

Key to the New World genera of Euphorinae (Hymenoptera: Ichneumonoidea: Braconidae) and synopses of the genera

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Abstract

This is an updated overview of the New World (Western Hemisphere) members of the subfamily Euphorinae, including Greenland and the Caribbean Islands. It is a revision of the key by Shaw (1997a). It includes a key to the New World genera and a synopsis of each genus. The synopses include the following sections: diagnosis, biology, diversity, distribution, publications, and notes. There are 35 genera in the New World and about twice that number worldwide.

Shaw, S.R. 1997. Subfamily Euphorinae, pp.234-254. In: Wharton, R.A., Marsh, P.M., and Sharkey, M.J. (eds). Manual of the New World Genera of the Family Braconidae (Hymenoptera). Special Publication of the International Society of Hymenopterists, 439 pp.

Accepted April 03 2025

Published online January 30 2026

Introduction

Euphorinae is a large subfamily containing approximately 52 genera, 35 of which are found in the New World. This treatment of the New World genera of Euphorinae is a revision of that by Shaw (1997a) and is part of a comprehensive effort to treat all New World genera of Braconidae. To confirm a subfamily identification, the key by Sharkey et al. (2023) may be used. Readers using that key will be automatically directed here if they obtain an identification of Euphorinae. The present work includes a key to the New World genera and a synopsis of each genus. The synopses include the following sections: diagnosis, biology, diversity, distribution, publications, and notes. All images are by Sharkey unless noted otherwise. General morphological terminology can be found in Sharkey et al. (2023). More detailed information is in the morphology chapter of the New World manual (Sharkey and Wharton, 1997) and in the Hymenoptera Anatomy Ontology Portal (<http://portal.hymao.org/projects/32/public/ontology/>).

Overview of the subfamily

Phylogeny

Molecular phylogenetic analyses by Belshaw and Quicke (2002), Sharanowski et al. (2011), and Stigenberg et al. (2015) concluded that neoneurines are nested inside Euphorinae, corroborating the conclusion that the

neoneurines should be classified as a tribe in Euphorinae. Even before these publications, Belokobylskij (2000a) placed the neoneurines in the subfamily Euphorinae. Gómez, Durán and van Achterberg (2011) also adopted this placement. Stigenberg et al. (2015) conducted a phylogenetic analysis of the entire subfamily and placed genera in 14 tribes.

Biology

Euphorines are primarily solitary or (more rarely) gregarious koinobiont endoparasitoids of adult insects including Coleoptera, Lepidoptera, Hymenoptera, Diptera, Neuroptera, and perhaps Dermaptera, as well as of nymphal and adult Heteroptera and Psocodea. Some of the parasitoids that attack Coleoptera can also be larval parasitoids or attack the larval or pupal stage and emerge from the adult (details under the respective generic treatments). The members of Meteorini are endoparasitoids of larval Lepidoptera and Coleoptera. Euphorinae has a host range that is substantially broader than other braconid subfamilies. More information on euphorine biology is provided in Shaw and Huddleston (1991). Stigenberg et al. (2015) elucidated the evolution of host associations and summarized the host data for all tribes.

Common genera

Leiophron, *Meteorus*, and *Microctonus*.

Distribution

Cosmopolitan.

Distinguishing features

Euphorinae is morphologically diverse and difficult to diagnose. No members have crossvein 2cu-a in the forewing, however this absence is widespread in Braconidae. The first metasomal segment is usually constricted, at least basally. Eyes are often situated low on the face relative to other braconids. The second submarginal cell in the forewing is open (not closed by the r-m crossvein) in most members (however see key below), and in those with an open second submarginal cell the RS vein often curves towards the anterior margin and ends well before the wing apex. No members have a metasomal carapace and many genera have unique forewing venation.

Note. In the generic treatments we give rough estimates of the number of undescribed species that may occur in the New world, e.g., for *Centistes*, “There are 26 BINs (proxies for species) in the Barcode of Life Data System (BOLD) from Costa Rica (Oct. 13, 2024, <https://www.boldsystems.org>), suggesting that there are more than 200 hundred Neotropical species”. To arrive at these very conservative numbers we used estimates of the number of trees in Costa Rica compared to the remainder of the New World. Cazzolla Gatti et al. (2022) estimated there to be 40,123 species of trees in the New World. Nelson Zamora (personal communication), the leading Costa Rican botanist, estimates there to be 2,500 species of trees in Costa Rica, or ~6.2% of the New World fauna. Over the last ten years Dan Janzen, Winnie Hallwachs and their team have barcoded Malaise trap samples from all over Costa Rica, making it one of the best sampled countries in the Barcode of Live Data System, though it is far from complete. In the example above, if we were to assume that the 26 BINs represented 6.2% of the New World fauna we would arrive at an estimate of 419 species for the New World. However, we refrain from this detailed estimate and instead make the generalized and

conservative estimate of, “more than 200 Neotropical species

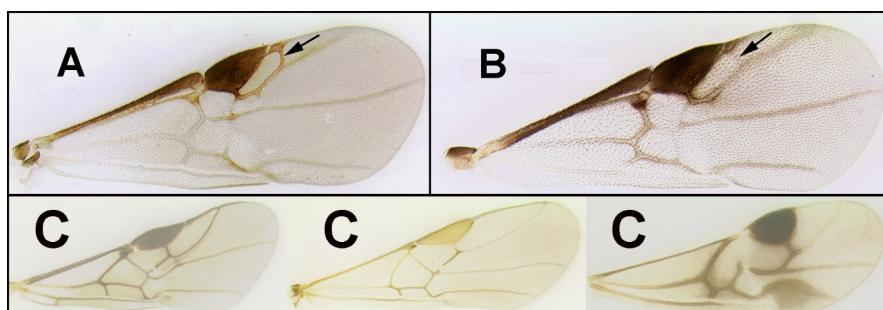
Table 1. List of New World genera of Euphorinae.

<i>Allurus</i> Foerster, 1863
<i>Aridelus</i> Marshall, 1887
<i>Betelgeuse</i> Shaw, 1989
<i>Bracteodes</i> de Saeger, 1946
<i>Centistes</i> Haliday, 1835
<i>Centistina</i> Enderlein, 1912
<i>Centistoides</i> van Achterberg, 1992
<i>Chrysopophthorus</i> Goidanich, 1948
<i>Cosmophorus</i> Ratzburg, 1848
<i>Cryptoxilos</i> Viereck, 1911
<i>Dinocampus</i> Foerster, 1863
<i>Ecclitura</i> Kokujev, 1902
<i>Elasmosoma</i> Ruthe, 1858
<i>Holdawayella</i> Loan, 1967
<i>Leiophron</i> Nees, 1816
<i>Litostolus</i> van Achterberg, 1985
<i>Marshiella</i> Shaw, 1985
<i>Meteorus</i> Haliday, 1835
<i>Microctonus</i> Wesmael, 1835
<i>Myiocephalus</i> Marshall, 1898
<i>Neoneurus</i> Haliday, 1838
<i>Orionis</i> Shaw, 1987
<i>Perilitus</i> Nees, 1819
<i>Peristenus</i> Foerster, 1863
<i>Plynops</i> Shaw, 1996
<i>Pygostolus</i> Haliday, 1833
<i>Ropalophorus</i> Curtis, 1837
<i>Spathicopis</i> van Achterberg, 1977
<i>Streblocera</i> Westwood, 1833
<i>Syntretus</i> Foerster, 1863
<i>Townesilitus</i> Haeselbarth and Loan, 1983
<i>Wesmaelia</i> Foerster, 1863
<i>Yanayacu</i> Zhang and Chen, 2015
<i>Zele</i> Curtis, 1832

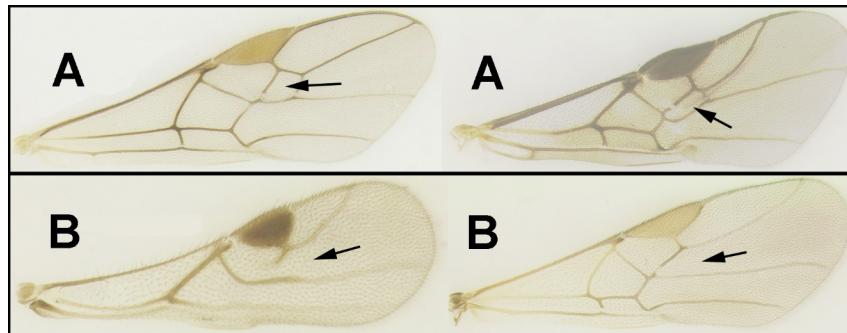
Key to the New World genera of Euphorinae

Clicking the hyperlinked text in the key below will take the reader to the corresponding couplet or genus synopsis.

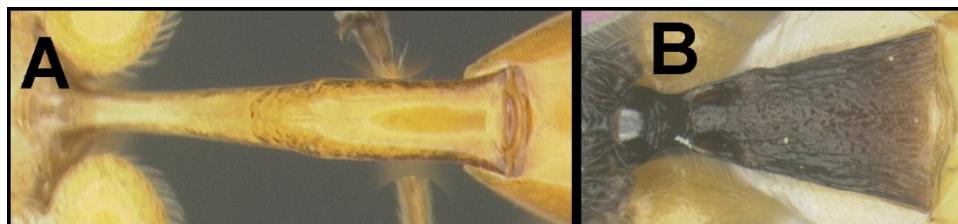
1. A. Forewing venation unique as in image, with a distinct split in vein RS. Nearctic. [***Neoneurus***](#)
- B. Forewing venation unique as in image, with a hint of a split in vein RS. Nearctic. [***Elasmosoma***](#)
- C. Forewing venation of many other designs, lacking any sign of a split in vein RS. Nearctic and Neotropical. [2](#)



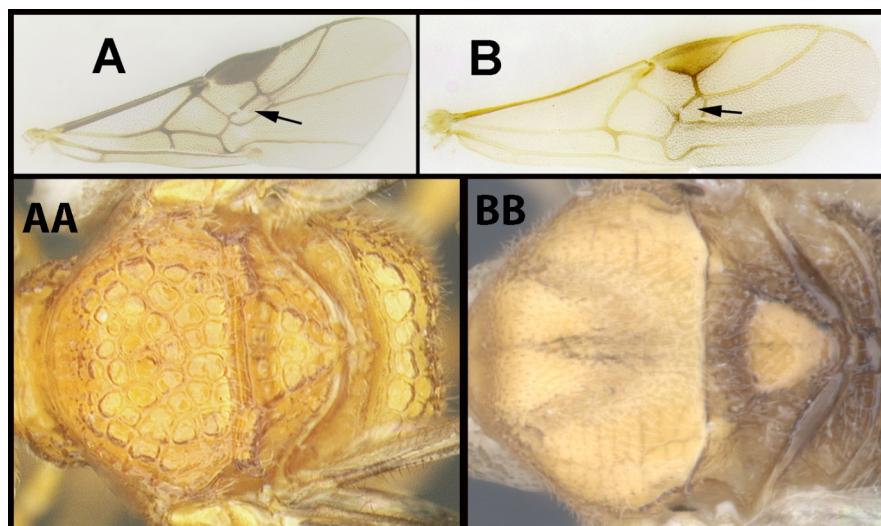
- 2(1). A. Forewing second submarginal cell closed distally..... 3
 B. Forewing second submarginal cell open, not closed or only partially closed distally..... 6



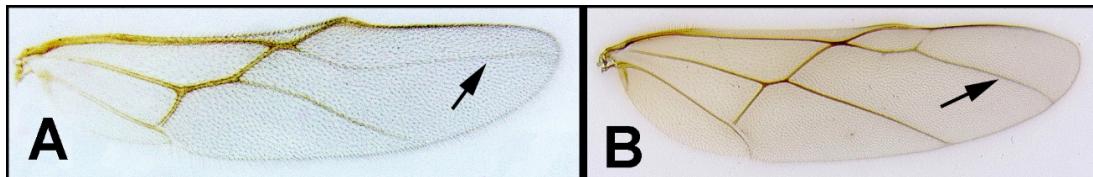
- 3(2). A. First metasomal segment much longer than wide and not more than 2x wider apically than basally..... 4
 B. First metasomal segment not so narrow and usually more than 2x wider apically than basally..... 5



- 4(3). A. Second submarginal cell wider than high, not triangular, and usually 5-sided. AA. Mesoscutum with large areolae..... *Aridelus*
 B. Second submarginal cell not wider than high, triangular or almost so, and 3- or 4-sided. BB. Mesoscutum with finer sculpture..... *Chrysopophthorus*



- 5(3). A. Hind wing vein RS bending towards anterior wing margin..... [Meteorus](#)
 B. Hind wing vein RS bending away from anterior wing margin..... [Zele](#)



- 6(2). A. Propodeum with projections laterally. Neotropical..... [7](#)
 B. Propodeum lacking projections laterally, rather rounded or flat. Widespread..... [8](#)



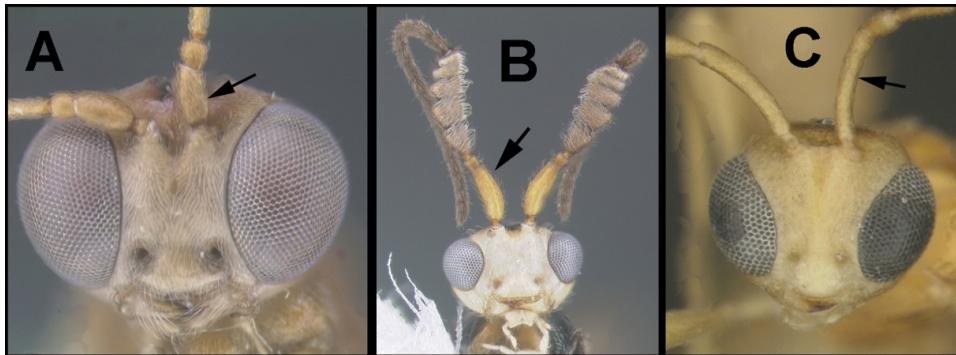
- 7(6). A. Face less rugose (image modified from Shaw 2012)..... [Yanayacu](#)
 B. Face more rugose..... [Betelgeuse](#)



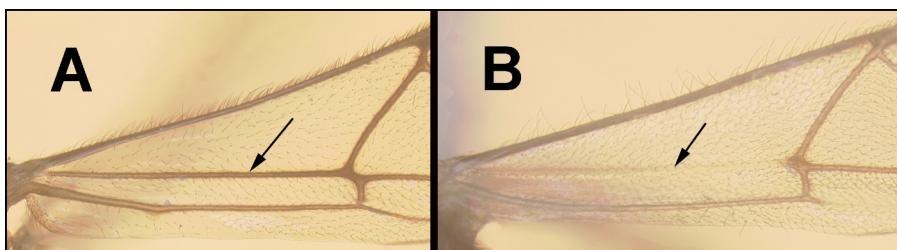
- 8(6). A. (RS+M)a vein of forewing absent..... [9](#)
 B. (RS+M)a vein of forewing present, rarely reduced in basal half or more, but always present apically..... [20](#)



- 9(8). A. Scape length less than 2.5 times scape width. Very common..... [10](#)
 B. Scape length 3-3.5 times scape width; female with setose pads on underside of basal flagellomeres. Males lack flagellar modifications but have similar dimensions of the scape. Rare..... [*Marshiella*](#)
 C. Scape length more than 4 times scape width. Rare..... [19](#)



- 10(9). A. Forewing vein M+Cu complete and mostly or entirely tubular..... [11](#)
 B. Forewing vein M+Cu reduced, mostly or entirely not tubular, or absent..... [13](#)



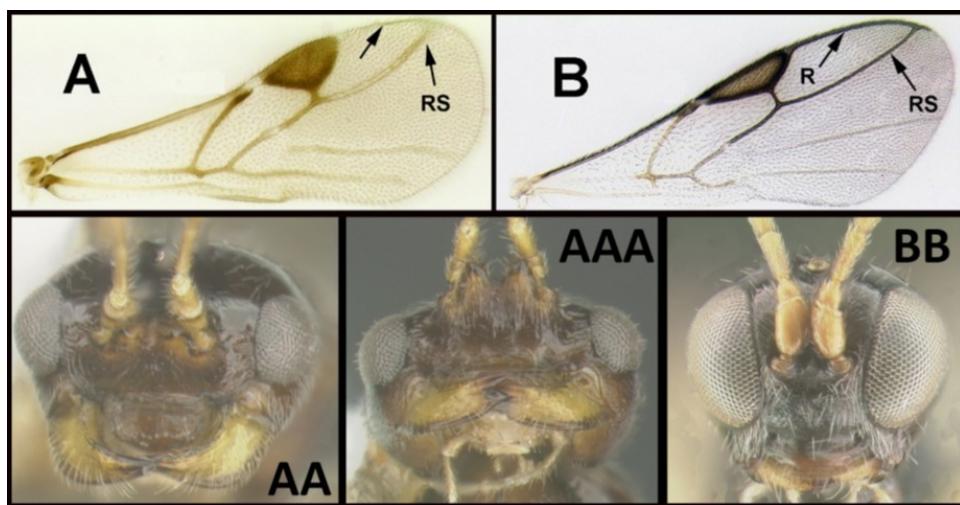
- 11(10). A. First metasomal segment greatly constricted basally and lacking pair of dorsal pits. Widespread. Common...
 [12](#)
 B. First metasomal segment slightly constricted basally and with pair of large dorsal pits. Nearctic. Rare..... [*Spathicopis*](#)



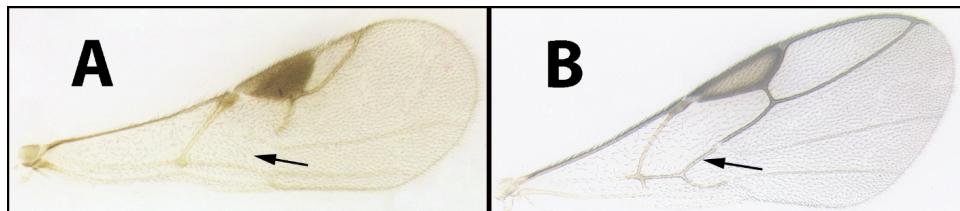
- 12(11). A. Propodeum entirely and evenly areolate-rugose, lacking a large pentagonal cell posteromedially and lacking more pronounced carinae.....*[Microctonus](#)*
 B. Propodeum, with a large pentagonal cell posteromedially and with some carinae more pronounced than others delimiting large cells.....*[Townesilitus](#)*



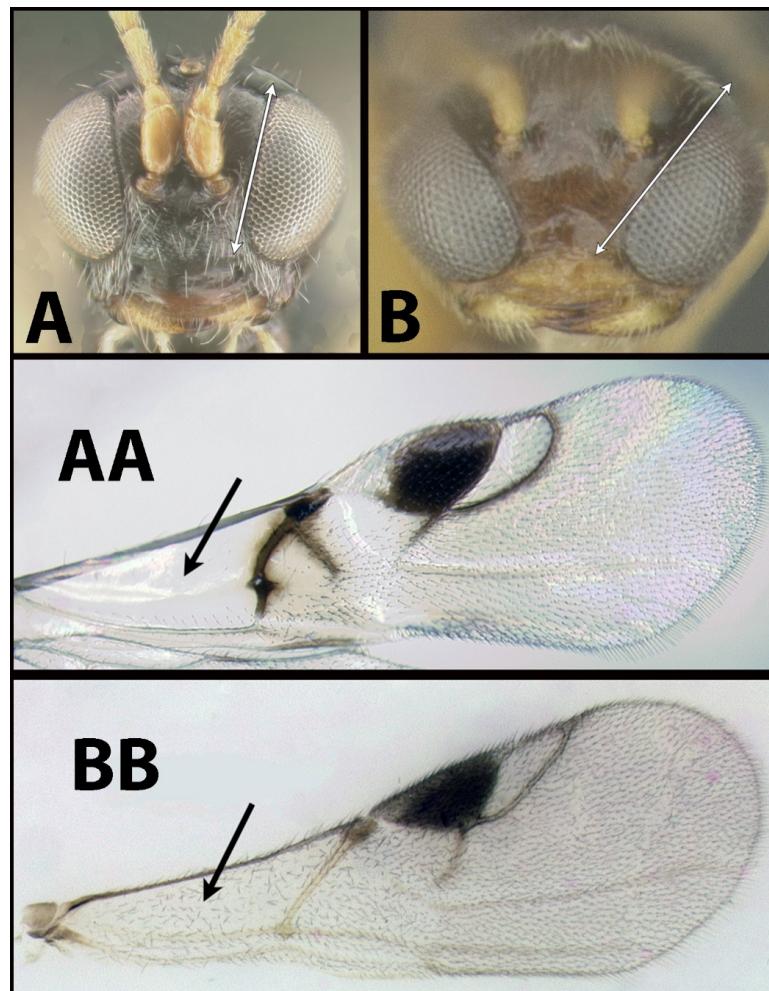
- 13(10). A. Forewing vein R absent distal to stigma. Forewing vein RS not complete to wing margin. AA. Mandibles massive. AAA. Antennae positioned on protuberances.....*[Cosmophorus](#)*
 B. Forewing vein R present distal to stigma. Forewing vein RS complete to wing margin. BB. Mandibles of normal dimensions. BBB. Antennae not positioned on protuberances.....*[14](#)*



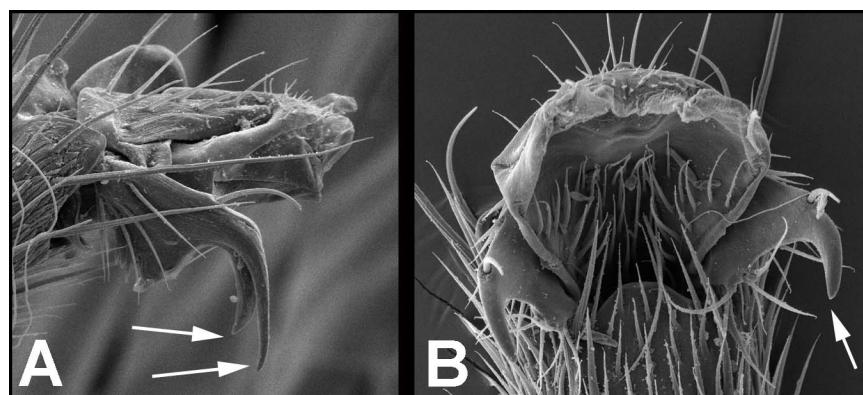
- 14(13). A. Forewing crossvein m-cu absent.*[15](#)*
 B. Forewing crossvein m-cu present.*[16](#)*



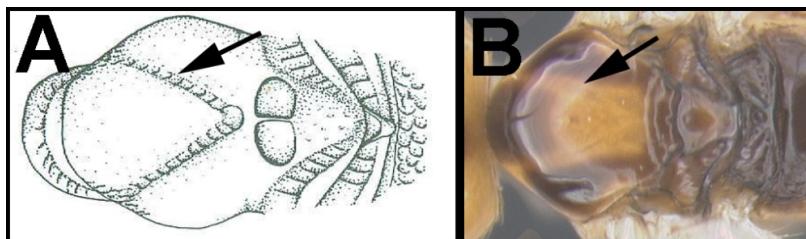
- 15(14). A. Face wide ventrally, eyes slightly converging, inner orbit of eye almost vertical. AA. Basal cell of forewing variable, but often glabrous. Common..... *Leiaphron* (in part)
 B. Face narrow ventrally, eyes converging ventrally, inner orbit of eye on a 45-degree angle. BB. Basal cell of forewing setose. Rare..... *Cryptoxilos* (in part)



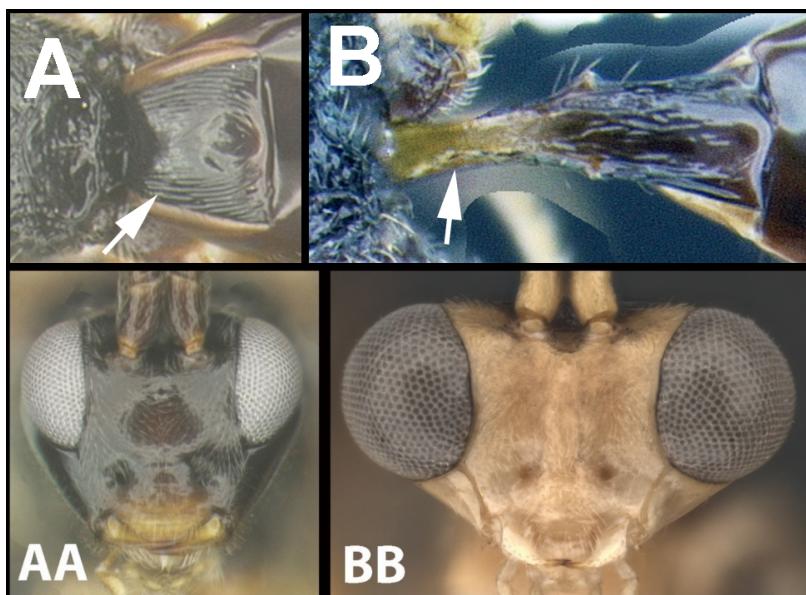
- 16(14). A. Tarsal claws cleft. First metasomal tergum and sternum completely fused throughout entire length..... [17](#)
 B. Tarsal claws simple. First metasomal tergum and sternum not fused..... [18](#)



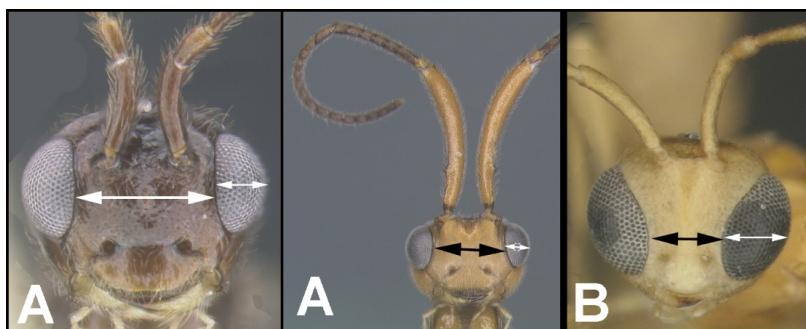
- 17(16). A. Notauli present and distinct (Image by van Achterberg). Rare. [*Bracteodes*](#)
 B. Notauli absent. Relatively common. [*Syntretus*](#)



- 18(16). A. First metasomal segment slightly narrowed basally. AA. Head about as wide as high in anterior view. [*Centistes*](#) (in part)
 B. First metasomal segment greatly narrowed basally. BB. Head much wider than high in anterior view. [*Myiocephalus*](#)



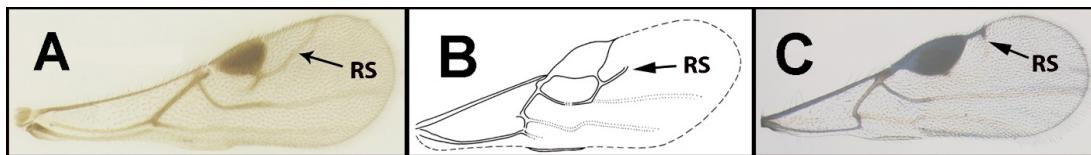
- 19(9). A. Shortest distance between eyes much longer than eye width in anterior view. Neotropical. Rare. [*Streblocera*](#)
 B. Shortest distance between eyes shorter than eye width in anterior view. Widespread. Rare. [*Ecclitura*](#)



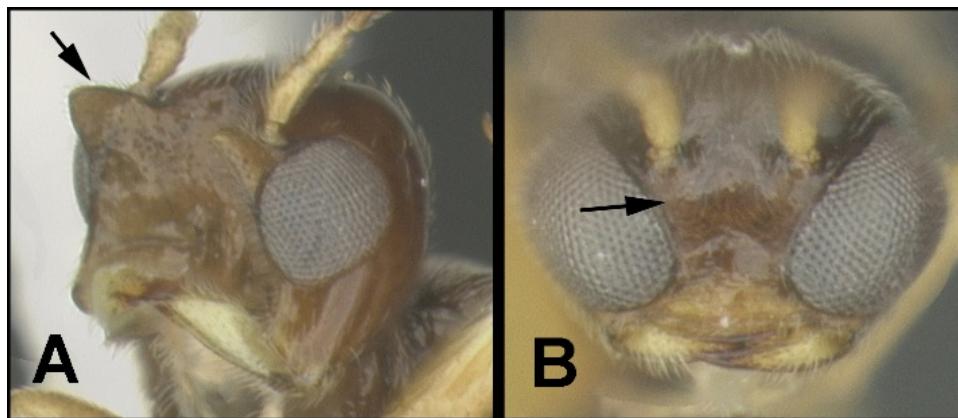
- 20(8). A. Forewing crossvein m-cu reduced or absent. [21](#)
 B. Forewing crossvein m-cu complete. [24](#)



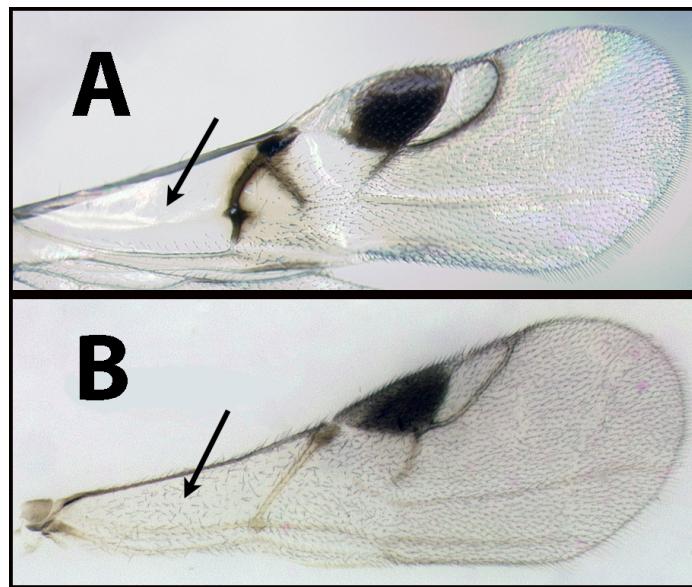
- 21(20). A. Forewing vein RS complete or almost complete to wing margin. Common. [22](#)
 B. Forewing vein RS reduced and less than ½ distance to wing margin (image modified from Shaw 1997a).
 Rare. [*Holdawayella*](#)
 C. Forewing vein RS absent except as a small stub distally. Common. [*Leiophron*](#) (subgenus *Euphoriella*)



- 22(21). A. Face with projections below antennae. Mandibles large and widely spaced. Rare. [*Plynops*](#)
 B. Face without projections below antennae. Mandibles normal. Common. [23](#)



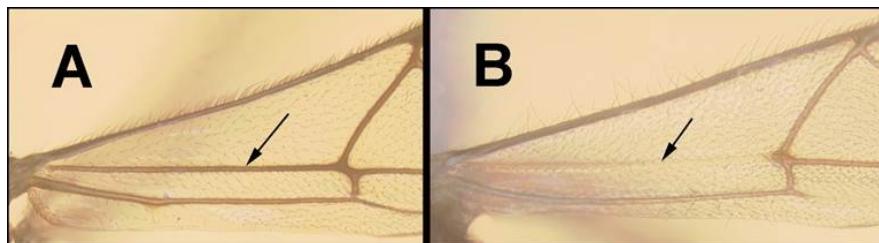
- 23([22](#)). A. Basal cell of forewing mostly glabrous. Common *[Leiophron](#)* (in part)
 B. Basal cell of forewing mostly setose. Rare *[Cryptoxilos](#)* (in part)



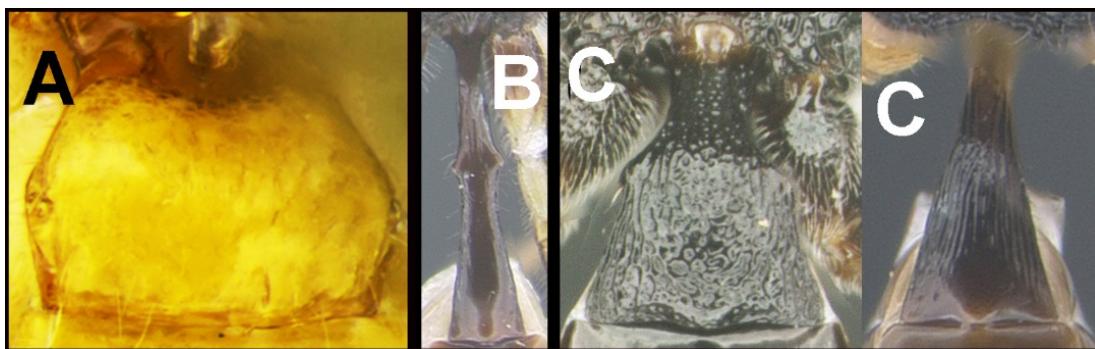
- 24([20](#)). A. Antenna short with 7-9 flagellomeres. Nearctic. Rare *[Ropalophorus](#)*
 B. Antenna longer with many more than 9 flagellomeres. Widespread. Relatively common [25](#)



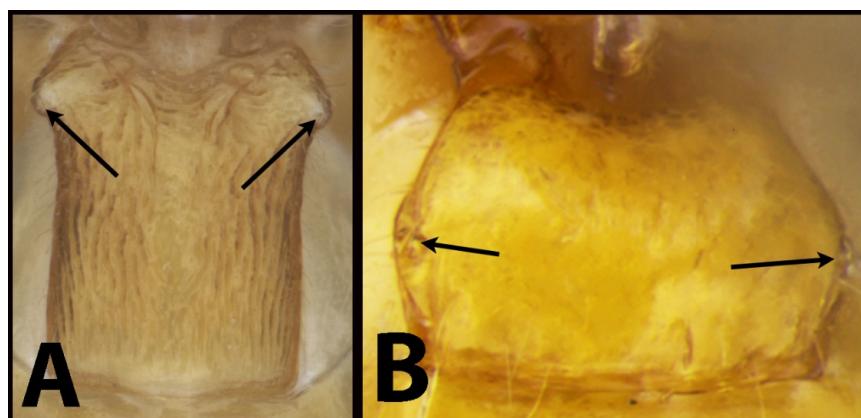
- 25([24](#)). A. Forewing vein M+Cu complete and tubular [26](#)
 B. Forewing vein M+Cu reduced, not tubular for most of its length [30](#)



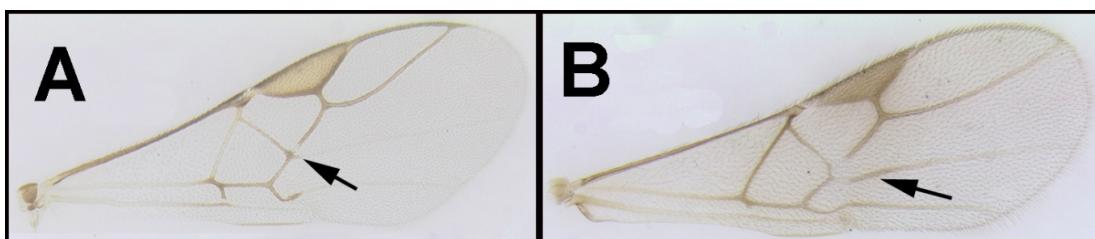
- 26(25). A. First metasomal tergum wide, almost as wide basally as apically (image modified from de Almeida and Penteado-Dias 2018). Widespread. Rare 27
 B. First metasomal tergum much narrower at base than apex, tergum long and thin. Neotropical. Rare *Orionis*
 C. First metasomal tergum, narrower at base than apex, but not nearly as long and thin as in B. Widespread. Common 28



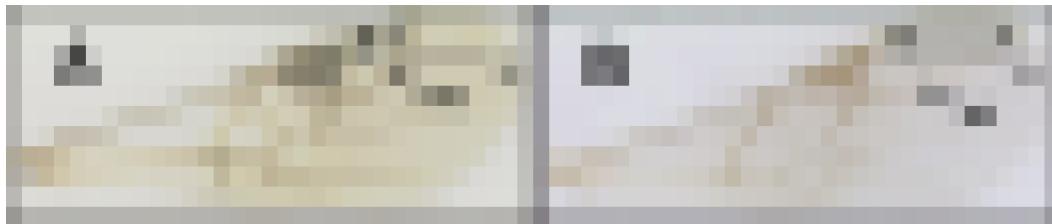
- 27(26). A. First metasomal tergum with straight sides with spiracles situated basally on small prominences. Widespread. Rare *Pygostolus* (in part)
 B. First metasomal tergum with rounded sides with spiracles situated posterior to mid-length (image modified from de Almeida and Penteado-Dias 2018). Neotropical. Rare *Centistoides*



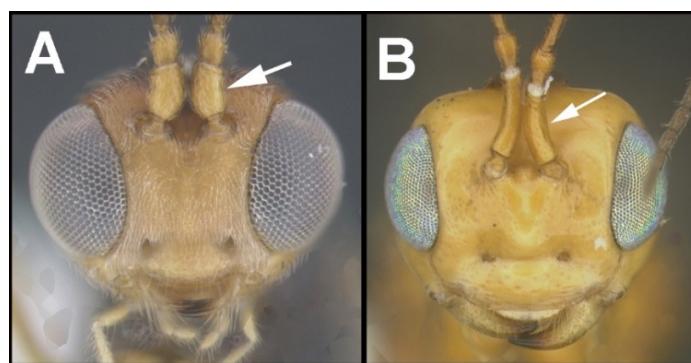
- 28(26). A. Forewing vein 2M reduced to a small stub *Perilitus*
 B. Forewing vein 2M longer 29



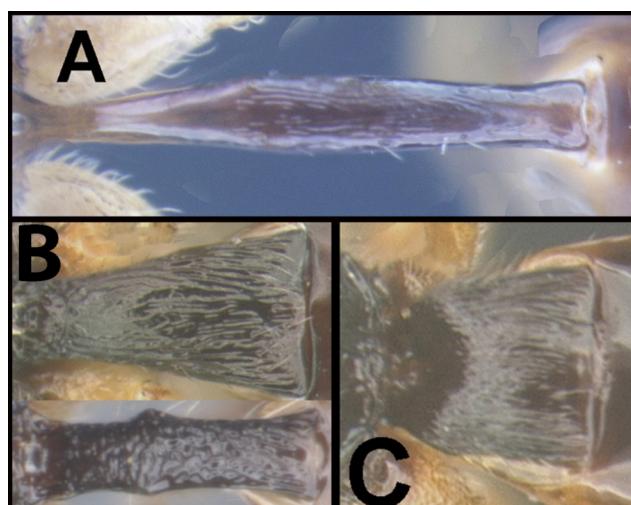
- 29(28). A. Distance from stigma to apex of RS much less than half distance from stigma to apex of wing, i.e., RS ending far from wing margin..... [*Dinocampus*](#)
 B. Distance from stigma to RS much greater than half distance from stigma to apex of wing, i.e., RS ending near wing margin..... [*Litostolus*](#)



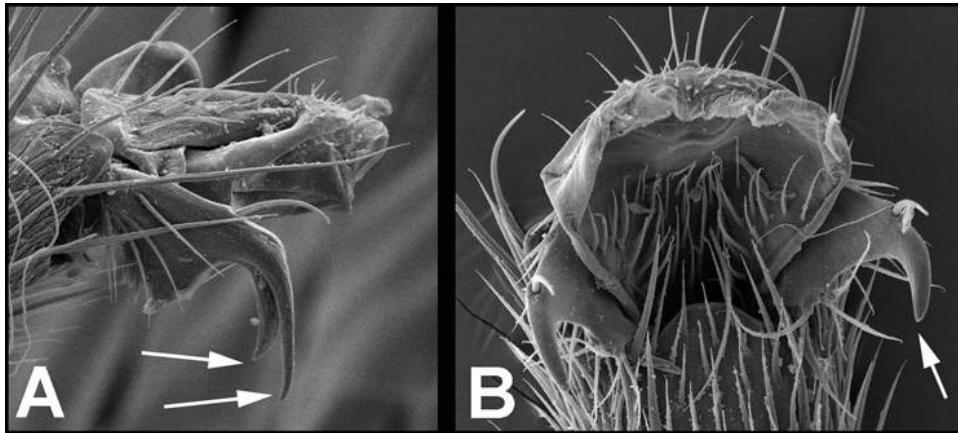
- 30(25). A. Scape length less than 2 times scape width..... [**31**](#)
 B. Scape length more than 3 times scape width..... [*Centistina*](#)



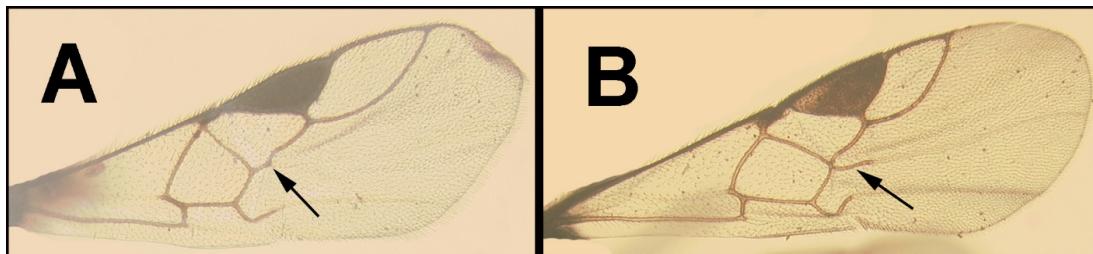
- 31(30). A. First metasomal segment narrow along entire length, and more than 6 times wider than long, exceptionally long and thin. Rare..... [*Wesmaelia*](#)
 B. First metasomal segment constricted near base or tube-like and less than 4 times longer than apical width. Common..... [**34**](#)
 C. First metasomal segment slightly constricted near base, as wide near base as it is apically or almost so. Common..... [**32**](#)



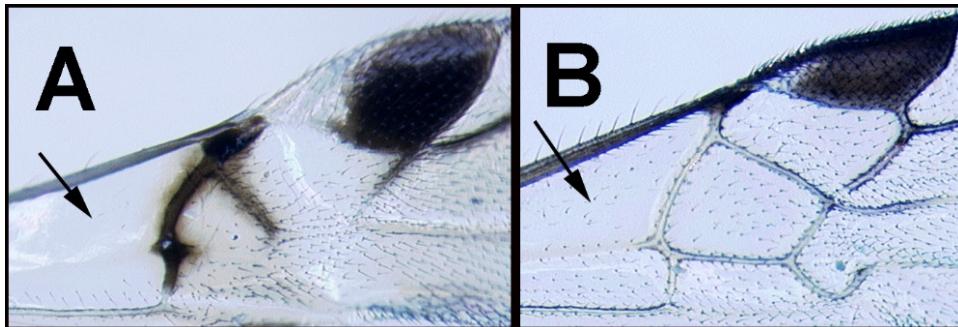
- 32(31). A. Tarsal claws cleft. Nearctic. Rare *Allurus*
 B. Tarsal claws simple. Widespread. Common [33](#)



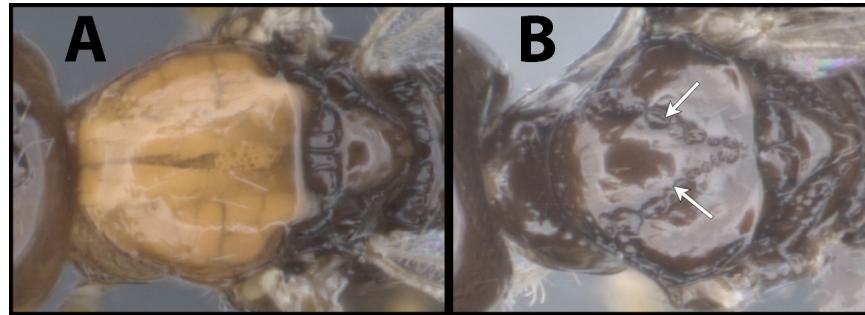
- 33(32). A. Forewing 2M desclerotized and reduced to only a short stub or absent. Common *Centistes*
 B. Forewing 2M sclerotized and present as a short but distinct branch. Rare *Pygostolus* (in part)



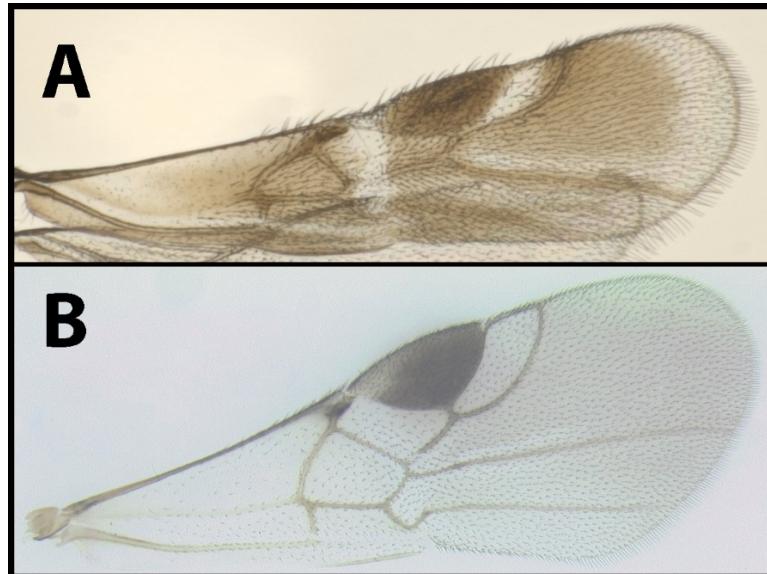
- 34(33). A. Basal area of forewing glabrous (lacking setae) or almost so. *Leiophron* (in part)
 B. Basal area of forewing setose. [35](#)



- 35(34). A. Notauli lacking or restricted to anterior margin of mesoscutum. *Leiophron* (in part)
 B. Notauli present and complete to posterior margin of mesoscutum..... [36](#)



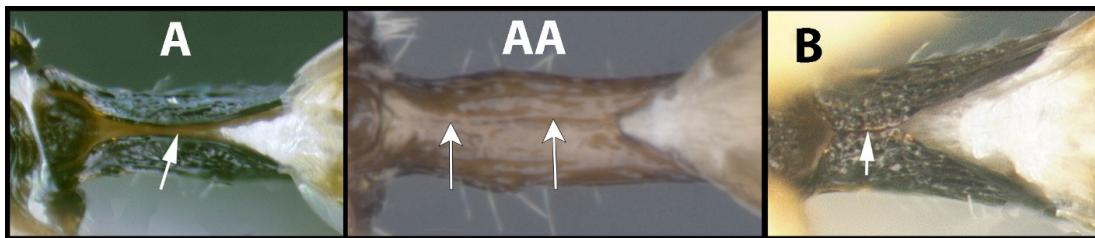
- 36(35). A. Forewing patterned with infuscate areas. *Leiophron* (in part)
 B. Forewing clear, or weakly and evenly infuscate, or slightly darkening apically. [37](#)



- 37(36). A. First metasomal tergum tubular, not or only slightly wider posteriorly. *Leiophron* (in part)
 B. First metasomal tergum, distinctly wider apically than basally. [38](#)



- 38(37). A. First metasomal tergum not fused ventrally, OR AA. fused or touching along most of its length.....
 *Leiophron* (in part)
 B. First metasomal tergum fused or touching ventrally in anterior portion only. *Peristenus*



Generic treatments

Allurus Foerster, 1863

Fig. 1

Diagnosis. Tarsal claws cleft (couplet 15A). Forewing vein 3RS complete to wing margin (Fig. 1B). Forewing vein M+Cu reduced, not tubular for most of its length (Fig. 1B). (RS+M)a vein of forewing present (Fig. 1B). First metasomal tergum (T1) not greatly narrowed basally, i.e., widely attached to propodeum (Fig. 1D).

Biology. Parasitoids of adult Curculionidae (Jackson 1920; Aeschlimann 1980).

Diversity. There are three species described, one of which occurs in the Nearctic. There are likely a few undescribed species.

Distribution. Holarctic and Oriental realms.

Publications. Stigenberg and van Achterberg (2016) reviewed the genus.

Aridelus Marshall, 1887

Fig. 2

Diagnosis. Shape of second submarginal cell (SSC) of forewing unique (Fig. 2C). Mesosoma covered with coarse honey-combed, areolate sculpture (Figs 2B, E). First metasomal segment narrow and elongate (Fig. 2E).

Biology. Parasitoids of late instar nymphs and adults of Pentatomidae.

Diversity. About 50 species are described worldwide, three Nearctic, and one Neotropical. Many more are undescribed. Presently there are 11 BINs (proxies for species) from Costa Rica on BOLD (Oct. 21, 2024) suggesting that there are around 100 Neotropical species.

Distribution. Cosmopolitan, in the New World from Canada to Argentina.

Publications. Papp (1965) provided a key to species.

Betelgeuse Shaw, 1989

Fig. 3

Diagnosis. Mesosoma and head entirely coarsely rugose to rugose-punctate (Figs 3A, B, D). Basal flagellomeres of female antenna serrate along outer margin. Flagellum with 13 flagellomeres. Scape (SC) about 5x longer than

wide (Fig. 3D). Basal flagellomere (F) about 8 times longer than wide (Fig. 3D). Forewing venation unique (Fig. 3E). Male unknown.

Biology. Unknown.

Diversity. Three described species, perhaps several more undescribed.

Distribution. Neotropical (Mexico).

Publications. Shaw (1989) erected the genus and Shaw (2002) added two species and provided a key to species.

Bracteodes de Saeger, 1946

Fig. 4

Diagnosis. Notauli present and distinct (Fig. 4D). Tarsal claws cleft (couplet 32A). Forewing vein M+Cu reduced, mostly or entirely not tubular (Fig. 4C). (RS+M)a vein of forewing absent (Fig. 4C). Scape (SC) length is less than 2.5 times width (Fig. 4B).

Biology. The Asian species *B. ceranae* is a parasitoid of the Asian honeybee, *Apis cerana* Fabricius (You and Zhou, 1991).

Diversity. Two described species one from Africa and the other from China. Shaw reported an undescribed species from the southwestern USA and Mexico in the Euphorinae chapter in the Manual of New World Braconidae (Shaw, 1997a). There is a Costa Rican specimen and a Colombian specimen (Fig. 4) in the Hymenoptera Institute collection.

Distribution. Afrotropical, Oriental, Nearctic, Neotropical (southwestern USA to Colombia).

Publications. None of interest to the New World fauna except the details mentioned in Shaw (1997a).

Centistes Haliday, 1835

Fig. 5

Diagnosis. First metasomal segment not greatly narrowed basally (Fig. 5C). Tarsal claws simple. Forewing vein M+Cu reduced, mostly or entirely not tubular (Figs 5D, E). Vein M absent as a tubular vein or tubular portion present as a very short stub (Figs 5D, E). Vein (RS+M)a variable, usually complete but varying from complete (Fig. 5D), to present as a stub apically (Fig. 5E), to completely absent.

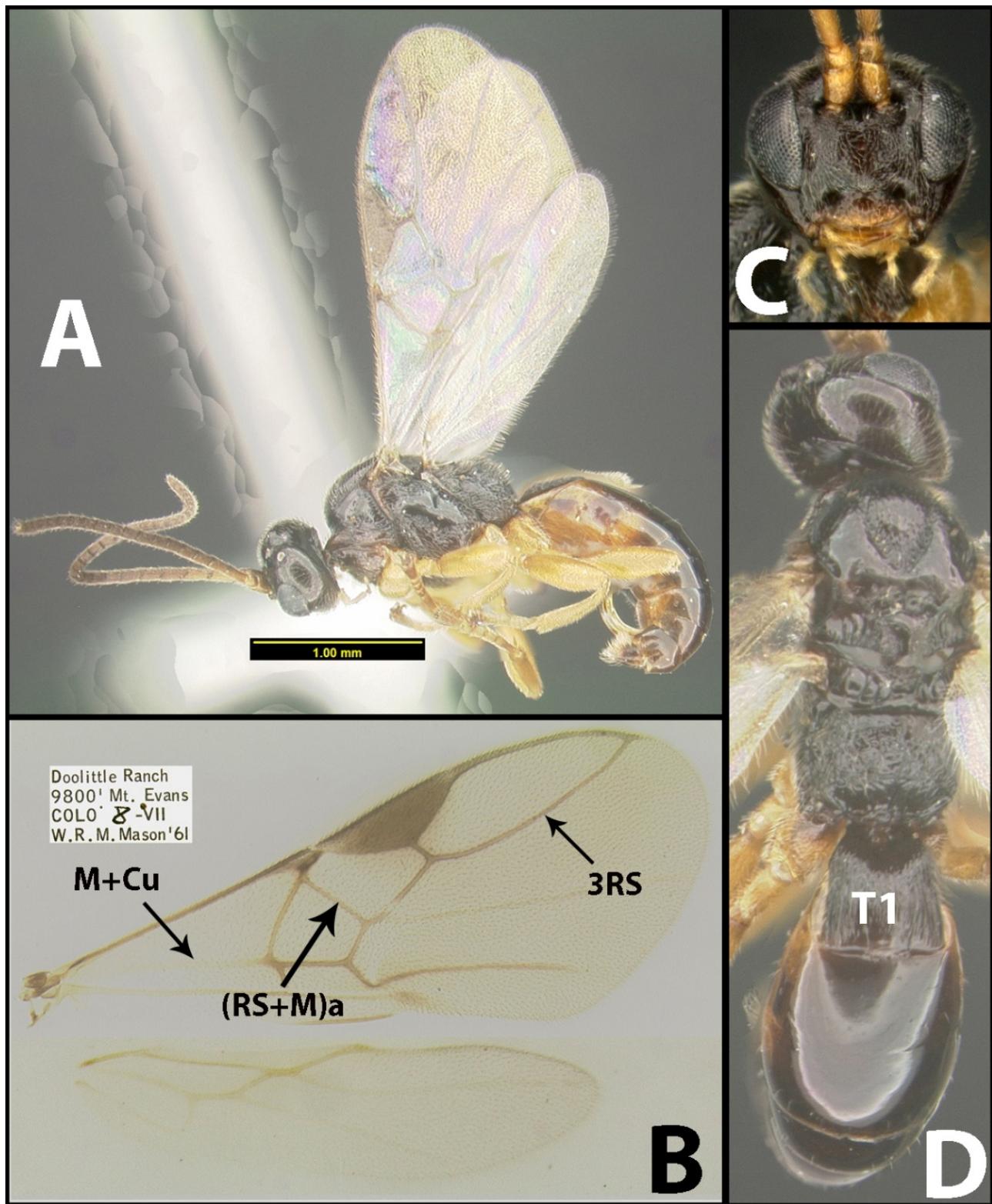


Figure 1. *Allurus* sp. nr. *A. muricatus*.

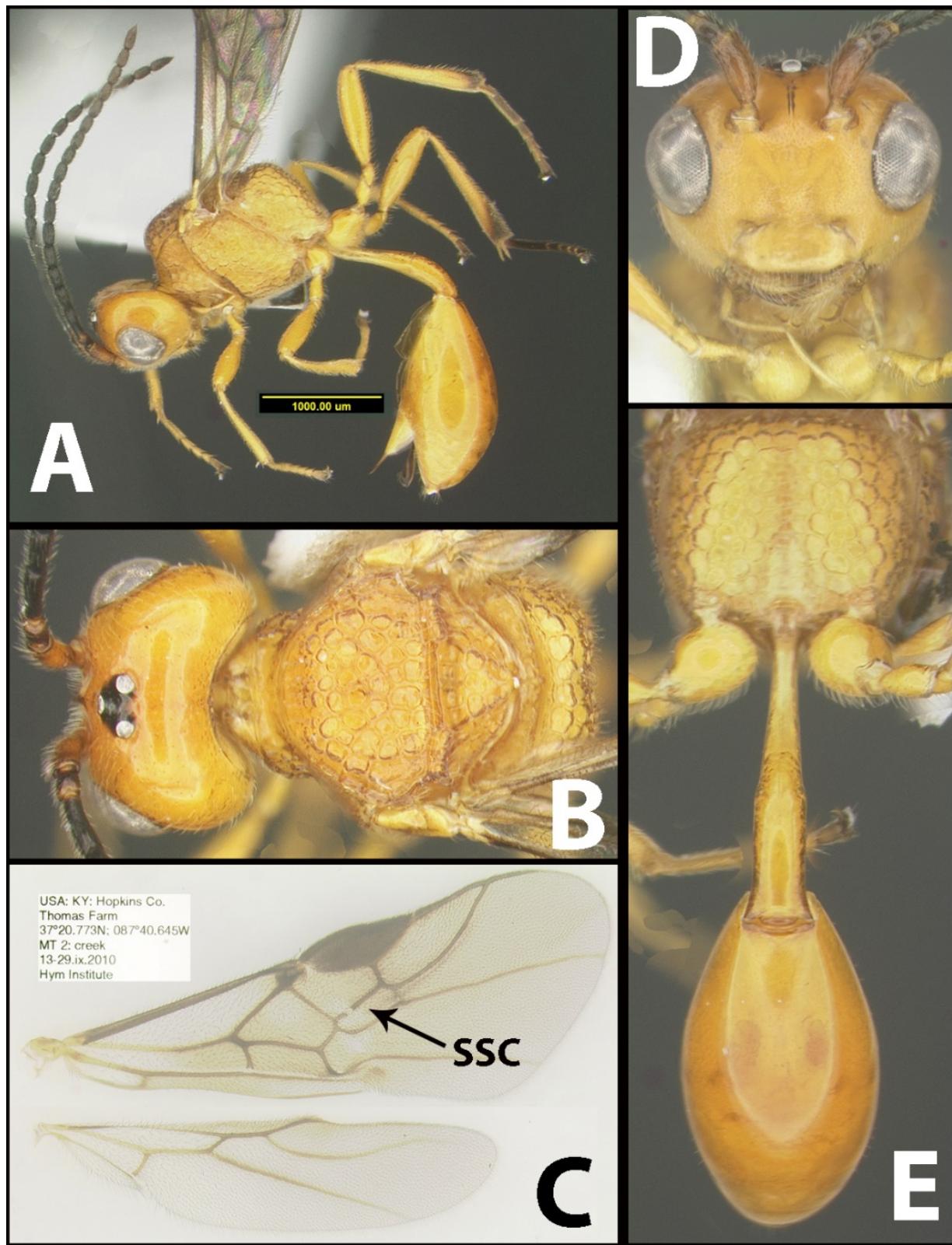


Figure 2. *Aridelus* sp.

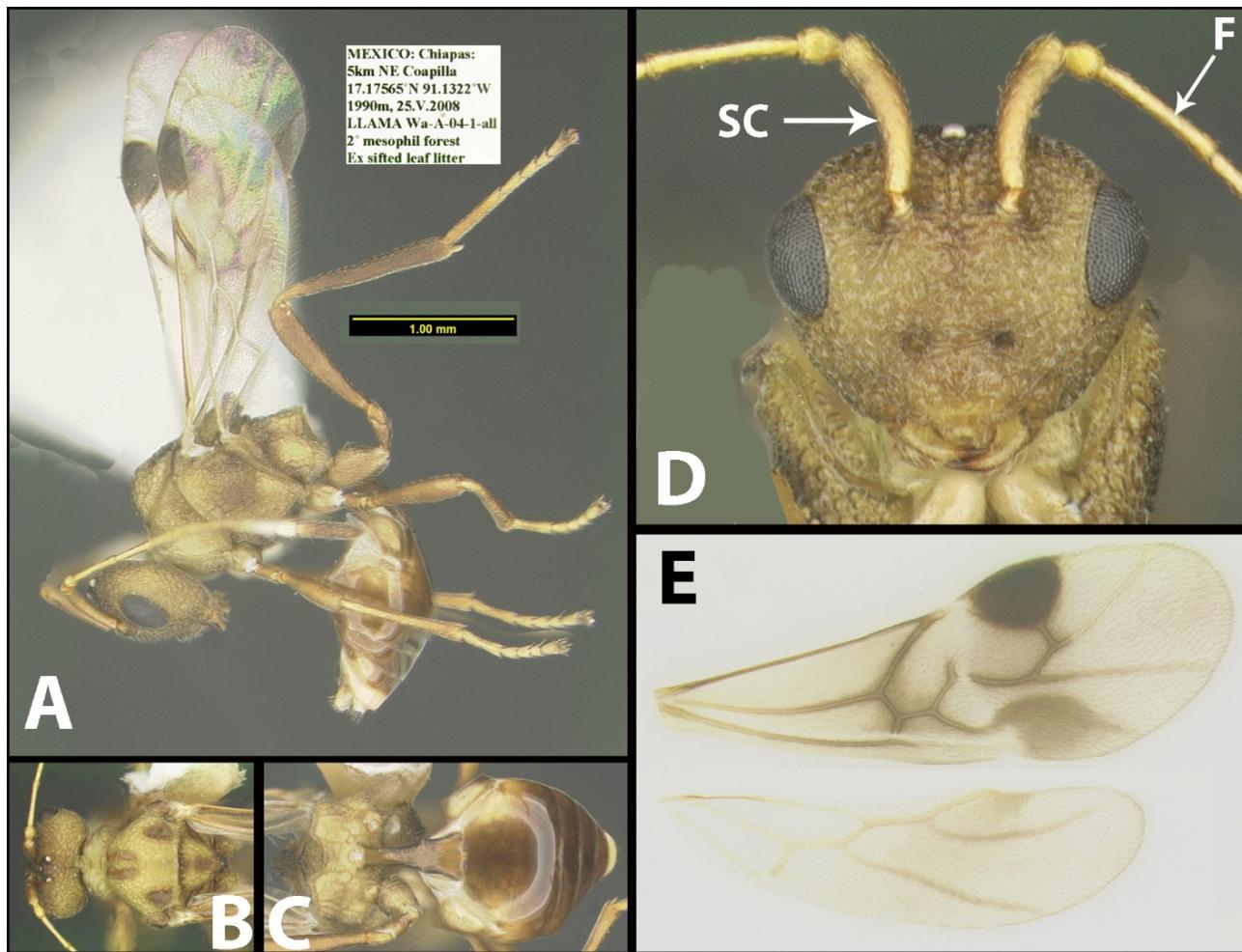


Figure 3. *Betelgeuse aztecus* Shaw.

Biology. Parasitoids of adult beetles, especially Curculionidae, Chrysomelidae, and Carabidae (Shaw, 1995).

Diversity. About 70 species are described worldwide and approximately nine in the New World. There are 26 BINs (proxies for species) in BOLD from Costa Rica (Oct. 13, 2024) suggesting that there are more than 200 hundred Neotropical species.

Distribution. Cosmopolitan with many undescribed Neotropical species.

Publications. Aguirre et al. (2017) revised the Costa Rican fauna, described 23 new species and provided a key to all Neotropical species.

Note. Members of the subgenus *Syrrhizus* Foerster have forewing (RS+M)a vein reduced (Fig. 5E) or absent.

***Centistina* Enderlein, 1912**

Fig. 6

Diagnosis. Scape 4 or more times longer than wide (Fig. 6D). Clypeus (C) relatively wide; scape (SC) relatively thin compared to *Dinocampus* (Fig. 6D). Antenna with many more than 8 flagellomeres. Forewing vein M+Cu complete and tubular (Fig. 6B). (RS+M)a vein of

forewing present (Fig. 6B). Propodeum (PP) rounded in lateral view (Fig. 6A).

Biology. Unknown

Diversity. Six described species, and few are undescribed.

Distribution. Afrotropical, Neotropical, and southwestern Nearctic. Only two species are described from the New World, both are from Costa Rica.

Publications. Van Achterberg and Shaw (2000) described the two Costa Rican species.

Note. *Eodinocampus* Belokobylskij is a junior synonym (Belokobylskij, 2001).

***Centistoides* van Achterberg, 1992**

Figs 7, 8

Diagnosis. Dorsope absent. Maxillary palp with 3 segments; labial palp with 1 segment. Female hypopygium deeply incised medially. Forewing vein 2M sclerotized and present as a short but distinct branch (Fig. 7A). Forewing 3RS fully developed (Fig. 7A). First metasomal tergum not greatly constricted basally, almost as wide basally as apically (Figs 7G, 8G).

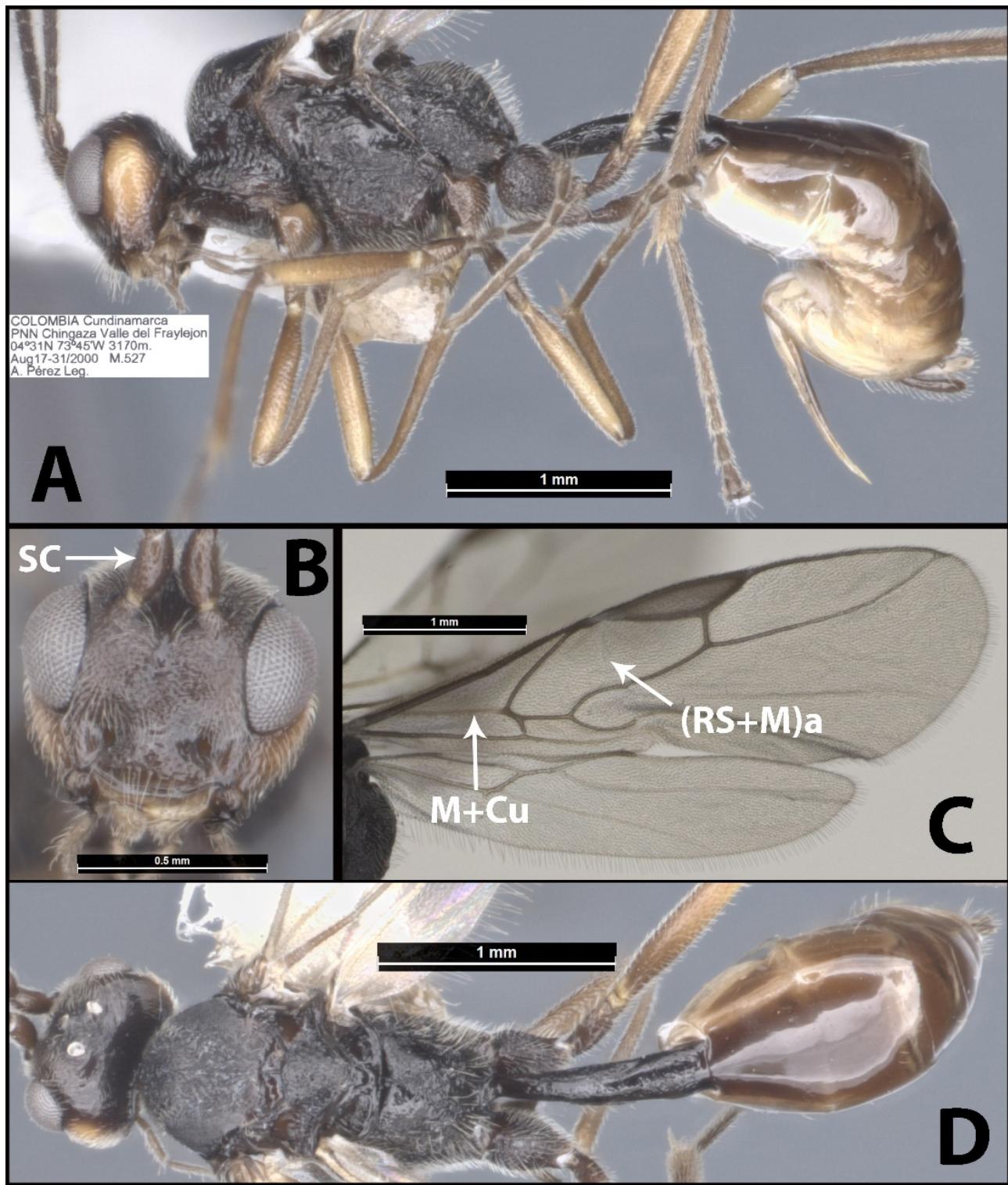


Figure 4. *Bracteodes* sp.

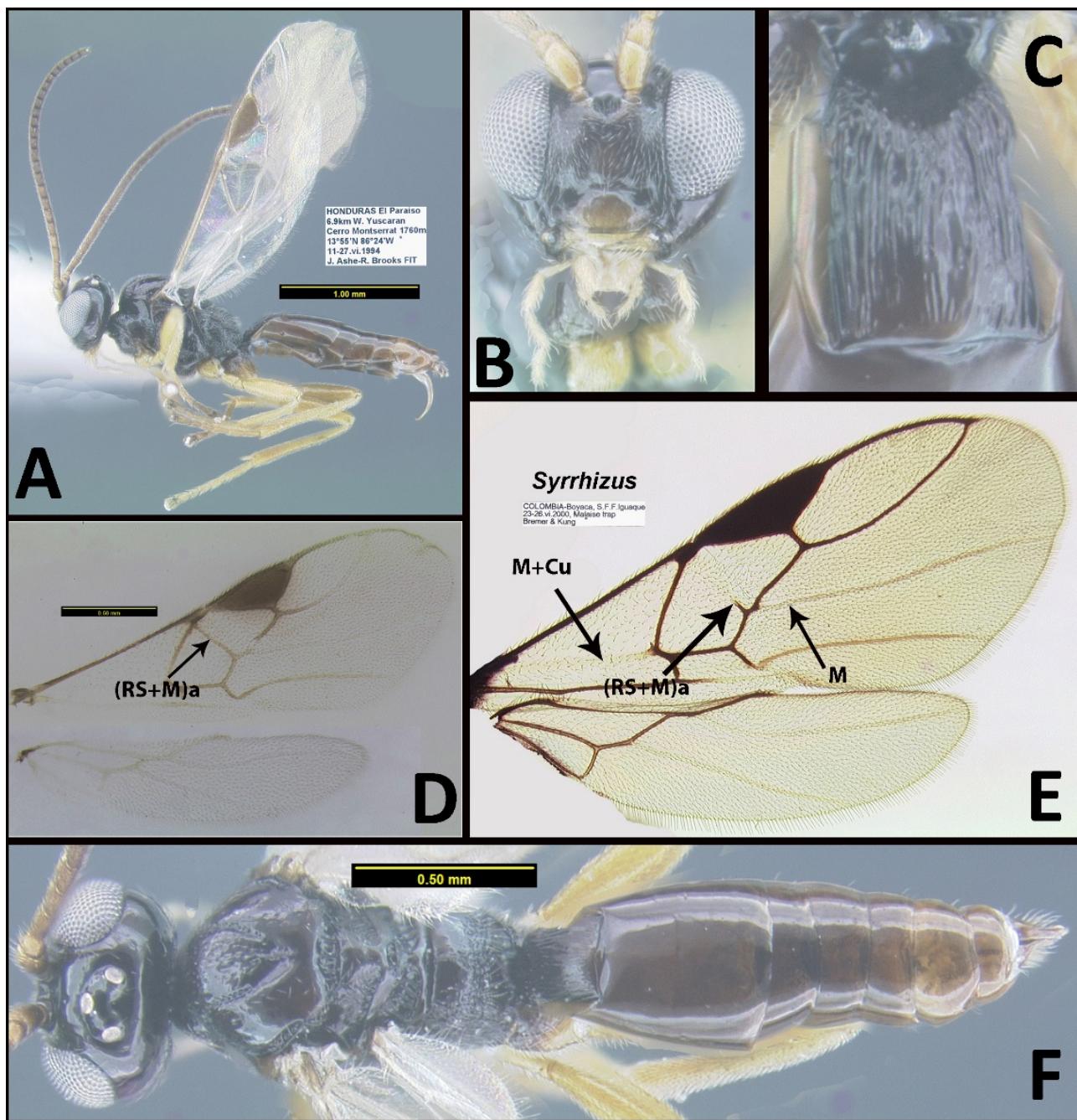


Figure 5. *Centistes* spp.

Biology. Unknown

Diversity. Two described species, undoubtedly a few undescribed species exist.

Distribution. Neotropical, only known from Surinam and Brazil.

Publications. Van Achterberg (1992a) erected the genus. Almeida and Penteado-Dias (2018) described the Brazilian species and distinguished it from the Surinam species.

Chrysopophthorus Goidanich, 1948

Fig. 9

Diagnosis. Forewing r-m present, thus second submarginal cell closed (Fig. 9B). Mesosoma without honey-combed or areolate sculpture except on propodeum. Mesoscutum punctate and with distinct notaui (Fig. 9D). First metasomal segment as long as or longer than remainder of metasoma (Fig. 9D).

Biology. Parasitoids of adult Chrysopidae.

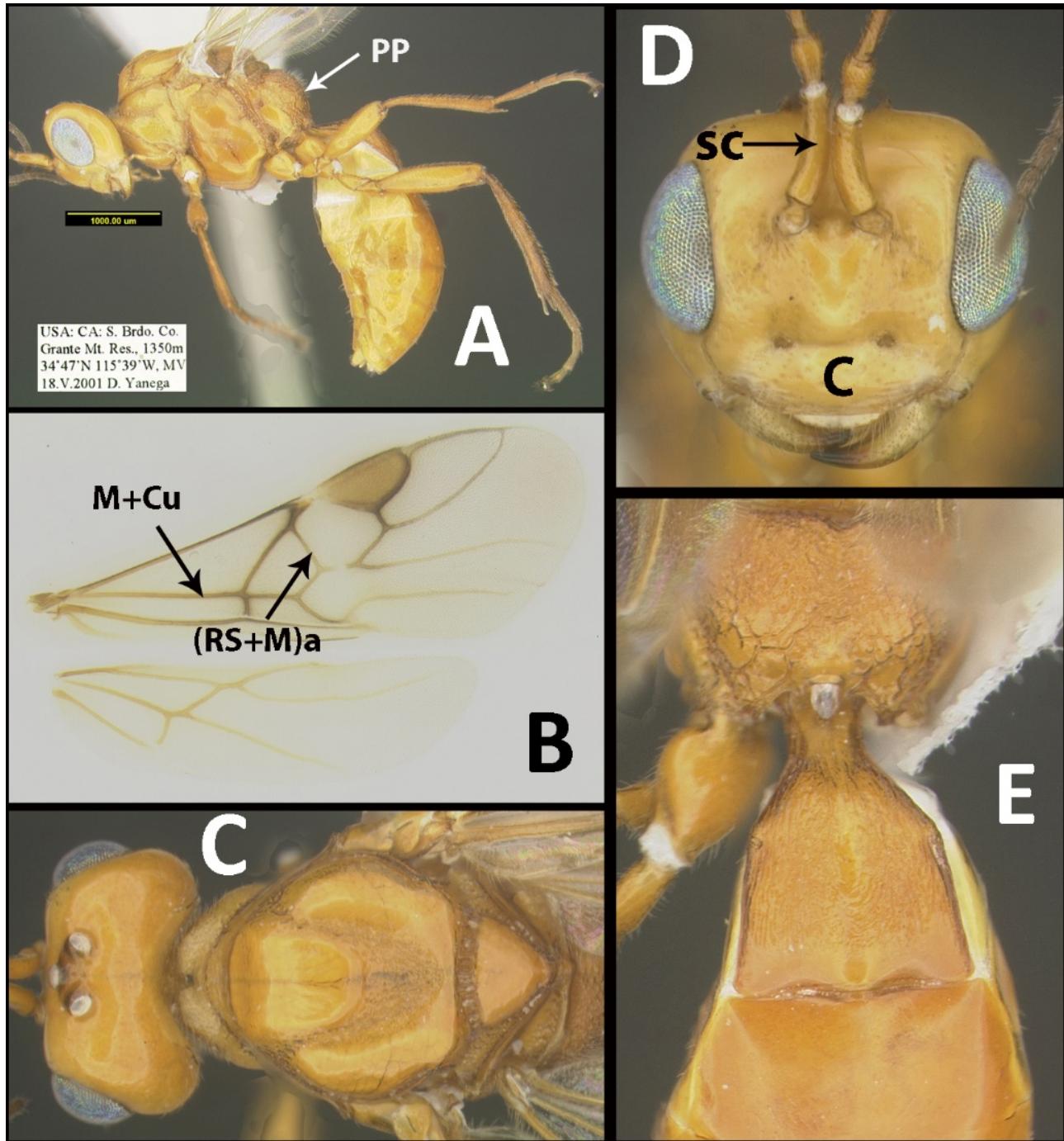


Figure 6. *Centistina* sp.

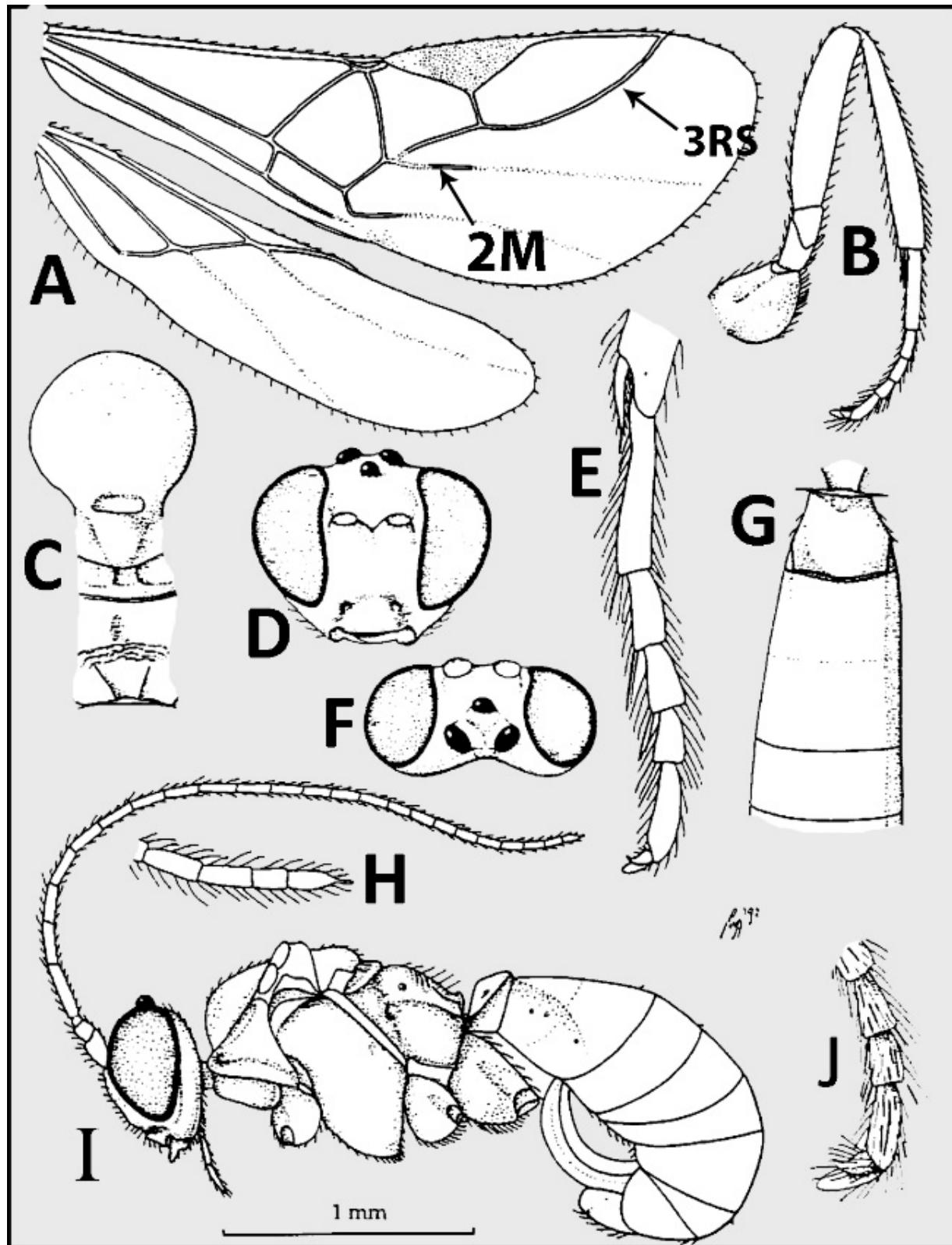


Figure 7. *Centistoides doesburgi* van Achterberg, modified from van Achterberg (1992a).

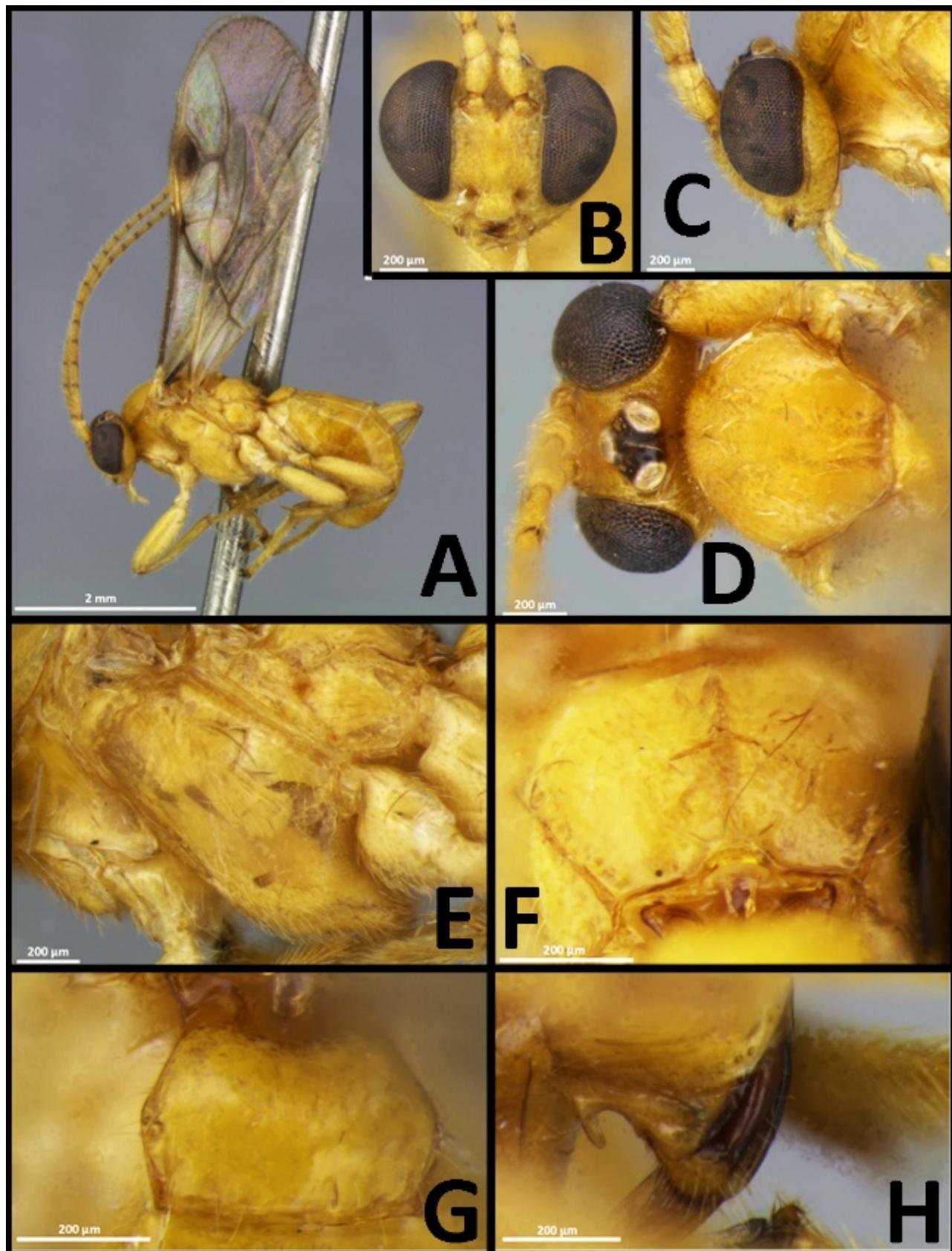


Figure 8. *Centistoides manoeli* de Almeida and Penteado-Dias, modified from de Almeida and Penteado-Dias (2018).

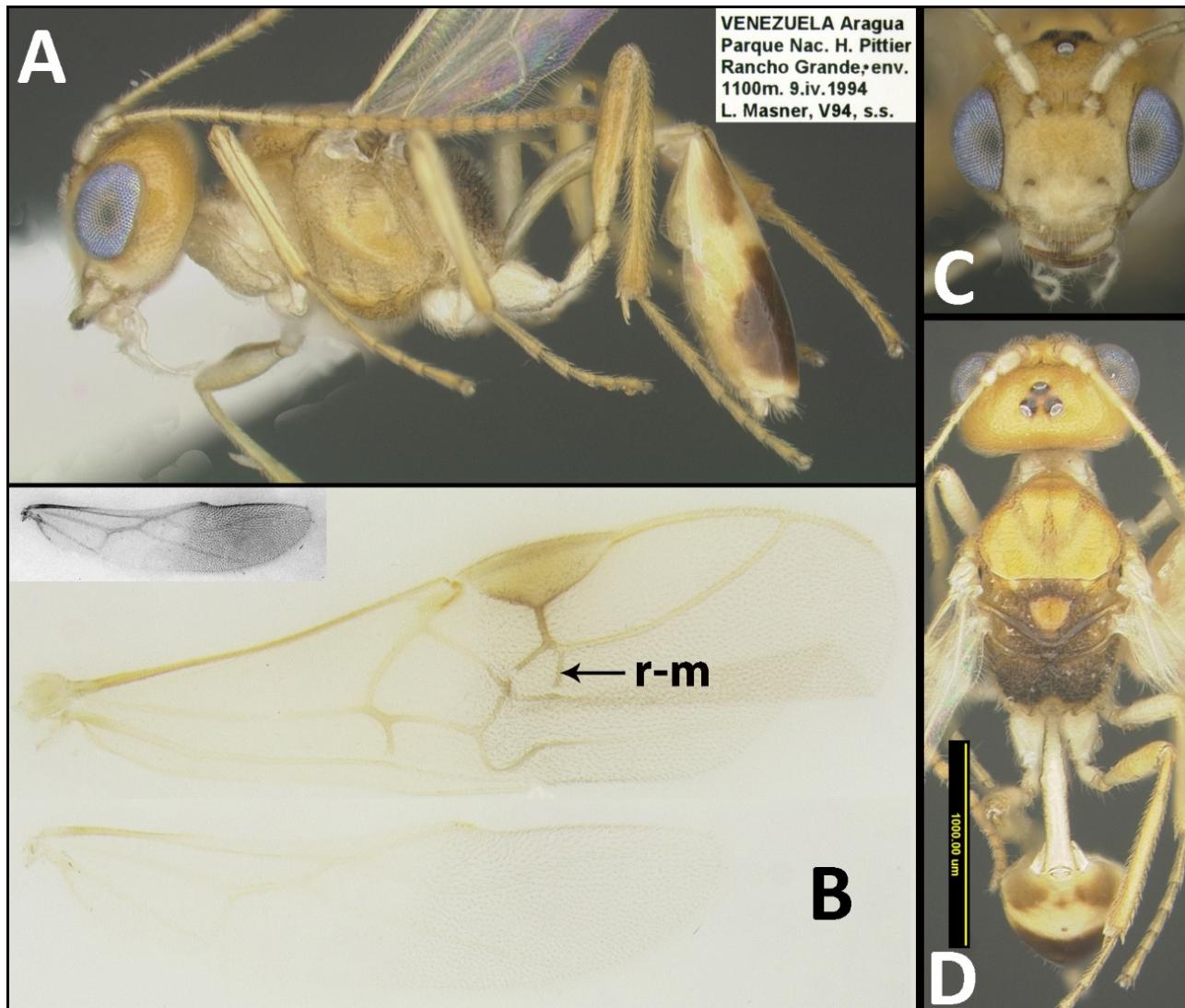


Figure 9. *Chrysopophthorus* sp.

Diversity. Eight described species, one Nearctic and three Neotropical.

Distribution. Cosmopolitan.

Publications. Mason (1964) provided a key to the New World species. Van Achterberg (1994) revised the Palearctic species and summarized what is known of their biology.

***Cosmophorus* Ratzeburg, 1848**

Fig. 10

Diagnosis. Antennae each inserted on large protuberances (Fig. 10E). Labrum (L) large and occupying the large space between mandibles and clypeus (Fig. 10D). RS not quite reaching the wing margin (Fig. 10A).

Biology. Parasitoids of adult Scolytinae (Curculionidae) (Loan and Matthews, 1973).

Diversity. 33 described species including five Nearctic species. None of the Neotropical species is described.

Distribution. Cosmopolitan.

Publications. The Nearctic species were most recently treated by Loan and Matthews (1973).

***Cryptoxilos* Viereck, 1911**

Fig. 11

Diagnosis. Eyes converging ventrally (Fig. 11E). Wing venation reduced with the m-cu crossvein absent (Fig. 11D).

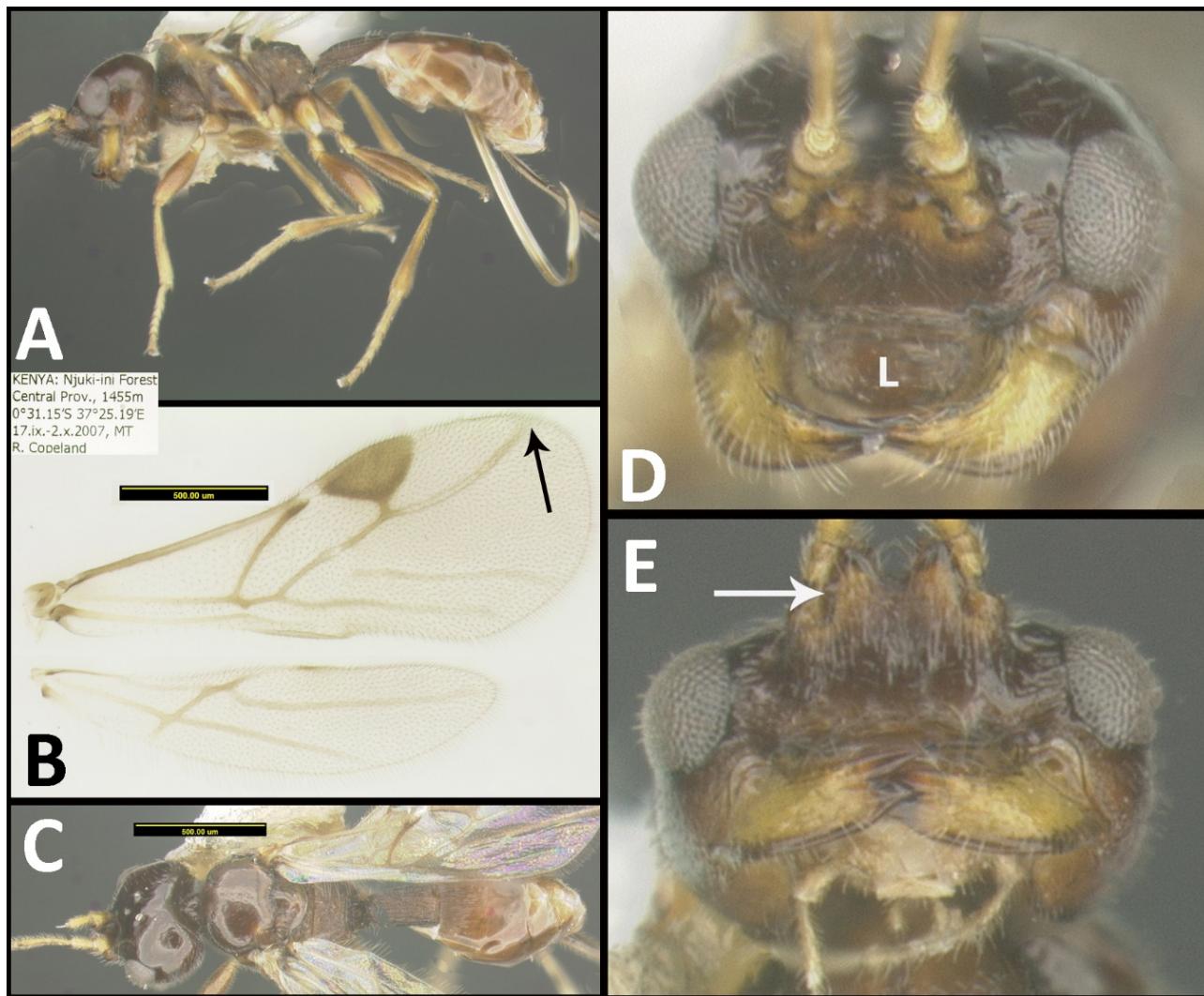


Figure 10. *Cosmophorus* sp.

Biology. Parasitoids of adult Scolytinae (Curculionidae) (Deyrup, 1981).

Diversity. Eight described species, including three from the Nearctic and one from the Neotropical realm. A small number undoubtedly remain undescribed.

Distribution. All realms except Afrotropical and Australian.

Publications. Deyrup (1981) gives a thorough description of the biology of *C. lymantori*.

***Dinocampus* Foerster, 1863**

Fig. 12

Diagnosis. Scape more than 2.5 x longer than wide (Fig. 12D). Labial palp with 2 segments. Distance from stigma (S) to RS is much less than half the distance from the stigma to the apex of the wing, i.e., RS ending far from the wing margin (Fig. 12C).

Biology. Parasitoids of adult Coccinellidae. A symbiotic virus is correlated with the manipulation of host behavior (Dheilly *et al.*, 2015). Records for Curculionidae as hosts almost certainly refer to *Perilitus* species and not species that are now assigned to *Dinocampus*.

Diversity: There is one species described, and it may be the only one in existence.

Distribution. Cosmopolitan.

Publications. Dheilly *et al.* (2015) give an interesting summary of biology.

***Eclitura* Kokujev, 1902**

Fig. 13

Diagnosis. Scape more about 5 x longer than wide (Fig. 13C). Forewing vein (RS+M)a absent (Fig. 13D). Face narrow, i.e., the shortest distance between eyes is shorter than one eye width in anterior view (Fig. 13C).

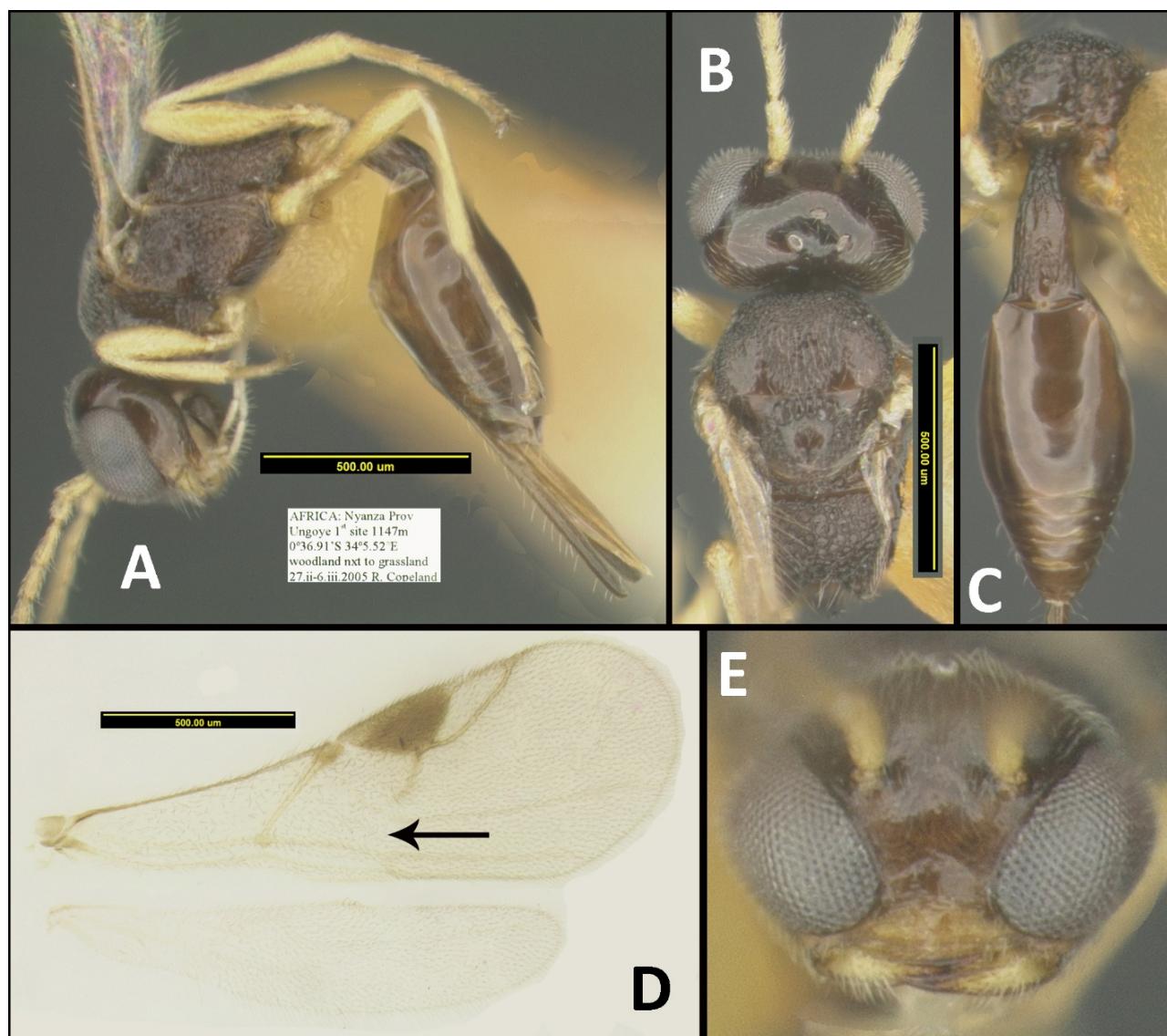


Figure 11. *Cryptoxilos* sp.

Biology. Unknown.

Diversity: Three described species. Two from the Palearctic and one from Brazil. The few Nearctic species are not described.

Distribution. Holarctic, Neotropical.

Publications. De Almeida et al. (2019) described the Brazilian species.

Elasmosoma Ruthe, 1858

Fig. 14

Diagnosis. The forewing venation of *Elasmosoma* (Fig. 14D) and *Neoneurus* are similar and unique amongst Euphorinae and indeed Hymenoptera. The two genera may be distinguished with a number of characters including the forewing of *Elasmosoma* having RS descleritized or absent apically, usually indicated apically only by spectral venation (Fig. 14D).

Biology. Parasitoids of adult formicine ants (Poinar, 2004). Gómez Durán and Achterberg (2011) described the oviposition behavior and included a link to a film clip showing this (<https://www.youtube.com/watch?v=GYGdEoaMYWs>).

Diversity: 19 described species, six of which are Nearctic. There are 14 Nearctic BINs (proxies for species) in BOLD (Oct. 21, 2024) suggesting that there are likely more than 30 Nearctic species.

Distribution. Holarctic and northern Oriental.

Publications. Shaw (2007) provided a key to the Nearctic species.

Note. Stigenberg et al. (2015) showed that Neoneurini (*Elasmosoma* and *Neoneurus*) belong in the Euphorinae. Previously the tribe had subfamily status, Neoneurinae (Shaw, 1997a).

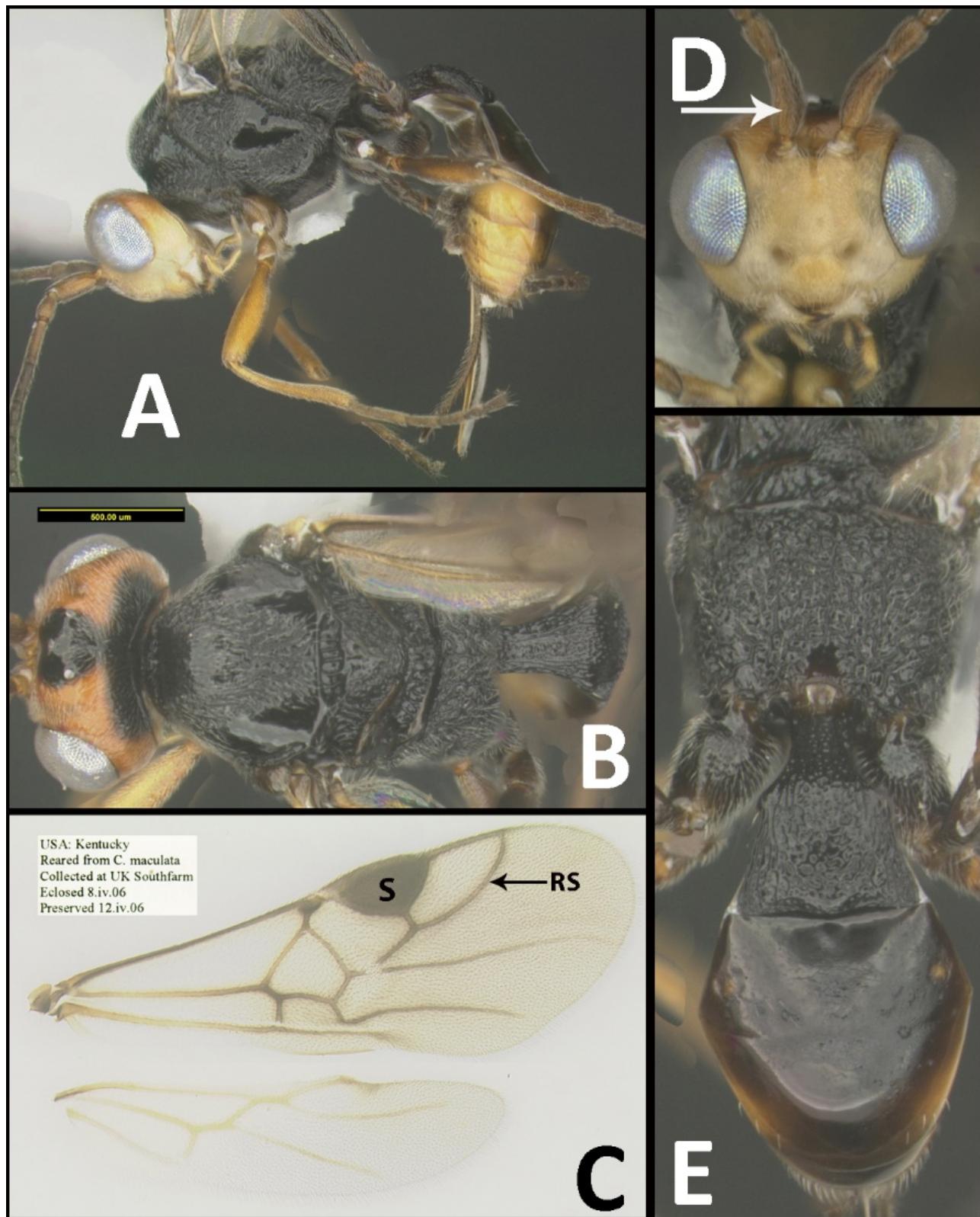


Figure 12. *Dinocampus coccinellae* Schrank.

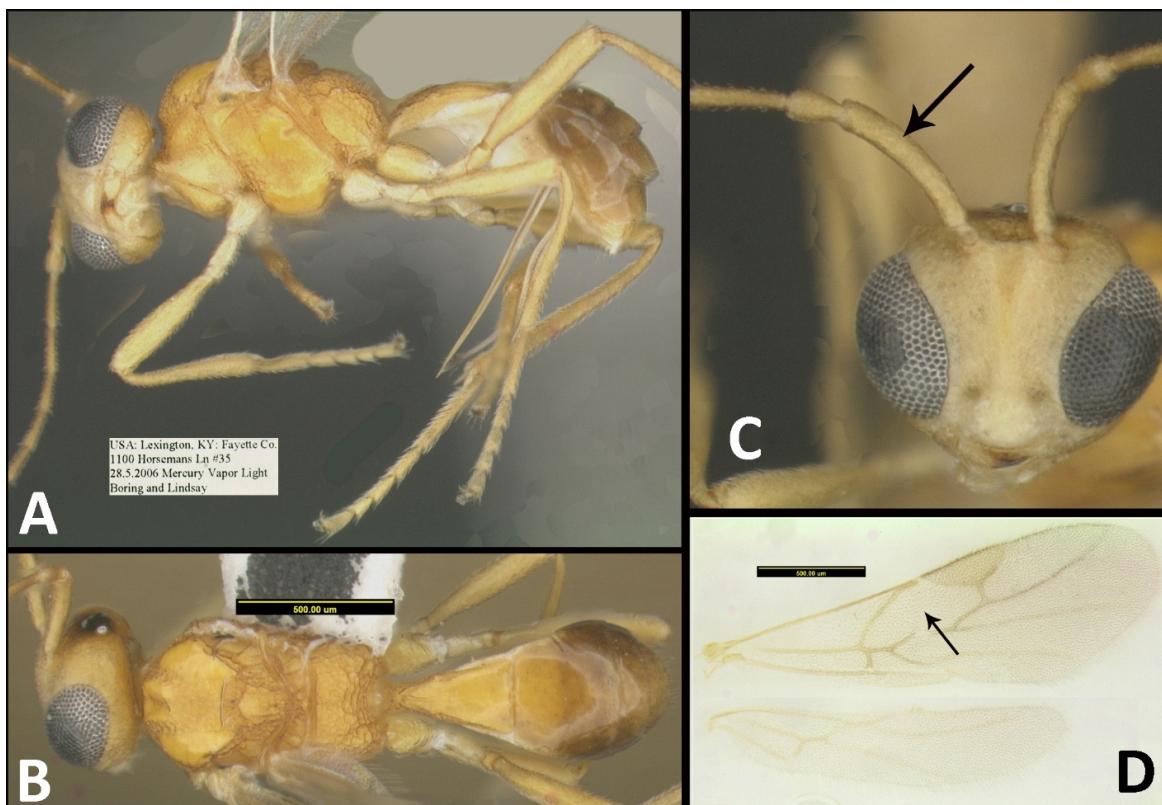


Figure 13. *Ecclitura* sp.

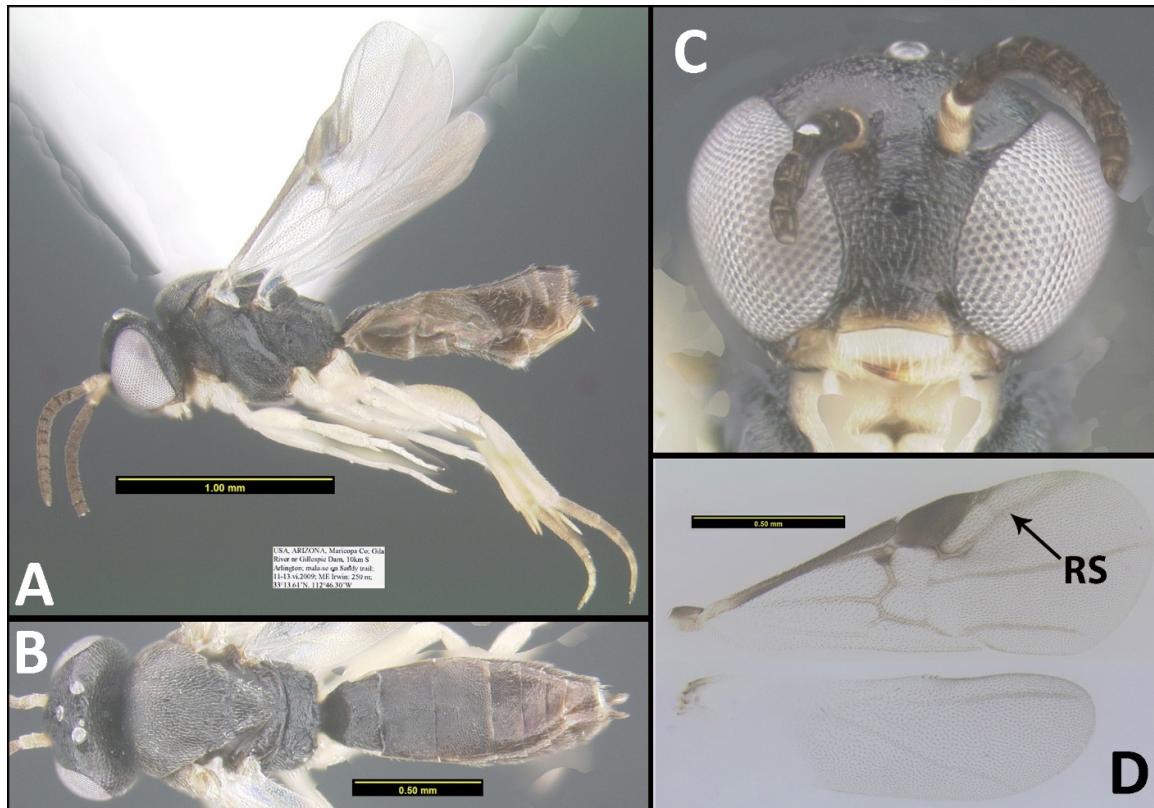


Figure 14. *Elasmosoma* sp.

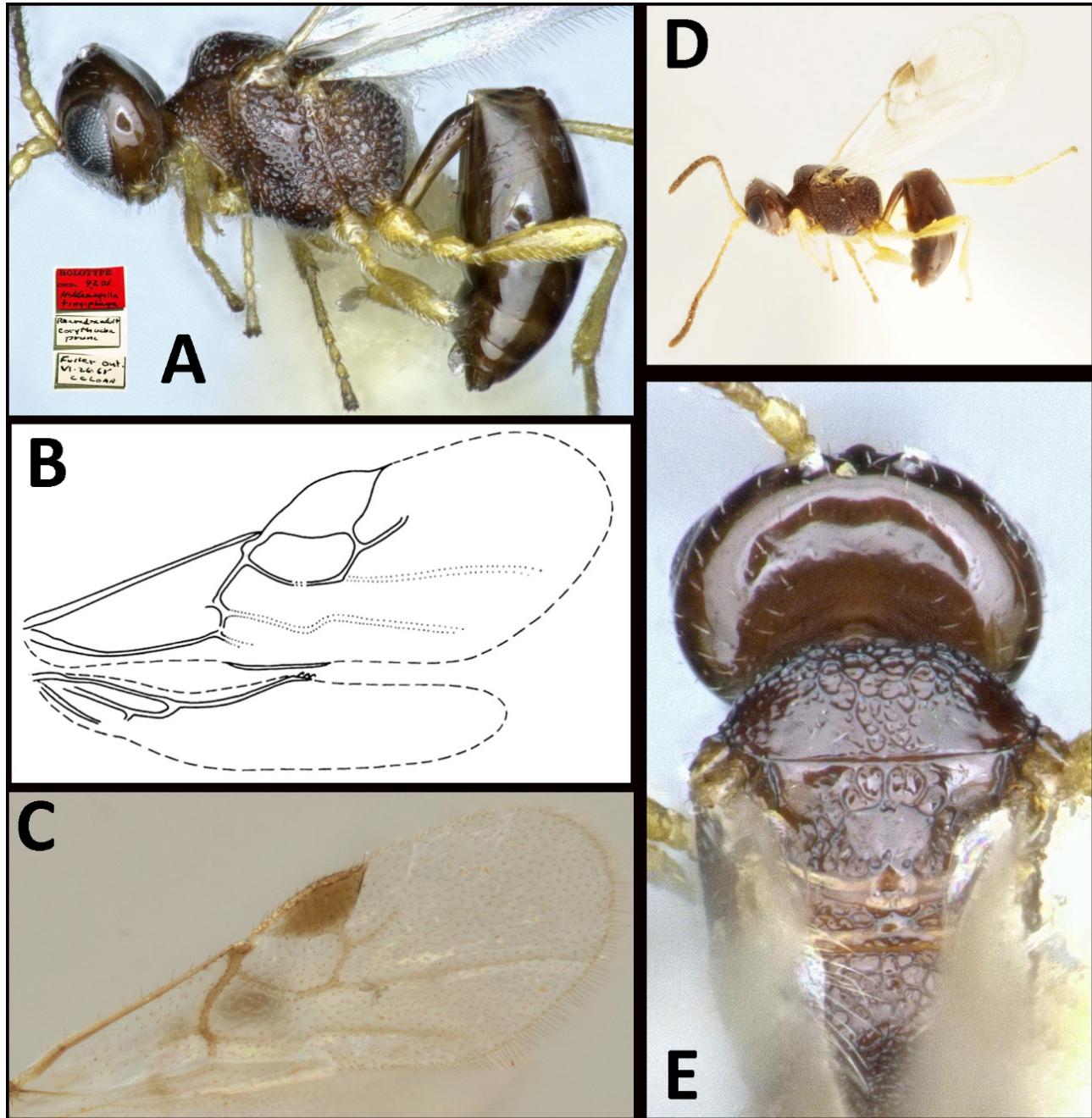


Figure 15. *Holdawayella tingiphaga* Loan. Drawing (15B) modified from Shaw (1997a). Other images by the staff at the Canadian National Collection.

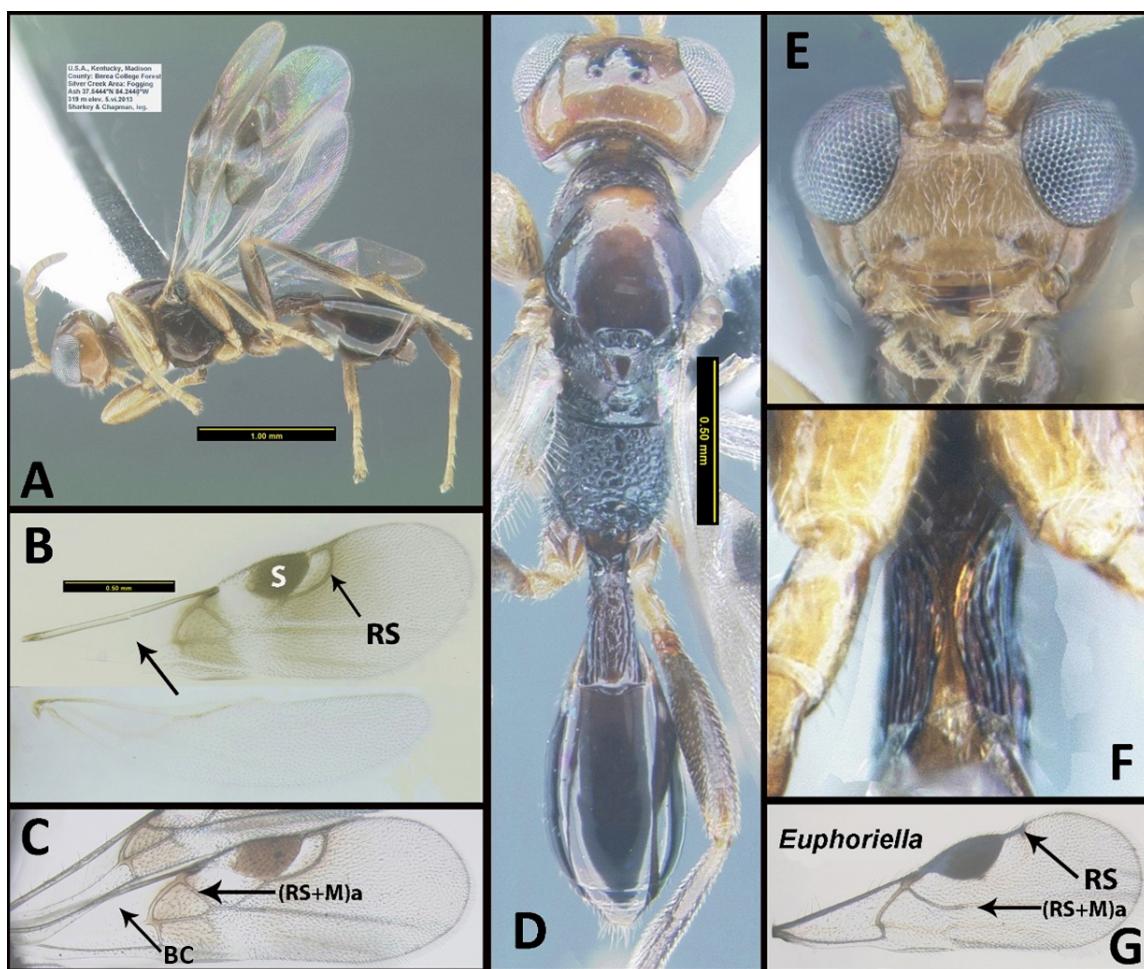
Figure 16. *Leiophron* spp.***Holdawayella*** Loan, 1967

Fig. 15

Diagnosis. The forewing venation is unique (Fig. 15B).**Biology.** Parasitoids of late instar nymphs and adults of Tingidae.**Diversity:** Two described Nearctic species, and at least one undescribed Neotropical species.**Distribution.** Nearctic and Neotropical.**Publications.** Loan et al. (1971) distinguished the two Nearctic species. Stigenberg et al. (2015) synonymized *Ussurarideles* Tobias and Belokobylskij with *Holdawayella*, however, van Achterberg and Soethof (2023) reinstated the genus. Since the two genera appear to be sister taxa this is simply a subjective decision.***Leiophron*** Nees, 1816

Fig. 16

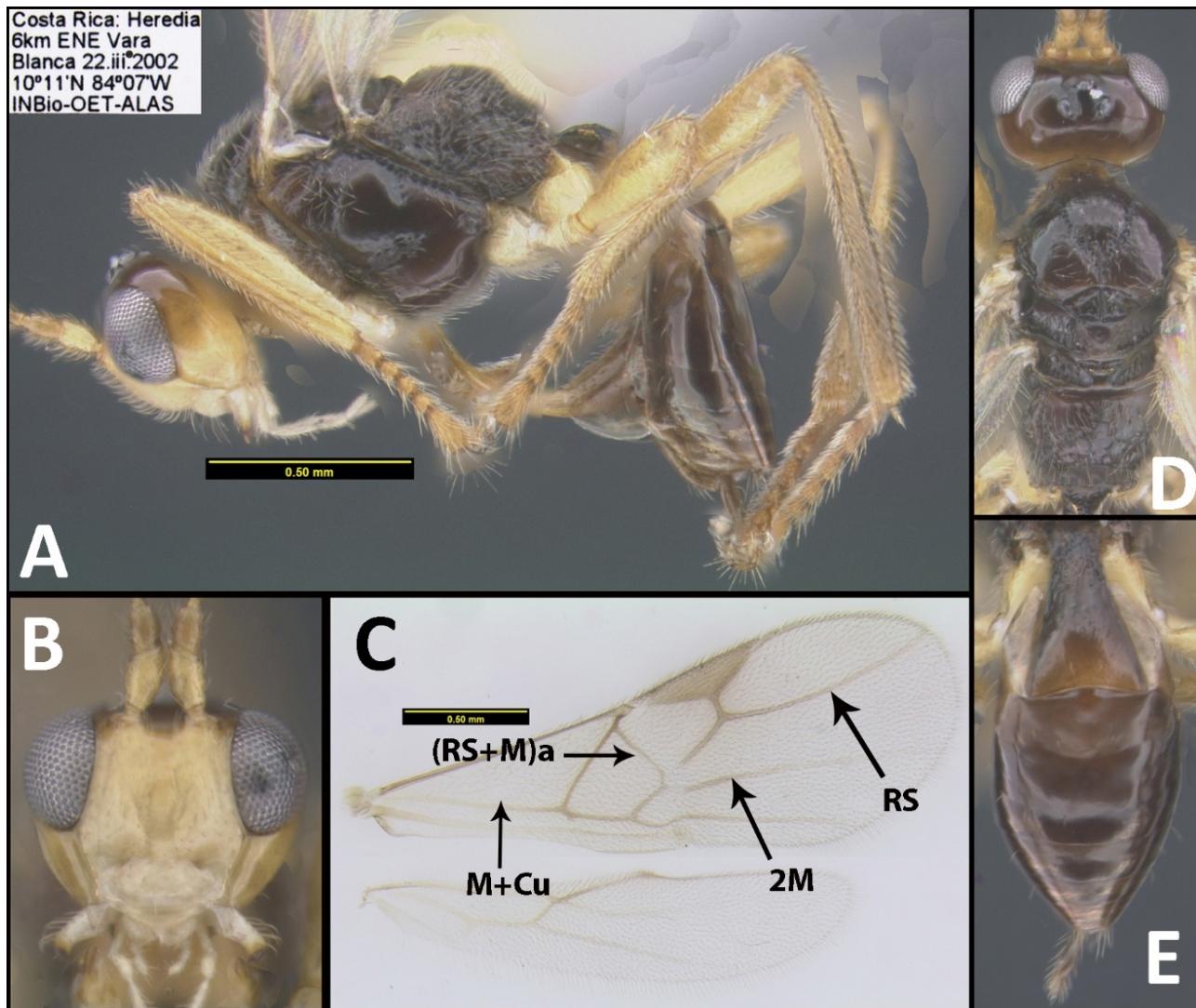
Diagnosis. Very similar to *Peristenus*. Basal cell (BC) of forewing often mostly or entirely glabrous (90%) (Figs 16B, C). First metasomal segment with tergum and sternum entirely separate, not fused ventrally at the base of the segment (Fig. 16F, couplet 34A), or fused throughout entire length (couplet 34AA). RS vein of

forewing ending nearer stigma (S) than apex of wing and (RS+M)a vein of forewing present (Figs 16B, C, G). In specimens formerly placed in *Euphorielia* Ashmead (now considered a subgenus) the RS vein of the forewing is mostly absent and usually present only as a small stub on the wing margin (Fig. 16G). M+Cu vein of forewing mostly or entirely weak and non-tubular (Figs 16B, C, G). None of these characteristics will separate all species from *Peristenus*.

Biology. Parasitoids of late instar nymphs and adults of Hemiptera (Miridae and Lygaeidae) and Psocodea (Psocidae). The early instar nymph of the host is parasitized, and the mature larva emerges from the mature host nymph or adult (Zhang et al., 2018).

Diversity. Over 200 described species, about 70 in the Nearctic and a handful in the neotropics. There are 125 BINs (proxies for species) from Costa Rica on BOLD (March 28, 2025) suggesting that there are more than 1,000 undescribed species in the New World.

Distribution. Cosmopolitan.**Publications.** Goulet and Mason (2006) reviewed the species attacking the *Lygus* bug. Zhang et al. (2018) redefined the limits of the genus.

Figure 17. *Litostolus* sp.

Notes. Stigenberg et al. (2015) synonymized *Euphoiriella* with *Leiophron* and it is recognized here as a subgenus. Zhang et al. (2018) synonymized *Mama* Belokobylskij with *Leiophron*.

Litostolus van Achterberg, 1985

Fig. 17

Diagnosis. Distance from stigma to RS is much greater than half the distance from stigma to the apex of the wing, i.e., RS ending near wing margin (Fig. 17C). Forewing vein 2M long, not simply as a stub (Fig. 17C). Forewing vein M+Cu complete and tubular (Fig. 17C). Forewing crossvein m-cu complete (Fig. 17C). (RS+M)a vein of forewing present (Fig. 17C). Forewing second submarginal cell open, not closed or only partially closed distally (Fig. 17C). First metasomal tergum much wider apically than at base (Fig. 17E). Propodeum lacking projections laterally, weakly rounded or flat (Fig. 17A).

Biology. Unknown.

Diversity. Only one species is described occurring in USA and Canada. There are probably 20 or more undescribed New World species. 14 BINs are presently represented in BOLD (Oct. 14, 2024).

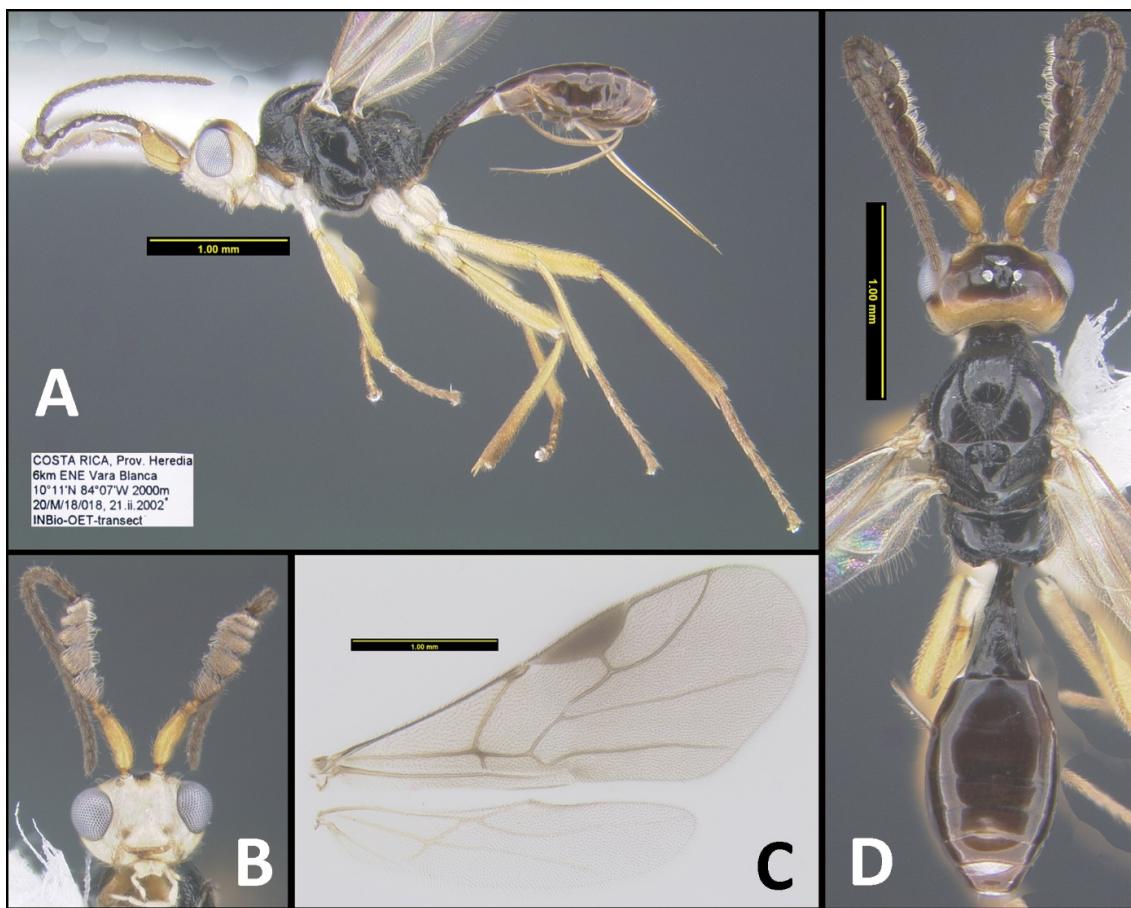
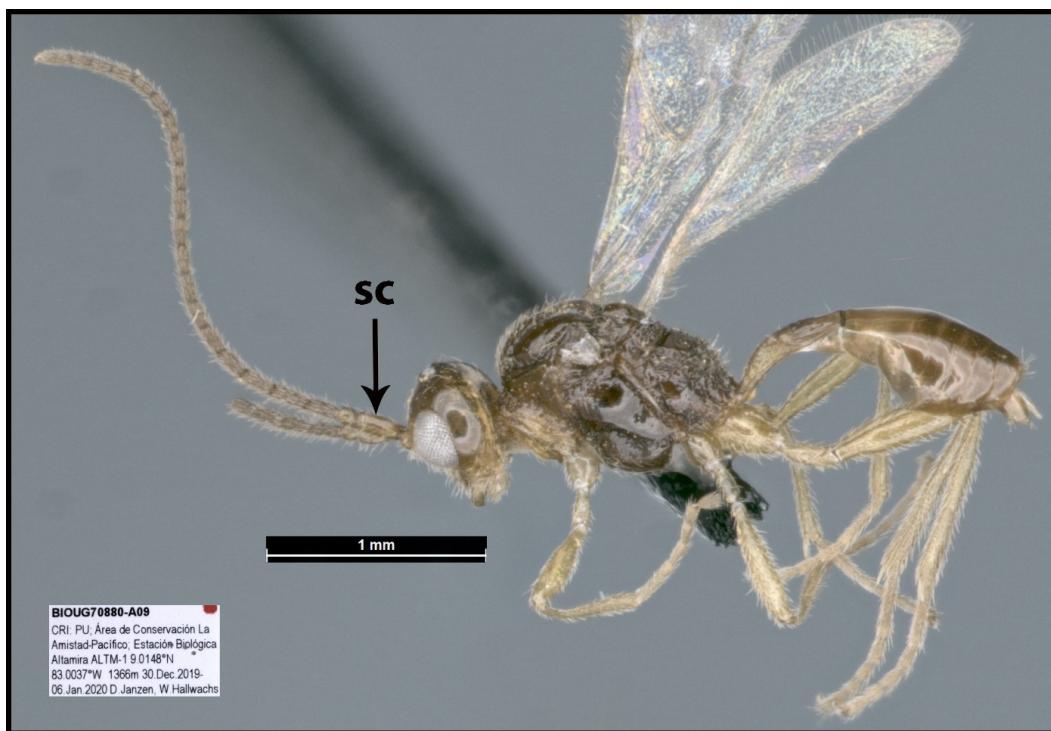
Distribution. Restricted to the New World (Canada to Brazil).

Publications. Van Achterberg (1985) described the sole species.

Marshiella Shaw, 1985

Figs 18, 19

Diagnosis. Scape length is 3-3.5 times scape width. Female with setose pads on underside of basal flagellomeres (Fig. 18B). Males do not have the highly modified flagellomeres, but the scape (SC) is 3 times longer than wide (Fig. 19) thus distinguishing them from *Microctonus* and *Townesilitus*.

Figure 18. *Marshiella* sp.Figure 19. *Marshiella* sp., male.

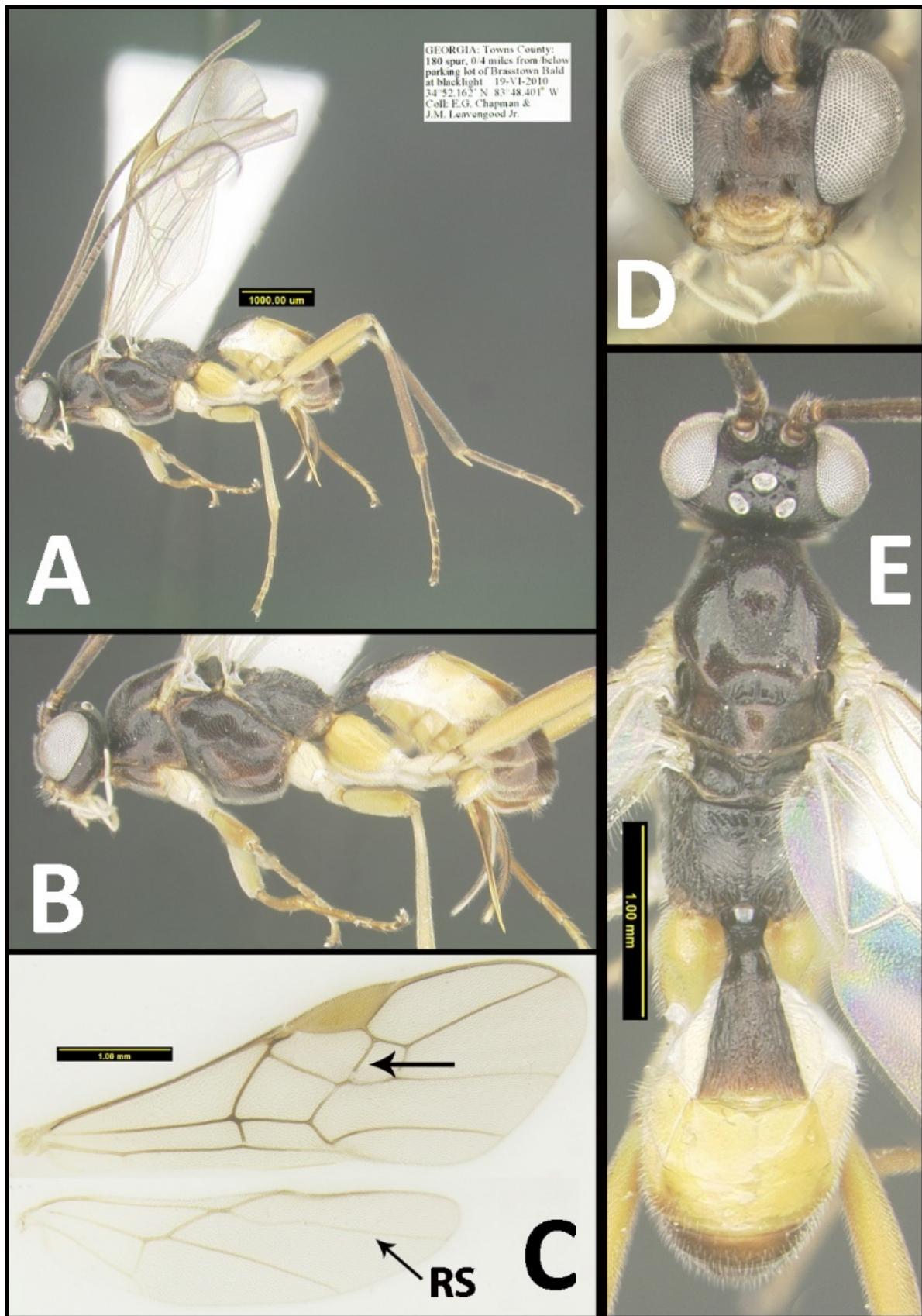


Figure 20. *Meteorus* sp.

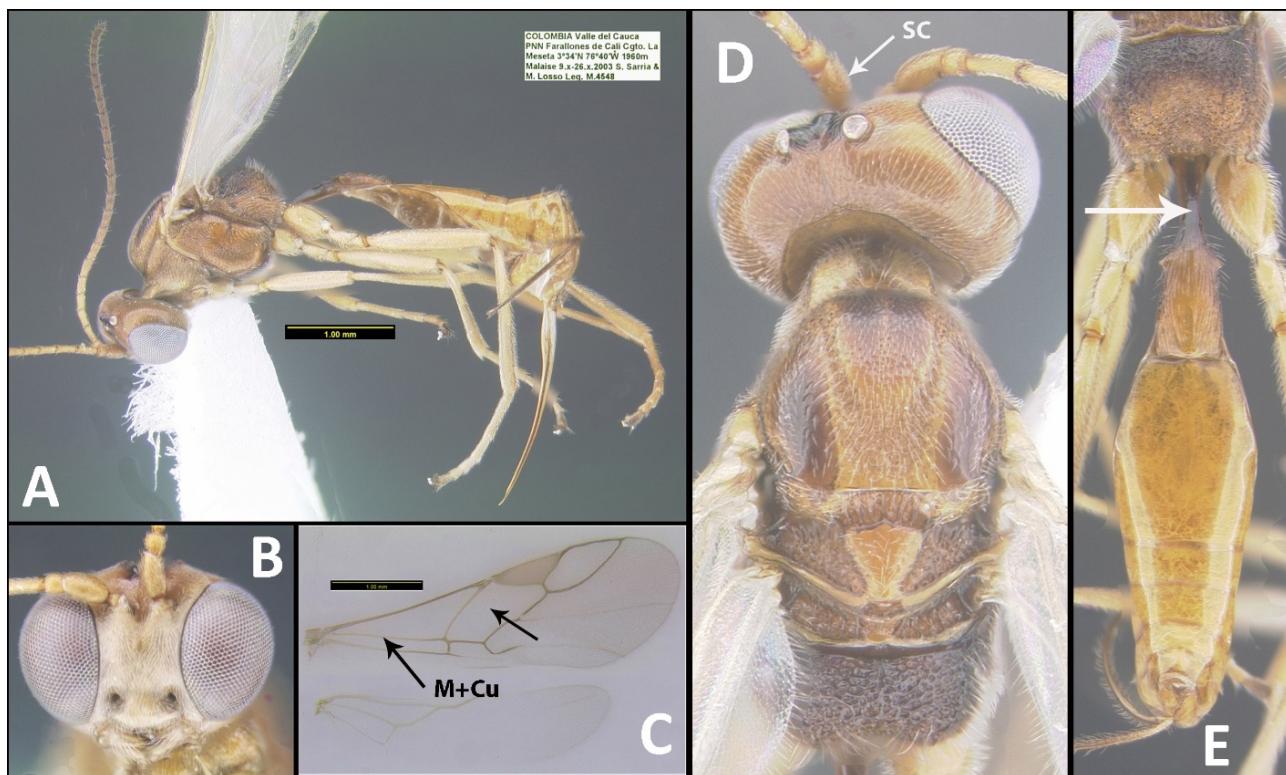


Figure 21. *Microctonus* sp.

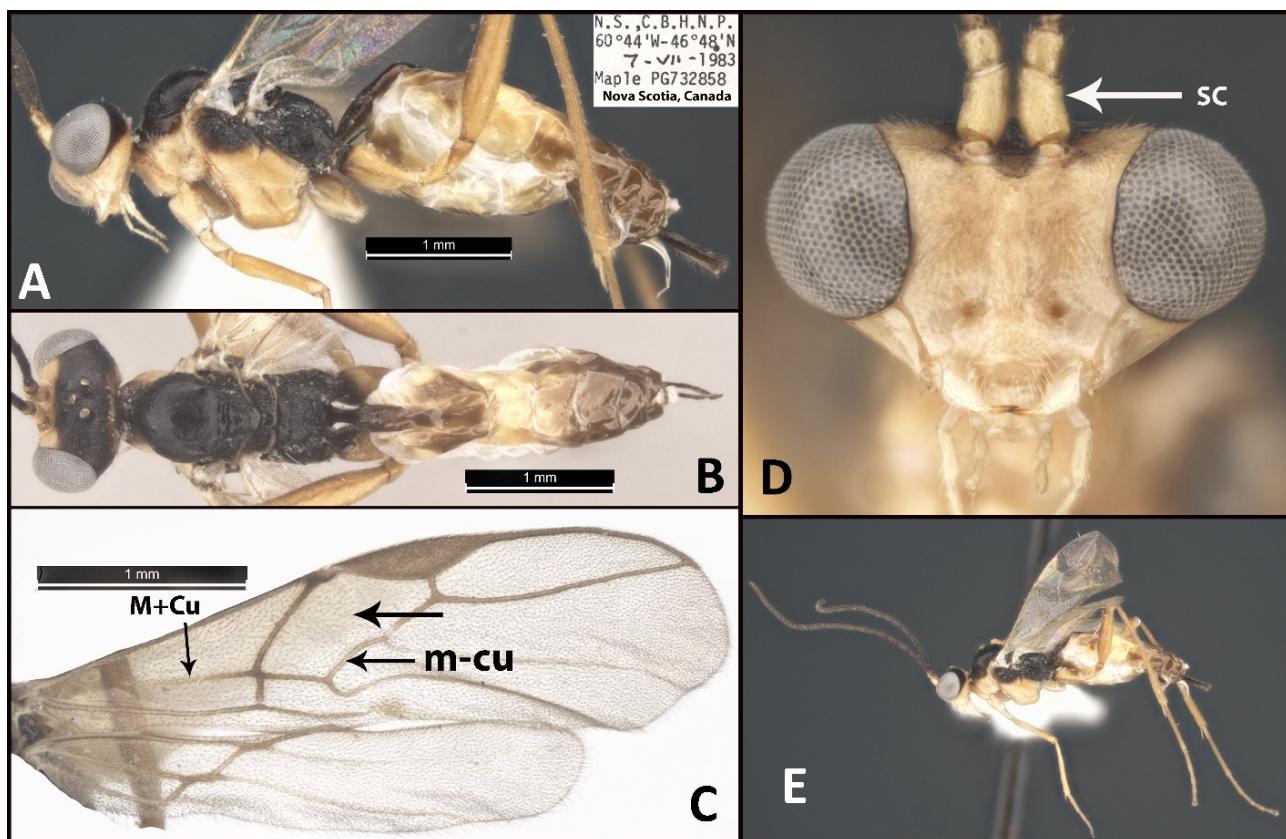


Figure 22. *Myiocephalus* sp.

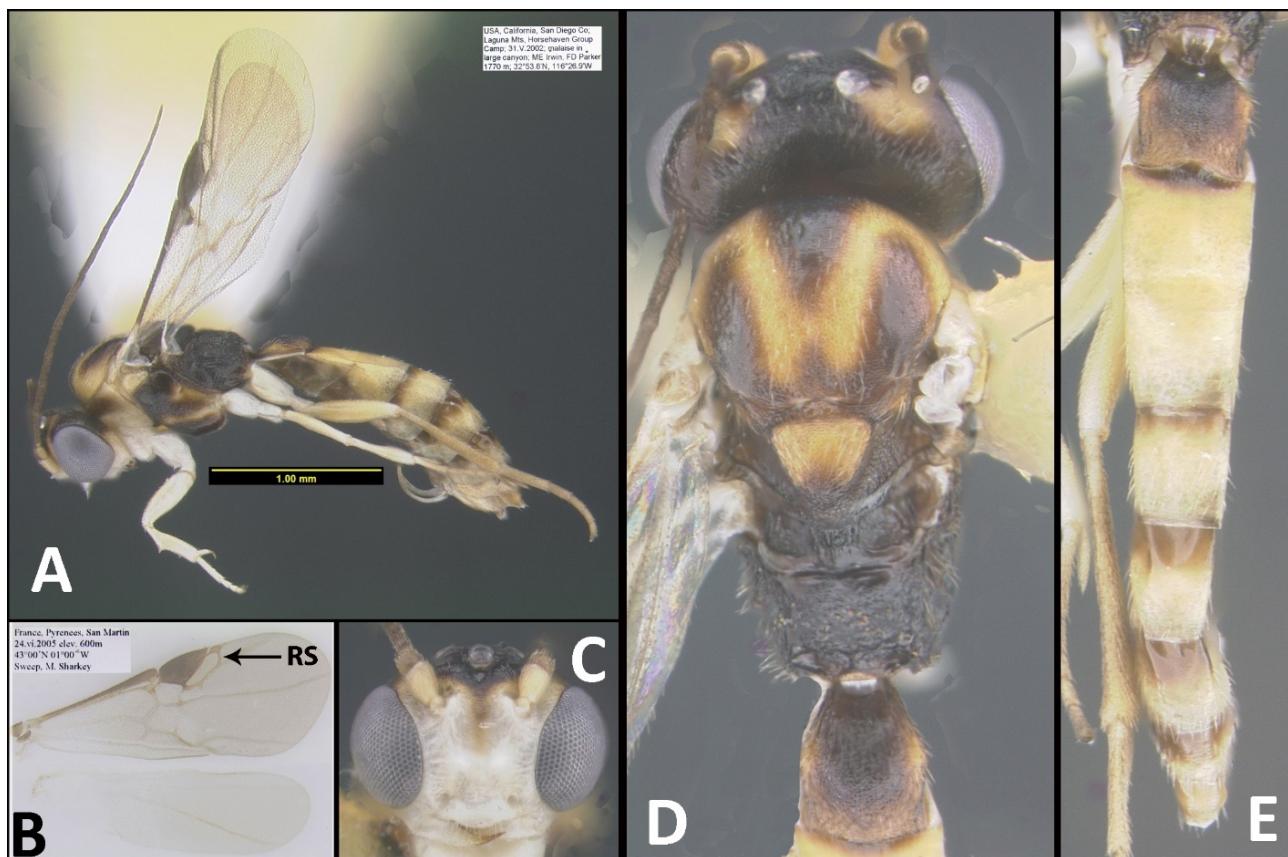


Figure 23. *Neoneurus* sp.

Biology. Reared from Anthicidae (Coleoptera) (Gornitz, 1937; Smith 1953).

Diversity. 10 described species, perhaps that many or more undescribed.

Distribution. Holarctic, Oriental, Neotropical (Canada to Brazil).

Publications. Shaw and Marsh (2000) revised the genus, described three new species, and provided a key to New World species. De Almeida et al. (2019) described a new species from Brazil.

Note: A male specimen (Fig. 19) is recorded here for the first time. It was identified using COI barcode data on BOLD. The Sample ID on BOLD is BIOUG70880-A09.

Meteorus Haliday, 1835

Fig. 20

Diagnosis. Forewing second submarginal cell present and 4-sided (Fig. 20C). Basal segment of metasoma usually more than 2x wider apically than basally (Fig. 20E). Hind wing vein RS straight (Fig. 20C) or bending towards anterior wing margin

Biology. Primarily endoparasitoids larval Lepidoptera (caterpillars), and occasionally larvae of Coleoptera.

Diversity. Over 300 described species, about 40 in the Nearctic and 70 in the Neotropics. Hundreds more species remain undescribed. Presently (Oct. 21, 2024) there are

101 BINs (proxies for species) in BOLD from Costa Rica alone.

Distribution. Cosmopolitan.

Publications. The Nearctic species have not been revised since Muesebeck's (1923) treatment. Nearctic species have been published in scattered publications since then. Aguirre et al. (2015) summarized the described Neotropical species, added 11 new species, and included a key to species.

Microctonus Wesmael, 1835

Fig. 21

Diagnosis. First metasomal segment greatly constricted basally and lacking anterior dorsolateral pits (Fig. 21E). Forewing vein M+Cu tube-shaped and complete (Fig. 21C). (RS+M)a vein of forewing absent (Fig. 21C). Scape (SC) length less than 2.5 times width (Fig. 21B).

Biology. Endoparasitoids of adult and sometimes larval beetles, especially Curculionidae, Chrysomelidae, and Carabidae.

Diversity. There are about 40 described species, hundreds more are undescribed. For example, presently (Oct. 12, 2024) there are 73 BINs (proxies for species) in BOLD from Costa Rica alone.

Distribution. Cosmopolitan.

Publications. Pucci (2013) revised the Canadian and USA

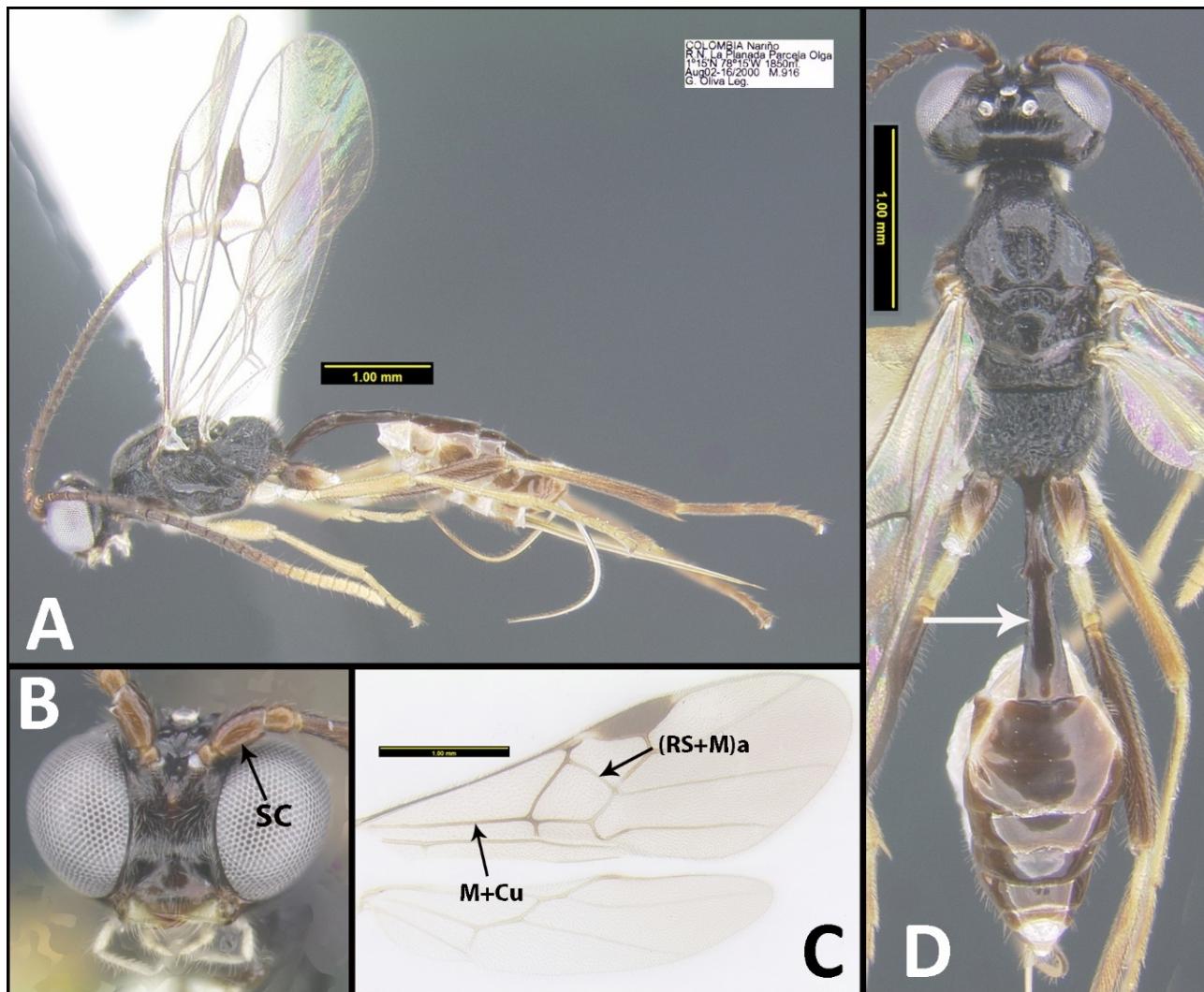


Figure 24. *Orionis* sp.

species but most species in this region remain undescribed.

Note. Stigenberg et al. (2015) showed that *Microctonus* is nested within *Perilitus* but suggested that generic status be retained pending further phylogenetic research. Other authors such as van Achterberg et al. (2000) and Belokobylskij (2000b) have treated *Microctonus* as a subgenus of *Perilitus*.

***Myiocephalus* Marshall, 1898**

Fig. 22

Diagnosis. Head triangular in frontal view; eyes bulging, and head much wider than long in dorsal view (Fig. 22D). First metasomal segment greatly narrowed basally (Fig. 21B). Tarsal claws simple. Forewing crossvein m-cu present (Fig. 22C). Forewing vein RS complete to wing margin (Fig. 22C). Forewing vein M+Cu reduced, mostly or entirely not tubular (Fig. 22C). (RS+M)a vein of forewing absent (Fig. 22C). Forewing second submarginal cell open (Fig. 22C). Scape (SC) length is less than 2.5 times the scape width (Fig. 22D).

Biology. Associated with ants, but not reared (Donisthorpe, 1927).

Diversity. Five described species, several undescribed species occur in the southwestern USA and Mexico. There are 37 sequences and six BINs (proxies for species) in BOLD (Oct. 18, 2024). Three are from Finland and three from Canada; none is shared between the Old and New World. Canada and Finland are the only two Holarctic countries with extensive, public barcodes on BOLD for this group.

Distribution. Holarctic, Oriental, and Central American (Mexico).

Publications. Li et al. (2020) revised the world's species.

Note. Foissner and van Achterberg (1997) showed that the genus name *Loxocephalus* Foerster was preoccupied, therefore the correct name for the genus is *Myiocephalus*.

***Neoneurus* Haliday, 1838**

Fig. 23

Diagnosis. The forewing venation of *Elasmosoma* and *Neoneurus* are similar, and both are unique. The two

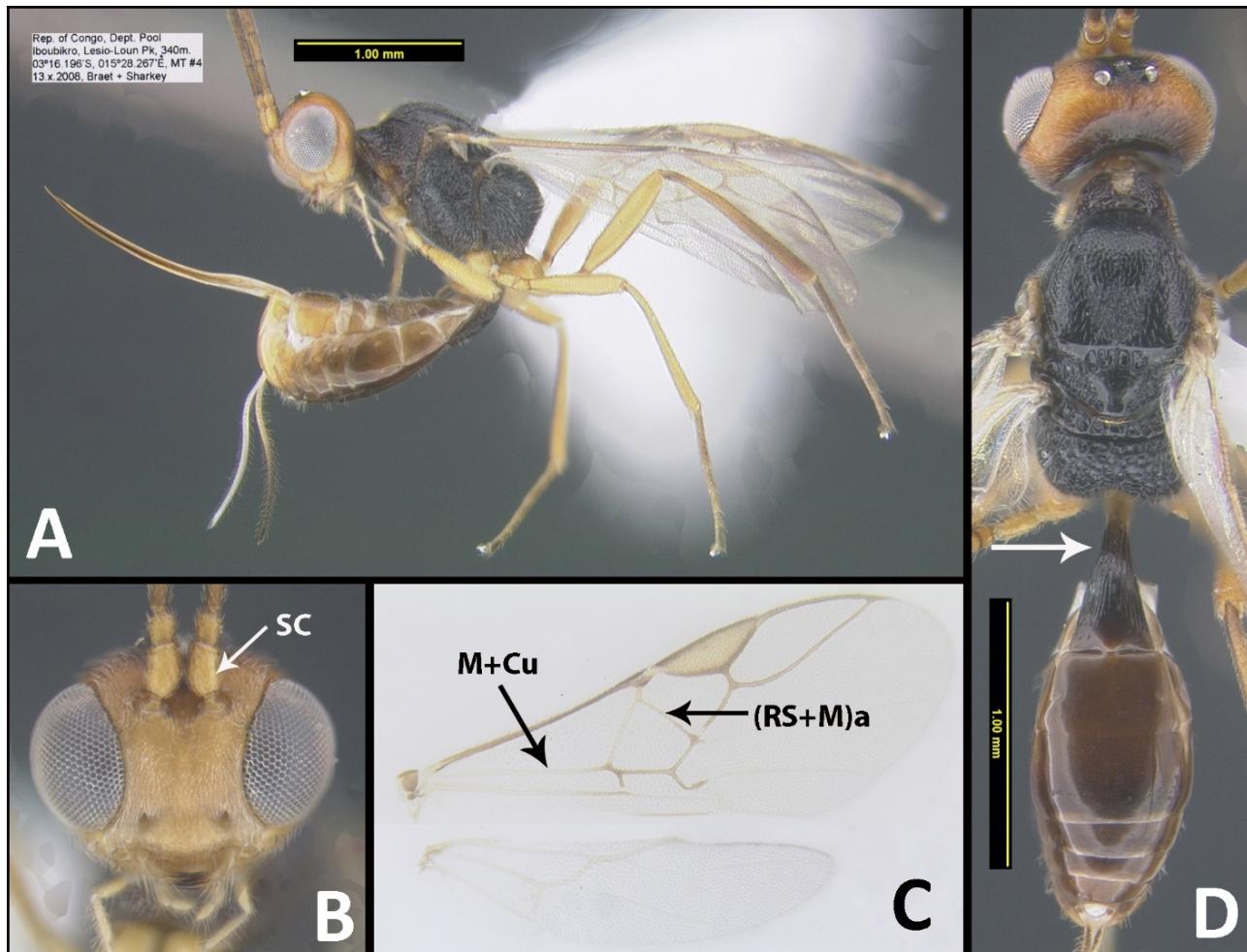


Figure 25. *Perilitus* sp.

genera may be distinguished with several characters including the forewing of *Neoneurus* having RS sclerotized and present apically (Fig. 23B).

Biology. Endoparasitoids of adult ants of the genus *Formica*. Gómez Durán and van Achterberg (2011) document the oviposition behavior of three genera of Neoneurini, including *Neoneurus*. They include links to film clips of the behaviour which can be viewed on YouTube (<https://www.youtube.com/watch?v=GYGdEoaMYWs>).

Diversity. Sixteen species are described, seven in the Nearctic. There are 10 BINs (proxies for species) from Canada and the USA in BOLD (Oct. 21, 2024) suggesting that there are at least twice that number of species in the Nearctic.

Distribution. Holarctic.

Publications. Shaw (1992) revised the Nearctic species. Stigenberg et al. (2015) showed that Neoneurini (*Elasmosoma* and *Neoneurus*) belong in the Euphorinae. Previously the tribe had subfamily status, Neoneurinae (Shaw, 1997a).

***Orionis* Shaw, 1987**

Fig. 24

Diagnosis. First metasomal segment constricted near base and 5 or more times longer than apical width (Fig. 24A). Scape (SC) length is less than 2.5 times width (Fig. 24B). Forewing vein M+Cu complete and tubular (Fig. 24C). (RS+M)a vein of forewing complete. Second submarginal cell open, not closed apically (Fig. 24C).

Biology. Unknown; however, a European species has been photographed attacking an adult earwig (Dermoptera) (Bendixen and Shaw, 2024).

Diversity. Ten described species, four of which are Neotropical, not a species-rich genus but undescribed species remain.

Distribution. Neotropical, Palearctic, and Oriental.

Publications. Bortoni et al. (2016) revised the Neotropical species and provided a key. Broad and Stigenberg (2021) revised the Old World species and provided a key. Gupta et al. (2024) described new species from India and included a key to the Old World species.

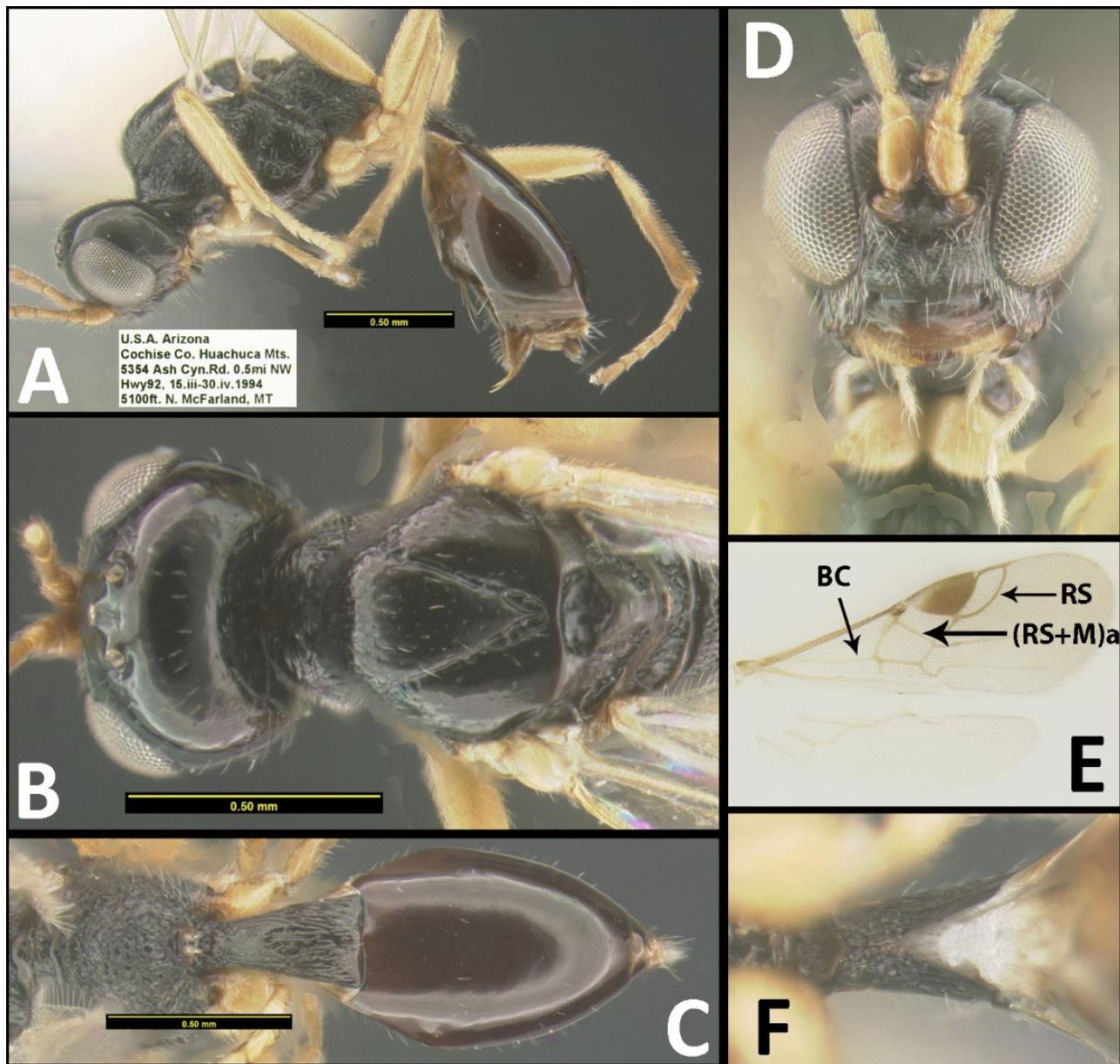


Figure 26. *Peristenus* sp.

***Perilitus* Nees, 1819**

Fig. 25

Diagnosis. First metasomal segment greatly constricted basally and lacking dorsal pits (Fig. 25D). Forewing vein M+Cu present and tubular (though this does not show well in the overexposed image in Fig. 25C). (RS+M)a vein of forewing present (Fig. 25C). Scape (SC) length is less than 2.5 times width (Fig. 25B).

Biology. Endoparasitoids of adult and sometimes larval beetles, especially Curculionidae, Chrysomelidae, and Carabidae.

Diversity. About 140 species are described but only about 12 from the New World. Many more are undescribed.

Distribution. Cosmopolitan.

Publications. There are no treatments of the few described New World species.

Note. Stigenberg et al. (2015) showed that *Microctonus* is nested within *Perilitus* but chose to maintain it as a separate genus pending further phylogenetic study. Van Achterberg et al. (2000) and Belokobylskij (2000b) treated *Microctonus* as a subgenus of *Perilitus*.

***Peristenus* Foerster, 1863**

Fig. 26

Diagnosis. Basal cell (BC) of forewing setose, though less so than other forewing cells (Fig. 26E, couplet 32B). Notauli present. Tergum of first metasomal segment fused

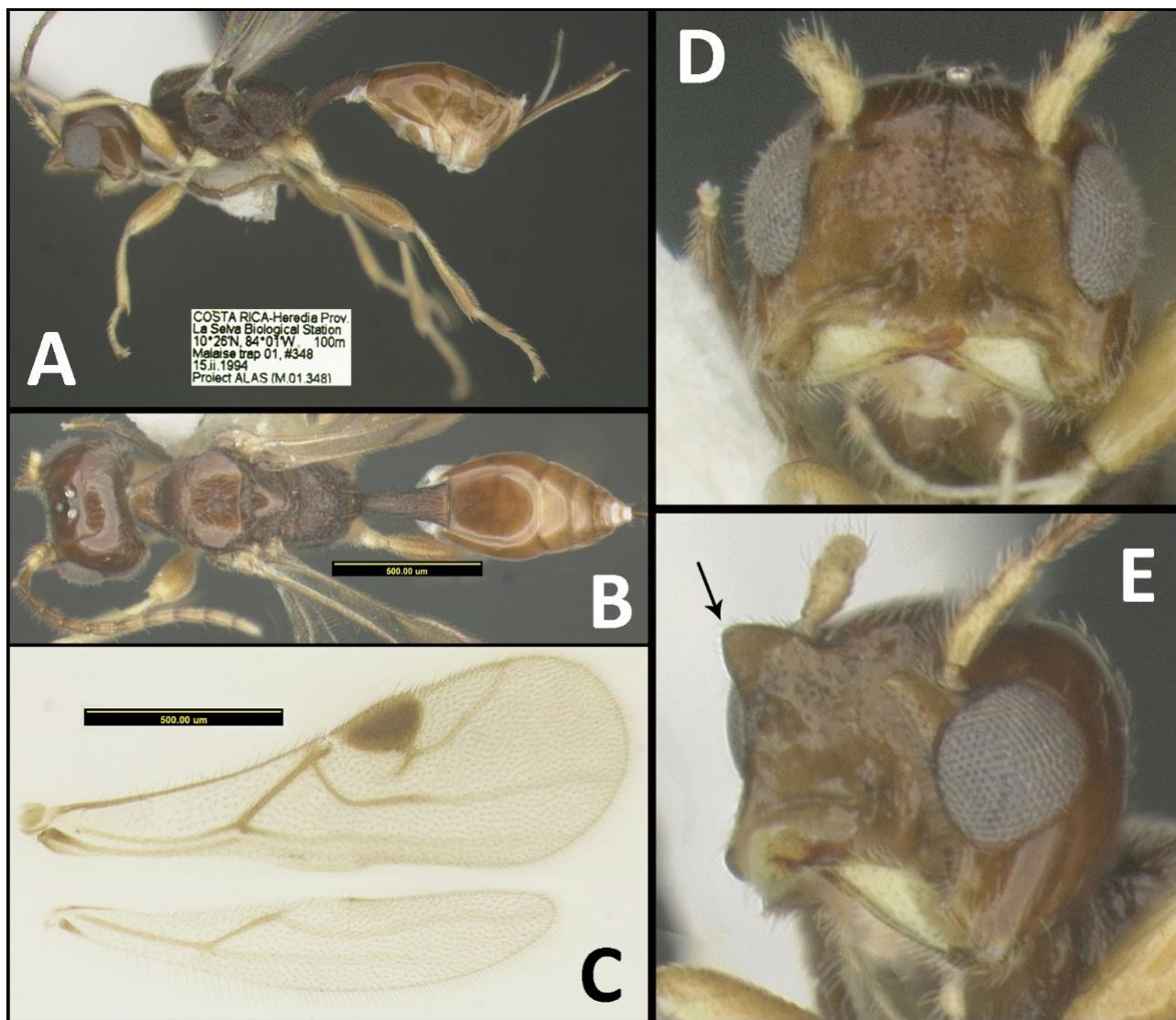


Figure 27. *Plynops* sp.

or touching ventrally in anterior portion only (Fig. 26F). Forewing not banded (see *Leiophron* image Fig. 16B). RS vein of forewing ending nearer stigma than apex of wing (Fig. 26E). (RS+M)a vein of forewing present (Fig. 26E). None of these characteristics will separate all species from *Leiophron*.

Biology. Koinobiont endoparasitoids of late instar nymphs and adults of Miridae (Hemiptera). Early instar nymphs are parasitized, and the mature parasite larvae emerge from either the mature host nymphs or the adults (Zhang et al., 2018).

Diversity. About 140 described species, about 40 of these in the Nearctic. None is described from neotropics, but a few undescribed species occur there. Presently there are 42 BINs (proxies for species) in BOLD (Oct. 18, 2024) from Canada implying that there should be more than 100 species in the Nearctic.

Distribution. Cosmopolitan, but concentrated in the Holarctic.

Publications. Goulet and Mason (2006) reviewed, and Zhang et al. (2017) revised the species attacking the *Lygus* bug. Zhang et al. (2018) redefined the limits of the genus. Loan (1974) revised the Nearctic species.

***Plynops* Shaw, 1996**

Fig. 27

Diagnosis. Face with projections below antennae (Fig. 27E). Forewing venation unique, similar or identical to Fig. 27C.

Biology. Unknown.

Diversity. 10 described species and about that number are probably undescribed.

Distribution. Restricted to the New World from southern Florida to Brazil.

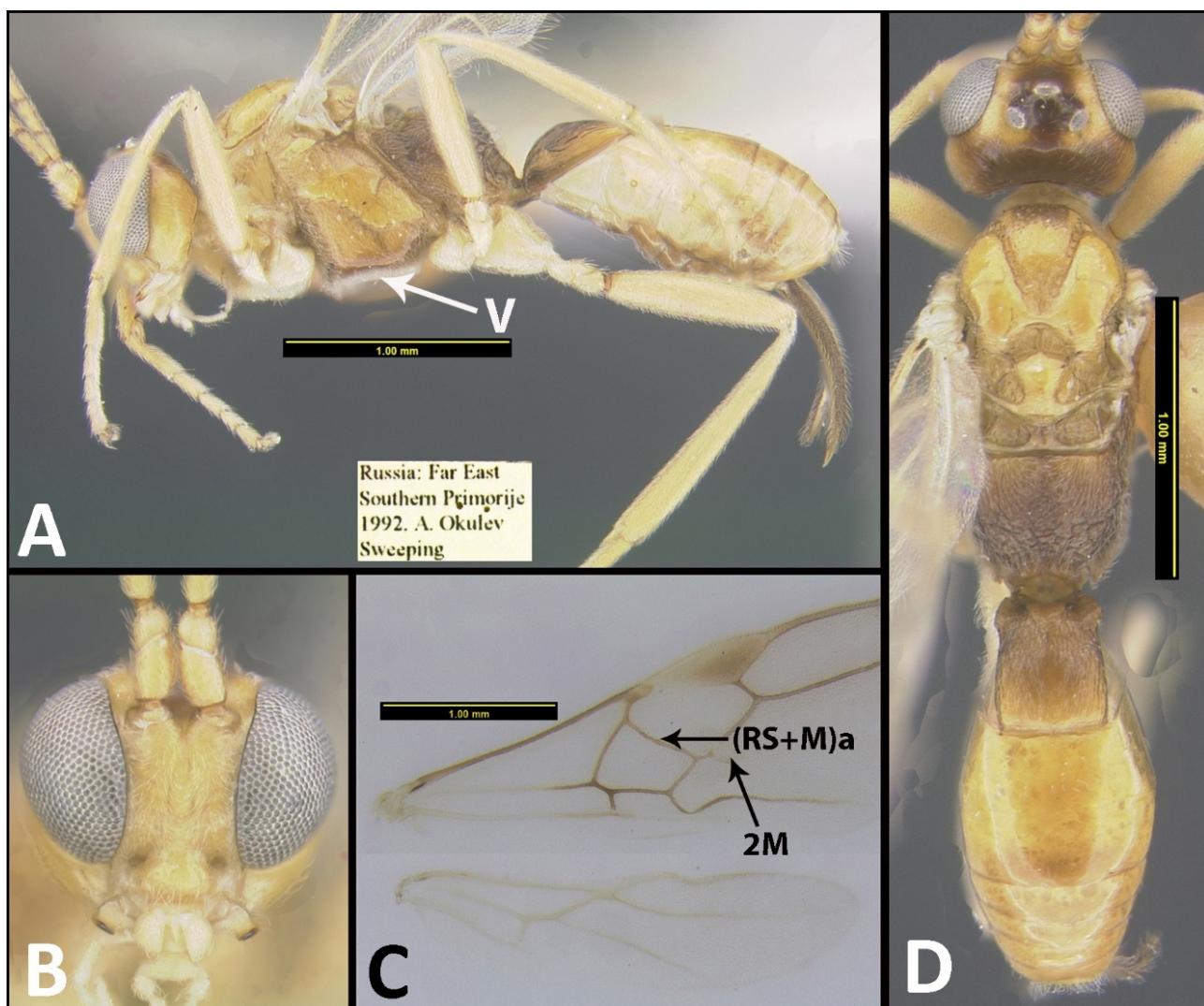


Figure 28. *Pygostolus* sp.

Publications. Shaw (1996) erected the genus and described and keyed the 10 species.

***Pygostolus* Haliday, 1833**

Fig. 28

Diagnosis. Forewing 2M sclerotized and present as a short but distinct branch (Fig. 28C). (RS+M)a vein of forewing present (Fig. 28C). Tarsal claws simple. Females of most species have the venter (V) of the mesosoma flattened and setose (Fig. 28A). First metasomal segment only slightly constricted near base, almost as wide near base as it is apically (Fig. 28D). Apical flagellomere with a sharp terminal spine.

Biology. Usually endoparasitoids of adult Curculionidae, but larval or pupal stages may also be attacked with emergence always coming from the adult (van Achterberg, 1992b).

Diversity. Fourteen described (extant) species, four of which occur in the Nearctic. These same four also occur in the Palearctic (van Achterberg, 1992b).

Distribution. Holarctic and Neotropical including Chile.

Publications. Van Achterberg (1992b) revised the Holarctic species.

***Ropalophorus* Curtis, 1837**

Fig. 29

Diagnosis. The short antennae with 8 flagellomeres are unique among Euphorinae (Fig. 29C).

Biology. Endoparasitoids of adult Scolytidae (Yang et al., 2003).

Diversity. Four described species, perhaps a few undescribed.

Distribution. Holarctic, three species in China and one in the Nearctic (Shaw, 1985).

Publications. Yang et al. (2003) provided a key to the world species.

Note. *R. wisconsinensis* Shenefelt was synonymized with *R. clavicornis* (Wesmael) (Yang et al., 2023).

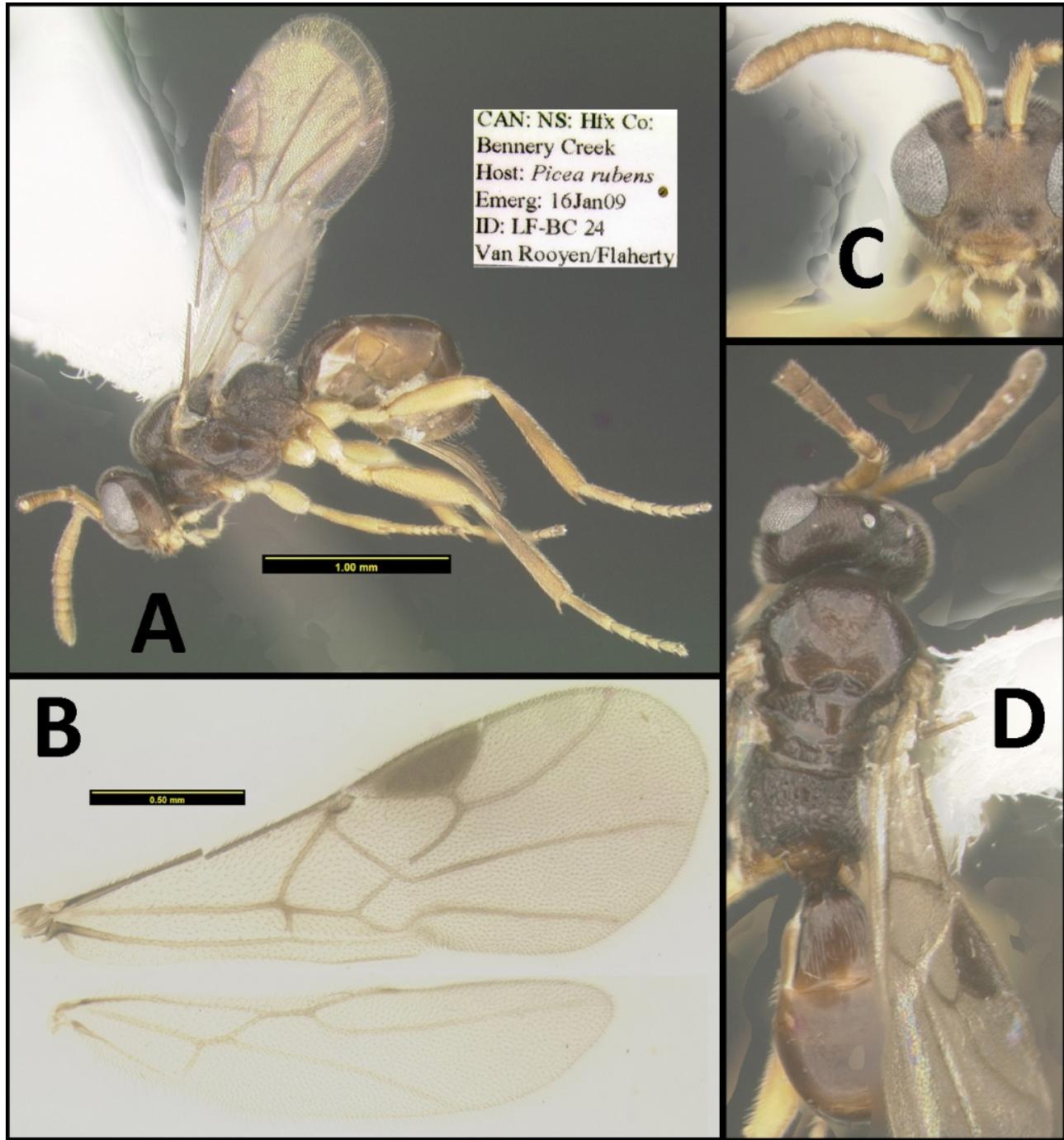


Figure 29. *Ropalophorus* sp.

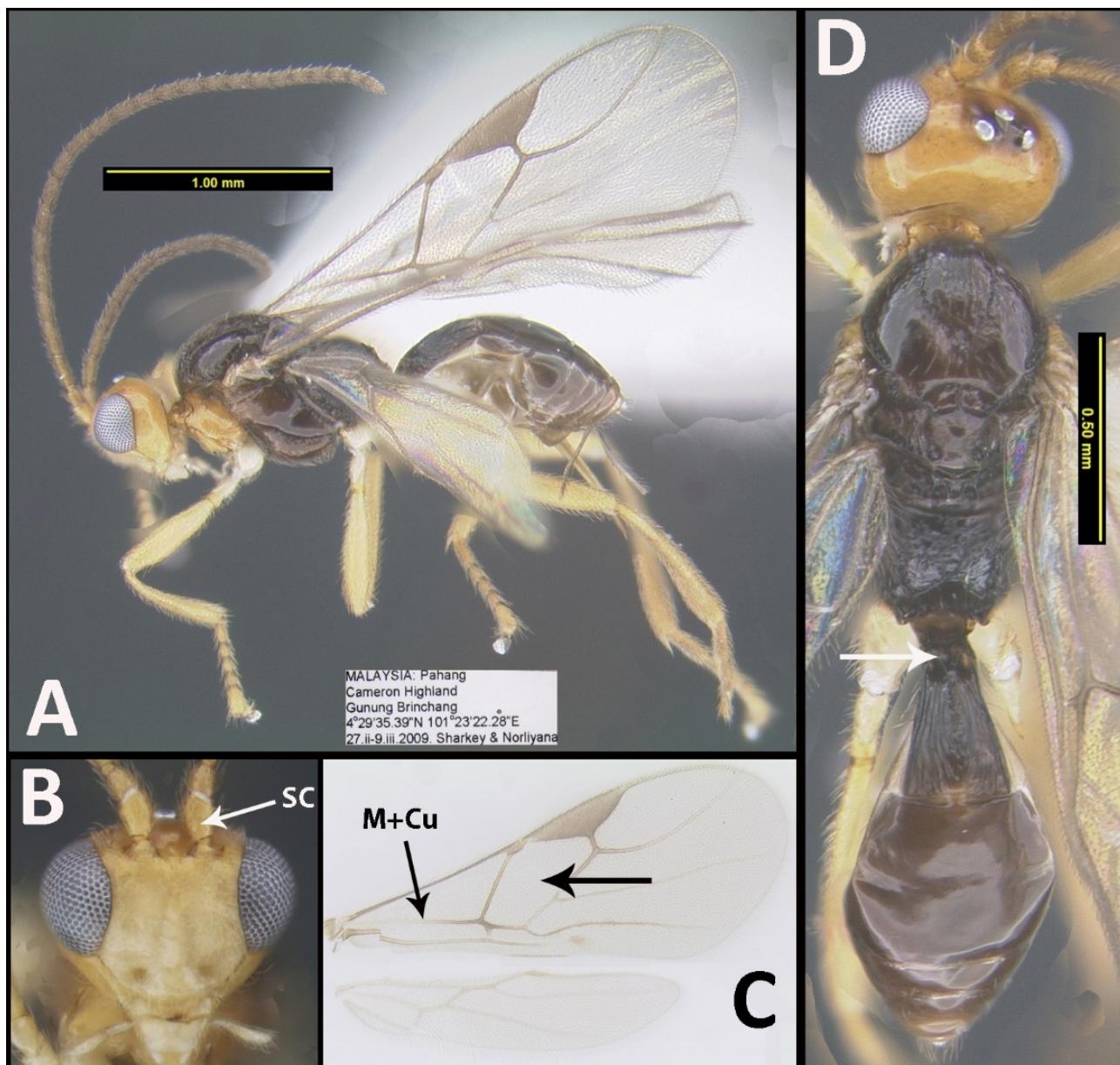


Figure 30. *Spaticopis* sp.

Spaticopis van Achterberg, 1977

Fig. 30

Diagnosis. First metasomal segment with large basal dorsal pits (Fig. 30D). Forewing vein M+Cu reduced, mostly or entirely not tubular (Fig. 30C). (RS+M)a vein of forewing absent (Fig. 30C). Scape (SC) length is less than 2.5 times width (Fig. 30B).

Biology. Unknown.

Diversity. There is one species described, and several are undescribed.

Distribution. Oriental and Aftrotropical (new record), Holarctic, U.S.A. and Canada in the Nearctic.

Publications. Van Achterberg (1977) described the sole species.

Streblocera Westwood, 1833

Fig. 31

Diagnosis. The shortest distance between eyes is much longer than eye width in anterior view (Fig. 31B). Scape length more than 4 times scape width (Fig. 31B). (RS+M)a vein of forewing mostly or entirely absent (Fig. 31C). Propodeum rounded, lacking projections laterally (Fig. 31A). Female antennae of one undescribed Neotropical species and a described species from Brazil are raptorial (as in Fig. 31A) whereas all males and all other females in the New World have elongated scapes but otherwise unmodified antennae.

Biology. Endoparasitoids of adult Chrysomelidae, summarized in Chen and van Achterberg (1997).

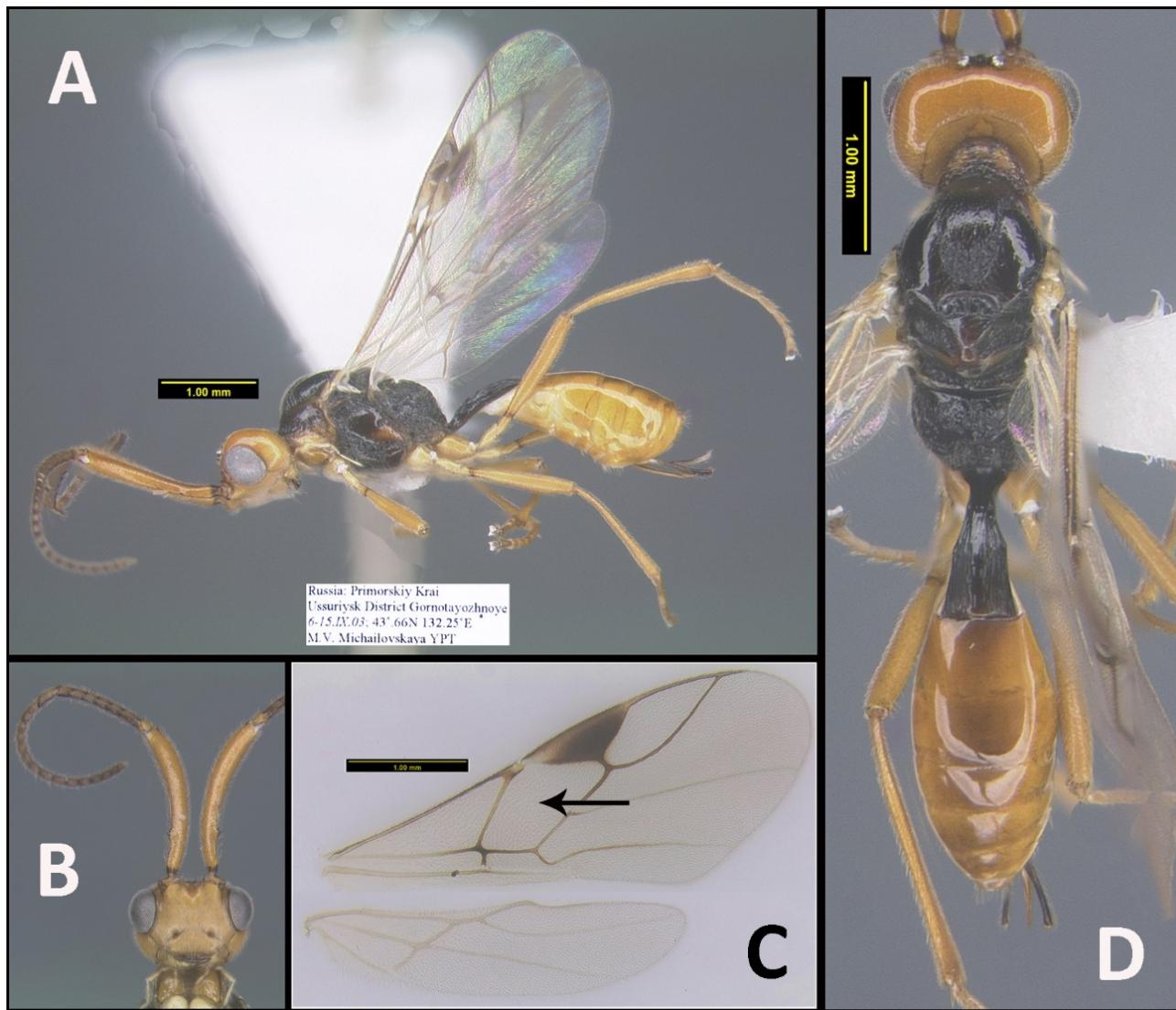


Figure 31. *Streblocera* sp.

Diversity. More than 100 described species worldwide, but few in the New World. There are four undescribed species from Costa Rica on BOLD (Nov. 7, 2024) suggesting that there are several dozen species in the Neotropics.

Distribution. Pantropical, Oriental, and Palearctic.

Publications. De Almeida et al. (2019) described a species from Brazil.

Notes. A species of *Streblocera* from Canada described by Walley and MacKay (1963) was transferred to *Marshiella*, *M. pulvillicornis* (Walley and Mackay) by Shaw (1985). *Lecythodella* is now considered a subgenus of *Streblocera* following Stigenberg et al. (2015).

***Syntretus* Foerster, 1863**

Fig. 32

Diagnosis. Notauli absent (Fig. 32D). Tarsal claws cleft. Forewing vein M+Cu reduced, mostly or entirely not

tubular (Fig. 32C). (RS+M)a vein of forewing mostly or entirely absent (Fig. 32C).

Biology. Endoparasitoids of adult Ichneumonidae, the adults of several species of bees as well as *Drosophila*. Details are in Moore et al. (2024) who also summarize the biology of the genus. Folly et al. (2025) reported the presence of polydnavirus in nine European species of *Syntretus*.

Diversity. 62 described species, 7 in the Nearctic and 7 in the Neotropical region. There are 39 BINs (proxies for species) in BOLD from Costa Rica (Oct. 14, 2024). This implies that there may be several hundred species in the Neotropical region alone.

Distribution. Cosmopolitan.

Publications. Papp and Shaw (2000) revised the species of the subgenus *Falcosyntretus* Tobias from the New World with five new species and a key to species. Van Achterberg and Haeselbarth (2003) revised the *Syntretus*

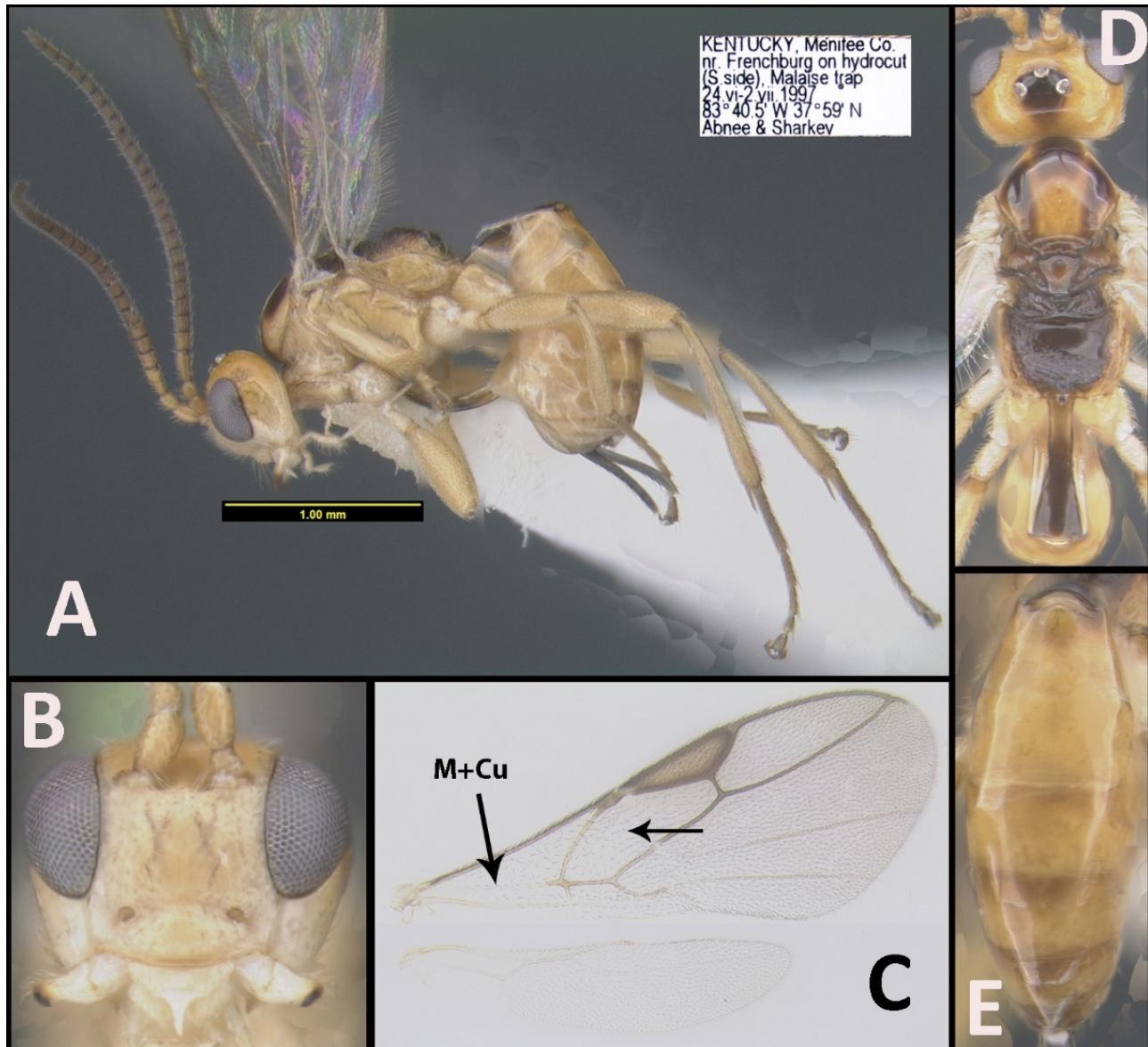


Figure 32. *Syntretus* sp.

species of Europe, summarized the taxonomy and biology of the genus. There are no recent treatments of the Nearctic species except for that of Moore et al. (2024).

Note. Van Achterberg and Haeselbarth (2003) treated *Falcosyntretus* as a junior synonym of *Syntretus*.

Townesilitus Haeselbarth and Loan, 1983

Fig. 33

Diagnosis. Very similar to *Microctonus*. Head circular in frontal view and eyes not bulging (Fig. 33D). First metasomal segment greatly narrowed basally (Fig. 33C). Tarsal claws simple. Forewing vein M+Cu mostly or entirely tubular (Fig. 33B). (RS+M)a vein of forewing absent (Fig. 33B). Scape (SC) length less than 2.5 times scape width (Fig. 33D). Propodeum not evenly areolate

rugose. The presence of areolate rugose sculpture is variable, however there are carinae delimiting larger cells on the propodeum and these are not present in 90% of *Microctonus* species. Except for the last feature these states also diagnose members of *Microctonus*. Features to distinguish between these two genera that have been used in the past include: 1. Clypeus with blister-like sculpture on apical margin (barely discernable in Fig. 33D) or clypeus with a flattened apical margin. These states are found in only a few New World species and are difficult to see but work well when present. 2. First tergite in front of spiracles closed ventrally, tube-shaped and rounded laterally. This condition is also found in many New World species of *Microctonus*.

Biology. Endoparasitoids of adult flea beetles (Alticinae: Chrysomelidae) (Stigenberg, 2017).

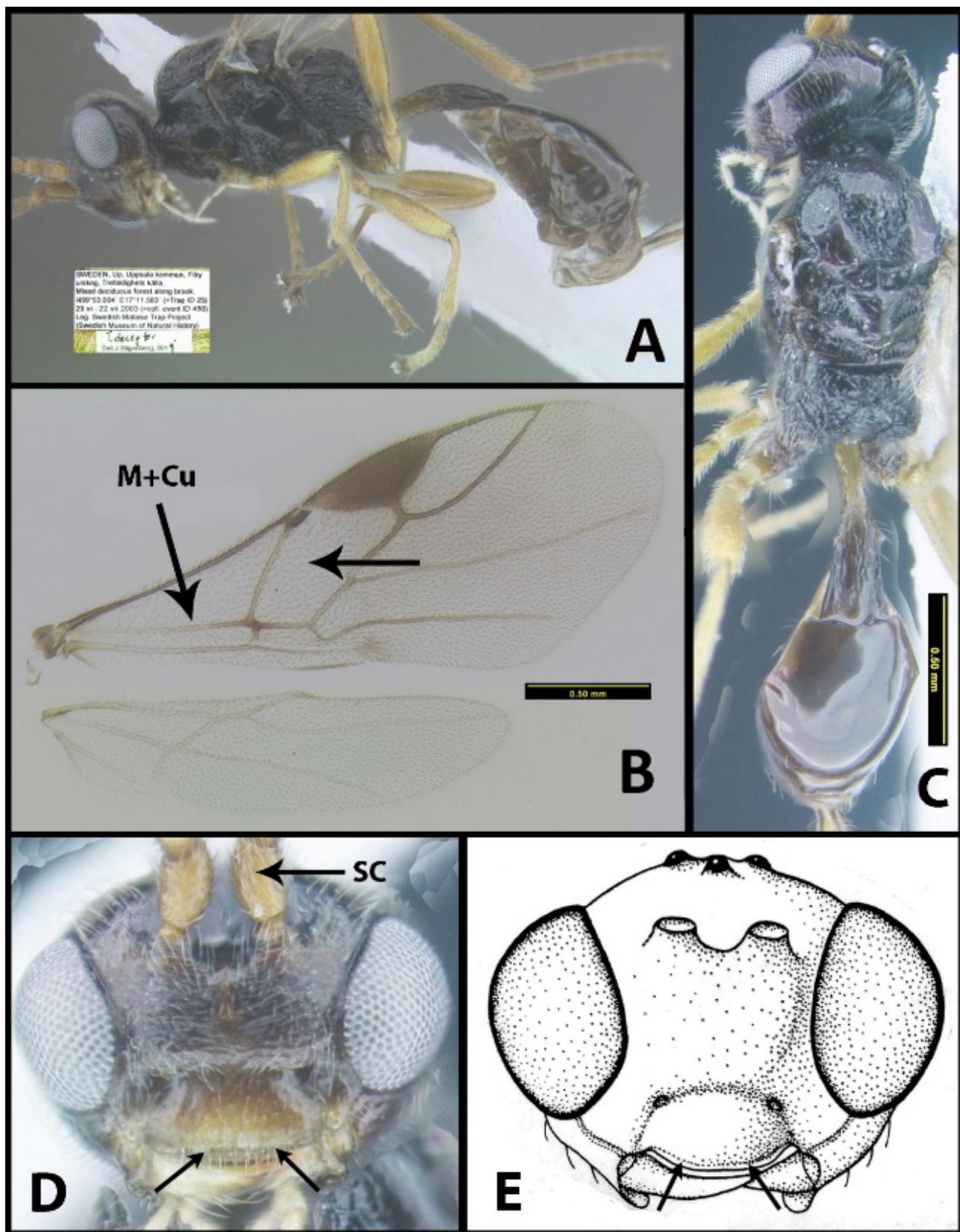


Figure 33. *Townesilitus deceptor* Wesmael.

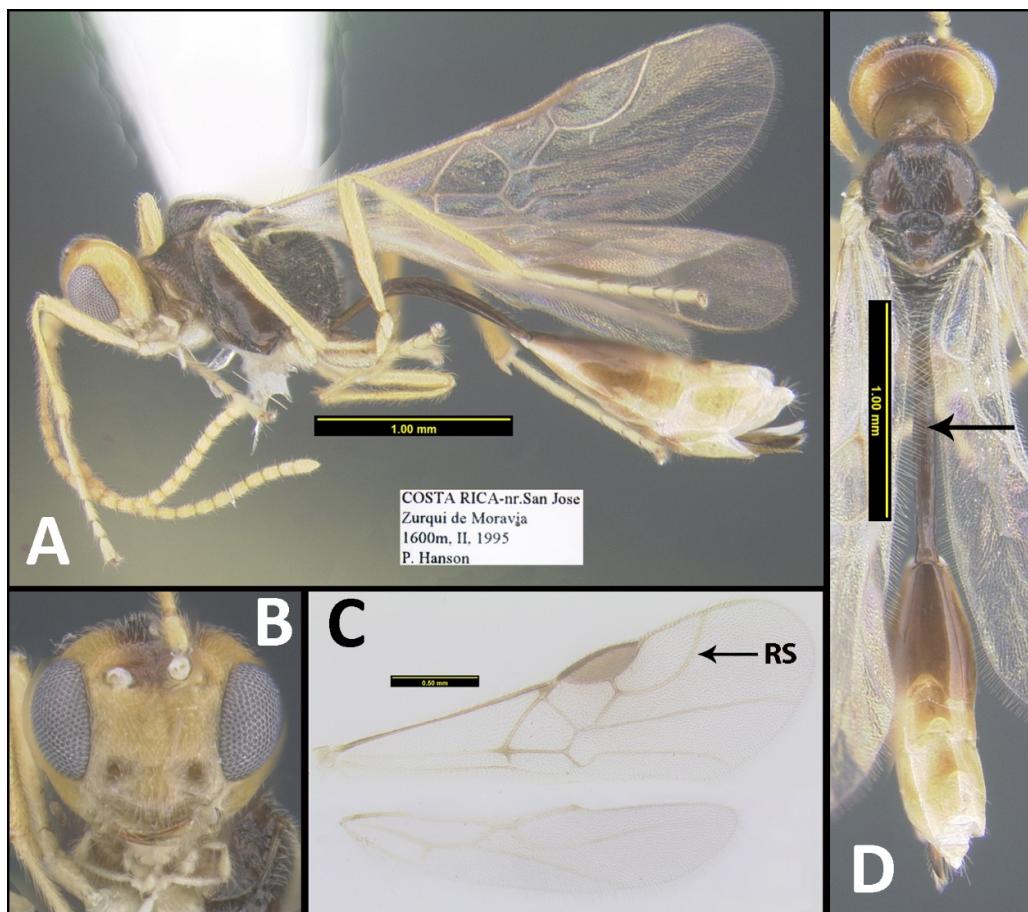


Figure 34. *Wesmaelia lizanoi* Shaw.

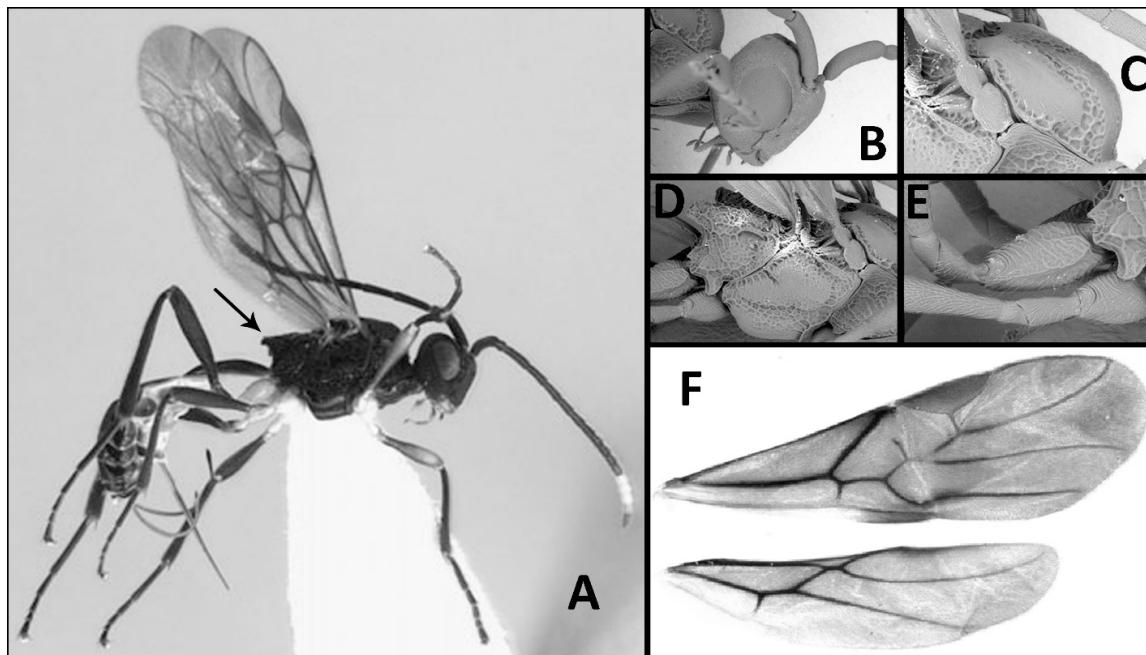


Figure 35. *Yanayacu* sp. Images modified from Shaw (2012).

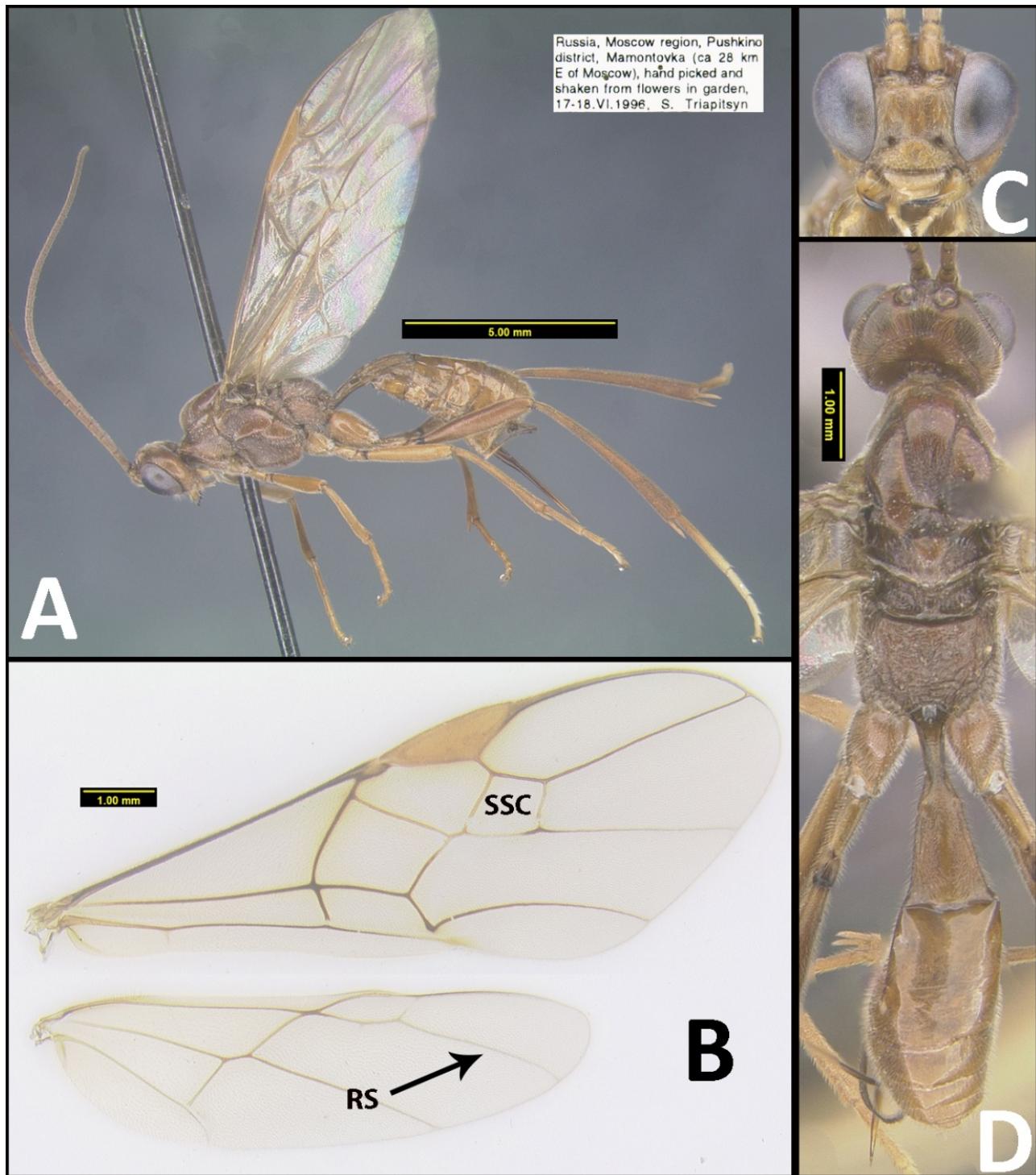


Figure 36. *Zele* sp.

Diversity. 12 described species, including three Nearctic species. Perhaps a dozen more undescribed Nearctic species. Presently in BOLD (Oct. 19, 2024) there are four BINs (proxies for species) from Costa Rica and six from Canada.

Distribution. Holarctic, Neotropical and Oriental.

Publications. No general treatments for the Nearctic region. Some species were originally described under *Microctonus*.

Note. According to co-author van Achterberg, *Gamosecus* Provancher, 1880 (type species: *G. mellinus* Provancher, 1880) either belongs to the large group of Nearctic *Microctonus* with the basal half of the first tergum tube-shaped or to *Townesilitus*. In the latter case *Gamosecus* is the senior name for what is now called *Townesilitus*. The drawing in Fig. 33E shows the “lips” on the margin of the clypeus typical of some species of *Townesilitus*. Unfortunately, the identification of the specimen is questionable and the type specimen of *G. mellinus* needs to be checked.

***Wesmaelia* Foerster, 1863**

Fig. 34

Diagnosis. First metasomal segment is exceptionally long and thin throughout its length (Fig. 34D). Forewing second submarginal cell open, not closed apically (Fig. 34C). RS vein of forewing ending well before wing apex (Fig. 34C).

Biology. Endoparasitoids of late instar nymphs and adults of Nabidae (Hendrick and Stern, 1970).

Diversity. About 12 species are described. One Nearctic and one Neotropical species are described. There may be about a dozen undescribed species.

Distribution. Cosmopolitan, except Australian and African realms.

Publications. Shaw (1997b) described a species from Costa Rica and provided a key to the two New World species.

***Yanayacu* Zhang and Chen, 2015**

Fig. 35

Diagnosis. Basal flagellomere about 5x longer than wide (Fig. 35B). Propodeum with projections laterally (Fig. 35A).

Biology. Unknown.

Diversity. Only known by the type species. A few more are expected to be discovered.

Distribution. Neotropical.

Publications. Shaw (2012) proposed the genus *Napo* and described the sole species. The mating and defensive behavior of *Yanayacu townsendi* Shaw (as *Napo townsendi*) was explored by Robinson et al. (2015)

Note. Zhang and Chen (2015) showed that the generic name *Napo* was preoccupied by a deltocephaline leafhopper genus and changed the name of this braconid genus to *Yanayacu*.

***Zele* Curtis, 1832**

Fig. 36

Diagnosis. Forewing second submarginal cell (SSC) 4-sided (Fig. 36B). Hind wing vein RS bending away from anterior wing margin (Fig. 36B).

Biology. Endoparasitoids of lepidopteran larvae.

Diversity. About 30 species are described, about 13 in the New World. A few dozen may be undescribed.

Distribution. Cosmopolitan, except Australia.

Publications. Muesebeck (1923) revised the USA and Canadian species under *Meteorus*. Van Achterberg (1979) revised the world species, and added species (van Achterberg, 1984).

Note. Stigenberg et al. (2015) and previous authors showed that *Zele* is nested within *Meteorus* and may not deserve separate status.

Acknowledgements

Thank you to reviewers Caroline Boudreault and José Fernandez for their valuable comments and to the editors at CJAI for their dedication. DLJQ was supported by the Rachadaphisek Somphot Fund for postdoctoral fellowship, Graduate School, Chulalongkorn University, Thailand. Research funding for SRS and imaging equipment was provided by National Science Foundation grants DEB-10-20751 and DEB 14-42110 (Dimensions of Biodiversity Program). Additional research support for SRS was provided by McIntire-Stennis Grant Project number WYO-612-20, Studies of Parasitoid Wasps of Forest Ecosystems.

References

- Aeschlimann, J. 1980. The *Sitona* (Coleoptera: Curculionidae) species occurring on *Medicago* and their natural enemies in the Mediterranean region. *Entomophaga*, **25**: 139–153. <https://doi.org/10.1007/BF02374316>
- Aguirre, H., de Almeida, L.F., Shaw, S.R., and Sarmiento, C.E. 2015. An illustrated key to Neotropical species of the genus *Meteorus* Haliday (Hymenoptera, Braconidae, Euphorinae). *ZooKeys*, **489**: 33–94. <https://doi.org/10.3897/zookeys.489.9258>
- Aguirre, H., de Almeida, L.F., and Shaw, S.R. 2017. Revision of the genus *Centistes* (Hymenoptera: Braconidae: Euphorinae: Centistini) of Costa Rica. *Zootaxa*, **4216**(1): 4–26 <https://doi.org/10.11646/zootaxa.4216.1.1>
- Amat, Z., Achterberg, C.V., Zhao, G.-S., Fang, Y., Tang, P. & Li, Q. 2025. Unveiling a new taxon belonging to *Marshiella* Shaw (Hymenoptera: Braconidae). *Zootaxa*, **5679**: 143–147. <https://doi.org/10.11646/zootaxa.5679.1.9>
- Belokobylskij, S.A. 2000a. Euphorinae. pp.192–399. In: Ler PA. (ed.) Key to the insects of Russian Far East. Vol. IV. Neuropteroidea, Mecoptera, Hymenoptera. Pt 4. Opredelitel nasekomykh Dalnego Vostoka Rossii. T. IV. Setchatokryloobraznye, skorpionnitsy, pereponchatokrylye. Ch. 4. Dalnauka, Vladivostok. 651 pp.
- Belokobylskij, S.A. 2000b. New species of the subfamily

- Euphorinae (Hymenoptera, Braconidae) from east Palaearctic. Part 3. Far Eastern Entomologist, **89**: 61–88. <http://www.zin.ru/labs/insects/Hymenopt/Personalia/Belokobylskij/pdf/111-2000.pdf>
- Belokobylskij, S.A. 2001. First record of the genus *Centistina* Enderlein, 1912 from the Palaearctic Region (Hymenoptera: Braconidae. Euphorinae). Zoosystematica Rossica, **10**: 166.
- Belshaw, R., and Quicke, D.L.J. 2002. Robustness of ancestral state estimates: evolution of life history strategy in ichneumonoid parasitoids. Systematic Biology, **51**: 450–477. <https://doi.org/10.1080/10635150290069896>
- Bendixen, L., and Shaw, M.R. 2024. Are Dermaptera the hosts of the genus *Orionis* (Hymenoptera: Braconidae: Euphorinae)? Entomologist's Monthly Magazine, **160**(4): 263–265. <https://doi.org/10.31184/M00138908.1604.4279>
- Bortoni, M.A., Shimbori E.M., Shaw S.R., de Souza-Gessner C., and Penteado-Dias, A.M. 2016. A review of the genus *Orionis* Shaw (Hymenoptera: Braconidae: Euphorinae) and first records of the genus from South America and the Oriental Region. Zootaxa, **4208**: 249–260. <https://doi.org/10.11646/zootaxa.4208.3.4>
- Broad, G.R., and Stigenberg, J. 2021. The genus *Orionis* Shaw (Hymenoptera, Braconidae, Euphorinae) in the Old World. Journal of Hymenoptera Research, **88**: 133–145. <https://doi.org/10.3897/jhr.88.76177>
- Chen, X.X., and van Achterberg, C. 1997. Revision of the subfamily Euphorinae (excluding the tribe Meteorini Cresson) (Hymenoptera: Braconidae) from China. Zoologische Verhandelingen, **313**: 1–217.
- de Almeida, L.F.V. and Penteado-Dias, A.M. 2018. First record of the genera *Centistoides* van Achterberg and *Pygostolus* Haliday (Hymenoptera: Braconidae) in Brazil, with the description of new species. Zootaxa, **4457**: 465–473. <https://doi.org/10.11646/zootaxa.4457.3.8>
- de Almeida, L.F.V., Souza-Gessner, C.D.S., and Penteado-Dias, A.M. 2019. Three new species of the subfamily Euphorinae (Hymenoptera: Braconidae) from Brazil. Zootaxa, **4638** (2), 255–263. <https://doi.org/10.11646/zootaxa.4638.2.5>
- Donisthorpe, H. 1927. The guests of British ants. London. 244 pp.
- Deyrup, M. 1981. A new species of *Cryptoxilos* (Hymenoptera: Braconidae) attacking adult *Lymantor decipiens* LeConte (Coleoptera: Scolytidae). Entomological News, **92**: 177–180.
- Dheilly, N.M., Maure, F., Ravallec, M., Galinier, R., Doyon, J., Duval, D., Leger, L., Volkoff, A.N., Missé, D., Nidelet, S. and Demolombe, V. 2015. Who is the puppet master? Replication of a parasitic wasp-associated virus correlates with host behaviour manipulation. Proceedings of the Royal Society B: Biological Sciences, **282**(1803): 20142773. <https://doi.org/10.1098/rspb.2014.2773>
- Foissner, W., and van Achterberg, C. 1997. The valid name for the genus *Loxocephalus* Foerster, 1862 (Insecta, Hymenoptera: Braconidae), preoccupied by *Loxocephalus* Eberhard, 1862 (Protozoa: Ciliophora). Zoologische Mededelingen, **71**: 31–32.
- Folly, A.J., Porter, H.R., Galloway, J.A., Schmidt, S., Shaw, M.R., Broad, G.R., Gammans, N., Brown, M.J., Barnes, I. and Brace, S. 2025. DNA from museum samples of a parasitoid wasp genus (Braconidae: *Syntretus*) offers novel insights into host-parasitoid interactions. Insect Conservation and Diversity. <https://doi.org/10.1111/icad.12803>
- Gatti, C., R., Reich, P. B., Gamarra, J. G., Crowther, T., Hui, C., Morera, A., ... & Liang, J. 2022. The number of tree species on Earth. Proceedings of the National Academy of Sciences, **119**: e2115329119. <https://doi.org/10.1073/pnas.2115329119>
- Gómez, Durán J.M., and van Achterberg, C. 2011. Oviposition behaviour of four ant parasitoids (Hymenoptera, Braconidae, Euphorinae, Neoneurini and Ichneumonidae, Hybrizontinae), with the description of three new European species. ZooKeys, **125**: 59–106. <https://doi.org/10.3897/zookeys.125.1754>
- Goulet, H., and Mason, P.G. 2006. Review of the Nearctic species of *Leiophron* and *Peristenus* (Hymenoptera: Braconidae: Euphorinae) parasitizing *Lygus* (Hemiptera: Miridae: Mirini). Zootaxa **1323**: 1–118. <https://doi.org/10.11646/zootaxa.1323.1.1>
- Gupta, A., van Achterberg, C., Pattar, R., Kumar, H.M.H., and Sushil, S.N. 2024. Review of the genera *Orionis* Shaw and *Stenothremma* Shaw (Braconidae) from India, with description of three new species. European Journal of Taxonomy, **943**: 218–238. <https://doi.org/10.5852/ejt.2024.943.2597>
- Hendrick, R.D., and Stern, V.M. 1970. Biological studies of three parasites of *Nabis americanus* (Hemiptera: Nabidae) in southern California. Annals of the Entomological Society of America, **63**: 382–391.
- Jackson, D.J. 1920. Bionomics of weevils of the Genus *Sitones* injurious to leguminous crops in Britain. Annals of Applied Biology, **7**: 269–298. <https://doi.org/10.1111/j.1744-7348.1920.tb05310.x>
- Li, J., van Achterberg, C., Zheng, M.-L., Chen, J.H. 2020. A new species of *Myiocephalus* Marshall (Hymenoptera, Braconidae, Euphorinae) from China. ZooKeys, **933**: 95–105. <https://doi.org/10.3897/zookeys.933.49607>
- Loan, C.C. 1974. The North American species of *Leiophron* Nees and *Peristenus* Foerster (Hymenoptera: Braconidae: Euphorinae). Transactions of the Royal Entomological Society of London, **126**: 207–238.
- Loan, C.C., Gerber, G.H., and Reid, D.G. 1971. Biosystematics of the Tingid parasite *Holdawayella* in Ontario (Hymenoptera: Braconidae). Canadian Entomologist, **103**: 1273–1284.
- Loan, C.C., and Matthews, R.W. 1973. *Cosmophorus capeki* n. sp. from New York (Hymenoptera: Braconidae). Proceedings of the Entomological

- Society of Washington, **75**: 205–208.
- Mason, W.R.M. 1964. The genus *Chrysopophthorus* Goidanich (Hymenoptera: Braconidae). The Canadian Entomologist, **96**: 1005–1017.
- Moore, L.D., Amuwa, T.C., Shaw, S.R., and Ballinger, M.J. 2024. *Drosophila* are hosts to the first described parasitoid wasp of adult flies. Nature, **633**: 840–847. <https://doi.org/10.1038/s41586-024-07919-7>
- Muesebeck, C.F.W. 1923. A revision of the North American species of Ichneumon-flies belonging to the genus *Meteorus* Haliday. Proceedings of the United States National Museum, **63**: 1–44.
- Papp, J. 1965. A monograph of the genus *Aridelus* Marshall. (Hymenoptera: Braconidae). Acta Zoologica Hungaricae, **11**: 181–201.
- Papp, J., Shaw, S.R. 2000. A study of the genus *Falcosyntretus* Tobias from the new world with five new species and a key to known species (Hymenoptera: Braconidae: Euphorinae). Proceedings of the Entomological Society of Washington, **102**: 634–642. <https://biostor.org/reference/56982>
- Poinar, G. 2004. Behavior and development of *Elasmosoma* species (Braconidae: Hymenoptera), an endoparasitoid of *Formica* ants (Formicidae: Hymenoptera). Parasitology, **128**: 1–11. <https://doi.org/10.1017/S0031182004004809>
- Pucci, T.M. 2013. Contributions to the classification of the North American *Microctonus* (Braconidae: Euphorinae). Zootaxa, **3725**: 1–150. <https://doi.org/10.1017/S0031182004004809>
- Robinson, W., Dority, D., Kulikowski, A., Shaw, S. 2015. The recently described parasitoid braconid wasp, *Napotownsendi* (Hymenoptera: Braconidae: Euphorinae: Dinocampini), forms leks and deters predators in the Ecuadorian cloud forest. International Journal of Tropical Insect Science, **35**: 103–116. <https://doi.org/10.1017/S1742758415000107>
- Sharanowski, B.J., Dowling, A.P., and Sharkey, M.J. 2011. Molecular phylogenetics of Braconidae (Hymenoptera: Ichneumonoidea), based on multiple nuclear genes, and implications for classification. Systematic Entomology, **36**: 549–572. <https://doi.org/10.1111/j.1365-3113.2011.00580.x>
- Sharkey, M.J., and Wharton, R.A. 1997. Morphology and terminology, pp.19–37. In: Wharton, R.A., Marsh, P.M., and Sharkey, M.J. (eds). Manual of the New World Genera of the Family Braconidae (Hymenoptera). Special Publication of the International Society of Hymenopterists, 439 pp.
- Sharkey, M., Athey, K.J., Fernández-Triana, J.L., Penteado-Dias, A.M., Monckton, S.K. and Quicke, D.L. 2023. Key to the New World subfamilies of the family Braconidae (Hymenoptera: Ichneumonoidea). Canadian Journal of Arthropod Identification, **49**: 1–43. <https://doi.org/10.3752/cjai.2023.49>
- Shaw, M.R., and Huddleston, T. 1991. Classification and biology of braconid wasps (Hymenoptera: Braconidae). Handbooks for the Identification of British Insects **7**: 1–126.
- Shaw, S.R. 1985. A phylogenetic study of the subfamilies Meteorinae and Euphorinae (Hymenoptera: Braconidae). Entomography, **3**: 277–370.
- Shaw, S.R. 1989. A new Mexican genus and species of Dinocampini with serrate antennae (Hymenoptera: Braconidae: Euphorinae). Psyche, **95**: 289–297.
- Shaw, S.R. 1992. Seven new North American species of *Neoneurus* (Hymenoptera: Braconidae). Proceedings of the Entomological Society of Washington, **94**: 26–47.
- Shaw, S.R. 1995. A new species of *Centistes* from Brazil (Hymenoptera: Braconidae: Euphorinae) parasitizing adults of *Diabrotica* (Coleoptera: Chrysomelidae) and key to New World species. Proceedings of the Entomological Society of Washington, **97**: 153–160.
- Shaw, S.R. 1996. *Plynops*, a peculiar new genus and ten new species in the tribe Euphorini (Hymenoptera: Braconidae). Journal of Hymenoptera Research, **5**: 166–183.
- Shaw, S.R. 1997a. Euphorinae. In: Wharton, R.A., Marsh, P.M., and Sharkey, M.J. Eds. Manual of the New World genera of the family Braconidae (Hymenoptera). International Society of Hymenopterists. Special Publication No. 1. 439 pp., pp. 234–254.
- Shaw, S.R. 1997b. The Costa Rican species of *Wesmaelia* Foerster with description of a new species (Hymenoptera: Braconidae: Euphorinae). Pan-Pacific Entomologist, **73**: 103–109.
- Shaw, S.R. 2002. Two new species of *Betelgeuse* from Mexico (Hymenoptera: Braconidae: Euphorinae). Pan-Pacific Entomologist, **78**: 188–196. <https://biostor.org/reference/245418>
- Shaw, S.R. 2007. A new species of *Elasmosoma* Ruthe (Hymenoptera: Braconidae: Neoneurinae) from the northwestern United States associated with western thatching ants, *Formica obscuripes* Forel, and *Formica obscuriventris clivea* Creighton (Hymenoptera: Formicidae). Proceedings of the Entomological Society of Washington, **109**: 1–8. <https://biostor.org/reference/55327>
- Shaw, S.R. 2012. A new genus and new species of Dinocampini (Hymenoptera: Braconidae: Euphorinae) from Napo province in Ecuador. International Journal of Tropical Insect Science, **32**: 101–107. <https://doi.org/10.1017/S1742758412000112>
- Shaw, S.R., and Marsh P.M. 2000. Revision of the enigmatic genus *Marshiella* Shaw in the New World with description of three new species (Hymenoptera: Braconidae, Euphorinae). Journal of Hymenoptera Research, **9**: 277–287. <https://biostor.org/reference/276>
- Smith, O.J. 1953. Species, distribution, and host records of the braconid genera *Microctonus* and *Perlitus* (Hymenoptera: Braconidae). Ohio Journal of Science, **53**: 173–178.
- Stigenberg, J., Boring, C.A., and Ronquist, F. 2015. Phylogeny of the parasitic wasp subfamily Euphorinae (Braconidae) and evolution of its host preferences.

- Systematic Entomology, **40**: 570–591. <https://doi.org/10.1111/syen.12122>
- Stigenberg, J. 2017. Review of the genus *Townesilitus* (Hymenoptera, Braconidae) in Sweden, with description of a new species and a molecular characterization. Entomologisk Tidskrift, **138**: 137–150.
- Stigenberg, J., and van Achterberg, C. 2016. Review of the Palaearctic (and Oriental) *Allurus* (Braconidae, Euphorinae) based on material from Sweden. Biodiversity Data Journal, **4**: e7853. <https://doi.org/10.3897/BDJ.4.e7853>
- van Achterberg, C. 1977. A new Holarctic genus, *Spathicopis* gen. nov., belonging to the Euphorinae, Centistini (Hymenoptera: Braconidae). Entomologische Berichten, **37**: 27–31.
- van Achterberg, C. 1979. A revision of the subfamily Zelinae auct. (Hymenoptera: Braconidae). Tijdschrift voor Entomologie, **122**: 241–479.
- van Achterberg, C. 1984. Addition to the revision of the genus *Zele* Curtis (Hymenoptera: Braconidae). Entomologische Berichten, **44**: 110–112.
- van Achterberg, C. 1985. The genera and subgenera of Centistini, with the description of two new taxa from the Nearctic Region (Hymenoptera: Braconidae: Euphorinae). Zoologische Mededelingen, **59**: 348–362.
- van Achterberg, C. 1992a. *Centistoides* gen. nov. (Hymenoptera: Braconidae: Euphorinae) from Suriname. Zoologische Mededelingen, **66**: 15–348.
- van Achterberg, C. 1992b. Revision of the European species of the genus *Pygostolus* Haliday (Hymenoptera: Braconidae: Euphorinae), with a key to the Holarctic species. Zoologische Mededelingen, **66**: 349–358.
- van Achterberg, C. 1994. The Palaearctic species of the genus *Chrysopophthorus* Goidanich (Hymenoptera: Braconidae: Euphorinae). Zoologische Mededelingen, **68**: 301–307.
- van Achterberg, C., and Haeselbarth, E. 2003. Revision of the genus *Syntretus* Foerster (Hymenoptera: Braconidae: Euphorinae) from Europe. Zoologische Mededelingen, **77**: 9–78.
- van Achterberg, C., Kenis, M., and Sileshi, G. 2000. *Perilitus* (*Microctonus*) *larvicida* spec. nov. (Hymenoptera: Braconidae: Euphorinae) from Zambia. Zoologische Mededelingen, **74**: 57–62.
- van Achterberg, C., and Shaw, S.R. 2000. Two new species of the genus *Centistina* Enderlein (Hymenoptera: Braconidae: Euphorinae) from Costa Rica. Zoologische Mededelingen, **74**: 63–73.
- van Achterberg, C. and Soethof, R. 2023. A genus of Euphorinae (Hymenoptera, Braconidae) new for Europe, with the description of a new species from the Netherlands. Entomologische Berichten, **83**: 92–95.
- Walley, G.S., and MacKay, M.R. 1963. The discovery of *Streblocera* in Canada (Hymenoptera: Braconidae). Canadian Entomologist, **95**: 999–1001.
- Yang, Z., Gu, Y., and Song, Y. 2003. A new species in the genus *Ropalophorus* Curtis (Hymenoptera: Braconidae) from China, parasitizing adults of the bark beetle *Ips subelongatus* (Coleoptera: Scolytidae), with a key to world species of the genus. Zoologische Mededelingen, **77**: 631–636.
- You, L., and Zhou, Z. 1991. A new species of *Bracteodes* attacking *Apis cerana* Fabricius, 1793 (Hymenoptera: Braconidae: Euphorinae). Entomofauna, **12**: 157–164.
- Zhang, D.W., and Chen, J. 2015. New substitute name for the genus *Napo* Shaw, 2012 (Hymenoptera: Braconidae: Euphorinae). Zootaxa, **3946**(1): 149. <https://doi.org/10.11646/zootaxa.3946.1.10>
- Zhang, Y.M., Ridenbaugh, R.D. and Sharanowski, B.J. 2017. Integrative taxonomy improves understanding of native beneficial fauna: revision of the Nearctic *Peristenus pallipes* complex (Hymenoptera: Braconidae) and implications for release of exotic biocontrol agents. Systematic Entomology, **42**: 596–608. <https://doi.org/10.1111/syen.12233>
- Zhang, Y.M., Stigenberg, J., Meyer, J.H., and Sharanowski, B.J. 2018. Multilocus phylogeny of the parasitic wasps in the tribe Euphorini (Hymenoptera: Braconidae) with revised generic classifications. PeerJ **6**: e4783. <https://doi.org/10.7717/peerj.4783>