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Comprehensive phylogeny of *Simulium* (*Psilopelmia*) Enderlein (Diptera: Simuliidae) – classification tested against comparative morphology

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Abstract. A comprehensive phylogenetic analysis of *Simulium* (*Psilopelmia*) is made, using 67 of the 69 valid species and with indepth reinterpretation of comparative morphology. The analysis tested the monophyly of the subgenus, its species-groups, and evaluated the phylogenetic structure within them. The data matrix, composed by 87 terminal taxa and 73 characters obtained from adult, pupa, and larva, was analyzed under parsimony implied weighting, with a wide range of concavities. The searches found ten categories of k, grouped when they found the same MPTs, and the nodal stability was estimated via parameter sensitivity analysis. According to our results, *Simulium* (*Psilopelmia*) is monophyletic only if the species from the groups Blacasi and Oviedoi are excluded, as they fail to group with the remaining species-groups. *Simulium* (*Psilopelmia*), *S.* (*Notolepria*), *S.* (*Chirostilbia*), and *S.* (*Psilozia*) form a clade, where *S.* (*Psilopelmia*) and *S.* (*Psilozia*) are sister-groups. Each of the species-groups of *S.* (*Psilopelmia*), Dinellii, Escomeli, Perflavum, and Romanai were recovered as monophyletic and stable, but Bicoloratum is not stable. The species-groups Callidum and Virescens were proposed to tentatively accommodate the species of *S.* (*Psilopelmia*) that did not fit into any of the traditional groups. We propose a new subgenus for Blancasi species-group, *Simulium* (*Eremulium*) **subgen.n**.

Key words. America continent, black fly, cladistics, Culicomorpha, implied weighting, Insecta, morphology, systematics, taxonomy.

1. Introduction

From the 2,331 extant species of Simuliidae, 1,905 belong to *Simulium* Latreille, 1802, which are organized in at least 37 subgenera and 110 species-groups around the world (Adler 2020). Until a phylogeny that includes most of the *Simulium* groups is analysed, we cannot see the big picture concerning the relationships among *Simulium* subgenera, only some clues. Adler et al. (2004) considered three major clades in *Simulium* phylogeny: *S.* (*Hellichiella*) Rivosecchi & Cardinali, 1975, "*S.* (*Boreosimulium*) Rubtsov & Yankovsky, 1982 to *S.* (*Wallacellum*) Takaoka, 1983", and "*S.* (*Wilhelmia*) Enderlein, 1921 to *S.* (*Simulium*)". According to this perspective, all Neotropical *Simulium* subgenera belong to the latter clade. Gil-Azevedo et al. (2012) proposed that the Neotropical *Simulium* subgenera are polyphyletic and could be divided in four clades: **(1)** *S.* (*Pternaspatha*) Enderlein, 1930; **(2)** *S.* (*Trichodagmia*) Enderlein, 1934 + *S.* (*Hemicnetha*) Enderlein, 1934; **(3)** *S.* (*Aspathia*) Enderlein, 1935 + *S.* (*Psaroniocompsa*) Enderlein, 1934 + *S.* (*Inaequalium*) Coscarón & Wygodzinsky, 1984; and **(4)** *S.* (*Notolepria*) Enderlein, 1930 + *S.* (*Chirostilbia*) Enderlein, 1921 + *S.* (*Psilopelmia*) Enderlein, 1934.

There are 15 subgenera and 378 species of *Simulium* in the American Continents. *Simulium* (*Psilopelmia*) (sensu Adler 2020) is the largest subgenus, with 69 species, and the most widespread. The subgenus is endemic to the American Continents, being found in almost all continental countries (except Uruguay), and in many islands, such as Cuba, Hispaniola, Galapagos, Jamaica, Puerto Rico, and Trinidad (Adler 2020).

Simulium (*Psilopelmia*), as proposed by Adler (2020), is far from unanimous among authors. In the second half of

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the 20th century, in a series of papers, Coscarón established the group as two closely related subgenera, *S.* (*Ectemnaspis*) Enderlein, 1934 (type-species *Ectemnaspis macca* Enderlein, 1934 [= *Simulium bicoloratum* Malloch, 1912]) and *S.* (*Psilopelmia*) (type-species *Psilopelmia rufidorsum* Enderlein, 1934 [= *Simulium escomeli* Roubaud, 1909]) (Coscarón 1984, 1987, 1990; Coscarón et al. 1996). Coscarón's scheme organized *S.* (*Ectemnaspis*) in four species-groups: Bicoloratum, Dinellii, Perflavum, and Romanai. But Crosskey (1988; and Crosskey & Howard 1997, 2004) disagreed with Coscarón's subgenera limits and proposed another organization. They restricted *S.* (*Ectemnaspis*) to the Bicoloratum species-group, and transferred the Dinellii, Perflavum and Romanai species-groups to *S.* (*Psilopelmia*). They assigned Coscarón's *S.* (*Psilopelmia*) and all Nearctic species to the Escomeli species-group. Despite the discordance over the subgenera limits, Coscarón's and Crosskey's views, which culminated in Coscarón et al. (2008) and Adler & Crosskey (2010) schemes respectively, are quite similar regarding species-groups limits. The five species-groups are grounded in comparative morphology and phylogenetic studies (Coscarón 1984, 1987, 1990, 1991; Coscarón et al. 1996; Coscarón & Coscarón-Arias 2007).

Shelley et al. (1989) threw doubt on the necessity for two subgenera, and later formally proposed the synonymy of *S.* (*Ectemnaspis*) with *S.* (*Psilopelmia*) (Shelley et al. 2010). Despite our disagreement with the authors' arguments, it is not a contentious issue, since comparative studies always indicate that they are sister groups (e.g. Coscarón 1987; Gil-Azevedo et al. 2012). But they ignored all Coscarón's endeavor to organize the species-groups, who analyzed all Neotropical species and proposed many characters to corroborate his scheme. Shelley et al. (2010) discarded all of Coscarón's characters, based mainly in bibliographical analysis, with neither examination of the material, nor proper methodological-based refutation. Shelley's scheme took only one morphological structure into consideration, the cibarium, for definition of the subgenus and its species-groups (Shelley et al. 2010; followed by Adler & Crosskey 2011–2018 and Adler 2019–2020). They designated four types of cibaria (Bicoloratum, Dinellii, Perflavum and Romanai) and forced all the species within their concept of *S.* (*Psilopelmia*) into these categories. Shelley et al. (2010) discarded the Escomeli species-group, because it did not have a cibarium "type" and scattered its components among the remaining species-groups. But Escomeli was considered phylogenetically external in relation to the other species-groups (Coscarón 1987), which makes Shelley's scheme lose any phylogenetic meaning. To increase the confusion, the two most problematic species-groups of Neotropical *Simulium*, Blancasi and Oviedoi, which until 2007 were considered unplaced to subgenus, were added to *S.* (*Psilopelmia*) by Coscarón & Coscarón-Arias (2007) and Hernández-Triana (2011), respectively. To fit into Shelley's scheme, those species-groups were also discarded, and their species included in the Bicoloratum species-group (Adler & Crosskey 2011–2018; Adler 2019–2020). Bicoloratum cibarium type is toothless, a plesiomorphic state for *Simulium* (Adler et al. 2004; Gil-Azevedo et al. 2012). So, if most of the *Simulium* species would be considered *S.* (*Psilopelmia*), they would be included in the Bicoloratum species-group according to Shelley's scheme. For more details about the historical background of *Simulium* (*Psilopelmia*) see Miranda-Esquivel & Muñoz de Hoyos (1996) and Shelley et al. (2010).

Shelley et al. (2010: p. 364) also stated that phylogenetic analyses on *S.* (*Psilopelmia*) and *S.* (*Ectemnaspis*) were based "purely on morphological characters that are frequently poorly researched and biased by existing morphological arrangements". We partly agree with this criticism, although we think this is no excuse to base the classification on personal beliefs, rebooting all comparative morphology made before, and proposing a new scheme based solely upon one structure. There have been few phylogenetic studies with species of *S.* (*Psilopelmia*) (Coscarón 1987; Miranda-Esquivel & Muñoz de Hoyos 1993; Coscarón et al. 1996; Adler et al. 2004; Gil-Azevedo et al. 2012), but they suffer from huge sample bias. Poor sampling of characters is preponderant, but the worst is the sampling of taxa. None of the analyses come close to include the 69 species of *S.* (*Psilopelmia*). The largest sampling was done in the phylogeny of Neotropical *S.* (*Psilopelmia*) sensu Coscarón (Coscarón et al. 1996), with 21 species. The other analyses have much smaller sampling. The analysis of Coscarón et al. (1996) used only one outgroup, which made it impossible to test the monophyly of *S.* (*Psilopelmia*) sensu Coscarón. All previous analyses failed in test the monophyly of the supra-specific taxa involved, both subgenera and species-groups.

In the present study, a cladistic analysis was performed to test the monophyly of *Simulium* (*Psilopelmia*) and its species-groups, and to evaluate the phylogenetic structure within it. A comprehensive phylogenetic analysis of the subgenus is made for the first time, using almost all its species, and with indepth reinterpretation of comparative morphology.

2. Material and methods

2.1. Terminal taxa and specimens

The ingroup consists of all currently valid species of *Simulium* (*Psilopelmia*), except *S. flavipictum* Knab, 1914 and *S. jacobsi* Dalmat, 1953. The former species is known only by the female holotype and the latter is known only by the larval stage. Their exclusion resulted in 67 terminal taxa representing a group with 69 species. The 20 species chosen as outgroups were representatives of the three *Simulium* clades proposed by Adler et al. (2004): **(1)** "clade *Hellichiella*" – with one representative, where the analyses were rooted; **(2)** "clade *Boreosimulium* to *Wallacellum*" – with three *Simulium* subgenera represented; and **(3)** "clade *Wilhelmia* to *Simulium*", where *S.* (*Psilopelmia*) is included – with eight *Simulium* subgenera represented. We included representatives of *S.* (*Chirostilbia*), *S.* (*Notolepria*), *S.* (*Psaroniocompsa*) and *S.* (*Psilozia*), because they are considered closer to *S.* (*Psilopelmia*) (Adler et al. 2004; Gil-Azevedo et al. 2012). Six species of *S.* (*Chirostilbia*), three from each species-group, were taken to test the monophyly of the subgenus in relation to *S.* (*Psilopelmia*) (Gil-Azevedo et al. 2012). We also added representatives of *S.* (*Pternaspatha*) and *S.* (*Hemicnetha*) to evaluate its possible relationship with the Blancasi and Oviedoi species-groups, respectively. The Appendix (chapter 7) provides the list of species used as ingroup and outgroup in the analysis, and indicated the material used.

The specimens studied herein are deposited in the following institutions: Museo de La Plata (MLP, Argentina), Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ, Brazil), Coleção do Laboratório de Simulídeos e Oncocercose, Instituto Oswaldo Cruz (CSIOC, Brazil) and Royal Ontario Museum (ROM, Canada). Whenever possible, we examined specimens of the three developmental stages (larva, pupa, and adult) (Appendix). To improve the data about species morphology, we consulted original descriptions, all the papers cited herein, and additionally: Peterson & Kondratieff (1995); Moulton (1998); Hamada & Adler (1998); Hamada & Grillet (2001).

2.2. Terminology and characters

We followed the morphological terminology of Adler et al. (2004), with the addition of terms from Gil-Azevedo & Maia-Herzog (2007). Based on an extensive morphological study, we identified the characters and proposed hypotheses of primary homology (Pinna 1991). The logic employed in the preparation of characters followed Fitzhugh (2006) and Sereno (2007). We codified those hypotheses in a data matrix using the program Mesquite (Maddison et al. 1997; Maddison & Maddison 2017). Characters were preferentially coded reductively (Wilkinson 1995) and were treated as unordered (Fitch 1971). When two or more states of a character were found in one terminal taxon, the character was treated as polymorphic and both states were coded in the matrix.

Characters without a clear nomenclature based on shape were described with the help of a comparison between two structures (ratio), in order to provide a more detailed description and make it easier to be interpreted by the readers. These characters were constructed in such a way that there is always a gap between the states and are not truly morphometric.

2.3. Phylogenetic analyses

The dataset was analyzed under parsimony equal weighting (**EW**) and implied weighting (**IW**, Goloboff 1993; Goloboff et al. 2008b), where characters were downweighted based on their degree of homoplasy. We chose to use implied weighting for our data because "if weighting against homoplasy, a larger number of supported groups are likely to remain supported when new characters or taxa are found in the future", as demonstrated by Goloboff et al. (2008a). Some authors are against weighting arguing that it increases arbitrary assumptions, but equal weighting does not avoid that issue, as it presupposes that all the characters are equally congruent and reliable (Wheeler 1995; Giribet 2003; Goloboff et al. 2008a).

"Given that no weight strength seemed to have a significant better performance over all data sets and for all measures" and "there may not be one unique, 'true' value of concavity constant – **k** (e.g., they may vary over the tree, and these parameters certainly are not intended to reflect exact probabilities of events in a stochastic model)" (Goloboff et al. 2008a), we chose to explore different parameters of the k. The searches were carried out under a wide range of concavities (values of k between 1 and 100) through heuristic algorithms RAS (random addition sequences) + TBR (tree bisection-reconnection branch swapping). The parameters of the search were as follows: 5 000 replications and TBR with 1 000 trees saved per replication (EW and IW). The searches by IW phylogenetic analyses (k = 1 to 100) were grouped when they found the same Most Parsimonious Trees – **MPTs** in k-values. We performed analyses under EW with the same parameters of IW.

We chose this more conservative approach to minimize the chance of spurious nodes. The most important criterium considered here, on the discussions about the groups, synapomorphies, and for taxonomic decisions, is the nodal stability (Giribet 2003). The nodal stability was estimated via parameter sensitivity analysis – **PSA** (Wheeler 1995; Whiting et al. 1997; Prendini 2000; Giribet 2003). The premise behind the PSA is: "If a group is monophyletic only under a very specific combination of parameters, less confidence may be placed in the supposition that the data robustly support its monophyly than may be placed in a group which is monophyletic under a wider range and combination of parameters" (Whiting et al. 1997). The PSA is represented graphically using the "Navajo rugs" (Wheeler 1995; Prendini 2000; Giribet 2003), where the black squares represent that the clade was recovered in the analysis under this parameter, and the white squares were not. We used searches under EW and IW (with all k-values employed here) as parameters for the PSA. The size of the black area gives a measure of the stability of the clade (Wheeler 1995). The following criteria were used here to measure the stability of the clade: "If a high fraction of the total analysis space supports a group, the group is generally supported by the data because most combinations of analytical parameters will yield that clade. If, however, the areas in which the clade is supported are broken up and distributed over the space, this group would be unstable because small perturbations in analysis would lead to a new result" (Wheeler 1995).

For each k, we calculated its value in the normalized Fit function (since K = (F×S)/(1 − F); and if K = S, then F = 50%) (Mirande 2009; Reemer & Stahls 2013). The average homoplasy per character (S) was calculated based on the shortest trees found in EW analysis, where S = (shortest trees extra steps / minimum steps). We consider EW and all IW k-searches in the measure of nodal stability, but IW k-values between 50% and 90% of the normalized Fit function had a great weight in our decisions.

The nodal support was evaluated through bootstrap Poisson independent reweighting as frequency differences values (GC) (Goloboff et al. 2003), with 5000 replications with RAS + TBR, and relative Bremer support, calculated as the ratio between the favorable and the contradictory evidence (relative fit difference; Goloboff & Farris 2001). We used Subtree Pruning Regrafting moves – **SPRm** to compare trees, which measures the minimum number of SPRm required to transform one tree in the other (Goloboff 2008; Mirande 2009). We used the TNT program for all searches (Goloboff et al. 2008b).

3. Results

3.1. Phylogenetic analyses

The data matrix comprises 87 terminal taxa and 73 characters obtained from adult (43), pupa (22), and larval specimens of the final instar (8) (Tables 1, 2). The list of characters used in this analysis is given in Table 1.

The shortest 136 MPTs found in analysis with EW have 343 steps (Table 3), so the average homoplasy per character (S) in our matrix is 3.23 homoplastic steps. The searches by IW phylogenetics analyses (k = 1 to 100) found ten categories of k, grouped when they found the same MPTs (Table 3). Based on this, we calculated, for each k, its value in the normalized Fit function (Table 3). In IW searches, we found six k-values within the 50% to 90% homoplasy range, and they could be divided in two clusters, according to tree topologies similarity measured by SPRm: (1) k4, k5, and k6 – 9; (2) k10 – 17, k18 – 21, and k22 – 25 (Table 3). We choose the k-categories k6 – 9 (k = 6 strict consensus tree, Fig. 7) and k10 – 17 (k = 10 strict consensus tree, Fig. 8) for the graphical representation of the data, because it is where the cluster breaks occur. We also chose k6 strict consensus tree to plot the nodal stability (PSA) and support values (bootstrap and Bremer) (Fig. 7), and to obtain character scores (Table 1). The synapomorphies common to the analyses with k5 to k17 are presented in Table 4. To compare, we also present the strict consensus of EW trees in the 'Navajo rugs' box (Fig. 7).

According to our results, *Simulium* (*Psilopelmia*) is monophyletic only if the species from the groups Blacasi and Oviedoi are excluded, as they fail to group with the remaining species-groups (Bicoloratum, Dinellii, Escomeli, Romanai, and Perflavum) (Figs. 7, 8). The Oviedoi species-group was recovered closer to *S*. (*Hemicnetha*) (nodes 7 and 8), and of Blancalsi is in the base of the clade "*Wilhelmia* to *Simulium*" (nodes 1 and 5). *Simulium* (*Psilopemia*) form a monophyletic group with *S*. (*Notolepria*), *S*. (*Chirostilbia*), and *S*. (*Psilozia*) (node 4), being sister-group of the latter (node 15).

The species-groups Dinellii, Escomeli, Perflavum, and Romanai were all recovered as monophyletic in our analyses (Figs. 7, 8, nodes 28, 16, 42, and 37, respectively). The Bicoloratum species-group is not stable, only being recovered in analyses with k-value k3 to k6 – 9.

3.2. Taxonomy

Based on our data we propose the following classification for the species originally included in *Simulium* (*Psilopelmia*) sensu Adler (2020). More details in Discussion.

3.2.1. *Simulium* (*Eremulium*) subgen.n.

Figs. 1A, 6A

Type-species. *Simulium tenuipes* Knab, 1914.

Diagnosis. ***Adult*:** scutum uniformly gray leaden (both sexes); and without 1+1 lateral silver stripes, in contrast to the presence of 1+1 lateral silver stripes in other Neotropical *Simulium* subgenera. ***Female*:** cibarium cornua straight (with parallel lateral edges), in contrast to cornua expanded (with irregular and enlarged lateral edges) in other Neotropical *Simulium* subgenera; and unarmed. Mandible teeth well developed on both sides. Leg claw without sub-basal tooth. ***Male*:** gonostylus elongated subcylindrical, with pointed apex. ***Pupa*:** cephalothorax with only simple trichomes. Gill with four long branches. Cocoon anterior open, in lateral view, with dorsal border projecting forward beyond level of ventral border. ***Larva*:** abdomen without ventral tubercles; and rectal papillae with only three simple lobes.

Etymology. *Eremulium* – from Latin *eremus* (desert) + -ulium, termination of *Simulium*. We avoid the usage of the entire word to keep reasonable length in the name of the new subgenus. Grammatical gender neuter (as in *Simulium*).

Simulium (*Eremulium*) *blancasi* Wygodzinsky & Coscarón, 1970
Simulium (*Eremulium*) *penai* Wygodzinsky & Coscarón, 1970
Simulium (*Eremulium*) *tenuipes* Knab, 1914

3.2.2. *Simulium* (*Hemicnetha*) Enderlein, 1934

Type-species. *Hemicnetha mexicana* Enderlein, 1934 (= *Simulium paynei* Vargas, 1942).

Oviedoi species-group

Diagnosis. ***Female*:** cibarium cornua short, as long as wide. Leg claw with sub-basal tooth, reaching about half

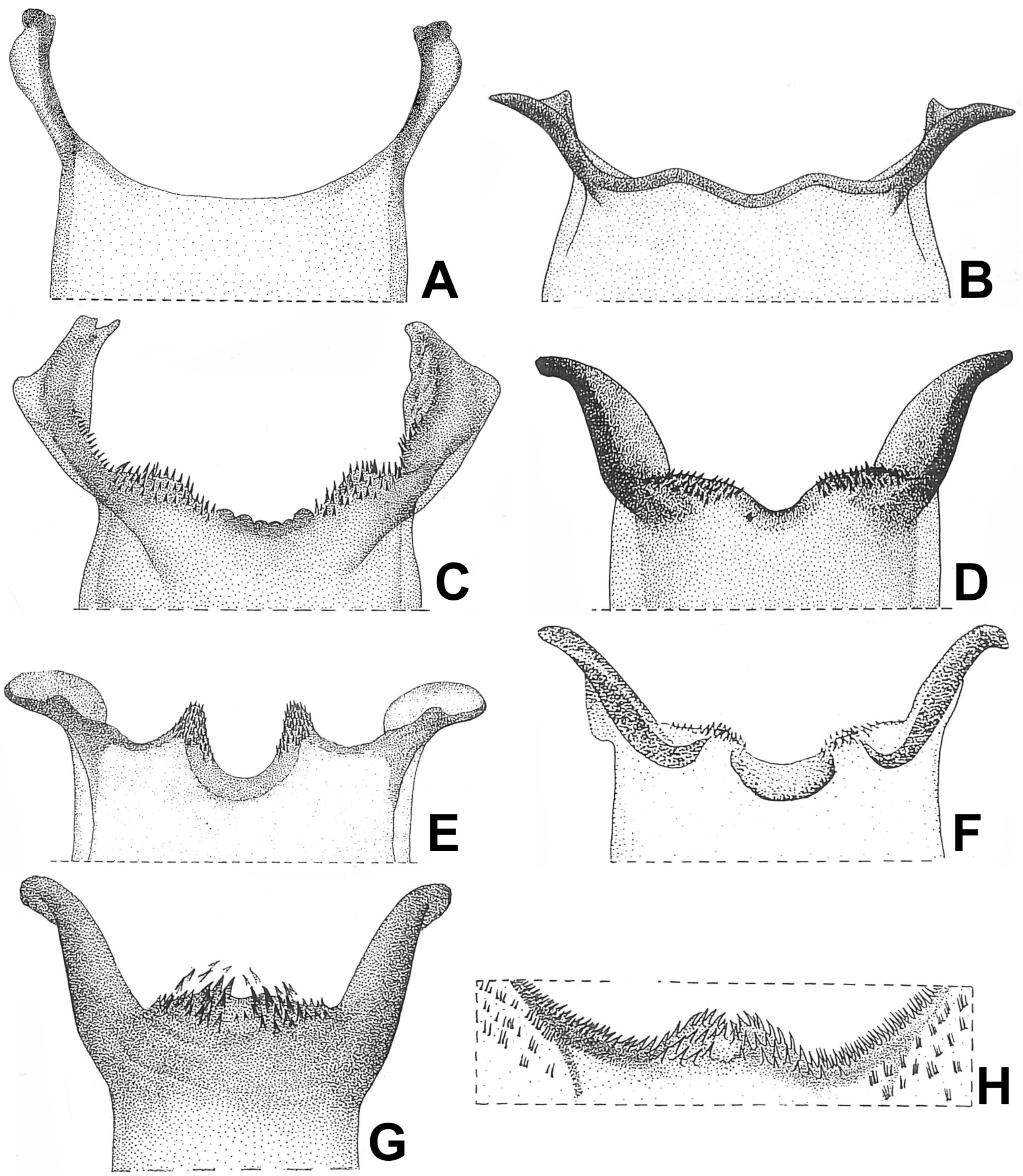

Fig. 1. Female cibarium, anterior view: (**A**) *Simulium tenuipes*; (**B**) *S. rubiginosum*; (**C**) *S. romanai*; (**D**) *S. escomeli*; (**E**) *S. dinellii*; (**F**) *S. trivittatum*; (**G**) *S. kabanayense*; (**H**) *S. perflavum* (detail).

of the length of main tooth. ***Male***: gonostylus markedly longer than gonocoxite, with pointed apex. ***Pupa***: cephalothorax with multibranched trichomes. Gill short (less than 1/2 of cocoon length). Cocoon boot-shaped. ***Larva***: hypostoma with medial and lateral teeth about twice as high as sublateral teeth.

Simulium (*Hemicnetha*) *oviedoi* Ramírez-Pérez, 1971
Simulium (*Hemicnetha*) *rivasi* Ramírez-Pérez, 1971

3.2.3. *Simulium* (*Psilopelmia*) Enderlein, 1934

Figs. 1B–H, 2A–I, 3A,B, 4, 5A–C

Simulium (*Ectemnapis*) Enderlein, 1936. Type-species: *Ectemnaspis macca* Enderlein, 1934 (= *Simulium bicoloratum* Malloch, 1912).

Type-species. *Psilopelmia rufidorsum* Enderlein, 1934 (= *Simulium escomeli* Roubaud, 1909).

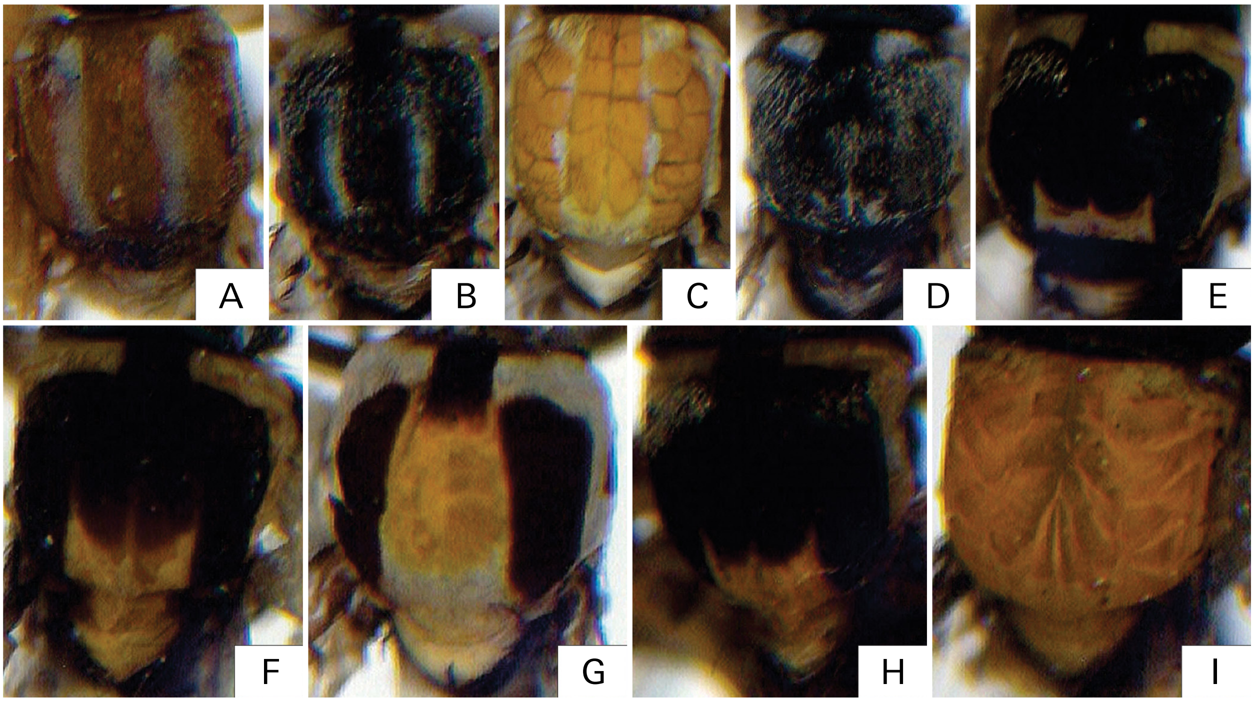

Fig. 2. Female thorax, dorsal view (**A–D**): (**A**) *Simulium escomeli*; (**B**) *S. mangaberai*; (**C**) *S. pseudocallidum*; (**D**) *S. mayuchuspi*. Male thorax, dorsal view (**E–I**): (**E**) *S. bicoloratum*; (**F**) *S. tunja*; (**G**) *S. pautense*; (**H**) *S. romanai* (black form); (**I**) *S. romanai* (yellow form).

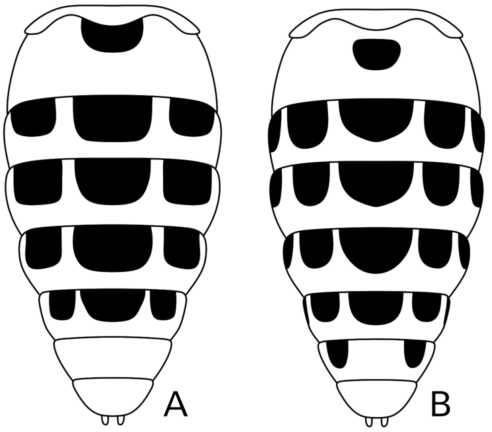

Fig. 3. Female abdomen, dorsal view: (**A**) *Simulium iracouboense*; (**B**) *S. escomeli*.

Fig. 4. Female of *S. bicoloratum*, lateral view (photo by Morgan D. Jackson).

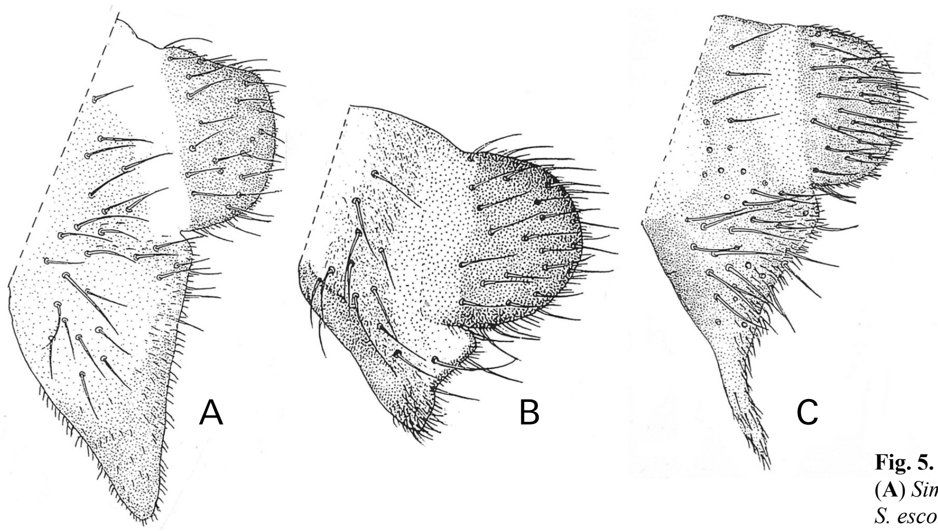

Fig. 5. Anal lobe and cercus, lateral view: (**A**) *Simulium callidum*; (**B**) *S. dugesi*; (**C**) *S. escomeli*.

Fig. 6. Pupa and cocoon, lateral view: (**A**) *Simulium tenuipes*; (**B**) *S. lutzianum*.

Table 1. Character list (L = length; CI = consistency index; RI = retention index). Character scores from parsimony implied weighting analysis with k = 6

[1] For this paper purposes, we consider all anteromedial border pigmented color as equal. But there are distinct levels of sclerotization in them, which should be investigated further, employing more and fresh material.

[2] The taxonomy of *Simulium* (*Psilopelmia*) is strongly influenced by the study of the cibarium morphology. The characters of shape of the cibarium were present in all the diagnoses of its species-groups (e.g. Coscarón & Coscarón-Arias 2007; Shelley et al. 2010), and the subgenus presents a quite information-rich cibarium. We tried to explore all the diagnoses proposed so far in the literature in the characters 5 – 12, with many adaptations to fit in the phylogenetic analysis. But some of the characters present in previous diagnoses could not be considered in this paper, such as the size of the teeth (characters 8 and 10 of Coscarón et al. 1996), due the lack of enough material to carry out such measures.

[3] The U-shape 1+1 lobes in the Perflavum species-group is distinctly smaller than in the Dinellii species-group, because the size of the area between 1+1 lobes is smaller in the Perflavum species-group [Character 8(1)], which forms the anteromedial convex border sensu Coscarón.

[4] We preferred to use a broader description of background color because it is harder to define narrower categories and those, in our experience, also lead to noise in phylogenetic signal. We preferred to adopt a more conservative coding of color (dark and light) which causes considerably less noise and some patterns emerge. But we are not completely comfortable with this decision, as we know that in a colorful group like *S.* (*Psilopelmia*) we are losing information. More studies on ultrastructure of thorax setae could help to propose more accurate coloration characters. In our present coding, if the species had specimens in both forms (some dark and some light), it was coded as 0 and 1. If the species were half dark and half light, in the same specimen, it was coded as inapplicable.

[5] We observed variations in this pattern (more or less expanded), which we considered homologous, but we did not explore this variation here.

[6] The male scutum 'bird pattern' are present in all species of the Bicoloratum and Romanai species-groups, except when the species lacks sexual dimorphism in thoracic coloration, the male scutum being equal to female. For example, in *S. romanai* there are males with scutum different from females (which presents 'bird pattern', Fig. 2h) and males with scutum equal to females (homogenous yellow, Fig. 2i). So, the 'bird pattern' is probably a synapomorphy of Bicoloratum and/or Romanai which is jumbled by the absence of sexual dimorphism in scutum coloration. This lack of sexual dimorphism appears many times among Neotropical *Simulium* species, but it is very confusing in the Bicoloratum, Dinellii, Perflavum, and Romanai species-groups. In those groups many species do not have dimorphism, males with appearance typical of females, or even females with typical pattern of males (as *S. bicoloratum*, Fig. 4), and in many species the scutum of the male are polymorphic (with or without dimorphism). This profuse variation in scutum coloration should be carefully investigated further to clarify the phylogenetic signal of the male scutum pattern.

[7] Unlike Gil-Azevedo et al. (2012), we did not consider reduced spurs as absent, because as we examined exemplars of all *S.* (*Psilopelmia*) species, a wide variation in the reduced shape was observed.

[8] Three meristic characters widely used in *S.* (*Psilopelmia*) taxonomy were added to test their phylogenetic signal.

[9] The 2-dimensional gill filament arrangement is a synapomorphy of *S.* (*Chirostilbia*) + *S.* (*Notolepria*) + *S.* (*Psilozia*) + *S.* (*Psilopelmia*). In *S.* (*Psilopelmia*), at least nine reversions to 3-dimensional arrangement occur besides intermediary states, which would be interesting to investigate further.

[10] *Simulium* (*Chirostilbia*) *pertinax* and *S.* (*C.*) *spinibranchium* have an intermediate type of cocoon that sometimes appears as slipper-shaped type and others as boot-shaped. Here we coded those species with both states.

[11] The thickened anterior rim should be investigated at the ultrastructural level, which probably will reveal that this condition in the Bicoloratum species-group is not homologous to the condition in the Escomeli species-group. But by only weak indications are revealed using light microscopy.

[12] The absence of 1+1 ventral tubercles is a synapomorphy of *S.* (*Chirostilbia*) + *S.* (*Notolepria*) + *S.* (*Psilozia*) + *S.* (*Psilopelmia*), with a reversion in node 22.

Characters		**L**	**Fit**	**CI/RI**	**Summary**
Adult – Female					
01	Mandible teeth: **(0)** well developed in both sides; **(1)** developed in the internal side and scarcely developed or undeveloped on external side	3	0.25	0.33/0.77	Modified from character 2 of Gil-Azevedo et al. (2012: sd 1)
02	Cibarium, cornua, shape: **(0)** straight, compact lateral edges (Fig. 1a); **(1)** expanded, irregular and enlarged lateral edges (Fig. 1b – g)	1	0.00	1/1	Modified from character 10 of Gil-Azevedo & Maia-Herzog (2007: 43)
03	Cibarium, cornua, length: **(0)** long, about 2 × longer than wide; **(1)** short, as long as wide	1	0.00	1/1	Character 6 of Gil-Azevedo et al. (2012: sd 1)
04	Cibarium, anteromedial border, coloration: **(0)** unpigmented or slightly pigmented (Fig. 1a); **(1)** distinctly pigmented (Fig. 1b – f,h)[1]	2	0.14	0.50/0.95	Character 4 of Gil-Azevedo et al. (2012: sd 1)
05	Cibarium, anteromedial border, surface: **(0)** unarmed (Fig. 1a,b); **(1)** distinctly armed (Fig. 1c–h)[2]	4	0.33	0.25/0.92	Character 203 of Adler et al. (2004: 157), 5 of Gil-Azevedo et al. (2012: sd 1)

Table 1. continued.

Characters		L	Fit	CI/RI	Summary
Adult – Female					
06	Cibarium, anterior border, shape: **(0)** regular; **(1)** irregular – wrinkled or indented	2	0.14	0.50/0.87	—
07	Cibarium, anteromedial border, 1+1 lobes, shape: **(0)** blunt or substraight (Fig. 1a–d,f); **(1)** acute projections – U-shape (Fig. 1e,g,h)[3]	3	0.25	0.33/0.81	Modified from characters 29, 31 and 33 of Coscarón (1987: 5); and 10 of Coscarón et al. (1996: 41)
08	Cibarium, anteromedial border, area between 1+1 lobes, size: **(0)** about as long as 1/2 of anteriomedial border – area between the cornuae (Fig. 1a–f); **(1)** distinctly smaller than 1/4 of the anteromedial border – anteromedial border convex (Fig. 1g–h)	1	0.00	1/1	Modified from characters 29, 31 and 33 of Coscarón (1987: 5); and 10 of Coscarón et al. (1996: 41)
09	Cibarium, anteromedial border, half-moon area – distinctly sclerotized rim, smooth and unarmed: **(0)** absent; **(1)** present (Fig. 1d–f)	2	0.14	0.50/0.92	Character 9 of Coscarón et al. (1996: 40)
10	Cibarium, medial area, transversal medial depression: **(0)** absent; **(1)** present	1	0.00	1/1	—
11	Cibarium, medial area, transversal medial depression, shape: **(0)** enlarged – as a channel; **(1)** slowly depressed	1	0.00	1/1	—
12	Cibarium, medial area, surface, plates: **(0)** absent; **(1)** present (Fig. 1c)	2	0.14	0.50/0.87	—
13	Thorax, scutum, background coloration: **(0)** dark– black to dark brown (Fig. 2b,d); **(1)** light– light brown to yellow (Fig. 2a,c)[4]	11	0.62	0.09/0.64	Character 7 of Gil-Azevedo et al. (2012: sd 1).
14	Thorax, scutum, pattern, adorned with silvery spots and/or stripes: **(0)** absent; **(1)** present (Fig. 2a–c,d)	2	0.14	0.50/0.75	Character 195 of Adler et al. (2004: 157), 8 of Gil-Azevedo et al. (2012: sd 1)
15	Thorax, scutum, pattern, silvery spots and/or stripes, 1+1 submedian longitudinal: **(0)** present (Fig. 2a–c,d); **(1)** absent	4	0.33	0.25/0.72	—
16	Thorax, scutum, pattern, 1+1 submedian longitudinal silvery spots and/or stripes, length: **(0)** does not cross the anterior half area (Fig. 2d); **(1)** crossing since anterior to posterior border (Fig. 2a–c)	4	0.33	0.25/0.86	Modified from character 1 of Coscarón et al. (1996: 40)
17	Thorax, scutum, pattern, 1+1 lateral silver stripes which join together forming an arch in posterior area: **(0)** absent; **(1)** present	1	0.00	1/1	—
18	Thorax, scutellum, background coloration: **(0)** dark – black to dark brown; **(1)** light – light brown to yellow	10	0.60	0.10/0.60	—
19	Legs, coloration pattern: **(0)** simple – almost homogeneous; **(1)** markedly – forming bands	4	0.33	0.25/0.50	Character 196 of Adler et al. (2004: 157)
20	Hind legs, pedisulcus, shape: **(0)** shallow; **(1)** deep	uninformative			Modified from characters 173 and 177 of Adler et al. (2004: 154), 16 of Gil-Azevedo & Maia-Herzog (2007: 44)
21	Hind legs, claw, sub-basal tooth: **(0)** present; **(1)** absent	7	0.50	0.14/0.81	Character 5 of Coscarón & Coscarón-Arias (1997: 114), 142 of Adler et al. (2004: 152), 17 of Gil-Azevedo & Maia-Herzog (2007: 44), and 11 of Gil-Azevedo et al. (2012: sd 1)
22	Hind legs, claw, sub-basal tooth, length: **(0)** developed, reaching about 1/2 of the main tooth; **(1)** reduced, smaller than 1/3 of the main tooth	5	0.40	0.20/0.63	Character 198 of Adler et al. (2004: 157), 18 of Gil-Azevedo & Maia-Herzog (2007: 44)
23	Wing, basal sector of the vein R, setae: **(0)** present; **(1)** absent	11	0.62	0.90/0.70	Character 4 of Coscarón & Coscarón-Arias (1997: 114), 200 of Adler et al. (2004: 157), 24 of Gil-Azevedo & Maia-Herzog (2007: 45), 13 of Gil-Azevedo et al. (2012: sd 1)
24	Abdomen, coloration pattern, 1+1 submedian longitudinal silver rows – in tergite lateral edges: **(0)** absent; **(1)** present (Fig. 3a–b)	1	0.00	1/1	Modified from character 7 of Coscarón et al. (1996: 40) [divided into two 24 and 25]
25	Abdomen, coloration pattern, 1+1 sublateral longitudinal silver rows: **(0)** absent (Fig. 3a); **(1)** present (fig. 3b)	2	0.14	0.50/0.90	Modified from character 7 of Coscarón et al. (1996: 40)
26	Abdomen, tergite II, background coloration: **(0)** dark color – black to dark brown; **(1)** light color – light brown to yellow	6	0.45	0.16/0.86	Modified from character 14 of Gil-Azevedo et al. (2012: sd 1)
27	Abdomen, tergite III, background coloration: **(0)** dark color– black to dark brown; **(1)** light color – light brown to yellow	7	0.50	0.14/0.81	Modified from character 14 of Gil-Azevedo et al. (2012: sd 1)
28	Abdomen, tergite IV, background coloration: **(0)** dark color – black to dark brown; **(1)** light color – light brown to yellow	2	0.14	0.50/0.75	Modified from character 14 of Gil-Azevedo et al. (2012: sd 1)
29	Abdomen, segment V, coloration: **(0)** homogeneous; **(1)** tergite dark brown to black contrasting with pleura and sternum orange to yellow (Fig. 4)	2	0.14	0.50/0.92	—
30	Anal lobe, length in relation to cercus: **(0)** distinctly less than 2 x long; **(1)** distinctly longer than 2 ×	12	0.65	0.08/0.59	Modified from character 31 of Gil-Azevedo & Maia-Herzog (2007: 48)
31	Anal lobe, length in relation to the width of base – in lateral view: **(0)** equally size; **(1)** distinctly longer	3	0.25	0.33/0.88	Modified from character 44 of Coscarón (1987: 3)
32	Anal lobe, distal portion narrowed forming a tail-like process: **(0)** absent (Fig. 5a); **(1)** present (Fig. 5b–c)	2	0.14	0.50/0.95	Modified from character 48 of Coscarón (1987: 5)
33	Anal lobe, distal portion, tail-like process, length: **(0)** smaller than 1/2 of the basal width of the anal lobe (Fig. 5b); **(1)** as long as the basal width of the anal lobe (Fig. 5c)	1	0.00	1/1	Modified from character 48 of Coscarón (1987: 5)
34	Anal lobe, distal border, shape: **(0)** sub-square; **(1)** hemispheric, distinctly rounded; **(2)** triangular – with base smaller than the height	3	0.14	0.66/0.93	Character 15 of Gil-Azevedo et al. (2012: sd 1)
35	Anal lobe, internal border – border closer to cercus, shape: **(0)** straight or convex; **(1)** concave.	2	0.14	0.50/0.91	Character 17 of Gil-Azevedo et al. (2012: sd 1)
36	Genital fork, stem, length in relation to lateral arms: **(0)** equally sized; **(1)** about 2 × longer or more	13	0.67	0.07/0.53	Character 18 of Gil-Azevedo et al. (2012: sd 1)

Table 1. continued.

Characters		L	Fit	CI/RI	Summary
Adult – Male					
37	Thorax, scutum, background coloration: **(0)** dark color – black to dark brown; **(1)** light color – light brown to yellow[4]	9	0.57	0.11/0.78	Character 20 of Gil-Azevedo et al. (2012: sd 2)
38	Thorax, scutum, pattern, dark pattern formed by a medial stripe touching anterior border but not posterior border and 1+1 submedial stripes touching posterior border but not anterior border – "bird pattern": **(0)** absent; **(1)** present (Fig. 2e–h)[5 and 6]	5	0.40	0.20/0.63	—
39	Gonopod, length between gonostylus and gonocoxite: **(0)** gonostylus subequal in length to or shorter than gonocoxite; **(1)** gonostylus markedly elongate, much longer than gonocoxite	3	0.25	0.33/0.83	Character 204 of Adler et al. (2004: 157)
40	Gonostylus, shape: **(0)** cylindrical or subcylindrical; **(1)** flattened dorsoventrally	3	0.25	0.33/0.94	Character 201 of Adler et al. (2004: 157)
41	Gonostylus, apex, shape: **(0)** pointed or narrowly rounded; **(1)** subquadrate – truncated	1	0.00	1/1	Character 202 of Adler et al. (2004: 157)
42	Gonostylus, apex, spurs: **(0)** present; **(1)** absent[7]	1	0.00	1/1	Character 8 of Coscarón & Coscarón-Arias (1997: 114), and 23 of Gil-Azevedo et al. (2012: sd 2)
43	Gonostylus, longitudinal ridge: **(0)** absent; **(1)** present	1	0.00	1/1	Character 24 of Gil-Azevedo et al. (2012: sd 2)
Pupa					
44	Gill, length in relation to cocoon: **(0)** about or longer; **(1)** less than 1/2 long	8	0.54	0.12/0.65	Modified from character 16 of Coscarón et al. (1996: 41)
45	Gill trunk, length: **(0)** long – well evident; **(1)** short – reduced	6	0.45	0.16/0.70	—
46	Gill, main branch, shape: **(0)** slender – similar caliber with terminal branches; **(1)** thick – more than 3 × larger than terminal branches	2	0.14	0.50/0.50	—
47	Gill filaments, number: **(0)** 6; **(1)** 8; **(2)** 4–5; **(3)** 10; **(4)** about 20, or more[8]	26	0.78	0.15/0.35	Modified from character 12 of Coscarón & Coscarón-Arias (1997: 114); 28 of Gil-Azevedo et al. (2012: sd 2)
48	Gill filaments, arrangement, spatial distribution: **(0)** 3-dimensional; **(1)** 2-dimensional[9]	10	0.60	0.10/0.66	Character 30 of Gil-Azevedo et al. (2012: sd 2)
49	Trichomes, aspect: **(0)** only simple; **(1)** multibranched	3	0.25	0.33/0.80	Cited by Coscarón (1987). Character 66 of Gil-Azevedo & Maia-Herzog (2007: 53)
50	Trichomes, number of branches – maximum: **(0)** 2–3 branches; **(1)** 4–14 branches; **(2)** 25–40 branches[8]	7	0.45	0.28/0.83	Modified from character 26 of Gil-Azevedo et al. (2012: sd 2)
51	Trichomes, basal portion, shape: **(0)** sub-straight; **(1)** coiled	4	0.33	0.25/0.40	—
52	Trichomes, caliber: **(0)** thin; **(1)** thick	5	0.40	0.20/0.82	—
53	Trichomes, shape: **(0)** erected; **(1)** curved	7	0.50	0.14/0.82	—
54	Trichomes, length in relation to the basal width of frontoclypeus: **(0)** shorter than a 1/2; **(1)** longer than a 1/2	8	0.54	0.12/0.63	—
55	Abdomen, aspect: **(0)** weakly sclerotized – only T I-II or T I-III sclerotic and with tubercles; **(1)** not sclerotized – membranous plates and without tubercles	2	0.14	0.50/0.83	Modified from character 188 of Adler et al. (2004: 155); 71 of Gil-Azevedo & Maia-Herzog (2007: 53)
56	Cocoon, shape in lateral view: **(0)** slipper-shaped – anterior opening next to the substratum; **(1)** boot-shaped – anterior opening separated from substratum, upward directed[10]	2	0.14	0.50/0.75	Modified from character 205 of Adler et al. (2004: 157). Character 34 of Gil-Azevedo et al. (2012: sd 2)
57	Cocoon, anterior open, shape in lateral view: **(0)** ventral border projecting forward beyond the level of dorsal border (Fig. 6b); **(1)** dorsal border projecting forward beyond level of ventral border (Fig. 6a)	1	0.00	1/1	Cited by Coscarón & Coscarón-Arias (2007)
58	Cocoon, fabric, aspect: **(0)** compact; **(1)** spongy – felt aspect	3	0.25	0.33/0.66	Modified from character 90 of Coscarón (1987: 5); and 15 of Coscarón et al. (1996: 41)
59	Cocoon, compact fabric, thickness: **(0)** thin; **(1)** distinctly thick	4	0.33	0.25/0.75	Modified from character 90 of Coscarón (1987: 5); and 15 of Coscarón et al. (1996: 41)
60	Cocoon, fabric, structure: **(0)** with visible fine threads; **(1)** with visible thick threads; **(2)** homogeneous – without distinct threads	20	0.75	0.10/0.57	Character 35 of Gil-Azevedo et al. (2012: sd 2)
61	Cocoon, dorsal longitudinal crest: **(0)** absent; **(1)** present	4	0.33	0.25/0.62	Modified from character 90 of Coscarón (1987: 5)
62	Cocoon, anterior dorsal projection: **(0)** present; **(1)** absent	4	0.33	0.25/0.57	—
63	Cocoon, anterior rim, shape: **(0)** thickened; **(1)** not thickened[11]	9	0.57	0.11/0.65	Character 178 of Adler et al. (2004: 154); 91 of Gil-Azevedo & Maia-Herzog (2007: 55); 36 of Gil-Azevedo et al. (2012: sd 2)
64	Cocoon, anterior rim, shape: **(0)** regular; **(1)** irregular	1	0.00	1/1	Cited by Gil-Azevedo et al. (2005)
65	Cocoon, anterior rim, open loops: **(0)** absent; **(1)** present	3	0.25	0.33/0.66	—
Larva					
66	Cephalic apoteme, coloration: **(0)** present; **(1)** absent	9	0.57	0.11/0.27	—
67	Cephalic apoteme, coloration, pattern: **(0)** positive – light background; **(1)** negative – dark background	8	0.54	0.12/0.22	Character 38 of Gil-Azevedo et al. (2012: sd 3)
68	Hypostoma, medial and lateral teeth, height in relation to sublateral teeth: **(0)** about 2 × as high; **(1)** similar	5	0.40	0.20/0.66	—
69	Postgenal bridge, length: **(0)** long, about as longer as hypostoma; **(1)** short, distinctly shorter than hypostoma	7	0.50	0.14/0.84	—
70	Postgenal cleft, shape: **(0)** subsquare; **(1)** oval; **(2)** subtriangular; **(3)** narrow subpentagon	8	0.45	0.37/0.86	Character 109 of Gil-Azevedo & Maia-Herzog (2007: 58); 44 of Gil-Azevedo et al. (2012: sd 3)

Table 1. continued.

Characters		L	Fit	CI/RI	Summary
Larva					
71	Rectal papillae, main lobes, branching: **(0)** absent – only simple lobes; **(1)** present – lobes multiramified	3	0.25	0.33/0.84	Character 179 of Adler et al. (2004: 155), 119 of Gil-Azevedo & Maia-Herzog (2007: 59)
72	Rectal papillae, number of branches on each main lobe: **(0)** 2–6; **(1)** 7–20[8]	9	0.57	0.11/0.63	—
73	Abdomen, 1+1 ventral tubercles: **(0)** present; **(1)** absent[12]	4	0.33	0.25/0.80	Character 113 of Gil-Azevedo & Maia-Herzog (2007: 58), 45 of Gil-Azevedo et al. (2012: sd 3)

Table 2. Data matrix for the cladistic analyses. — ***Symbols***: **–** codes for character inapplicable to taxon, ? for information unavailable in taxon, **a** = 0&1, **b** = 0&2, **c** = 1&3.

	0000000001111111111222222222233333333334444444444555555555560000000007777
	1234567890123456789012345678901234567890123456789012345678901234567890123
S. (*Hellichiella*) *nebulosum*	0000000000-000---000000000000000-000000000000000-00000000000000000000-0
S. (*Byssodon*) *meridionale*	0000000000-000---001001000000000-000000000110400-0100000000010000011100
S. (*Eusimulium*) *aureum* complex	0000000000-000---001000000000000-000000000010200-01000000000100000000-0
S. (*Nevermannia*) *pugetense* complex	0000000000-000---00100?000000000-000000000000200-0100000000010000001100
S. (*Hemicnetha*) *rubrithorax*	0110000000-0110111110110000000100-010a010000110100-0000110000-1010100211 1
S. (*Hemicnetha*) *canadense*	0110000000-00100101101100000000 10-010001000011--00-010011000201100 1-002111
S. (*Simulium*) *venustum* complex	0100000000-0010100111-1000000000-00000100000000000-00101000000100 01-111100
S. (*Aspathia*) *metallicum*	1100000000-0010110110110000000 00-1000010000000001000111000010110001001100
S. (*Psilozia*) *vittatum*	?100100000-0010110111-1000000110-210000110000041 0-000?100000001010001 01a01
S. (*Chirostilbia*) *pertinax*	1100000000-0010110110100000001 10-2100001111100111100111a00020100001112111
S. (*Chirostilbia*) *spinibranchium*	1100000000-0010110110100000001 10-2100001111110111100111a00010100001112111
S. (*Chirostilbia*) *distinctum*	1100000000-0110111110100000001 10-210100111111031110000110 1-1011-101112111
S. (*Chirostilbia*) *subpallidum*	1100000000-0a10111111-0001100110-210a0011110001111001110000000100000111111
S. (*Chirostilbia*) *papaveroi*	1100000000-0110111111-0000000110-2100001111000111100111000000100000111111
S. (*Chirostilbia*) *brunnescens*	1100000000-0110111111-0001100110-2101001111000011100111000000100000111??1
S. (*Notolepria*) *exiguum*	1100000000-000---0111-10000001010211000110010011110011100001011000011111 1
S. (*Pternaspatha*) *barbatipes*	0100000000-0010110110110000000 00-0010001100100001000101000020110 01-112101
S. (*Pternaspatha*) *nigristrigatum*	0100000000-0010110110110000000 00-0010001100100101000101000020100 01-112101
S. (*Psaroniocompsa*) *stellatum*	1101100000-0010110110110000000 00-1000001100000201000111000000000000101110
S. (*Psaroniocompsa*) *quadrivittatum*	11011-1000-0010110110110000000 00-1000001100000101000111000000100000003100
S. oviedoi	1110000000-00100?01100?000000100-01000100001100011001011000 20-1000000211 1
S. rivasi	1110000000-00100?01100?000000100-01000100001100011001011000 20-1000000211 1
S. blancasi	0000000000-0010001111-1000000000-00100000000002 00-00001010000110000003 0-1
S. penai	0000000000-0010001111-1000000000-00100000000010200-000010100001100000 0-0-1
S. tenuipes	0000000000-0010001111-1000000000-00100000000010200-000010100001100000 0-0-1
S. albanense	11011?00010111001101011001000010-2111101100000101101111000100101001112101
S. anaimense	???????????11?????0101???????????????10?????00001111110100010110100011211 1
S. antonii	1101000000-01100111101100110111 0-210??????????????????????????????????????
S. arcabucense	1101000000-0110??11101100110101 0-21?1100100000011111110001001010 1-112111
S. bicoloratum	1101000000-0110011110100011011 10-21011001000001112011110001011010001121 11
S. bicornutum	1101000000-0110011110110011011 10-2101100100101--1101111000100001001112111
S. bivittatum	1101100000-0110110111-1100000111021100011000001110000110000101010001 01a00
S. bobpetersoni	1101100010-0110111111-11100001111210000110000010100000100001010100010110 1
S. callidum	1101000000-0110111110100011001 10-21110011000001111001110000101010001011 11
S. clarum	1101100000-0a10110111-1110000111021000011000000c110000?1000010101000101 0-0
S. cormonsi	1101000000-0110011110100011011 10-211110010000000112011110001011010001121 11
S. dandrettai	1101100010-0-10111111-1100000011021100011000001110000110000101010001 01???
S. dinellii	1101111000-0110011110100011101 10-211100010000011110011100001011101-112101
S. downsi	1101100010-0-10111111-0111100111121110011000001110000110000101010011011 01
S. dugesi	1101100000-0-10111111-1100000001021100011000001110000110000000101000111 0-1
S. escomeli	1101100010-0a10111111-111aaa01111211a00110000011100001100001010100010110 1
S. furcillatum	1101000000-0110011110110011011 10-2101100100101--1101111000100001000112111
S. gabaldoni	110110000101111-11110100010000 10-2111000100000011101111000101101 0???????
S. gonzalezherrejoni	1101100010-0110111111-1110000111121000011000001010000110000101010001011 01
S. griseum	1101100010-0110111111-1110000111021000011000000111000 0?1000000101 01-1010-0
S. haematopotum	1101100000-0010111111-1100000011021000011000001110000110000101010001011 01
S. ignacioi	11011011011 0111-1111000001100110-21010101001104111001110 01-1011110011211 1
S. ignescens	1101010000-0110011110100011011 10-2101000100000311101111000000000100011211 1

Table 2. continued.

	0000000001111111111222222222233333333334444444444555555555560000000007777
	1234567890123456789012345678901234567890123456789012345678901234567890123
S. iracouboense	1101100000-0110111111-010110011102111001100000111000011001-10111000101101
S. jaimeramirezi	1101000000-011001111010001101110-21111001000000112011110001011010????????
S. kabanayense	110110110110111-1111000001000110-210101010001031110011100001011101-012111
S. longithallum	1101100010-0110111111-111000011112100001100000101000011000010101000101101
S. lutzianum	110110000101111-1111010001000110-2111000100000111101111000101101000112111
S. mangabeirai	1101100010-0010111111-111000011112100001100000211000011000010101000101111
S. maroniense	110110110110111-1111000001100110-2101010100110411100111001-10111100112111
S. mayuchuspi	110110000101010010111-0000000110-2100100100000111101111000101101000112111
S. mediovittatum	1101100000-0-10110111-1100000011021100011000001110000110000001010001010-0
S. notatum	1101100010-0010111111-111000011102100001100000111000011000000101000101-00
S. nuneztovari	1101111000-01????11101?001110110-2101000100?001?11001110000101110????????
S. ochoai	1101100000-0-10111111-1100000001021100011000001110000110000101010001110-1
S. ochraceum	1101111000-011001111000001110010-210100010000011110011100001011101-112111
S. panamense	1101100000-011011111010001100110-2101001100000401100111000010101000101111
S. pautense	1101010000-011011111011001101110-2111100100000011111110000000101000112111
S. perflavum	110110110111111-1111010001110110-2101010100110111100111000010111000112111
S. pifanoi	1101010000-011001111011001101110-2101000100000101111110000010101000112111
S. pseudocallidum	1101000000-011011111011001100110-2101001100000111100111000010101000101111
S. romanai	110110000101111-1111010000000110-2111a01100000111101111000111101000112111
S. roquemayu	1101010000-0111-1111010001101110-210???????0001111111100001011010????????
S. rorotaense	110110110110111-1111000001100110-2101010100110411100111001-10111100112111
S. rubiginosum	1101010000-011001111010001101110-2101100100000111101111000000001000112111
S. samboni	1101100000-0110111111-010110011102101001100000101000011000010101000101101
S. shewellianum	1101111000-011001111010001110010-210100010000011110011100001011101-112111
S. suarezi	110110110110111-1111000001100110-2101010100110411100111001-10111100112111
S. tolimaense	?101000000-01100111101?????????????????????100211111111000-200010????????
S. travisi	1101000000-011011111011001100110-2101001100?00111100111????????????101111
S. trivittatum	1101100010-0110111111-111000011112100001100000011000011000000101000101101
S. trombetense	110110110110111-1111010001100110-2101010100111401100111001-10111100112111
S. tunja	1101000000-011001101011001101110-211110010000031100001100001010101-112111
S. veracruzanum	1101100010-0010111111-111110011112110001100000101000001000000101000101101
S. venator	1101100000-0a10111111-1??000011102100001100000111 0000?100000010101-1010-0
S. wolffhuegeli	110110000101111-1111010001000110-2111101100000111101111000010101000112101
S. zempoalense	1101100010-0010111111-111000001102110001100000001000001000010101000101111
S. labellei	1101100010-0010111111-1??0000011021000011000001111000?10000001010001010-0
S. meyerae	1101100000-01101?0111-110000011102100001100000b010000?10000001010011010-?
S. robynae	1101100010-0110111110111?0000011021010011000001111000?10000001010001010-0
S. virescens	11011001010101001011011001001010-2100000100110011000101000020111000101111
S. machetorum	?1010???????0????01?010??????110-21?00?01000000111011?1000000001001112111

Table 3. Summary of scores and topological differences among the Most Parsimonious Trees (MPTs) obtained by analysis with Equal Weights (**EW**) and Implied Weights (**IW**). IW analyses were carried out under Concavity Constant (**k**) 1 to 100, which were grouped when the searches resulted in the same trees, totaling 10 k-categories. — ***Abbreviations***: **%Fit** = k-value in the normalized Fit Function; **CI** = consistency index; **RI** = retention index; **SPRm** = subtree pruning regrafting moves of strict of consensus tree; **T** = target; **stb** = strict consensus tree before.

Analysis	%Fit	MPTs	Fit < k	Length	CI / RI	SPRm T = stb	SPRm T = EW
EW	—	136	—	343	0.23 / 0.78	—	—
IW k1–2	< 40%	18	42.265422	368	0.22 / 0.76	—	17
IW k3	48%	64	30.32107	362	0.22 / 0.76	7	17
IW k4	55%	32	26.78941	357	0.22 / 0.77	5	15
IW k5	60%	16	24.057593	355	0.22 / 0.77	2	15
IW k6–9	65–74%	16	21.86872	354	0.22 / 0.77	1	14
IW k10–17	75–84%	32	16.1849	348	0.23 / 0.77	11	6
IWk18–21	85–87%	8	10.72027	347	0.23 / 0.77	1	7
IW k22–25	87–88%	8	9.19142	346	0.23 / 0.78	3	6
IW k26–35	89–91%	8	8.04809	344	0.23 / 0.78	8	1
IW k40–100	92–97%	8	5.60485	343	0.23 / 0.78	5	0

Table 4. List of synapomorphies common to the 64 trees found under searches carried under implied weights with k5 to k17. Bold are unambiguous synapomorphies. * sensu this paper.

Node n°	Node name	Synapomorphies
1	—	**14(1)**; **19(1)**; **55(1)**
2	—	**2(1)**
3	—	**17(1)**
4	*S.* (*Notolepria*) + *S.* (*Chirostilbia*) + *S.* (*Psilozia*) + *S.* (*Psilopelmia*) *	**34(2)**; 35(1); **48(1)**
5	*Simulium* (*Eremulium*) subgen.n.	18(1); 36(1); **57(1)**; 73(1)
6	*S. penai* + *S. tenuipes*	45(1)
7	*S.* (*Hemicnetha*) *	**3(1)**; 35(1); 45(1); 56(1); 72(1)
8	*S. oviedoi* + *S. rivasi*	1(1); 22(0)
9	*S.* (*Pternaspatha*)	66(1)
10	*S.* (*Chirostilbia*)	**42(1)**; **43(1)**
11	Subpallidum species-group	13(1); 18(1)
12	*S. subpallidum* + *S. brunnescens*	26(1); 27(1)
13	Pertinax species-group	67(1); 70(2)
14	*S. spinibranchium* + *S. distinctum*	45(1)
15	*S.* (*Psilopelmia*) *	**64(1)**
16	Escomeli species-group *	**24(1)**; 32(1)
17		30(1); **33(1)**
18		36(0)
19		13(1)
20		48(0)
21		31(0); 69(1)
22		18(0); 73(0)
23		25(1)
24		18(1)
25		9(1)
26		30(0); 50(1)
27		—
28	Dinellii species-group	6(1); 28(1)
29	*S. ochraceum* + *S. shewellianum*	30(0)
30		**50(2)**
31		36(1)
32		6(1)
33		51(1); 55(0)
34		23(1)
35		62(0)
36		38(0)
37	Romanai species-group	—
38		15(1); 36(1)
39		47(0)
40		40(1)
41		61(0); 72(0)
42	Perflavum species-group	**11(1)**; 15(1); 39(1)
43		58(1); 65(1); 47(4)

Diagnosis. ***Female***: anal lobe triangular, with length distinctly longer than width (in lateral view), except *S. dugesi* and *S. ochoai*. ***Pupa***: cocoon with irregular anterior rim. ***Larva***: hypostoma with similar teeth height.
For species-groups diagnosis see Table 5.

Bicoloratum species-group

S. antonii Wygodzinsky, 1953
S. arcabucense Coscarón, 1990
S. bicoloratum Malloch, 1912
S. bicornutum Wygodzinsky & Coscarón, 1982
S. cormonsi Wygodzinsky, 1971
S. furcillatum Wygodzinsky & Coscarón, 1982
S. ignescens Roubaud, 1906
S. jaimeramirezi Wygodzinsky, 1971
S. machetorum Mantilla, Moncada, Matta & Adler, 2013
S. pautense Coscarón & Takaoka, 1989
S. pifanoi Ramírez-Pérez, 1971
S. roquemayu Coscarón, 1985
S. rubiginosum (Enderlein, 1934)
S. tolimaense Coscarón, 1985
S. tunja Coscarón, 1990

Callidum species-group

S. callidum (Dyar & Shannon, 1927)
S. panamense Fairchild, 1940
S. pseudocallidum Díaz Nájera, 1965
S. travisi Vargas, Vargas & Ramírez-Pérez, 1993

Table 5. *Simulium* (*Psilopelmia*) Enderlein, 1934 species-group diagnoses.

Characters	***Simulium* (*Psilopelmia*)**						
	Bicoloratum	**Callidum**	**Dinellii**	**Escomeli**	**Perflavum**	**Romanai**	**Virescens**
Female							
Cibarium, surface of anteromedial border	unarmed	unarmed/ armed	armed	armed	armed	armed	armed
Cibarium, shape of 1+1 lobes of anteromedial border	blunt	blunt	acute projections (large U-shape)	blunt	acute projections (small U-shape)	blunt	blunt
Cibarium, size of the area between 1+1 lobes	about ½ of anterio-medial border	about ½ of anterio-medial border	about ½ of anterio-medial border	about ½ of anterio-medial border	smaller than ¼ of anterio-medial border	about ½ of anterio-medial border	smaller than ¼ of anterio-medial border
Cibarium, transversal medial depression in medial area	absent	absent	absent	absent	slowly depressed	enlarged	enlarged
Abdomen, with 1+1 submedian longitudinal silver rows – in tergite lateral edges	absent	absent	absent	present	absent	absent	absent
Abdomen, tergites II–IV background coloration	II and III light, IV dark	II and III light, IV dark	II to IV light	II and III variable, IV dark	II light, III and IV variable	II variable, III and IV dark	II light, III and IV dark
Abdomen, segment V coloration	tergite dark brown to black contrasting with pleura and sternum orange to yellow	homogeneous	homogeneous	homogeneous	homogeneous	homogeneous	tergite dark brown to black contrasting with pleura and sternum orange to yellow
Abdomen, anal lobe distal portion narrowed forming a tail-like process	absent	absent	absent	present	absent	absent	absent
Male terminalia							
Length of gonostylus relative to gonocoxite	subequal or shorter	subequal or shorter	subequal or shorter	subequal or shorter	markedly longer	subequal or shorter	subequal or shorter
Pupa							
Gill trunk	long	long	long	long	short	long	short
Cocoon anterior rim	thickened	thickened	not thickened	thickened (except *S. iracouboense*)	not thickened	thickened	not thickened

Dinellii species-group

S. dinellii (Joan, 1912)
S. nuneztovari Ramírez-Pérez, Rassi & Ramírez, 1977
S. ochraceum Walker, 1861
S. shewellianum Coscarón, 1985

Escomeli species-group

S. bivittatum Malloch, 1914
S. bobpetersoni Coscarón, Ibáñez-Bernal & Coscarón-Arias, 1996
S. clarum (Dyar & Shannon, 1927)
S. dandrettai Vargas, Martínez Palacios & Díaz Nájera, 1946
S. downsi Vargas, Martínez Palacios & Díaz Nájera, 1946
S. dugesi Vargas, Martínez Palacios & Díaz Nájera, 1946
S. escomeli Roubaud, 1909
S. gonzalezherrejoni Díaz Nájera, 1969
S. griseum Coquillett, 1898
S. haematopotum Malloch, 1914
S. iracouboense Floch & Abonnenc, 1946
S. labellei Peterson, 1993
S. longithallum Díaz Nájera & Vulcano, 1962
S. mangabeirai Vargas, 1945
S. mediovittatum Knab, 1915
S. meyerae Moulton & Adler, 2002
S. notatum Adams, 1904
S. ochoai Vargas, Martínez Palacios & Díaz Nájera, 1946
S. robynae Peterson, 1993
S. samboni Jennings, 1915
S. trivittatum Malloch, 1914
S. venator Dyar & Shannon, 1927
S. veracruzanum Vargas, Martínez Palacios & Díaz Nájera, 1946
S. zempoalense Vargas, Martínez Palacios & Díaz Nájera, 1946

Perflavum species-group

S. ignacioi Ramírez-Pérez & Vulcano, 1973
S. kabanayense Ramírez-Pérez & Vulcano, 1973
S. maroniense Floch & Abonnenc, 1946
S. perflavum Roubaud, 1906
S. rorotaense Floch & Abonnenc, 1946
S. suarezi Ramírez-Pérez, Rassi & Ramírez, 1977
S. trombetense Hamada, Py-Daniel & Adler, 1999

Romanai species-group

S. albanense Coscarón, 1990
S. anaimense Coscarón & Muñoz de Hoyos, 1995
S. gabaldoni Ramírez-Pérez, 1971
S. lutzianum Pinto, 1932
S. mayuchuspi Coscarón, 1990
S. romanai Wygodzinsky, 1951
S. wolffhuegeli (Enderlein, 1922)

Virescens species-group

S. virescens Hamada, Silva & Pereira, 2012

Species inquirenda

S. flavipictum Knab, 1914
S. jacobsi Dalmat, 1953

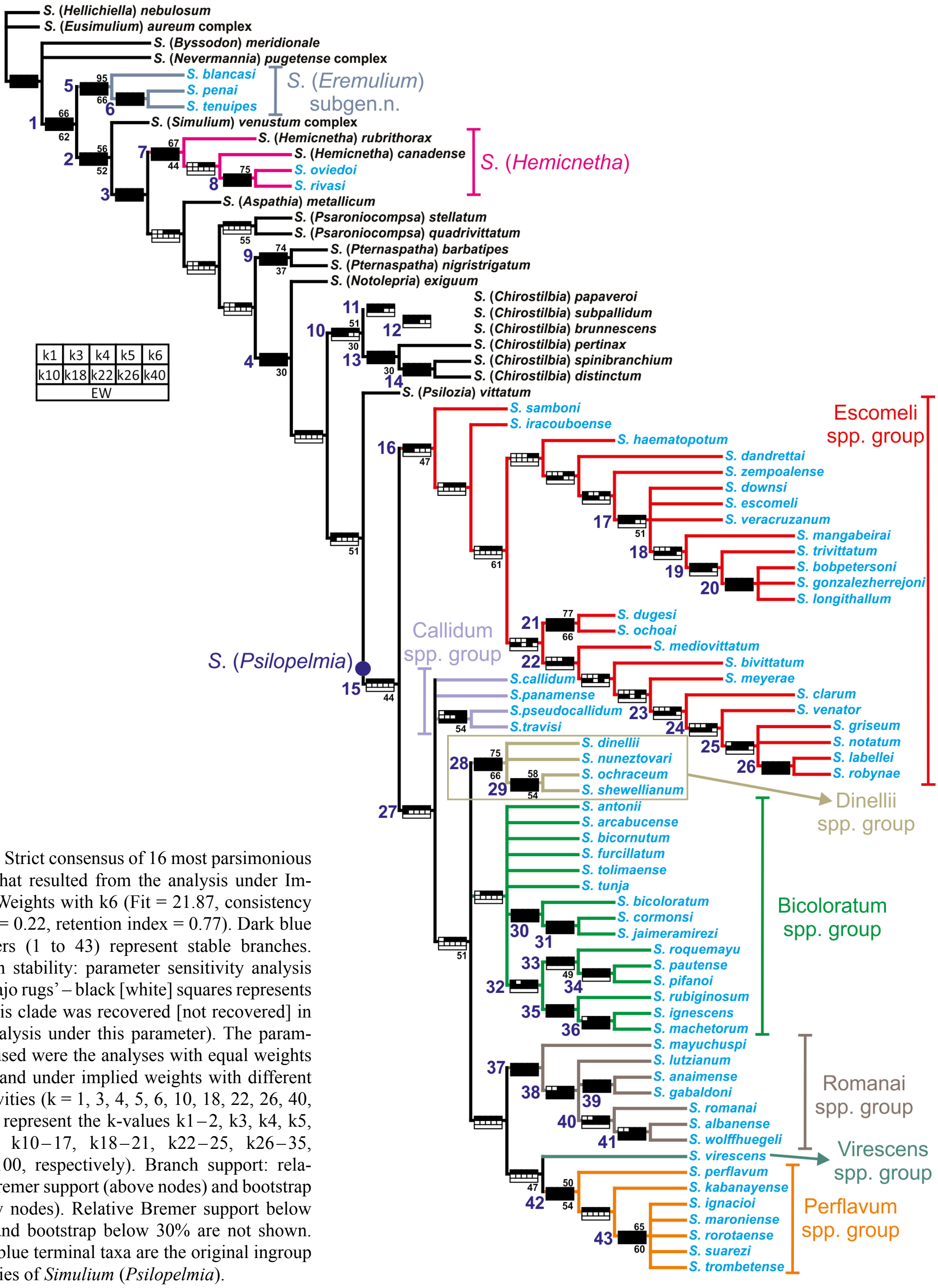

Fig. 7. Strict consensus of 16 most parsimonious trees that resulted from the analysis under Implied Weights with k6 (Fit = 21.87, consistency index = 0.22, retention index = 0.77). Dark blue numbers (1 to 43) represent stable branches. Branch stability: parameter sensitivity analysis ('Navajo rugs' – black [white] squares represents that this clade was recovered [not recovered] in the analysis under this parameter). The parameters used were the analyses with equal weights (EW) and under implied weights with different concavities (k = 1, 3, 4, 5, 6, 10, 18, 22, 26, 40, which represent the k-values k1–2, k3, k4, k5, k6–9, k10–17, k18–21, k22–25, k26–35, k40–100, respectively). Branch support: relative Bremer support (above nodes) and bootstrap (below nodes). Relative Bremer support below 50% and bootstrap below 30% are not shown. Light blue terminal taxa are the original ingroup – species of *Simulium* (*Psilopelmia*).

4. Discussion

Simulium (*Psilopelmia*) sensu Adler (2020) was not recovered in our analyses, because the species of the groups Blancasi (*Simulium blancasi*, *S. penai*, and *S. tenuipes*) and Oviedoi (*S. oviedoi* and *S. rivasi*) sensu Coscarón et al. (2008) do not group with Bicoloratum, Dinellii, Escomeli, Romanai, and Perflavum species-groups in all resulting trees (Figs. 7, 8, nodes 5, 8, and 15). *Simulium* (*Psilopelmia*) sensu Coscarón et al. (2008) is also not recovered, even without the Blancasi species-group, because *S. callidum*, *S. panamense*, *S. pseudocallidum*, and *S. travisi* are closer to the Bicoloratum, Dinellii, Perflavum, and Romanai species-groups (node 27) than to its remaining species (here as Escomeli species-group,

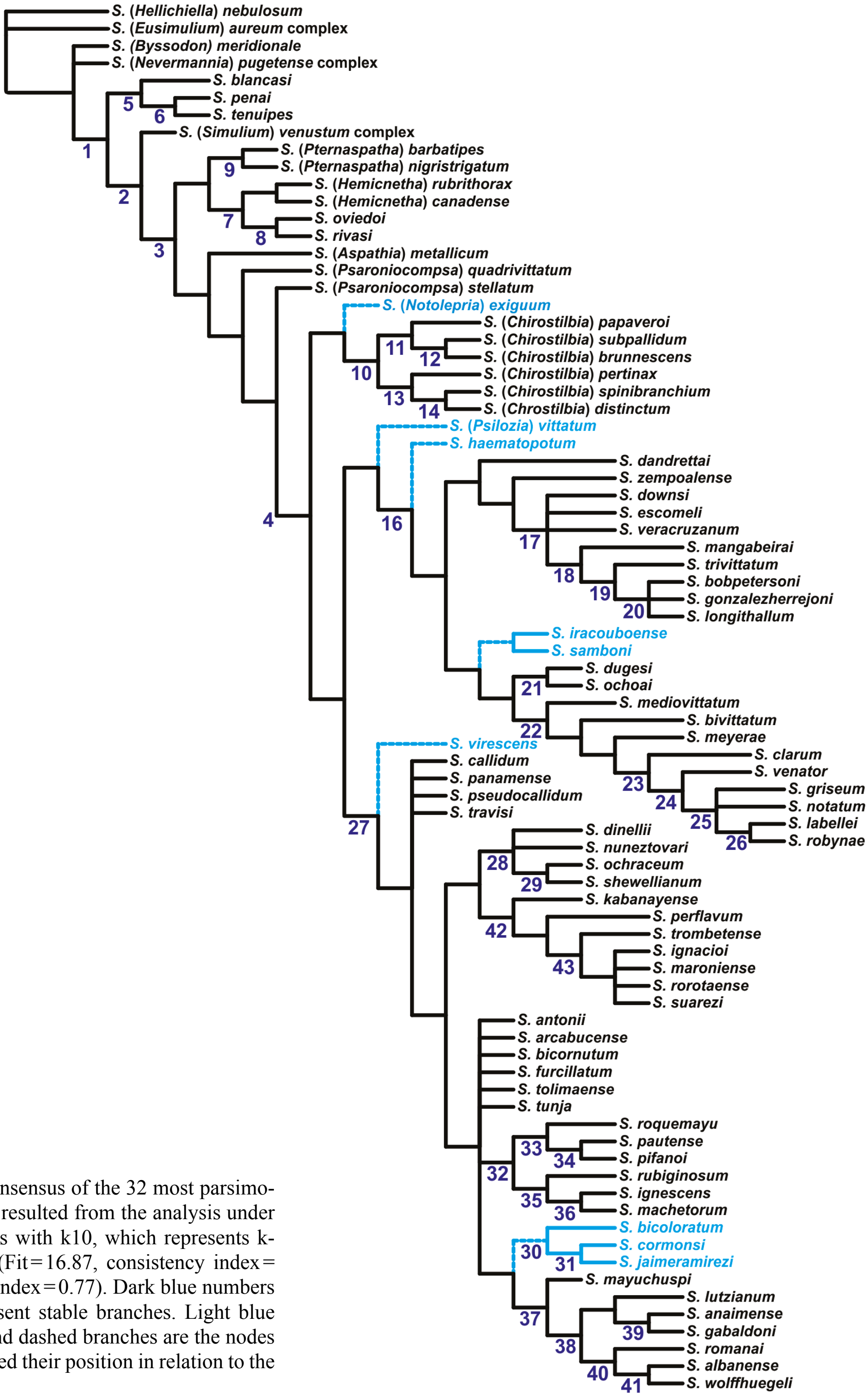

Fig. 8. Strict consensus of the 32 most parsimonious trees that resulted from the analysis under Implied Weights with k10, which represents k-value k10–17 (Fit=16.87, consistency index=0.23, retention index=0.77). Dark blue numbers (1 to 43) represent stable branches. Light blue terminal taxa and dashed branches are the nodes that have changed their position in relation to the tree in Fig. 7.

node 16). We obtained weak stability for *Simulium* (*Ectemnaspis*) sensu Coscarón (Bicoloratum, Dinellii, Perflavum, and Romanai species-groups), which was recovered in analyses with k-values k3 to k6–9 only. But when *S. callidum*, *S. panamense*, *S. pseudocallidum*, and *S. travisi* are included (node 27), the clade could be considered stable (recovered in analysis with k-values k1–2 to k10–17).

Based on our data and with the aim of taxonomic stability, we have three systematic arrangement options: (1) consider *Simulium* (*Psilopelmia*), without Blancasi and Oviedoi species-groups (recovered in analyses with k-value k1–2 to k6–9, node 15); (2) consider *S.* (*Psilopelmia*) (node 16) and *S.* (*Ectemnaspis*) (node 27) valid; or (3) synonymize *S.* (*Psilozia*) with *S.* (*Psilopelmia*) (k-values k1–2 to k10–17). The three proposed combinations form natural groups and could be considered for taxonomic purposes. Whereas the close relationship between *S.* (*Psilozia*) and *S.* (*Psilopelmia*) is widely accepted and form the most stable group (option

3), the synonymy of the two subgenera has never been proposed before, could be controversial, and should be further investigated. None of the proposals stand out for their stability, hence we chose to maintain the *status quo* (option 1) until new data can be added.

All analyses recovered the clade *S.* (*Notolepria*) + *S.* (*Chirostilbia*) + *S.* (*Psilozia*) + *S.* (*Psilopelmia*) (Figs. 7, 8, node 4), supported by three unambiguous synapomorphies (Table 4). Gil-Azevedo et al. (2012) found similar results in an analysis focused in *S.* (*Chirostilbia*), but with a larger number of representatives of Neotropical *Simulium* subgenera as outgroups, which reinforces that this group forms a stable clade inside the phylogeny of *Simulium*. Here we recovered *S.* (*Chirostilbia*) as monophyletic (Figs. 7, 8, node 10; Table 4), whereas Gil-Azevedo et al. (2012) did not. Gil-Azevedo et al. (2012) recovered both species-groups of *S.* (*Chirostilbia*), Pertinax and Subpallidum, as did we (Figs. 7, 8, nodes 11 and 13 respectively; Table 4), but found the Subpallidum species-group closer to *S.* (*Psilopelmia*) than to Pertinax. In this paper we expanded the number of terminal taxa of *S.* (*Psilopelmia*), sampling 62 against four in Gil-Azevedo et al. (2012), which invalidated some of the authors' apomorphies (as our character 23 [Wing, basal sector of the vein R, setae: (0) present; (1) absent]); we also changed the perspective on some characters that were reinterpreted here (i.e., characters 34 [Anal lobe, distal border, shape: (0) sub-square; (1) hemispheric, distinctly rounded; (2) triangular (base smaller than high)] and character 42 [Gonostylus, apex, spurs: (0) present; (1) absent]; see details in Table 1).

Simulium oviedoi and *S. rivasi* are similar species and both were unplaced to subgenus for 36 years until Coscarón & Coscarón-Arias (2007) placed them in *S.* (*Hemicnetha*). They based their decision on similarities of head and wings of the adult, but chiefly upon characteristics of the pupa. The same authors highlighted that terminalia and larvae from the Oviedoi species-group are quite different from typical *S.* (*Hemicnetha*). Hernández-Triana (2011), in a review of *S.* (*Trichodagmia*) sensu lato (including *S.* (*Hemicnetha*) species), considered that terminalia features should weigh more and included the Oviedoi species-group in *S.* (*Psilopelmia*). However, he recognized the general similarities between adults of Ovieidoi and *S.* (*Trichodagmia*). Oddly, he subsumes the species-group in the Bicoloratum species-group. In our analysis, the Oviedoi species-group does not fit in the clade *S.* (*Notolepria*) + *S.* (*Chirostilbia*) + *S.* (*Psilopelmia*). The position of this group closer to *S.* (*Heminetha*) is found in all analyses with five unambiguous synapomorphies (from adult head and terminalia, pupa, and larva) (Figs. 7, 8, node 7; Table 4). Based on this result, we propose the maintenance of Oviedoi as a species-group and its transferrence from *S.* (*Psilopelmia*) to *S.* (*Hemicnetha*), at least provisionally.

Simulium blancasi, *S. penai*, and *S. tenuipes* form a species-group endemic to the Atacama Desert (Chile-Peru). The group has been maintained as unplaced to subgenus for 37 years, until Coscarón & Coscarón-Arias (2007) putatively allocated it inside *S.* (*Psilopelmia*), as the species-group Blancasi. Shelley et al. (2010) sank the Blancasi group into the Bicoloratum species-group because they have unarmed cibarium (clearly a plesiomorphy). In our analyses, the position of the Blancasi species-group is always far outside *S.* (*Psilopelmia*). The group is found in all analyses, with stability and support, in the base of the clade "*Wilhelmia* to *Simulium*" (Figs. 7, 8, nodes 1, 2, and 5; Table 4). For example, in the character 02 [Cibarium, cornua, shape] the group presents the plesiomorphic state (0) straight, compact lateral edge, as opposed to state (1) expanded, irregular and enlarged lateral edges, which is a synapomorphy of all the other "*Wilhelmia* to *Simulium*" subgenera. The position of the Blancasi species-group reinforces the relictual aspect of the group, which should be fully investigated in future phylogenetic analyses of *Simulium*. Also, the Blancasi species-group is monophyletic (with stability and support), with four unambiguous synapomorphies from adult, pupa and larva (Figs. 7, 8, node 5; Table 4). As they form a natural group having distinctive features, and do not fit into any existing *Simulium* subgenera, we propose here a new subgenus to allocate its species.

Based in our data we grouped *Simulium* (*Psilopelmia*) into seven species-groups: Bicoloratum, Callidum, Dinellii, Escomeli, Perflavum, Romanai, and Virescens (Table 5). Dinellii (node 28), Perflavum (node 37), and Romanai (node 42) species-groups are stable, being recovered in all k-value analyses (Figs. 7, 8; Table 4). Escomeli species-group (node 16) is stable and recovered in analyses with k-value k1 – 2 to k18 – 21. The Bicoloratum species-group is not stable, only being recovered in analyses with k-value k3 to k6 – 9. We prefer to retain it as a putative species-group until its relationship is more fully investigated (see below for more details). Five species of *S.* (*Psilopelmia*) did not fit in any of the five species-groups: *S. callidum*, *S. panamense*, *S. pseudocallidum*, *S. travisi*, and *S. virescens*. The first four species have intermediate characters between *S.* (*Psilopelmia*) and *S.* (*Ectemnaspis*), both sensu Coscarón. In our analyses those four species appear either as a paraphyletic 'stem group' of *S.* (*Ectemnaspis*) sensu Coscarón or monophyletic as its sister-group. *Simulium callidum*, *S. pseudocallidum*, and *S. travisi* clustered in most of the recovered trees, especially the last two species. These three species appeared close to *S. panamense* in all analyses, in many trees they formed a clade. These four species have similar morphology (Coscarón & Coscarón-Arias 2007), and we tentatively propose the species-group Callidum to house them. But it is important to investigate this relationship further, with the help of molecular data if possible.

Simulium virescens is a bizarre species that presents characters of the Bicoloratum, Perflavum, and Romanai species-groups. We tentatively propose the species-group Virescens to accommodate it until its position is more thoroughly investigated.

Several comprehensive reviews on the subgenus *S.* (*Psilopelmia*) and their species-groups have been presented (Coscarón 1984, 1990; Peterson 1993; Coscarón et al. 1996; Coscarón & Coscarón-Arias 2007); however, only the Perflavum species-group was studied indepth at the species level. Hamada & Adler (1998) revised the group, defining its species based on morphological and chromosomal data and using material from several localities. Through this study, they confirmed/refuted synonyms and investigated the variability within constituent species. For example, they confirmed that *S. perflavum* is a single species, despite its wide distribution. The Bicoloratum, Callidum, Dinellii, Escomeli, and Romanai species-groups need better species level investigations. Many species of Bicoloratum and Romanai are known only by the type material, or based on scarce material from few localities, and six species of those groups lack descriptions of some stages, resulting in considerable amounts of missing data in the matrix. This is especially true in the Bicoloratum group, which could be the reason for its weak phylogenetic stability. Also, studies with partial sequences of the COI gene indicate cryptic diversity in some species of the subgenus (Hernández-Triana et al. 2015; Colorado-Garzón et al. 2017).

Within each species-group we observed some stable relationships between the species (Figs. 7, 8; Table 4): Escomeli (nodes 17–26); Dinellii (node 29); Bicoloratum (nodes 30–36); Romanai (nodes 38–41); and Perflavum (node 43). Approximately 40% of the internal nodes of the *S.* (*Psilopelmia*) species-groups were stable and fully resolved in our analyses. Romanai was the only group which was fully resolved; the remaining species-groups lacked some internal resolution.

Our morphological data detected phylogenetic signal in species-groups, subgenera, and at higher levels. The morphological data was able to appropriately answer the proposed problem (i.e., to test supra-specific classification) with a stable solution. But our analyses failed to estimate satisfactorily the relationship among species-groups and within them. Additional data from various sources such as molecular, cytological, or morphometric may solve those node levels. An integrative approach would be ideal, notably to investigate species-level relationships and their limits. Unfortunately, for *Simulium* (*Psilopelmia*), many species are known only by type material, based on scarce material from few localities, and contains some species that lack descriptions of some stages, all of which make an integrative approach for the entire group impossible at present. In the future, a better species level investigation is fundamental, as well as collection of fresh material to access other data types.

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7. Appendix – Material examined

Outgroup

***S.* (*Hellichiella*) *nebulosum* Currie & Adler, 1986**: CANADA: 2♂, 2♀, British Columbia, 1.1 mi S of Kaslo, 49°55′N 116°55′W, 22.v.1964, Wood GC & DM leg. (ROM, Paratypes); 3 larvae – **L**, British Columbia, Vancouver, University of British Columbia campus, 49°16′N 123°07′W, 9.v.1964 (ROM, Paratypes); 5 Pupae – **P**, British Columbia, E of Prince Rupert on Rt. 16, Diana Lake Prov. Pk., brown-water bog stream, 54°13′N 130°10′W, 15–25 cm, 08.vi.1991, Currie leg. (ROM). 1P, 1L, British Columbia, Vancouver Is., w of Parksville, 49°17′N 124°35′W, 50–75 cm bridge str., 5.vi.1991 (ROM); 3P, 3L, British Columbia, Vancouver, UBC, Endowment Lands (MNRJ#10,232). — USA: 3♂, 1♀, Oregon, St. Corvalis Oak Burn, trap, 1–30.iv.1994, Anderson leg. (ROM).

***S.* (*Byssodon*) *meridionale* Riley, 1887**: CANADA: 3♀, 3P, 3L, Alberta, Onetree Creek near Patricia (MNRJ #10.230).

***S.* (*Eusimulium*) *aureum* Fries, 1824 (complex)**: CANADA: 3P, 5L, British Columbia, Graham Island, 8km N. Port of Skidegate Hwy. (MNRJ#10,231); 3L, British Columbia, ditch drainage, 25 km N Tumbler Ridge on Hwy 29, 55°14′N 121°13′W, 3.vii.1987, Currie leg. (ROM); 20L, British Columbia, Graham Isl., 8 km N. Port of Skidegate on Hwy 16, 57°17′N 131°57′W, 3.vii.1984, Currie leg.; 2F, Quebec, Rigaud, 09.v.1994 (ROM). 2♂/exuviae – **ex**, New Brunswick, Restigouche Co., jcn Hwy 17 & Restigouche R. Rd, 4.vi.1994, Wood leg. (ROM). — USA: 1♂, 3♀, 1P, Oregon, Bento Co., s Philomath, 0.5–1.0 m trib., Beaver Cr. at Rt. 34 crossing, 44°27′N 123°20′W, 21.iii.1992, Currie leg. (ROM).

S. **(*Nevermannia*) *pugetense* (Dyar & Shannon, 1927) (complex)**: CANADA: 3P, 3L, Alberta, Cypress Hills, on Saskatchewan border (MNRJ#10,234).

S. **(*Hemicnetha*) *rubrithorax* Lutz, 1909**: BRAZIL: 2♀, 9P, 12L, Ceará, Ubajara (MNRJ#10,045, #10,046, #10,047, #10,049, #10,051, #10,052, #10,054, #10,055).

S. **(*Hemicnetha*) *canadense* Hearle, 1932**: CANADA: 2P, 5L, British Columbia, Vancouver Island, Golden Stream Province (MNRJ#10,233, alcohol). — USA: 4P, 9L, California, Saratoga to Santa Clara (MNRJ#10,270).

S. **(*Simulium*) *venustum* Say, 1823 (complex)**: 4♀, 4P, 5L, CANADA, Alberta, Ghost Pine Creek, near Huxley (MNRJ#10,237).

S. **(*Aspathia*) *metallicum* Bellardi, 1859**: MEXICO: 11P, 19L, Oaxaca (MNRJ#10,274). — VENEZUELA: 1♂, Mérida, Mucuruba, 2,350 m, 26.ii.1968, Wygodinsky P & B leg. (MLP); 1♀, Miranda, El Saman, without data, Iriarte leg. (MLP). — ECUADOR: 1♀/ex, Pichincha, Cutuglahua, 05.iii.1970 (MLP); 1P, Imbabura, Urcuquí– Salinas, Ao. Piguntucha, 25.v.2002, Coscarón leg., (MLP). 2♀, 1♂, without data (MLP).

S. **(*Psilozia*) *vittatum* Zetterstedt, 1838**: CANADA: 3♀, 3P, 10L, Alberta, Jasper National Park, outflow Patrick Creek (MNRJ#10,235).

S. **(*Chirostilbia*) *pertinax* Kollar, 1832**: BRAZIL: 1♀/ex, Rio de Janeiro, Rio de Janeiro, 18.vi.1984, Malaguti & Castro leg. (CSIOC); 1♂ (pinned), Rio de Janeiro, Rio de Janeiro, 13.viii.1984, Herzog & Malaguti leg. (CSIOC); 2♂, 1♀/ex, Rio de Janeiro, Rio de Janeiro, 18.ix.1984, Herzog & Malaguti leg. (CSIOC); 2L, Rio de Janeiro, Angra dos Reis, 24.v.2002, Nessimian leg. (CSIOC); 1♀, 1♂, Paraná, Apucarana, de Almeida leg. (MLP); 1♀/ex, Santa Catarina, Florianópolis, 04.xi.1981, Coscarón leg. (MLP); 1♂/ex, Santa Catarina, córrego Pindotiba, 05.xi.1981, Coscarón leg. (MLP); 1P, Santa Catarina (MLP). — ARGENTINA: 1♀/ex, Misiones, San Pedro, 18.x.1974, Coscarón leg. (MLP); 1♀, Misiones, Río Uruguay, 10.vi.1971, Coscarón leg. (MLP). 1L, Misiones, Ao. Yacuy Chico, 01.vii.1971, Coscarón leg., (MLP).

S. **(*Chirostilbia*) *spinibranchium* Lutz, 1910**: BRAZIL: 4♀, 6P, Ceará, Ubajara (MNRJ #10,044, #10,048, #10,053).

S. **(*Chirostilbia*) *distinctum* Lutz, 1910**: BRAZIL: 7P, São Paulo, Ubatuba, Rio Prumirim, 24.v.1979, Coscarón leg. (MLP). 1P, Minas Gerais, Bocaina de Minas (MNRJ# 10,000).

S. **(*Chirostilbia*) *subpallidum* Lutz, 1910**: BRAZIL: 5♂/ex, 7♀/ex, 7P, 62L, Rio de Janeiro, Casimiro de Abreu (MNRJ#10,089, #10,104, #10,106, #10,107, #10,109, #10,115, #10,117, #10,118, #10,119, #10,122, #10,123, #10,136, #10,163).

S. **(*Chirostilbia*) *papaveroi* Coscarón, 1982**: BRAZIL: 2♀/ex, 1♂/ex, 2L, Minas Gerais, Jaboticatuba, Serra do Cipó, 28.iv–02.v.1973. Coscarón leg. (MLP, Paratypes).

S. **(*Chirostilbia*) *brunnescens* Maia-Herzog et al., 2012**: BRAZIL 1♀/ex, Mato Grosso, Rosário do Oeste (CSIOC#2,748, holotype); 2♂/ex, 1P, Mato Grosso, Rosário do Oeste (CSIOC#2,749, paratypes); 4♀/ex, 6♂/ex, Mato Grosso, Acorizal (CSIOC#1,588, #2,768, #2,770, #2,771, #2,772, #2,773, #2,774, #2,775, #2,776, #2,777, #2,779, paratypes); 5L, Mato Grosso, Chapada dos Guimarães (CSIOC #ANE1–5, paratypes).

S. **(*Notolepria*) *exiguum* Roubaud, 1906**: ARGENTINA: 3♂, 4♀, 7P, 44L, Jujuy, Río Zora (MNRJ#10,275).

S. **(*Pternaspatha*) *barbatipes* (Enderlein, 1934)**: ARGENTINA: 1♀, Tucumán, Tafí del Valle, Wygodzinsky leg. (MLP); 1♂/ex, 1L, San Juan, El Leoncito, 02.ix.1993, Coscarón leg. (MLP).

S. **(*Pternaspatha*) *nigristrigatum* (Enderlein, 1930)**: ARGENTINA: 43P, 21L, Neuquén (MNRJ#10,277, #10,278); 1♀/ex, Río Negro, Choele Choel, 24.ix.1993, Coscarón leg. (MLP); 1♂, Río Negro, Cipolletti, María Elvira, 06.i.1994, Coscarón leg., (MLP); 1♀, Chubut, Río Tecka, 20 km N. Pueblo, 2.ii.1975, Coscarón leg. (MLP).

S. **(*Psaroniocompsa*) *stellatum* Gil-Azevedo, Figueiró & Maia-Herzog, 2005**: BRAZIL: 1♀/ex, Minas Gerais, Itamonte, Brejo da Lapa (CSIOC#006, holotype); 5♀/ex, 4♂/ex, 15P, 40L, Minas Gerais, Itamonte, Brejo da Lapa (CSIOC#007, paratypes).

S. **(*Psaroniocompsa*) *quadrivittatum* Loew, 1862**: GUATEMALA: 2♀/ex, 1L, Alta Verapaz, Coban, 19.xi.1944, Fairchild leg. (MLP). — PANAMA: 1L, Chiriquí, Gualaca, 82°14’W 8°37′N, Py-Daniel col., (MLP). — ECUADOR: 1♀/ex, Cayapas, Corriente Grande, 26.vi.2001, Coscarón leg. (MLP).

Ingroup – *S.* (*Psilopelmia*) sensu Adler (2020)

S. oviedoi **Ramírez-Pérez, 1971**: VENEZUELA: 1♀/ex, 1♂/ex, 2L, Mérida, Road Apartaderos – Sto. Domingo, 3,500m, 16–26.ii.1968, Wygodzinsky P & B leg. (MLP).

S. rivasi **Ramírez-Pérez, 1971**: VENEZUELA: 1♀\ex, 1♂\ex, 2L, Mérida, N of Apartaderos, 3,850 m, 13.ii.1968, Wygodzinsky P & B leg. (MLP). 1♀/ex, Mérida, Páramo, 4,100 m, 6.x.1980, Coscarón leg. (MLP).

S. blancasi **Wygodzinsky & Coscarón, 1970**: PERU: 4P, 5L, Lima (MNRJ#10,271); 1♀/ex, 5P, 5L, Valle del Rimac, Puente Verrugas, 28.ix.1983, Coscarón leg. (MLP). — CHILE: 1♂/ex, Taparacá, 20.ix.1979, Coscarón leg. (MLP); 1L, Antofagasta, 5.viii.1977, Solervicens leg. (MLP).

S. penai **Wygodzinsky & Coscarón, 1970**: CHILE: 7P, Arica y Parinacota, Socoroma, 3,000 m, 19.xii.1981, Henry leg. (MLP); 7P, Arica y Parinacota, Putre, without data (MNRJ#10,272).

S. tenuipes **Knab, 1914**: CHILE: 5P, 5L, Tarapacá, Río Azapa, km 70, 26.viii.1972, Valenzuela leg. (MLP). 1♀, Tarapacá, Río Camarones, Hacienda Cuja, 8.ix.72, Valenzuela leg. (MLP); 1♂, Tarapacá, Azapa, 17.ix.1979 (MLP); 1P, Taparacá, Río Lluta, km 40, 5.x.1972, Valenzuela leg. (MLP); 1♀, 1L, Arica y Parinacota, Arica, Río Lluta, vi.1981, Boabadilla leg. (MLP); 15P, 10L, Arica y Parinacota, Río Lluta (MNRJ#10,273).

S. albanense **Coscarón, 1990**: COLOMBIA: 1♀/ex, 1♀, 1♂/ex, 7P, 1L, Cudinamarca, 2 km SE de Albán, 24.viii.1967, Wygodzinsky leg. (MLP, paratypes).

S. anaimense **Coscarón & Muñoz de Hoyos, 1995**: COLOMBIA: 1♂/ex, 1L, Tolima, Río Potosí, 07.viii.1994, Coscarón leg. (MLP, paratypes).

S. antonii **Wygodzinsky, 1953**: PERU: 1♀, Cuzco, Quincemil, 1–15.xi.1962, Peña leg. (MLP).

S. arcabucense **Coscarón, 1990**: COLOMBIA: 1♀/ex, 3P, 6L, Boyacá, Valley of Río Pomeca, NW of Arcabuco, 09.vii.1967, Wygodzinsky P & B leg. (MLP, paratypes).

S. bicoloratum **Malloch, 1912**: VENEZUELA: 1L, Monagas, San Antonio, 11.iii.1972, Ramirez-Pérez leg. (MLP). — ECUADOR: 1♂/ex, Tungurahua, Río Verde, 5.xi.1986, Coscarón leg. (MLP). — PERU: 1♀/ex, 5P, 5L, Cuzco, Machupichu, 18.iv.1971, Coscarón leg. (MLP); 4P, 7L, Cuzco, Machupichu, 18.iv.1971, Coscarón leg. (MNRJ#10,281).

S. bicornutum **Wygodzinsky & Coscarón, 1982**: COLOMBIA: 1♂/ex, 1P, 1L, Cundinamarca, Bogotá, Páramo de Sumapaz, 2.vii.1965, Wygodzinsky leg. (MLP).

S. bivittatum **Malloch, 1914**: USA: 1♂, California, Bakersfield, 13.vi.1943, Galindo leg. (MLP). — MEXICO: 1♀/ex, 3P, 1L, Zacatecas, Jerez, 22.vi.1957, Díaz, Fuentes & Rodríguez leg. (MLP).

S. bobpetersoni **Coscarón, Ibáñez-Bernal & Coscarón-Arias, 1996**: MEXICO: 1♂/ex, 1L, Jalisco, Guadalajara, Sta. Ana, xi.1948, Macias leg. (MLP). 1♀, Veracruz, Escamela, 31.i.1948, Reyes leg. (MLP).

S. callidum **(Dyar & Shannon, 1927)**: MEXICO: 5P, Morelos, Temixco, 03.vii.1945, Díaz Nájera leg. (MLP); 1P, Oaxaca, Gelatao, x.1948, Luna leg. (MLP); 5♀, without data (MLP). — GUATEMALA: 5L, 1985, without data (MLP).

S. cormonsi **Wygodzinsky, 1971**: BOLIVIA: 5P, 5L, road to Chapare, 3,000 m, 18.xi.1971, Coscarón leg. (MLP).

S. dandrettai **Vargas, Martínez Palacios & Díaz Nájera, 1946**: MEXICO: 1♀/ex, 1♂/ex, 5P, Mexico, Lagunas de Zempoala, 10.ix.1969, Wygodzinsky P & B leg. (MLP); 1L, Río Frío, 3,000 m, Wygodzinsky P & B leg., without data (MLP).

***S. dinellii* (Joan, 1912)**: VENEZUELA: 1♂, Aragua, Rancho Grande, Parque Nacional Henry Pittier, 04.iii.1967 (MLP). — BRAZIL: 1P, Santa Catarina, Joinville, 01.x.1986, Moreira & Seidel leg. (MLP). — ARGENTINA: 5P, 5L, Salta, Tartagal, ix.1982, García leg. (MLP); 1P, Salta, Rosario de la Frontera, 21.viii.1948, Cuellar (MLP); 1♀, La Rioja, Olta, 30.iii.2000, Coscarón leg. (MLP); 1L, without data, except IMR 812 (MLP).

***S. downsi* Vargas, Martínez Palacios & Díaz Nájera, 1946**: MEXICO: 5P, 5L, Chiapas, Fca. Sta. Isabel Soc., iii.1947, Díaz Nájera leg. (MLP). — GUATEMALA: 1♀, 1♂, Chimaltenango, Yepocapa, 05.viii.1948, Dalmat leg. (MLP).

***S. dugesi* Vargas, Martínez Palacios & Díaz Nájera, 1946**: MEXICO: 1♂/ex, Tamaulipas, Xicoténcatl, iv.1949, Macias leg. (MLP); 1♀, 1P, 1L, San Luis Potosí, Río Verde, viii–ix.1948, Macias leg. (MLP); 3P, 4L, without data (MLP).

***S. escomeli* Roubaud, 1909**: ECUADOR: 1♂, 5P, 5L, San Pedro, 01.xi.1986, Coscarón leg. (MLP). — PERU: 8P, 18L, Lima, Sisicaya, Río Lurin (MNRJ#10,284). — CHILE: 1L, Arica y Parinacota, Río Lluta, 01.v.1972, Valenzuela leg. (MLP); 3♀, 3♂, 10P, Arica y Parinacota, Río Lluta (MNRJ#10,283).

***S. furcillatum* Wygodzinsky & Coscarón, 1982**: COLOMBIA: 1♀/ex, 1♂/ex, 2P, 2L, Cundinamarca, Bogotá, Páramo de Sumapaz, 30.vi.1965, Wygodzinsky P & B leg. (MLP).

***S. gabaldoni* Ramírez-Pérez, 1971**: VENEZUELA: 1♀/ex, 2♂/ex, Monagas, Otto, Caripe, Río Caripe, 730 m, without data, Gabaldon leg. (MLP).

S. gonzalezherrejoni Díaz Nájera, 1969: MEXICO: 3♀, 3P, 9L, Aguascalientes, San José de Gracias, Ao. Pabellon, 4 km San Luis Letras, vi.1992, Coscarón leg. (MLP).

***S. haematopotum* Malloch, 1914**: MEXICO: 1L, Veracruz, Jesús Carranza, iv.1946, Parras leg. (MLP); 1P, Michoacán, Apatzingán-Cancita, 24.x.1952, Díaz Nájera leg. (MLP); 5P, 5L, Guerrero, Ciudad Altamirano and Coyuca de Catalán, Río Balsas, 08.i.1984, 23.iii.1984, Rodriguez & Ibáñez leg. (MLP); 1♂, Guerrero, Arcelia, vi.1947, Díaz Nájera leg. (MLP); 2♀, Chiapas, Tuxtla Gutiérrez, 27.iv.1968, Molina leg. (MLP).

***S. ignescens* Roubaud, 1906**: COLOMBIA: 1♀/ex, Cauca, Río Piendamo, 2,250 m, 24.viii.1967, without collector (MLP); 2L, 29.i.1983, without collector (MLP). — VENEZUELA: 1L, Monagas, San Antonio, 2,150 m, 11.iii.1972, Ramirez-Perez (MLP). — ECUADOR: 5P, 5L, Pichíncha, Nono, 21.iv.2001, without collector (MLP). — PERU: 1♀, Cuzco, Machupichu, 18.iv.1971, Coscarón leg. (MLP). — BOLIVIA: 1P, Chapare, 17.xi.1977, Coscarón leg. (MLP).

***S. iracouboense* Floch & Abonnenc, 1946**: FRENCH GUIANA: 1♀/ex, 1♂/ex, 5P, 6L, Oiapoque, Maripá waterfall, 24–25.ix.1981, Py-Daniel leg. (MLP).

***S. kabanayense* Ramírez Pérez & Vulcano, 1973**: VENEZUELA: 1♀, 1♀/ex, 1♂/ex, Bolívar, 1,200 m, Ramírez Pérez leg., without data (MLP).

S. longithallum Díaz Nájera & Vulcano, 1962: MEXICO: 1♀, Jalisco, Guadalajara, El Salto, xi.1948, Macias leg. (MLP).

***S. lutzianum* Pinto, 1932**: COLOMBIA: 1♀/ex, 1♂/ex, Valle del Cauca, road Saladito to Anchicaya, 700 m, 19.viii.1967, Wygodzinsky P& B leg. (MLP). — ECUADOR: 5P, 5L, Chimborazo, Santiago, 1,130 m, 07.xi.1986, Coscarón leg. (MLP); 5P, 15L, Chimborazo, Santiago (MNRJ#10,285). — PERU: 1♀/ex, 1L, Huánuco, Tingo María, Río Cueva de las Pavas, 2.x.1983, Coscarón leg. (MLP).

***S. mangabeirai* Vargas, 1945**: MEXICO: 2♂/ex, México, Salazar, 3,005 m, 22.iii.1944, Díaz Nájera leg. (MLP); 5P, 5L, México, road México City to Tlamacas, W Popocatépetl, 3,500 m, 16.ix.1969, Wygodzinsky P & B leg. (MLP); 1L, Michoacán, Uruapan, vi–vii.1948, Macias leg. (MLP).

***S. maroniense* Floch & Abonnenc, 1946**: BRAZIL: 1♀/ex, Roraima, Igarapé Sta. Anita, 27.x.1987, without collector (MLP).

***S. mayuchuspi* Coscarón, 1990**: PERU 1♂/ex, 1L, Junín, Tarma, 3,000 m, 11.vii.1965, Wygodzinsky P & B leg. (MLP, paratypes); 1♂, Junín, 2,700 m, 14.vii.1965, Wygodinsky P & B leg. (MLP, paratypes). — ECUADOR: 1♀/ex, 5P, Pichincha, El Campito, 21.vi.2001 Coscarón leg. (MLP).

***S. mediovittatum* Knab, 1915**: MEXICO: 1P, 4L, Chihuahua, Delicias, Río Conchas, xi.1957, Tort leg. (MLP). 1♀/ex, 5P, 1L, Coahuila, Muzquíz, Las Salinas, 3–13.x.1976, Díaz Nájera leg. (MLP).

***S. ochoai* Vargas, Martínez Palacios & Díaz Nájera, 1946**: MEXICO: 1♂/ex, 5P, 4L, Veracruz, Tierra Blanca, Río Azufre, 28.i.1945, Lassman leg. (MLP).

***S. ochraceum* Walker, 1861**: MEXICO: 1P, Oaxaca, s\road175, km 57, 700 m, 13.vi.1992, Coscarón leg. (MLP). — GUATEMALA: 1♂, Chimaltenango, Acatenango, Vieja Margarita, 07.ix.1948, Dalmat leg. (MLP); 1L, 21.vi.1984, whithout data (except #32) (MLP). — COLOMBIA: 1♀, without data (MLP). — ECUADOR: 1♀/ex, Zapallo Grande, Río Cayapas, 25.vi.2001, without collector (MLP); 5P, 5L, Galápagos, Island of San Cristóbal, 27.ii.2002, Coscarón-Arias leg. (MLP).

***S. panamense* Fairchild, 1940**: COSTA RICA: 1♀, San José, El Cedial, M.O., 26.x.1985, Jeron leg. (MLP). —PANAMA: 1♀/ex, 1♂/ex, 1P, Chiriquí, Planes de Hornito, without data (MLP); 5P, 5L, without data.

***S. pautense* Coscarón & Takaoka, 1989**: ECUADOR: 1P, 2L, Paute, 05.vii.1989, Takaoka leg. (MLP, paratypes); 5P, 1L, Cuenca, 04.vii.1988, Takaoka leg. (MLP, paratypes); 1♀/ex, 1♂/ex, Pichincha, 08.vii.2001, Coscarón leg. (MLP).

***S. perflavum* Roubaud, 1906**: BRAZIL: 1♀/ex, Bahia, Ilhéus, 29.vii.1978, Coscarón leg. (MLP); 5♂/ex, 6♀/ex, 35P, 200L, Rio de Janeiro, Casimiro de Abreu, Reserva Biológica União, 27.vi.2013, Molina leg. (MNRJ #10,061, #10,076, #10,080, #10,085, #10,086, #10,091, #10,092, #10,096, #10,108, #10,110, #10,111, #10,113, #10,142, #10,146, #10,152, #10,183); 1♀/ex, São Paulo, Itú, Pau d'Alho, 06.vi.1979, Coscarón leg. (MLP); 1♂, Santa Catarina, between Orleans and Lauro Muller, 05.xi.1981, Coscarón leg. (MLP). — PARAGUAY: 5P, 5L, s\ruta 70, 80km E. of Asunción, 13.vii.1971, Coscarón leg. (MLP). — ARGENTINA: 1L, Misiones, Cataratas del Iguazú, 11.vii.1971, Coscarón leg. (MLP); 1P, Misiones, Ao. del Valle, 08.iv.2002, Coscarón leg. (MLP); 1L, Corrientes, road to Galarza, Estacíon 13, 10.ix.2002, Coscarón leg. (MLP).

***S. pifanoi* Ramírez-Pérez, 1971**: COLOMBIA: 1♀/ex, 1♂/ex, Cundinamarca, 2 km SE Albán, 2,400 m, 24.viii.1969, Wygodzinsky P & B leg. (MLP). 1♀/ex, 3P, 4L, Cundinamarca, road Sibaté, Aguadita, 2,300 m, 5.vii.1967, Wygodzinsky P & B leg. (MLP).

S. pseudocallidum Díaz Nájera, 1965: MEXICO: 5L, Veracruz, Santa Ana, 05.iii.1948, without collector (MLP). 1♂, 1♀, 1P, Oaxaca, Capulálpam de Méndez, x.1948, Luna leg. (MLP); 5P, Oaxaca, Oaxaca, S. Road 175 Km 57, 700 m, 13.vi.1995, Coscarón leg. (MLP).

***S. romanai* Wygodzinsky, 1951**: ECUADOR: 5P, 5L, Mindo, vii.2000, Coscarón-Arias leg., (MLP). — ARGENTINA: 7P, 18L, Jujuy, Normenta, Br. Chico NE, 25.vii.1997, Coscarón leg. (MNRJ#10,286); 1♀/ex, Salta, Quebrada de Escoipe, 13.ii.1996, Coscarón leg. (MLP); 1♀/ex, 1♂/ex, 1P, Salta, Cachí Adentro, 2,500 m, 12.x.1973, Coscarón leg. (MLP); 1♀/ex, Tucumán, San Javier, Ao. La Cascadita, 18.ix.1990, Coscarón leg. (MLP).

***S. roquemayu* Coscarón, 1985**: BOLIVIA: 1♀/ex, Cochabamba, Río Roquemayu, 2,900 m, 15.xi.1977, Coscarón leg. (MLP, holotype).

***S. rorotaense* Floch & Abonnenc, 1946**: BRAZIL: 7P, 5L, Amazonas, Manaus, Reserva Ducke, Igarapé Acará, 22.vii.1981, da Silva leg (MLP); 1♀/ex, 1♂/ex, Amazonas, Manaus, road Manaus–Itacoatiara km 29, CEPLAC, 04.ix.1976, Benedito & Inocencio leg. (MLP).

***S. rubiginosum* (Enderlein, 1934)**: PERU: 1♂, Cuzco, Urubamba, 2,300 m, 18.iv.1971, Coscarón leg. (MLP). — ARGENTINA: 1P, Tucumán, San Javier, Ao. La Cascadita, 18.ix.1990, Coscarón leg. (MLP); 5P, 5L, Tucumán, Tucumán, Reserva

Horco Molle, N de las Residencias, 10.vi.1983, Coscarón leg. (MLP). 1♀, 1♂, 8P, 6L, Tucumán, Tucumán, Reserva Horco Molle, N de las Residencias, 10.VI.1983, Coscarón leg. (MNRJ#10,287); 1P, San Juan, El Leoncito, 24.ix.1993, Coscarón leg. (MLP); 1♀, Buenos Aires, Sierra de la Ventana, Ao. El Loro, 23.xii.1972, Coscarón leg. (MLP); 1L, Buenos Aires, Sierra de la Ventana, Ao. El Loro, 19.viii.1973, Coscarón leg. (MLP).

***S. samboni* Jennings, 1915**: MEXICO: 1♀, 1♂, Veracruz, Córdoba, a Trindad, 14.vii.1948, Córdova leg. (MLP); 1L, Veracruz, Motzorongo, 23.i.1948, Reyes leg. (MLP). 1P, Oaxaca, Río Yetla, 160 m, 13.vi.1992, Coscarón leg. (MLP). — PANAMA: 1L, Panama, Torti, Río Torti, 19.i.1981, without collector (MLP). — VENEZUELA: 1L, Monaguas, San Antonio, without data, Ramírez-Pérez leg. (MLP).

***S. shewellianum* Coscarón, 1985**: COLOMBIA: 1♀/ex, Valle del Cauca, Valle del Río Dagua, 10 km West to Delfina, 400 m, 26.viii.1967, Wygodzinsky P & B leg. (MLP). 1♀/ex, Valle del Cauca, road Saladito to Anchicaya, 500–1,000 m, 19.viii.1967, Wygodzinsky P & B leg. (MLP). 1♂/ex, 1L, Valle de Cauca, road Aguadito to Anchicaya, 400 m, 19.viii.1967, Wygodzinsky P & B leg. (MLP).

***S. suarezi* Ramírez-Pérez, Rassi & Ramírez, 1977**: VENEZUELA: 1♀/ex, 1P, Amazonas, Mayobuteri, 20.iv.1990, Ramírez-Perez leg. (MLP).

***S. tolimaense* Coscarón, 1985**: COLOMBIA: 1♂/ex, Tolima, road Ibagué–Armenia, 14.viii.1967, Wyodzinsky P & B leg. (MLP).

***S. trivittatum* Malloch, 1914**: MEXICO: 1♀, 1♂, 1♂/ex, Coahuila, Múzquiz, 7–13.ix.1970, Diaz Nájera leg. (MLP); 2P, 3L, Jalisco, Guadalajara, Sta. Ana, xi.1948, Macias leg. (MLP).

***S. tunja* Coscarón, 1990**: COLOMBIA: 2♀/ex, 5P, 1L, Boyacá, Tunja, 2,900 m, 9.vii.1967. Wygodzinsky P & B leg. (MLP, paratypes); 2♂/ex, Cundinamarca, Albán, 2,400 m, 24.viii.1969, Wygodzinsky P & B leg. (MLP, paratypes).

***S. veracruzanum* Vargas, Martínez Palacios & Díaz Nájera, 1946**: MEXICO: 1♂, Veracruz, Huatusco, La Cuchilla, 25.viii.1948, Córdova leg. (MLP); 1♀, 2P, Michoacán, Uruapan, vi–vii.1948, Macias leg. (MLP); 1P, 1L, Chiapas, San Cristóbal, Río Mario, 14.viii.1983, Coscarón leg. (MLP). — GUATEMALA: 1P, Chimaltenango, Acatenango, 20.vi.1950, without collector (MLP).

***S. wolffhuegeli* (Enderlein, 1922)**: BOLIVIA: 1♀/ex, Cochabamba, Río Angostura, 2,600 m, 18.xi.1977, Coscarón leg. (MLP). — ARGENTINA: 1♀/ex, Salta, Capiaguti, ix.1982, García leg. (MLP); 5P, Córdoba, Alta Gracia, 23.vi.1995, Coscarón leg. (MLP); 5P, Córdoba, Río Cosquín, 22.vi.1995, Coscarón leg. (MLP); 3♀, 2♂, 30P, 10L, Córdoba, Rio Tercero, 23.vi.1995, Coscarón leg. (MNRJ#10,288); 1L, Mendoza, Uspallata, 01.iii.1989, Marino leg. (MLP); 1♂/ex, Mendoza, San Rafael, 29.i.1995, Coscarón leg. (MLP); 1♀, Buenos Aires, Tres Arroyos, Coscarón leg. (MLP); 1♂/ex, Río Negro, Gral. Fernández Oro, Canal de Riego, 31.i.1995, Coscarón leg. (MLP).

***S. zempoalense* Vargas, Martínez Palacios & Díaz Nájera, 1946**: MEXICO: 1♀, 3P, 1L, Morelos, Zempoala, 10.iii.1943, Vargas & Díaz Nájera leg. (MLP).

The following species were codified based only on the bibliography: *S. clarum* (Dyar & Shannon, 1927); *S. griseum* Coquillett, 1898; *S. ignacioi* Ramírez-Pérez & Vulcano, 1973; *S. jaimeramirezi* Wygodzinsky, 1971; *S. labellei* Peterson, 1993; *S. machetorum* Mantilla, Moncada, Matta & Adler, 2013; *S. meyerae* Moulton & Adler, 2002; *S. notatum* Adams, 1904; *S. nuneztovari* Ramírez-Pérez, Rassi & Ramírez, 1977; *S. robynae* Peterson, 1993; *S. travisi* Vargas, Vargas & Ramírez-Pérez, 1993; *S. trombetense* Hamada, Py-Daniel & Adler, 1998 (in Hamada & Adler); *S. venator* Dyar & Shannon, 1927; *S. virescens* Hamada, Silva & Pereira, 2012.

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