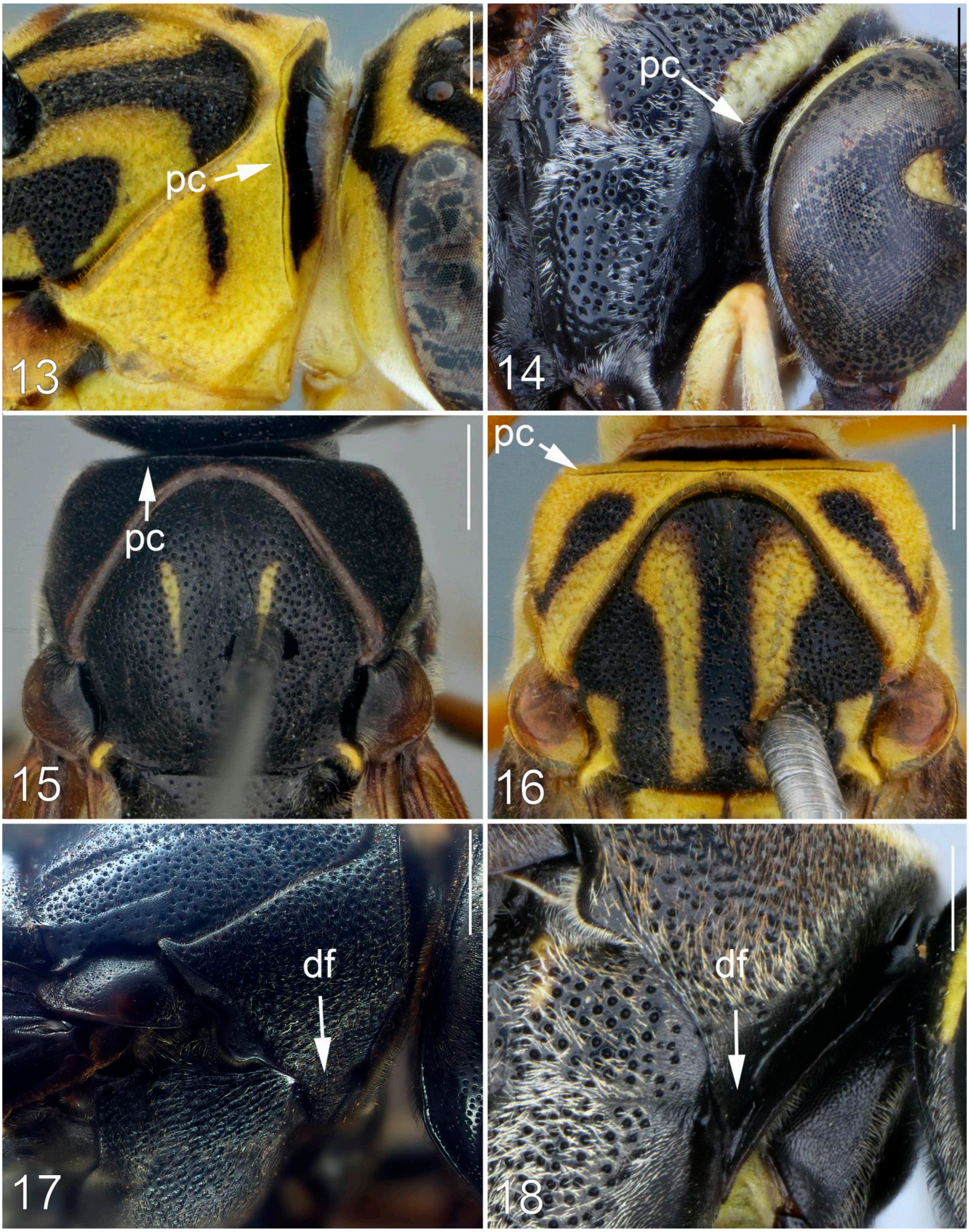
Figs. 1–6. The figures show the frontal and the dorsal views of the head. **1**: *Alphamenes campanulatus* Fabricius, 1804. **2**: *Monobia angulosa* Saussure, 1852. **3**: *Pararhaphidoglossa cressoniana* (Saussure, 1875). **4**: *Stenosigma imitans* (Ducke, 1911). Orientation: frontal view of the head (Scale bar: 0.5 mm). **5**: *Stenosigma testaceum* (Fox, 1899). **6**: *M. angulosa*. Orientation: dorsal view of the head. (Scale bar: 0.5 mm). — ***Abbreviations***: ca = clypeus apex; cm = lateral margin of clypeus; la = labrum apex; ir = interantennal region.

39. Cuspis, basis: **(0)** densely bristly (Oliveira et al. 2019: p. 78, fig. 8); **(1)** sparsely bristly (Ferreira et al. 2015: p. 121, fig. 14).

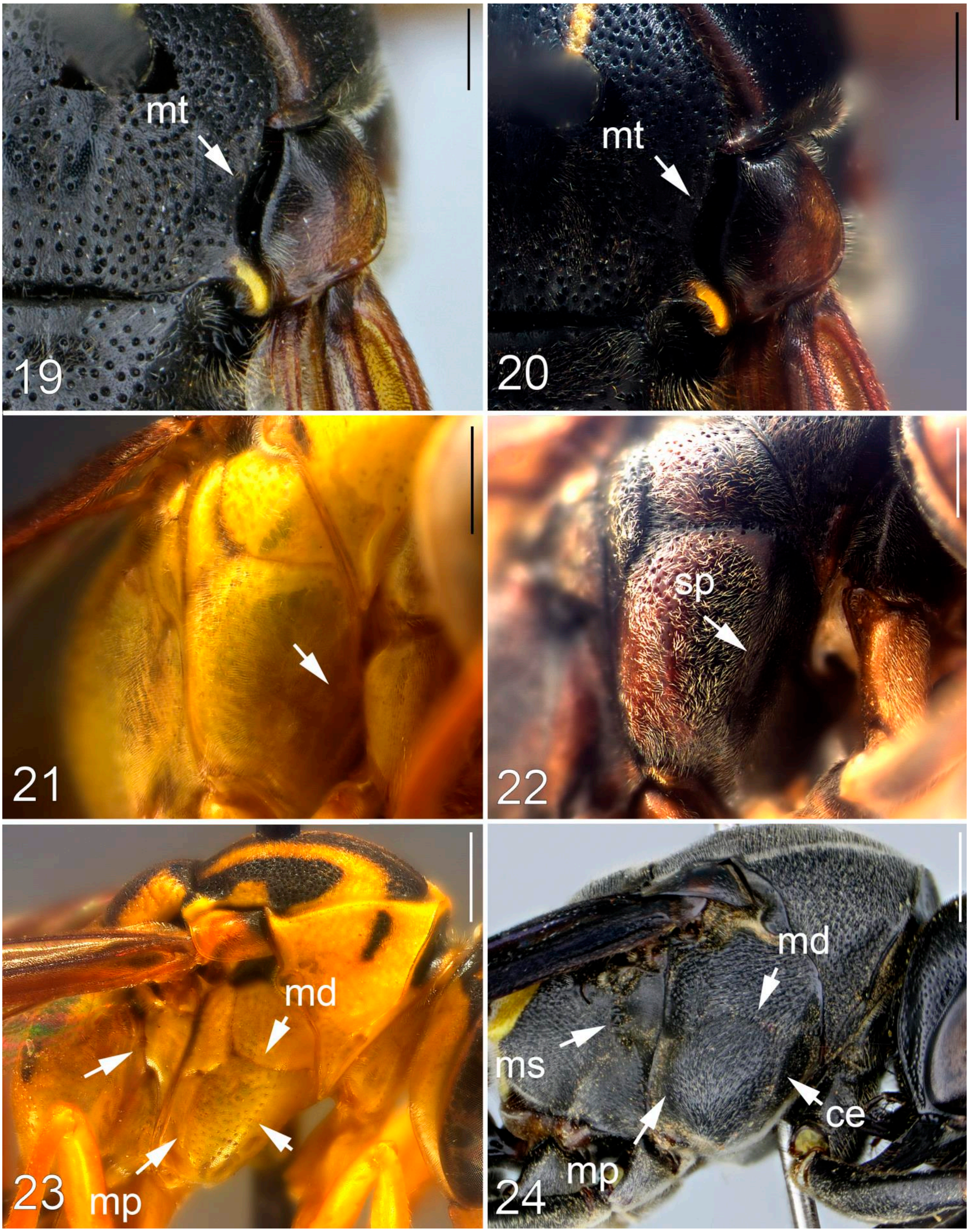
40. Cuspis: **(0)** without median projection adjacent to lamella (Oliveira et al. 2019: p. 78, fig. 8); **(1)** with median projection adjacent to lamella (Ferreira et al. 2015: p. 121, fig. 14).



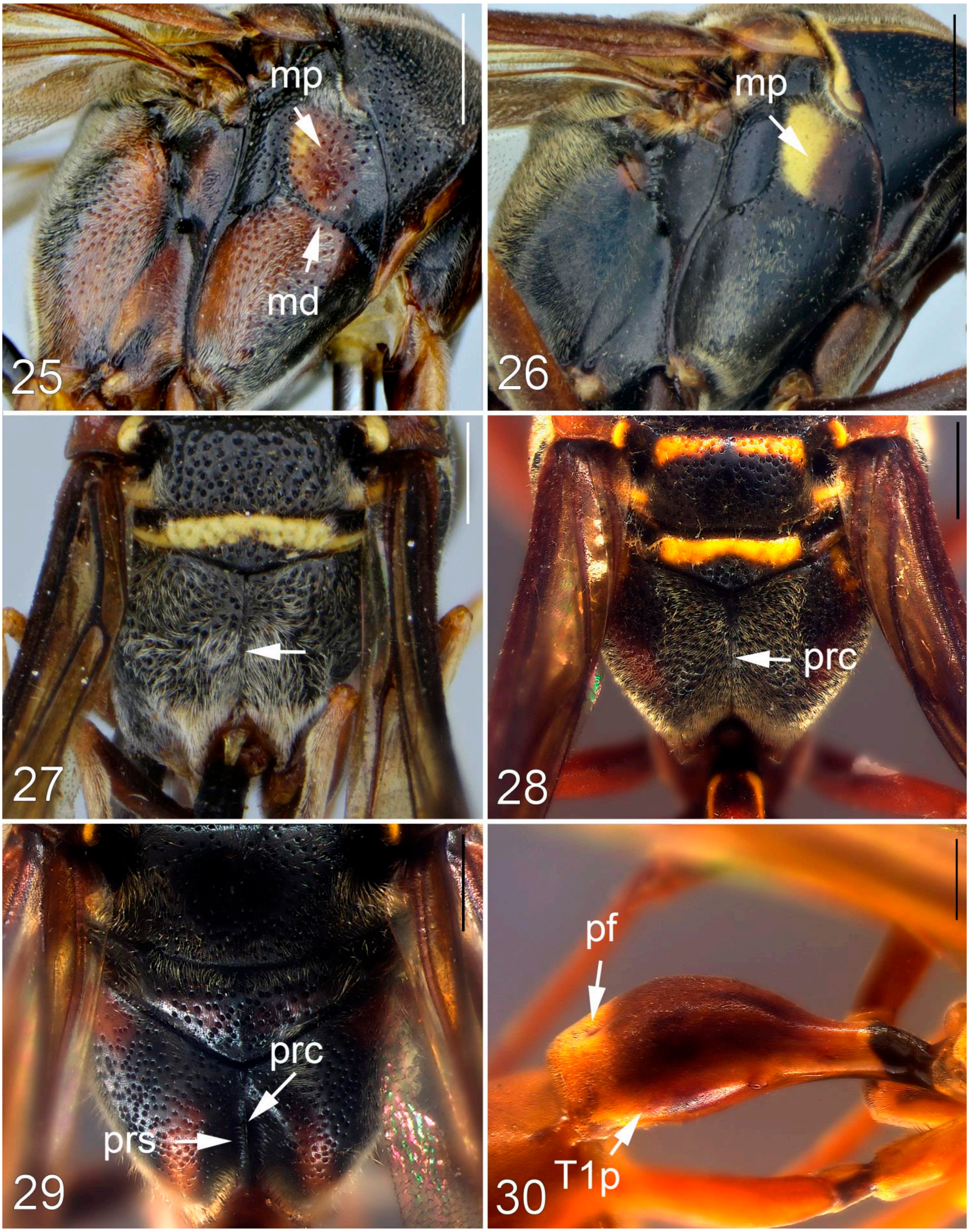
Figs. 7–12. The figures show the occipital carina, the antennal apex and a lateral view of the pronotum. **7**: *Pararhaphidoglossa cressoniana* (Saussure, 1875); **8**: *Monobia angulosa* Saussure, 1852. Orientation: dorsolateral view of the head (Scale bar: 0.5 mm). **9.** *M. angulosa*; **10**: *Stenosigma testaceum* (Fox, 1899). Orientation: ventral view of the apex of the male antenna (Scale bar: 0.5 mm). **11**: *Stenosigma allegrum* (Zavattari, 1912); **12**: *Stenosigma humerale* Giordani Soika, 1990. Orientation: mesosoma, dorsal view of the pronotum (Scale bar: 0.5 mm). — ***Abbreviations***: oc = occipital carina; f11 = flagellomere 11 of the male antenna; pp = punctuation on the dorsal surface of the pronotum; pc = pronotal carina; hm = humeral projection.



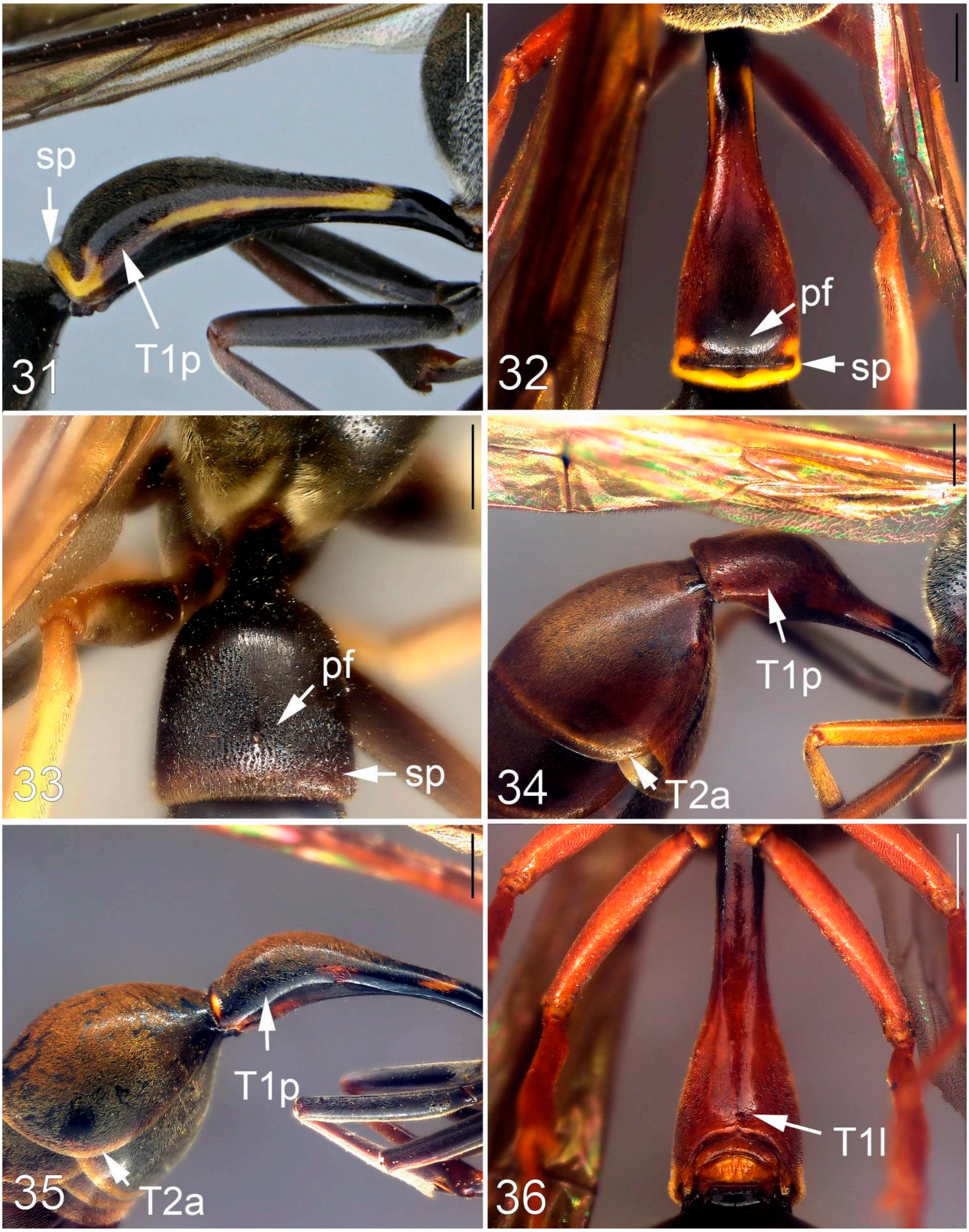
Figs. 13–18. The figures show the lateral and the dorsal views of the pronotum. **13**: *Stenosigma mariae* Ferreira & Hermes, 2018; **14**: *Pararhaphidoglossa pluviosa* (Zavattari, 1912). Orientation: mesosoma, lateral view of the pronotum (Scale bar: 0.5 mm). **15**: *Stenosigma allegrum* (Zavattari, 1912); **16**: *Stenosigma testaceum* (Fox, 1899). Orientation: mesosoma, dorsal view of the pronotum (Scale bar: 1 mm). **17**: *Monobia angulosa* Saussure, 1852; **18**: *Pararhaphidoglossa pluviosa* (Zavattari, 1912). Orientation: mesosoma, lateral view of the pronotum and mesepisternum (Scale bar: 0.5 mm). — ***Abbreviations***: pc = pronotal carina; df = distance between the pronotal fovea and mesepisternum.



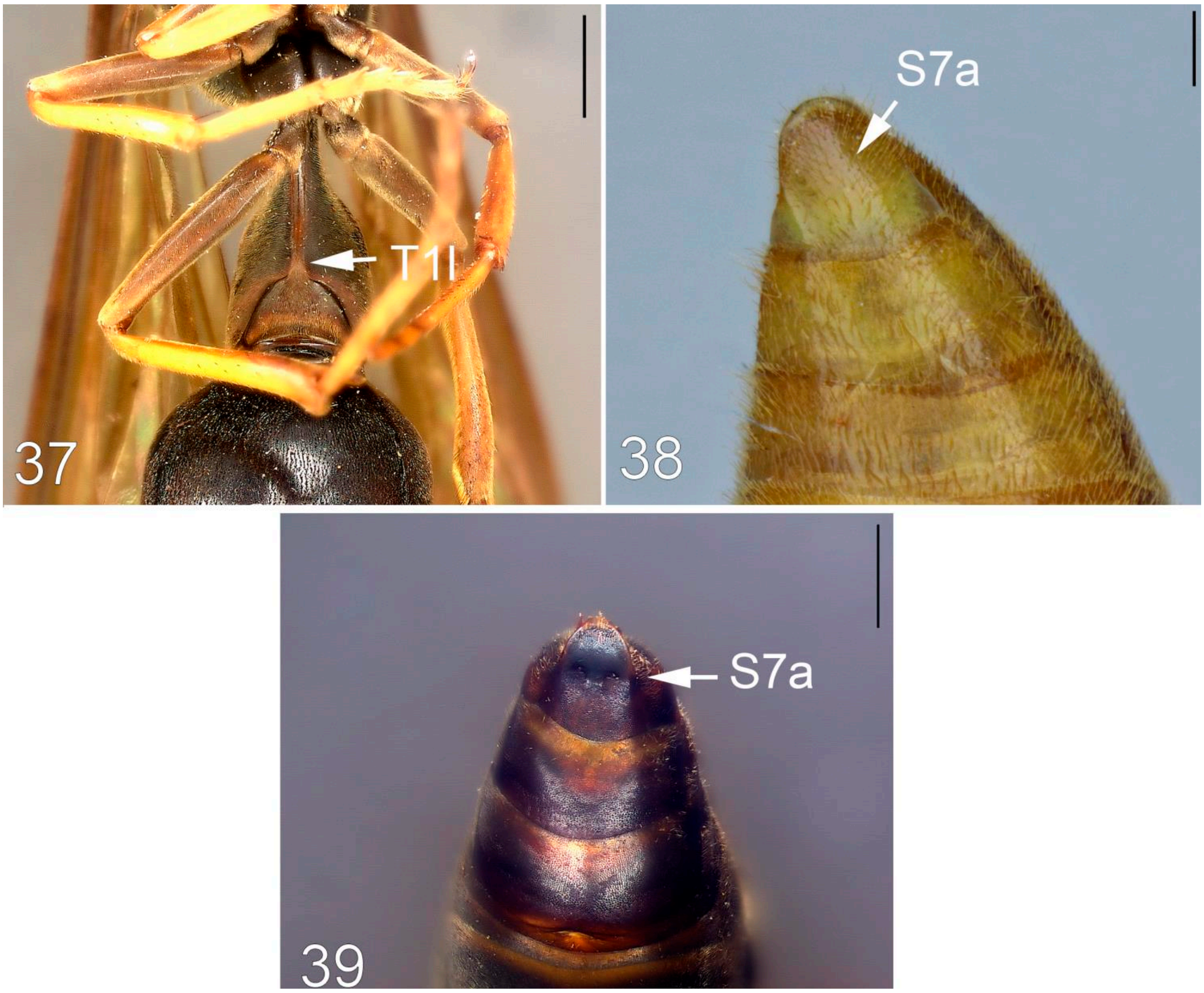
Figs. 19–24. The figures show the medial margin of the tegulae and the lateral view of the mesosoma. **19**: *Pararhaphidoglossa cressoniana* (Saussure, 1875); **20**: *Stenosigma allegrum* (Zavattari, 1912). Orientation: mesosoma, dorsal view of the mesonotum (Sacale bar: 0.5 mm). **21**: *Stenosigma testaceum* (Fox, 1899); **22**: *Stenosigma allegrum* (Zavattari, 1912). Orientation: mesosoma, lateral view of the mesepisternum (Scale bar: 0.5 mm). **23**: *Stenosigma mariae* Ferreira & Hermes, 2018; **24**: *Monobia angulosa* Saussure, 1852. Orientation: mesosoma, lateral view of the mesepisternum and metapleura (Scale bar: 1 mm). — ***Abbreviations***: mt = medial margin of the tegulae; sp = sternopleural carina; md = dorsal sulcus; ce = epicnemial carina; mp = region of mesepisternum posterior projection; ms = metapleura stratiation.



Figs. 25–30. The figures show the lateral and the postero-dorsal views of the mesosoma; and the lateral view of the metasomal tergum I. **25.** *Stenosigma allegrum* (Zavattari, 1912); **26.** *Stenosigma humerale* Giordani Soika, 1990 — Orientation: lateral view of the mesosoma (Scale bar: 1 mm). **27.** *Pararhaphidoglossa cressoniana* (Saussure, 1875); **28.** *Alphamenes campanulatus* Fabricius, 1804; **29.** *S. allegrum*. — Orientation: postero-dorsal view of the mesosoma: mesescutellum, metanotum and propodeum (Scale bar: 0.5 mm). **30.** *Stenosigma testaceum* (Fox, 1899). — Orientation: lateral view of the first metasomal tergum (Scale bar: 0.5 mm). — ***Abbreviations***: mp = mesepisternum dorsal punctuation; md = dorsal sulcus; prc = carina of the propodeum; prs = stration of the propodeum carina; T1p = sculpture of the first metasomal tergum; pf = preapical region.



Figs. 31–36. The figures show the metasomal terga I and II; and the metasomal sterna I. **31.** *Alphamenes campanulatus* Fabricius, 1804. — Orientation: lateral view of the first metasomal tergum (Scale bar: 0.5 mm). **32.** *A. campanulatus*; **33.** *Stenosigma humerale* Giordani Soika, 1990. — Orientation: dorsal view of the first metasomal tergum (Scale bar: 0.5 mm). **34.** *Stenosigma allegrum* (Zavattari, 1912); **35.** *A. campanulatus*. — Orientation: lateral view of the first and the second metasomal terga (Scale bar: 0.5 mm). **36.** *A. campanulatus*. — Orientation: ventral view of the first metasomal sternum (Scale bar: 1 mm). — ***Abbreviations***: T1l = lateral margins of the first metasomal tergum; T1p = sculpture of the first metasomal tergum; T2a = apex of the second metasomal tergum; pf = preapical region; sp = apex of the first metasomal tergum (preapical sulcus region).



Figs. 37–39. The figures show the first metasomal sterna and the apex of the metasoma. **37.** *Stenosigma humerale* Giordani Soika, 1990. — Orientation: ventral view of the first metasomal sternum (Scale bar: 1 mm). **38.** *Stenosigma testaceum* (Fox, 1899); **39.** *Alphamenes campanulatus* Fabricius, 1804. — Orientation: ventral view of the male metasomal sterna apex (Scale bar: 0.5 mm). — ***Abbreviations*:** T1l = lateral margins of the first metasomal tergum; S7a = apex of the seventh metasomal male sternum.

3.2. Cladistic results

The cladistic analysis with equal character weighing returned one most parsimonious tree, with length (L) = 57, consistency index (CI) = 73, and retention index (RI) = 83. The resampling analysis presented the same topology when compared to the equal weighing tree (the tree with the support values are presented in Figure 40; the character matrix is included in the Electronic Supplement S2).

Stenosigma was recovered as a monophyletic group in our analysis. The *Stenosigma* clade is supported in the present study by the following synapomorphies: lateral ocelli closer to each other than to the compound eye (char. 7[0]); dorsal sulcus of mesepisternum punctuated (char. 20[2]); presence of posterior median striation in the propodeum (char. 27[1]); and T1 with an evident preapical fossa (char. 30[1]).

The sister group relationship between *Stenosigma* and *Pararhaphidoglossa* was recovered in the present study. This clade is supported by four synapomorphies: pronotal carina dorsally developed (char. 13[0]); epicnemial carina absent (char. 18[0]); posterior projection in the mesepisternum undeveloped (char. 21[1]); and striation in the metapleura absent (char. 22[1]). The clade formed by the two *Alphamenes* species was recovered as a sister group of (*Stenosigma* + *Pararhaphidoglossa*).

Two distinct clades are recovered within *Stenosigma*: Clade 1 and Clade 2. Clade 1 is supported by one synapomorphy (char. 12[1]) and five homoplasies (chars. 4[1]; 15[1]; 25[1]; 29[1]; and 32[1]) with a high value of support (98). Clade 2 was supported by one synapomorphy (char. 5[1]) and one homoplasy (char. 26[1]) with low value of support (22).

4. Discussion

Stenosigma was recovered as a monophyletic group, corroborating the analysis by Hermes et al. (2014), who sampled only two species for the taxon (*S. allegrum* and

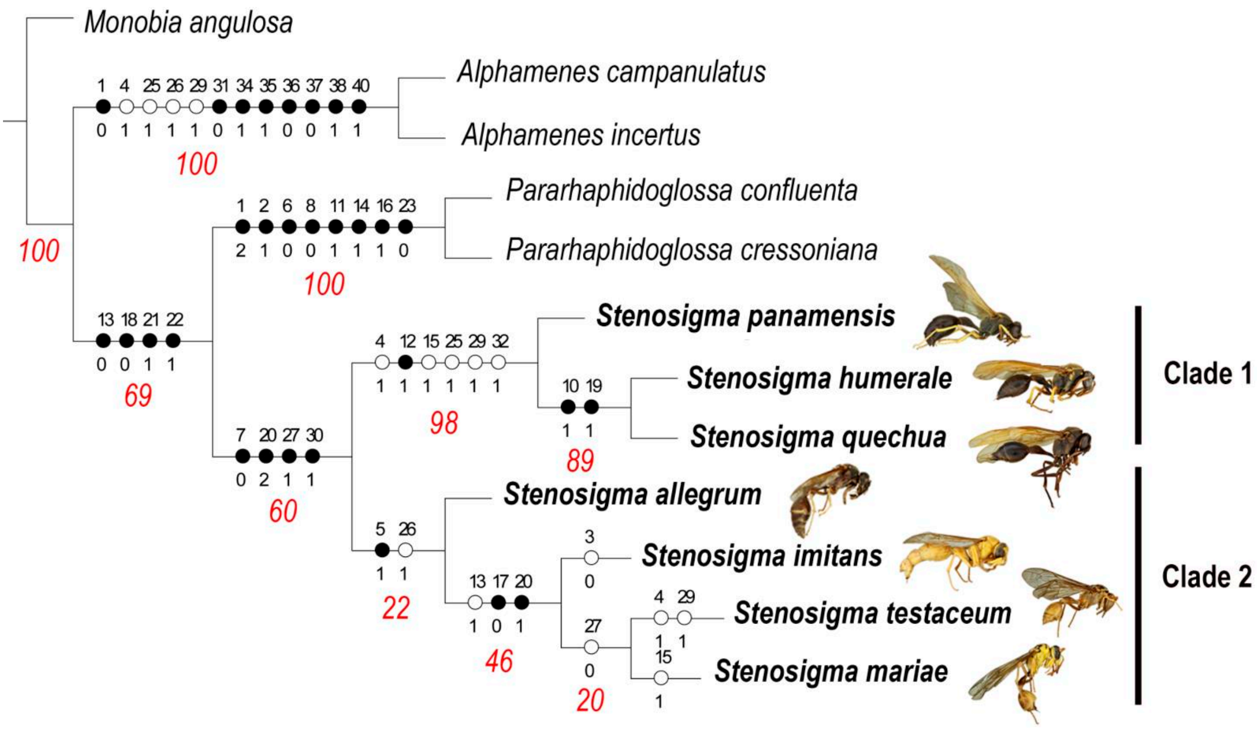


Fig. 40. Most parsimonious tree obtained with equal character weighing, with length (L) = 57; consistency index (CI) = 73; retention index (RI) = 83. Black circles correspond to unique transformations (synapomorphies) and white circles correspond to homoplasies. Support values (symmetric resampling) are given below branches (GC values). Only unambiguous changes are shown.

S. testaceum). Our results only contradict one character proposed by Hermes et al. (2014) – the presence of a developed lamella on T2 apex (ambiguous in the present analysis) and add one new character supporting the genus (char. 20[2]).

The sister group relationship between *Stenosigma* and *Pararhaphidoglossa* was recovered in the present study as well as in the results of Hermes et al. (2014). The two character states that support the monophyly of *Stenosigma* + *Pararhaphidoglossa* in Hermes et al. (2014) are not included in the present study because they are present both in *Alphamenes* and the outgroup *Monobia angulosa*. We suggest that a new analysis including other genera (like the closely related *Pirhosigma* Giordani Soika, 1978) and more species within *Pararhaphidoglossa*, a relatively diverse genus with about 50 species described (Cooper 2016), will better elucidate the validation of the sister group relationship between *Stenosigma* and *Pararhaphidoglossa*.

The clade formed by the two *Alphamenes* species was recovered as the sister group of *Stenosigma* + *Pararhaphidoglossa*. *Alphamenes* is a group with significant accumulation of autapomorphies, mainly related to the morphology of the male genitalia as already discussed in other studies (Oliveira et al. 2017, 2019; Hermes & Oliveira 2016). This genus represents an example of the diverse morphology of Eumeninae given the unique attributes found in the same character complexes. At the same time, *Alphamenes* is a good example of the morphological uniformity in a single genus, when considering the undistinguishable females of some species (Oliveira et al. 2017, 2019). In contrast, in *Stenosigma* we observed greater uniformity of male genitalia and a more variable female morphology.

Two distinct clades are recovered within *Stenosigma*: Clade 1 and Clade 2. In Clade 1, the recently described species *S. panamensis* (Ferreira et al. 2018) is the sister group of *S. humerale* + *S. quechua*. It is important to note that aspects of *S. panamensis* biology, including nesting behavior, have recently been described (Abrego & Santos 2018). The nest architecture reported by Abrego & Santos (2018) is interesting because of a supposed camouflage strategy: the rounded nest has protuberances on its surface that resemble the rough texture of the wall on which it was found (Abrego & Santos 2018, p. 493). Unfortunately, reports for the biology of Eumeninae species of the Neotropical region are quite scarce and there are no records in the literature for the other species of *Stenosigma* (Abrego & Santos 2018). Future studies focused on investigating these aspects of nest building and architecture would be interesting for proposing scenarios on the evolution of the nesting behavior within the genus.

The clade *S. humerale* + *S. quechua* was already expected given that these species present unique attributes related with tegument sculpture (e.g. punctures in the pronotum and mesepisternum are more spaced and deeper) (Ferreira et al. 2018; Hermes & Ferreira 2016). Also, the description of *S. quechua* was made based on the type material of *S. humerale* (Hermes & Ferreira 2016) undoing the taxonomic conflation of Giordani Soika (1990) due the morphological similarity between these species.

In Clade 2, *S. allegrum* emerges as the sister group of the clade formed by *S. imitans* + (*S. testaceum* + *S. mariae*). *Stenosigma allegrum* is a species with features intermediate between the species of Clade 1 and the other species of Clade 2. The postulated phylogenetic proximity between *S. humerale* and *S. allegrum* pointed out by Giordani Soika (1990, p. 155) is mainly due to the presence of plesiomorphic characters for the genus in these species and a well-demarcated melanic color, unlike the other species of *Stenosigma* described at the time (*S. imitans* and *S. testaceum*).

The close morphological proximity between *S. imitans* and *S. testaceum* was suggested and discussed by Giordani Soika (1990). The recently described *S. mariae* (Ferreira et al. 2018) is very similar morphologically to *S. testaceum* and *S. imitans*. However, as demonstrated by Ferreira et al. (2018), *S. imitans* in both sexes (contrary to Giordani Soika 1990) presents a shorter clypeus (wider than long – char. 2[1]), an autapomorphy within *Stenosigma*.

Interestingly, Clade 1 included only the *Stenosigma* species with a black body color with few yellow marks (*S. panamensis* + (*S. humerale* + *S. quechua*)). Additionally, the species in this clade are distributed in a possible biogeographical pattern: *S. humerale* and *S. quechua* have records for Bolivia, Peru and Colombia (Ferreira et al. 2018) in South America; and *S. panamensis* (as the epithet suggests) is endemic to Panama (Ferreira et al. 2018). Further studies with a larger sample and a biogeographic approach will be able to better clarify if the phylogenetic pattern found corresponds to the implied biogeographic pattern.

Clade 2 has *S. allegrum* as sister to *S. imitans* + (*S. testaceum* + *S. mariae*). *Stenosigma allegrum* has a characteristic brownish body color and is restricted to southeast and south Brazil (Ferreira et al. 2018). On the other hand, the species *S. imitans*, *S. testaceum* and *S. mariae* have a distinct yellowish body color and the geographical distribution these species are is associated with the Amazonian rainforest (Ferreira et al. 2018). It is likely that a new survey in central Brazil may find new species of *Stenosigma* that fill the gap that exists in the distribution of the genus given the disjunct distribution presented by the species in this clade.

5. Conclusions

This study presents the first phylogenetic hypothesis to include all currently described species of *Stenosigma*. Also, this is a contribution that complements and expands the results and discussions published in previous papers, especially Hermes & Ferreira (2016) and Ferreira et al. (2018). Through this contribution we tried to fill some of the gaps in our knowledge about this genus, especially considering the connections of geographical distribution and phylogenetic relationships.

We encourage more studies based in the Neotropical fauna and we think that now is a fertile time to explore the potter wasp phylogeny given the significance of the group in the recent discussions about the Vespidae evolutionary history: the hypothesis of the independent origins of eusociality in Vespidae depends on the phylogenetic position of solitary vespid wasps (Piekarski et al. 2018; Bank et al. 2017). With enough sampling, including Neotropical diversity, further studies may provide novel information on the variety of ways that wasps have evolved complex social behaviors.

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File 1: ferreira&hermes-stenosigma-asp2020-electronicsupplement-1.pdf — General remarks: list of specimens examined in the present study.

File 2: ferreira&hermes-stenosigma-asp2020-electronicsupplement-2.pdf — Character matrix for *Stenosigma* Giordani Soika (Hymenoptera, Vespidae, Eumeninae) and related taxa.

Authors' contributions

W.D.F. and M. G. H. have participated in the conception and execution of this study. The two authors contributed equally in the writing and revision of the manuscript.

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