Evolution of Philopotinae, with a revision and phylogeny of the New World spider fly genus *Philopota* Wiedemann (Diptera, Acroceridae)

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Philopotinae are hunchbacked spider flies represented by 63 fossil and extant species in 15 genera worldwide. *Philopota* Wiedemann, 1830, is the most species-rich genus within the subfamily. Here, the evolution of Philopotinae is discussed, and a revision and phylogeny of *Philopota* based on adult morphology are presented. Nine of the 12 extant Philopotinae genera were included in our analysis, and 22 species were recognized in *Philopota*, of which 13 are described as new. Seven new synonymies are proposed. The phylogenetic analysis included 33 terminal taxa (22 ingroup and 11 outgroup species) and used 53 morphological characters, resulting in a single most parsimonious tree under equal weights. The monophyly of *Philopota* is recovered, and the Palaearctic genus *Oligoneura* is hypothesized as its sister-group.

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INTRODUCTION

Spider flies (Diptera, Acroceridae) are a cosmopolitan family of infrequently collected lower brachyceran flies. The Acroceridae is comprised of approximately 530 species in 55 genera (Pape & Thompson, 2013; Schlinger, Gillung & Borkent, 2013) divided into three subfamilies: Acrocerinae, Panopinae, and Philopotinae (Schlinger, 1981). This traditional classification, however, is not supported by molecular data, which indicate that the Acrocerinae are polyphyletic (Winterton, Wiegmann & Schlinger, 2007).

Adult acrocerids are very distinctive, usually having either inflated or hunchbacked bodies (with the head close to the abdominal venter). They are generally covered with dense pilosity, but may also be smooth and shiny, and sometimes have a metallic coloration (Schlinger, 1981, 1987). Adults of ~20 genera have long, modified mouthparts used for nectar feeding, whereas the remaining ~35 genera probably do not feed as they have reduced or even absent mouthparts (Schlinger, 1981). Many species are specialized pollinators and are usually collected on or near flowers (Schlinger, 1960b; Goldblatt, Manning & Bernhardt, 1997; Gilbert & Jervis, 1998; Potgieter et al., 1999; Pujol-Luz, 2004; Barbola et al., 2006; Carvalho & Machado, 2006; Borkent & Schlinger, 2008a, b).

Acrocerid larvae are specialized endoparasitoids of true spiders (Araneae), with a hypermetamorphic life cycle consisting of four instars (Schlinger, 1981, 1987, 2009). Eggs are deposited in large numbers away from, but near their hosts, and they may be placed on the ground, dead branches, twigs, grass, or tree trunks (King, 1916; Cole, 1919a; Schlinger, 1960a, 1981; Cole & Schlinger, 1969; Adler, Reitz & Watson, 1997). First-instar larvae (i.e. maggots) are free-living planidia that either actively seek out a spider host by
crawling, looping or jumping, or sit and wait for the host to pass by (Cole, 1919a; Schlinger, 1987). The planidia often have well-developed setae, spines, and a caudal suction disc used to seek a host and enter its body (Nartshuk, 1997). Host records for acrocerid parasitizing spiders are known for approximately 60 species, and 23 spider families are recorded as hosts of acrocerid larvae (Schlinger, 1987, 2003; Cady et al., 1993). Panopinae are only known to attack mygalomorph spiders, and are recorded from the Antrodiaetidae, Ctenizidae, Dipluridae, Migidae, and Theraphosidae (Schlinger, 1987). Acrocerinae and Philopotinae, by contrast, are only known to attack araneomorph spiders (Schlinger, 1987, 2003). Acrocerinae are recorded from the Agelenidae, Anyphaenidae, Lycosidae, Miturgidae, Salticidae, and Segestriidae (Schlinger, 1987; Cady et al., 1993; Barraclough & Croucamp, 1997; Larrivée & Borkent, 2009), whereas Philopotinae are recorded from the Amaurobiidae, Miturgidae, Phyxelididae, and Salticidae (Schlinger, 1987, 2003).

Philopotinae contains 63 fossil and extant species placed in 15 genera (Gillung & Winterton, 2011; Schlinger et al., 2013). Flies in this subfamily are very distinctive, with varying degrees of arched body shape. The group is monophyletic, and characterized by enlarged postpronotal lobes that are contiguous dorsomedially, forming a collar behind the head (Winterton et al., 2007). Twelve extant genera are described in Philopotinae, of which nine were included in this study. Thylis Ericson and Africaterphis Schlinger are distributed in the Afrotropics, whereas Helle Osten Sacken is restricted to New Zealand. Megalybus Philippi, Neophilopota Schlinger, Philopota Wiedemann, Quasi Gillung & Winterton, and Terphis Ericson are New World genera, whereas Oligoneura Bigot is distributed in the Palaearctic and Oriental regions.

Philopota Wiedemann, 1830, is the most species-rich genus within Philopotinae, containing 16 valid species to date (Gillung & Carvalho, 2009; Pape & Thompson, 2013). Species of Philopota are characterized by a very hunchbacked body and conspicuous sexual dimorphism, in which the abdomen is strongly swollen in the females and slender and typically conical in the males (Fig. 1B vs. A respectively). The genus was originally described by Wiedemann (1830) for the species Philopota conica from Brazil. Loew (1844) described Philopota murina from the Palaearctic, and was followed by several authors who also described Palaearctic species in Philopota (Matsumura, 1916; Brunetti, 1920; Ouchi, 1938, 1942). Later, Bigot (1878) described the genus Oligoneura and its type species, Oligoneura aenea, from the Palaearctic, but then synonymized Oligoneura under Philopota based on their extreme morphological similarity (Bigot, 1888). The two genera were treated as synonymous by many authors for decades, until Schlinger (1971) resurrected Oligoneura and transferred all Palaearctic species from Philopota to this genus. Philopota can be readily differentiated from Oligoneura by the denser pilosity on its eyes, longer and more prominent frons, and the absence of maxillary palpi (Schlinger, 1971). Philopota is now restricted to the New World, with species found from north-eastern Mexico to southern South America.

Philopota is the most species-rich Neotropical genus of spider flies, and one of the largest genera of Acroceridae. Its evolutionary history is remarkable, with species showing an unparalleled degree of character plasticity and morphological variation for the Acroceridae. Wing venation, for instance, is strikingly more variable within Philopota than within any other acrocerid genus, with multiple reductions and deviations from the plesiomorphic, complete wing venation of Acroceridae. Moreover, species of Philopota are ecologically very important as flower visitors and even as pollinators (Pujol-Luz, 2004; Carvalho & Machado, 2006), and some species are amongst the most abundant spider flies in the Neotropics. Nonetheless, the genus has never been revised, and its most recently described species is Philopota flavolateralis Brunetti, 1926.

The first complete revision and phylogeny of Philopota are presented here, along with a dichotomous identification key to all 22 species, including the 13 described here as new. The cladistic analysis performed here sampled 33 terminal taxa, which represent nine of the 12 extant Philopotinae genera. This is the first phylogeny of the Acroceridae based on morphological data and, therefore, the 53 morphological characters constructed here are the first homology hypotheses ever proposed for the family.

MATERIAL AND METHODS

DEPOSITORIES
The material examined is deposited in the institutions listed in Table 1. Museum acronyms follow Evenhuis (2014).

TAXON SAMPLING
A total of 841 specimens of Philopota was studied. All primary types were examined, redescribed, and photographed, except for the holotype of Philopota limosa Walker, 1857, which was supposedly deposited in the British Museum (BMNH) (Pape & Thompson, 2013), but was not found in the BMNH material. No other identified material of this species was available for study, and the species was thus not included in the revision, as the original description is extremely short and inadequate for species-level identification, and no other author has commented on this species in taxonomic works on Philopota.

All descriptions and redescriptions are presented diagnostically, mainly taking into account phylogenetically informative characters, as the separation of many taxa is subtle and possible only through observing several characters. When both sexes were known, the males were initially described or redescribed, and only differing features in the females were described in a separate section. A male was designated as the holotype, whereas other males and the females were designated as paratypes. The only exception is *Philopota amazonensis* sp. nov., for which a female was chosen to be the holotype because it was the only specimen in the type series that bears a locality label, whereas the two male paratypes lack labels and information on their distribution (see further discussion under *P. amazonensis*). Descriptions were constructed in LUCID BUILDER 3.3, using a matrix database of character states that was exported into a text document using the natural language function. The information provided in the section 'Type material examined' is an exact transcription of the labels associated with the specimens. The quotation marks (”) indicate the different

<table>
<thead>
<tr>
<th>Collection</th>
<th>Location</th>
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<tbody>
<tr>
<td>AMNH: American Museum of Natural History</td>
<td>New York, NY, USA</td>
</tr>
<tr>
<td>BMNH: Natural History Museum</td>
<td>London, UK</td>
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<tr>
<td>CAS: California Academy of Sciences</td>
<td>San Francisco, CA, USA</td>
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<tr>
<td>CECL: Coleção de Entomologia Costa Lima, Instituto de Biologia da Universidade Federal Rural do Rio de Janeiro</td>
<td>Rio de Janeiro, RJ, Brazil</td>
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<tr>
<td>CEIOC: Coleção Entomológica do Instituto Oswaldo Cruz, Instituto Oswaldo Cruz</td>
<td>Rio de Janeiro, RJ, Brazil</td>
</tr>
<tr>
<td>CMNH: Carnegie Museum of Natural History</td>
<td>Pittsburgh, PA, USA</td>
</tr>
<tr>
<td>CUIC: Cornell University Insect Collection</td>
<td>Ithaca, NY, USA</td>
</tr>
<tr>
<td>DZUNB: Coleção Entomológica do Departamento de Zoologia da Universidade de Brasília</td>
<td>Brasília, DF, Brazil</td>
</tr>
<tr>
<td>DZUP: Coleção Entomológica Pe. Jesus Santiago Moure, Departamento de Zoologia da Universidade Federal do Paraná</td>
<td>Curitiba, PR, Brazil</td>
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<tr>
<td>EMEC: Essig Museum of Entomology, University of California Berkeley</td>
<td>Berkeley, CA, USA</td>
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<td>EMUS: Utah State University Insect Collection</td>
<td>Logan, UT, USA</td>
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<tr>
<td>IFML: Fundación y Instituto Miguel Lillo, Instituto Superior de Entomología, Universidad Nacional de Tucumán</td>
<td>Tucumán, Argentina</td>
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<tr>
<td>INBIO: Instituto Nacional de Biodiversidade</td>
<td>Santo Domingo de Heredia, Costa Rica</td>
</tr>
<tr>
<td>INPA: Instituto Nacional de Pesquisas da Amazônia</td>
<td>Manaus, AM, Brazil</td>
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<tr>
<td>KSUC: Museum of Entomological and Prairie Arthropod Research, Kansas State University</td>
<td>Manhattan, NY, USA</td>
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<tr>
<td>LACM: Natural History Museum of Los Angeles County</td>
<td>Los Angeles, CA, USA</td>
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<td>MNHN: Muséum National d’Histoire Naturelle</td>
<td>Paris, France</td>
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<tr>
<td>MNRJ: Museu Nacional da Universidade Federal do Rio de Janeiro</td>
<td>Rio de Janeiro, RJ, Brazil</td>
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<tr>
<td>MPEG: Museu Paraense Emílio Goeldi</td>
<td>Belem, PA, Brazil</td>
</tr>
<tr>
<td>MZSP: Museu de Zoolôgica da Universidade de São Paulo</td>
<td>São Paulo, SP, Brazil</td>
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<tr>
<td>NHRS: Naturhistoriska Riksmuseet</td>
<td>Stockholm, Sweden</td>
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<tr>
<td>NMW: Naturhistorisches Museum Wien</td>
<td>Vienna, Austria</td>
</tr>
<tr>
<td>OUMNH: Hope Entomological Collections, University Museum</td>
<td>Oxford, UK</td>
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<tr>
<td>RMNH: Naturalis Biodiversity Centre</td>
<td>Leiden, Netherlands</td>
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<tr>
<td>SEMC: Snow Entomological Museum, University of Kansas</td>
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<td>UCRC: University of California, Riverside</td>
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<td>UFPE: Coleção Entomológica da Universidade Federal do Pernambuco</td>
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<td>USNM: National Museum of Natural History, Smithsonian Institution</td>
<td>Washington DC, USA</td>
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<tr>
<td>UVGC: Universidad del Valle de Guatemala, Collección de Artrópodos</td>
<td>Guatemala City, Guatemala</td>
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<tr>
<td>ZMHB: Museum für Naturkunde, Humboldt-Universität</td>
<td>Berlin, Germany</td>
</tr>
<tr>
<td>ZUEC: Museu de Zoológia do Instituto de Biologia, Universidade Estadual de Campinas</td>
<td>Campinas, SP, Brazil</td>
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Note: In addition to the institutions above, the following acronym was used in the ‘Type material’ section of *Philopota truquii* Bellardi: MRSN, Museo Regionale di Scienze Naturali, Turin, Italy (Guido Pagliano), because material from this collection was mentioned but not examined.

labels for the same specimen, the slashes (/) indicate different lines on the same label, and italics indicate handwritten information. The total number of examined specimens in this revision is very large, and in order to save space herein the complete list of examined material is provided in Supporting Information Table S3; only the type material examined is provided for each species. Distribution maps were created using SIMPLEXMAPPR (Shorthouse, 2010). When GPS data were not available on the label, latitude and longitude were obtained by consulting online gazetteers. Georeferencing data are provided in Table S2.

MORPHOLOGICAL ANALYSIS
Terminology for general morphology follows Cumming & Wood (2009), with wing venation as in Gillung & Winterton (2011) and Winterton (2012), and antennae as in Stuckenberg (1999). Modifications of wing terminology as proposed by Saigusa (2006) were used, in which the dipteran vein A1 (anterior anal vein) (as used in Cumming & Wood, 2009) was homologized with CuP (posterior branch of cubitus) of Mecoptera. Consequently, the following wing venation terms are used here: CuA1 (first anterior branch of cubitus) (of Cumming & Wood, 2009) was homologized with CuP (posterior branch of cubitus) of Mecoptera. Consequently, the following wing venation terms are used here: CuA1 (first anterior branch of cubitus) (of Cumming & Wood) = M1, (fourth posterior branch of media), CuA2 (second anterior branch of cubitus) = CuA (anterior branch of cubitus), and A1 = CuP (posterior branch of cubitus). Homology of the wing veins and cells was inferred through comparison with the wing of species of Megalybus, the most closely related genus to Philopota, which has a complete (plesiomorphic) Philopotinae wing venation (Winterton et al., 2007; Gillung & Winterton, 2011). In plesiomorphic philopotine wing venation, the posterior branches of media M1, M2, M3, M4, as well as CuA are all present. Philopota, by contrast, has very reduced wing venation with some veins being incomplete (i.e. without connection to their stem veins; see vein M2 in Fig. 16B). The superposition of a Philopota wing with that of Megalybus allows the recognition of veins based on their relative position. For vein M2, the basal-most portion is absent, thus leaving a free spur vein (‘spur’ in Figs 14C, 16B, 17D).

External morphology was studied with a Leica MZ9.5 stereomicroscope, and genitalia were examined with a Leica DM2500 microscope. Dissections were carried out by detachment of the genitalia from the tip of the abdomen. The genitalia were subsequently cleared in a 10% KOH solution for 12–24 h, neutralized in acetic acid and ethanol, and stored in glycerine in a microvial and affixed on the pin with the rest of the specimen. The male genitalia of all recognized Philopota species of which the males are known were dissected. In addition, the male genitalia of the outgroup taxa were examined and illustrated. Owing to the absence of sufficient well-preserved material, characters of the female terminalia were not included in the phylogeny, and only drawings and a description of the female genitalia of Philopota tuberculata are presented. Measurements were taken from type and nontype material and are presented in millimetres; the range of the measurement and the number of specimens measured are presented in parentheses. Wing measurements were taken as the length from the base of the distal median plate to the wing tip. Body length was recorded as the distance from the anterior margin of the head to the posterior margin of abdominal segment VI in lateral view. Specimen images were taken at different focal planes using a Leica DFC420 digital camera attached to a Leica MZ16 stereomicroscope, which were then combined into a serial montage image using HELICON FOCUS (Helicon Soft Ltd).

PHYLOGENETIC ANALYSIS
The character matrix used in the phylogenetic analysis is presented in Table S1. Missing data were scored with a question mark, '?', and inapplicable data with a hyphen, ‘−’. All characters were given equal weights and were considered to be non-additive. Sexually dimorphic characters were separated in the matrix and their corresponding states for males and females were coded.

Representatives of all 22 species of Philopota were included as the ingroup (nine described plus 13 new species described herein). In order to test the monophyly of the genus, representatives of eight other extant Philopotinae genera were included as outgroup taxa: Africaterphis acroceroides Sabrosky, Helle rufescens Brunetti, Megalybus crassus Philippi, Megalybus obesus Philippi, Megalybus pictus Philippi, Neophilopota brevirostris Schlinger, Oligoneura itoi Schlinger, Oligoneura yasumatsui Schlinger, Quasi fisheri Gillung & Winterton, Terphis nodosa Ericson, and Thyllis crassa Fabricius. The molecular analysis of Winterton et al. (2007: 821) showed two clades within Philopotinae, one including both the Neotropical genera Megalybus, Terphis, and Philopota, and the Afrotropical genera Parahelle Schlinger and Thyllis, and the other clade including the Australasian genera Helle and Schlingeriella (cited as genus ‘New Caledonia’) Gillung & Winterton, 2011. Therefore, the resulting cladograms from our analyses were rooted using H. rufescens. The fossil genera Archaeaterphis Hauser & Winterton, Eulonchiella Meunier, and Prophilopota Hennig, as well as the extant genus Schlingeriella were not included in our analysis owing to unavailability of material. The Australasian genera Dimacrocolus Schlinger and Parahelle Schlinger were also not included because of their extreme morphological similarity to Thyllis, which indicates that they might be synonymous; further studies will test this hypothesis more thoroughly.
The character matrix was compiled and edited using the matrix and tree interfaces of WinClada (Nixon, 2002) and MESQUITE 3.0 (Maddison & Maddison, 2014). The characters were ordered in the matrix based on their sequence in the taxonomic descriptions. Parsimony analysis was performed with TNT 1.1 (Goloboff, Farris & Nixon, 2008). Ten thousand replications of random taxon addition and the tree-bisection-reconnection branch swapping algorithm were used to find the best trees under equal weights, saving 100 trees per replicate. Bremer support values (Bremer, 1988, 1994) were determined in TNT by performing a search for suboptimal trees that were up to ten extra steps longer. The cladograms were produced in MESQUITE with only unambiguous changes shown. They were then exported as a .svg file and edited using Adobe ILLUSTRATOR.

RESULTS

TAXONOMY

PHILOPOTA WIEDEMANN, 1830
(Figs 1–27, 28F–I, 29, 30, 31F–O, 32, 33F–I, 34, 35, 36A, 37)

Philopota Wiedemann, 1830: 17. Type species: Philopota conica Wiedemann (by monotypy). Macquart, 1834: 366 (diagnosis, reference to P. conica); Blanchar, 1840: 584 (diagnosis, reference to P. conica); Ericson, 1840: 152 (diagnosis, description of new species); Walker, 1855: 340 (diagnosis, reference to P. conica, Philopota maculicollis, Philopota liturata, Philopota ovata, Philopota tuberculata, Philopota histrio, Philopota turbinata, Philopota sobria, and Philopota temperata); Bigot, 1889 (senior synonym of Oligoneura); Bigot, 1890: 318 (key to some Philopotinae genera, comments); Williston, 1900: 185 (drawings of heads and wings, key to genera of Acroceridae); Coquillett, 1910: 588 (reference to P. conica); Cole, 1919a: 19 (diagnosis, key to North American species, comments), 1919b: 54 (comments); Brunetti, 1926: 561 (key to species, comments); Hennig, 1966: 5 (comments, drawings of heads and wings, comments); Schlinger, 1971: 188 (comments, resurrection of Oligoneura), 1981: 582 (key to genera, comments); Winterton et al., 2007: 14 (comments, phylogeny of Acroceridae); Gillung & Carvalho, 2009: 39 (comments, diagnosis, list of Brazilian species); Gillung & Winterton, 2011 (key to Philopotinae genera, comments); Schlinger et al., 2013 (discussion, key to New World Acroceridae genera).

Diagnosis: Philopota is morphologically similar to Neophilopota, Oligoneura, and Quasi, but it can be readily distinguished from all other philopotine genera by its well-developed and prominent frons, which are almost twice as long as wide. Philopota shares with both Neophilopota and Oligoneura the presence of pilose eyes, and elongate, tubular mouthparts. In Quasi, by contrast, the eyes are bare, and the mouthparts are greatly reduced and barely visible. Philopota differs from Neophilopota by the insertion of the antennae on the middle part of the frons, the lower facial margin with same width throughout its extension, and the clypeus as long or as longer than the antennae. Philopota can be differentiated from Oligoneura by its denser eye pilosity, longer and more prominent frons, and the absence of maxillary palpi.

Description: Coloration nonmetallic, body brown or black, usually with yellow markings; head spherical, slightly narrower than thorax width; eye pilose; three ocelli present, median ocellus slightly smaller than lateral ocelli; frons pilose, twice as long as wide and larger than ocellar triangle, raised and conspicuous, projecting over scape and pedicel; antenna shorter than to as long as frons height, situated in the midportion of head; postpedicel stylate with basal portion enlarged and distal portion thin; pedicel bare; frons narrow above antennal base, eyes contiguous; frons wide below antennal base, eyes not contiguous; lower facial margin uniformly widening along its length; clypeus as long as or longer than antenna; maxillary palpus absent; proboscs well developed, longer than head height; dorsomedial margin of fused postpronotal lobes as long as first tarsomere of foreleg; subscutellum usually not developed (except in Philopota dissimilis sp. nov., P. flavolateralis, P. tuberculata, and Philopota grossii sp. nov.); anepisternum usually without lateral tubercle (except in P. dissimilis sp. nov.); wing usually brown; male wing usually without markings (Fig. 14B, without markings vs. C, with markings); female wing usually with markings; costal vein ending before wing tip; radial veins directed to wing apex, reaching wing margin before wing apex; R1 usually not inflated at pterostigma (except in Philopota minut a sp. nov.); R2–3 usually straight; R4–5 present as a single vein, not reaching wing margin; crossovein 2r-m absent; cell r4+5 narrowly elongate, open distally; medial veins not reaching wing margin; M1 straight; M2 present or absent, when present usually with a spur vein; M3 usually absent, when present incomplete, without connection to base of M; discal cell open distally; cell m3 absent; M4 not reaching wing margin; CuA usually absent; anal lobe well developed; alula well developed; legs not elongated (except in P. dissimilis sp. nov.); pulvilli present; forecoxa inserted slightly dorsally relative to midcoxa (Fig. 26B); male abdomen usually conical (Fig. 27B), sometimes ovate (Fig. 27C); female abdomen almost globose (Fig. 27A). Male genitalia (Figs 28F–I, 29, 30, 31F–O, 32, 33F–I, 34, 35, 36A, 37). Cerci smooth; epandrium with posterior margin usually concave.
Philopota amazonensis sp. nov.

(Figs 1A, B, 14A, 20A, 28F, 31F, 33F)

Holotype female, MZSP. Type locality: Brazil, Amazonas, Ega.

Diagnosis: Philopota amazonensis is a distinctive species characterized by the dark body colour, usually black, and the proepisternum and forecoxa yellow. Abdomen is ovate in the male and almost globose in the female, and both sexes have wing without markings, and numerous yellow markings on the body. The species is similar to Philopota costaricensis sp. nov., but can be distinguished by the wider frons and the katepisternum bare on the anterior third.

Description: Holotype female (Fig. 1B). Body length: 7.7 mm, wing length: 8.1 mm (N = 1). Head (Fig. 20A). Slightly narrower than thorax width; vertex black, not raised in comparison to postocular ridge in lateral view; frons brown with apex yellow, narrower than vertex width; postpedicel shorter than frons; postocular ridge black, narrower than clypeus length; face black; clypeus brown, bare, longer than antenna; proboscis reaching posterior abdominal apex without exceeding it. Thorax (Fig. 1B). Black with yellow markings; postpronotum yellow, with median border brown and a brown posterior band; scutum black, without posterior tubercles; proepisternum yellow; anepisternum yellow with posteroventral margin brown, without lateral tubercle; katepisternum brown, pilose on the anterior third; anepimeron and katepimeron black; anatergite black with a yellow median stripe; katatergite and scutellum black; subscutellum small, barely visible; calyptr yellow, with margin brown. Wing (Fig. 14A). Brown, without markings; R4,5 well sclerotized, curved, extending for half of length of cell r4-5; M2 without spur vein; M3 and CuA absent. Leg (Fig. 1B). Not elongated; forecoxa yellow; mid- and hind coxae brown; femur brown with distal apex yellow; tibia brown with dorsal face light brown; tarsus brown. Abdomen (Fig. 1B).

Almost globose, segments III and IV of equal width; tergite I brown with posterior margin yellow; tergites II–VI brown, with posterolateral margin yellow; sternites entirely brown or brown on anterior half and yellow on posterior half. Male (Fig. 1A). Body length: 8.0 mm (7.4–8.0 mm, N = 2), wing length: 7.5 mm (7.5–7.9 mm, N = 2). Head. Vertex narrower than in female; frons slightly narrower and shorter; postocular ridge narrower. Thorax. Postpronotum yellow with median margin black; katepisternum yellow or brown. Abdomen. Slightly narrower than in female; tergites I–VI brown with posterior margin yellow; sternites yellow. Genitalia (Figs 28F, 31F, 33F). Epandrium with posterior margin concave; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus thinned.

Type material examined: Holotype female, MZSP.

Philopota lugubris and Philopota vitrialata sp. nov.; parameral sheath apex without constriction; dorsal surface of gonocoxite completely closed, forming a diamond-shaped opening; apex of gonostylus broadened (Fig. 35E) or thinned (Fig. 35D); gonocoxal apodemes present, usually fused (except in P. conica). Female genitalia (based only on P. tuberculata) (Fig. 37). Cerci well developed, with numerous terminal setae; hypoproct with numerous setulae on ventral surface; tergite 7 narrow, arch-shaped; tergite 8 as wide as tergite 7, arch-shaped; tergites 9 and 10 fused, wider than tergites 7 and 8, enlarged at apices, with numerous setae on dorsal surface; sternite 10 narrow, situated ventrally in relation to hypoproct; furca originated from sternite 9, small sized and ‘U’ shaped; sternite 9 divided into numerous small sclerites located laterally to furca; sternite 8 well developed, concave, with numerous setae and pile on ventral surface, with a cluster of setae on dorsal apex, right next to cerci; sternite 7 rectangular, with ventral surface covered by pile; two spermathecae present, faintly sclerotized, greatly elongated and globose at distal apex.

Geographical distribution: Mexico, Guatemala, El Salvador, Costa Rica, Panama, French Guiana, Suriname, Venezuela, Colombia, Ecuador, Peru, Bolivia, Brazil, Argentina.

Comments: Philopota is the type genus for the subfamily Philopotinae, and is also the most species rich within the subfamily. The genus is widespread and species rich throughout the Neotropical Region, with some species occurring also in the Nearctic portion of Mexico. All species are flower visitors with long mouthparts, and are readily identified based on the large and prominent frons, which is twice as long as wide.

1. Vein M₃ present (Figs 15D, 16A, B, 17A–D, 18C, 19A) .......................................................... 2
   • Vein M₃ absent (Figs 14A, B, 15A–C, 16C, D, 17B, C, 18A–D, 19B, C) ............................... 8
2 (1). Posterior portion of scutum with lateral tubercle; scutellum developed, dorsoventrally tall and overhanging by the scutellum (Figs 4B–D, 5B, 9D, 10A–C) ........................................................................ 3
   • Posterior portion of scutum without lateral tubercle; scutellum not developed, not dorsoventrally tall (Figs 1A, C, 3A, B, 6A–C) .............................................................. 5
3 (2). Scutum with yellow lateral longitudinal stripes (Fig. 4A–C); vein R₄+₅ extending for half of the length of cell r₂₃ (Fig. 15D) (northern South America) .......................... _Philopota flavolateralis_ Brunetti
   • Scutum uniformly brown or black, without yellow lateral stripes (Fig. 1C, D); vein R₄+₅ extending beyond half the length of cell r₂₃ (Figs 15B, 16B, 19A) ........................................ 4
4 (3). Frons brown; katepisternum bare on its anterior third (Fig. 5B); male abdomen ovate (Figs 5B, 27C) (Brazil) .......................................................... _Philopota grossii_ sp. nov.
   • Frons black with apex yellow; katepisternum pilose on its anterior third (Fig. 10B, C); male abdomen conical (Figs 10B, 13A) (Brazil) ............................................................. _Philopota tuberculata_ Westwood
5 (2). Katepisternum pilose on its anterior third (Fig. 26C) ............................................................. 6
   • Katepisternum bare on its anterior third (Fig. 26B) ................................................................. 7
6 (5). Clypeus bare (Fig. 23C); male wing without markings (Fig. 17A); male abdomen conical (Fig. 6D) (Central America) ................................................................. _Philopota longirostris_ sp. nov.
   • Clypeus pilose (Fig. 24B); male wing with markings (Fig. 17D); male abdomen ovate (Fig. 8B) (Mexico) ................................................................. _Philopota multivenata_ sp. nov.
7 (5). Proboscis not reaching posterior abdominal apex (Fig. 5A); scutellum brown; male wing with markings (Fig. 16A) (Mexico) ................................................................. _Philopota fuscofemorata_ sp. nov.
   • Proboscis exceeding posterior abdominal apex (Fig. 9B); scutellum brown with posterior margin yellow; male wing without markings (Fig. 18C) (Mexico) ................. _Philopota tepicensis_ sp. nov.
8 (1). Aneipisternum with lateral tubercle (Fig. 3C) (Brazil) ......................................................... _Philopota dissimilis_ sp. nov.
   • Aneipisternum without lateral tubercle (Figs 3D, 5A, 7B, C) .................................................. 9
9 (8). Postero medial portion of scutum with yellow markings (Figs 3D, 4A, 7B, C) .................... 10
   • Postero medial portion of scutum without yellow markings (Figs 2A–D, 12A, C) ................. 13
10 (9). Vertex elevated in comparison to postocular ridge in lateral view (Fig. 23D); postocular ridge lateromedially wider than clypeus width; katepisternum pilose on its anterior third (Fig. 7B, C) (Mexico) .............................. _Philopota lugubris_ Williston
   • Vertex not elevated in comparison to postocular ridge in lateral view (Figs 22A, 24C); postocular ridge lateromedially either narrower than or as wide as clypeus width; katepisternum bare on its anterior third (Figs 4A, 8C, D) ................................................................................................................................. 11
11 (10). Frons narrower than vertex width (see Figs 20D, 21B); postocular ridge as wide as clypeus width (Fig. 22A) (Mexico and Central America) ........................................ _Philopota flavimaculata_ sp. nov.
   • Frons as wide as vertex width (see Figs 20D, 21B); postocular ridge narrower than clypeus width (Figs 23A, 24C) (Brazil) ......................................................... _Philopota schlingeri_ sp. nov.
12 (11). Female wing with markings (Fig. 8D); male abdomen ovate (Fig. 8C) (Brazil) .................. _Philopota histrio_ sp. nov.
   • Female wing without markings (Fig. 6A); male abdomen conical (Fig. 5C) (Brazil) ............... _Philopota minuta_ sp. nov.
13 (9). Vein R₁ not inflated at pterostigma (Fig. 14B); medium-sized species (mean body length = 6 mm) .......................... 14
   • Vein R₁ inflated at pterostigma (Fig. 17C); small-sized species (mean body length = 4 mm) (Brazil) ................................................................. _Philopota castanea_ sp. nov.
14 (13). Antenna longer than frons length (see Fig. 20D); clypeus shorter than antenna (Fig. 20B); vein R₄+₅ straight (Fig. 14B); body extremely hunchbacked, thorax and abdomen dorsally forming an acute angle when seen in profile; scutum without yellow markings (Fig. 1C, D) (Brazil, Argentina) ....... _Philopota castanea_ sp. nov.
   • Antenna shorter than frons length (see Fig. 20D); clypeus as long as or longer than antenna (Figs 20C, D, 23B); vein R₄+₅ curved (Figs 14C, 16D); body moderately hunchbacked, thorax and abdomen forming an obtuse angle when seen in profile; scutum with yellow markings (Figs 2A, B, 6B, C) .................. 15
15 (14). Vein R₄+₅ extending beyond half of the length of cell r₂₃ (Figs 14C, 16D) ................. 16
   • Vein R₄+₅ extending only for half of the length of cell r₂₃ (Figs 15A, 18B) ....................... 17
specimens. The female was chosen to be the holotype because it is the only specimen in the type series that bears a locality label, whereas the two male paratypes lack labels. Association between males and females was possible as all three specimens bear identification labels written by Brunetti. It is highly likely that all individuals were collected at the same locality and at the same time, but because it could not be confirmed, the one bearing a label with collecting data was chosen as the holotype.

**Philopota castanea sp. nov.**

(Figs 1C, D, 14B, 20B, 28G, 31G, 33G)

Holotype male, MNRJ. Type locality: Argentina, Tucumán, Transcas.

**Diagnosis:** Philopota castanea is very distinct from all other Philopota species and is readily identified by an exclusive combination of characters, such as body color entirely brown, without yellow markings, in both the male and the female, clypeus shorter than the antenna and narrower than the postocular ridge, vein R4+5 faintly sclerotized and straight, and male abdomen ovate.

**Description:** Holotype male (Fig. 1C). Body length: 6.2 mm, wing length: 6.3 mm (N = 1). *Head* (Fig. 20B). Narrower than thorax vertex; clypeus brown, not raised in comparison to postocular ridge in lateral view; frons brown, narrower than vertex width; postpedicel longer than frons; postocular ridge brown, wider than clypeus length; face brown; clypeus brown, bare, shorter than antenna; proboscis not reaching posterior abdominal apex. *Thorax* (Fig. 1C). Brown, without yellow markings; postpronotum brown; scutum brown, without posterior tubercles; proepisternum brown; anepisternum brown, without lateral tubercle; katepisternum bare on anterior third; anepimeron, katapimeron, anatergite, katatergite, and scutellum brown; subscutellum small, barely visible; calypter yellow, with margin brown. *Wing* (Fig. 14B). Brown, without markings; R4+5 faintly sclerotized, narrower and paler than other veins, straight, extending beyond half of length of cell r2+3; M2 with spur vein; M3 and CuA absent. *Leg* (Fig. 1C). Not elongated; coxa, femur, tibia, and tarsus brown. *Abdomen* (Fig. 1C). Ovate, segments III and IV of equal width; tergites I–VI brown; sternites brown.


**Etymology:** The species epithet is derived from the Latin castanea (feminine, singular, meaning of the colour
of chestnuts, brown), in reference to the uniform brownish body colour of both male and female.

Geographical distribution (Fig. 40): Brazil (São Paulo); Argentina (Tucumán).

Comments: Philopota castanea sp. nov. is a rare South American species only known from a male and a female specimen. Similarly to Philopota schlingeri sp. nov., P. castanea has a disjunct distribution, occurring both in south-east Brazil and in north-west Argentina.

**PHILOPOTA CONICA** Wiedemann, 1830

(Figs 2A–D, 12A, B, 14C, D, 20C, D, 21A, B, 26B, 27A, B, 28H, 31H, 33H, 34A)

*Philopota conica* Wiedemann, 1830: 17. Holotype male, NMW. Type locality: 'Brazil'. Wiedemann, 1830: 17 (description, drawings of habitus, head, and wing); Macquart, 1834: 366 (diagnosis, drawing of habitus); 1838: 171 (drawings of habitus and head); Blanchard, 1840: 584 (diagnosis); Erickson, 1840: 154 (diagnosis); Walker, 1855: 340 (diagnosis); Westwood, 1848: 94 (comments); Hunter, 1900: 152 (catalogue); Brunetti, 1926: 562 (comments); Schlinger, 1971: fig. 1 (wing); Gillung & Carvalho, 2009: 39 (citation).

*Philopota maculicollis* Westwood, 1835: 447. Holotype female, OUMNH. Type locality: 'Brazili'. Wiedemann, 1830: 17 (synonym, Westwood, 1835: 447 (description), 1848: 93 (diagnosis, comments, synonymy with *P. vidua*); Erickson 1840: 153 (comments, comparison to *P. vidua*); Walker, 1855: 340 (diagnosis); Hunter, 1900: 152 (catalogue); Brunetti, 1926: 565 (holotype redescription, comments); Gillung & Carvalho, 2009: 39 (citation).


*Philopota nitida* Westwood, 1848: 94. Holotype male, OUMNH. Type locality: 'Brazil'. syn. nov. Westwood, 1848: 94 (description); Gillung & Carvalho, 2009: 39 (citation).

Diagnosis: Philopota conica is a very conspicuous species characterized by the absence of veins M₃ and CuA, male with the abdomen conical, and female with brown body coloration, seldom with a few yellow markings. Philopota conica is very similar to *P. liturata* as both species have bare clypeus and katepisternum, brown male and female wings, female wing with markings, and absence of vein M₃. Philopota conica is distinguished from *P. liturata* based on the more hunchbacked male body, the brown abdominal sternites, the yellow male postpronotum, and the female body usually entirely brown, with very scarce yellow markings.

Redescription: Holotype male (Fig. 2A). Body length: 8.0 mm (7.7–9.7 mm, N = 11), wing length: 10.0 mm (9.6–10.6 mm, N = 11). Head (Figs 20D, 21B, 26B). Slightly narrower than thorax width; vertex brown, not raised in comparison to postocular ridge in lateral view; frons brown with apex yellow, narrower than vertex width; postpedicel shorter than frons; postocular ridge brown, as wide as clypeus length; face brown; clypeus brown, longer than antenna, bare; proboscis not reaching posterior abdominal apex. Thorax (Figs 2A, 26B). Brown with yellow markings; postpronotum yellow; scutum brown, with yellow lateral stripes, without posterior tubercles; proepisternum yellow; anepisternum yellow with posteroventral margin brown, without lateral tubercle; katepisternum brown, bare on the anterior third; anepimeron and katepimeron brown; anatergite brown with a wide yellow median stripe; katatergite brown; scutellum brown; subscutellum small, barely visible; calypter pale yellow, with the ventral portion of the margin yellow and the anterior, posterior, and dorsal portions of the margin brown. Wing (Fig. 14D). Brown, without markings; R₄+₅ well sclerotized, curved, extending beyond half of length of cell r₄+₅; M₂ present, without spur vein; M₃ absent; CuA absent. Leg (Fig. 2A). Not elongated; coxa brown; femur brown with distal apex yellow; tibia brown with dorsal face light brown; tarsus brown. Abdomen (Figs 2A, 27B). Conical, each segment successively narrower lateromedially than the previous one; tergite I brown with posterior margin yellow; tergites II–III brown with posterolateral margin yellow; tergites IV–VI brown with lateral margin yellow; sternites brown. Genitalia (Figs 28H, 31H, 33H, 34A). Epedanium with posterior margin concave; parameral sheath apex bilobate; gonocoxal apodemes present, separate; apex of gonostylus broadened. Variation. Proboscis rarely not reaching posterior abdominal apex; vein M₂ seldom with a spur vein; abdominal tergites IV–VI rarely brown. Female (Figs 2C, D, 12B, 14C, 20C, 21A, 27A). Body length: 10.6–11.2 mm, wing length: 11.2–12.7 mm (N = 8). Head. Much narrower than thorax; frons longer and more prominent than in the male, almost as wide as vertex; postocular ridge wider than in the male; proboscis reaching posterior abdominal apex without exceeding it. Thorax. Wider than in the male, brown, usually without yellow markings; postpronotum brown, with a small yellow spot on the posterior apex; scutum brown, rarely with a narrow yellow lateral stripe; sclerites brown; calypter brown or white, with margin brown. Wing. With markings; vein M₂ usually without spur vein. Abdomen. Tergite I entirely brown or brown with posterior margin yellow.

Type material examined: Philopota conica Wiedemann. Holotype male, NMW, 'Brasilien' 'conica Wd./Coll. Wiedem.' Philopota nitida Westwood. Holotype male, OUMNH, 'Type of Philopota conica./nitidaWestw./Trans. Ent. Soc. L./1847-9, p 94./Coll. Hope Oxon.'

Additional material examined: Listed in Table S3.

Geographical distribution (Fig. 39): Brazil (Minas Gerais, Espírito Santo, Rio de Janeiro, São Paulo).

Comments: Philopota conica is only known so far from Brazil. Here, P. nitida Westwood, 1848, is considered a synonym of P. conica Wiedemann, 1830, based on the extreme morphological similarity shared by the two species. Philopota conica and P. nitida only differ in the shape and width of the yellow spots and stripes of the thorax, which is considered here as intraspecific variation. In addition, after the examination of a large series of specimens, P. maculicollis Westwood, 1835, was recognized as the female of P. conica. As a junior synonym of P. maculicollis, P. vidua Erichson, 1840, is also regarded as a synonym of P. conica.

**Philotopa costaricensis sp. nov.**

(Figs 3A, B, 15A, 21C, 28I, 31I, 33I)

Holotype male, USNM. Type locality: Costa Rica, San Mateo, Higuito.

**Diagnosis:** Philopota costaricensis is easily recognizable by its body coloration brown with yellow markings, postpedicel as long as frons, and male abdomen ovate. Females of P. costaricensis are distinctive as they can be almost entirely yellow, usually paler than the males. In other Philopota species the females tend to be brown or at least darker in colour than the males.

**Description:** Holotype male (Fig. 3A). Body length: 8.0 mm (7.0–8.7 mm, N = 32), wing length: 8.7 mm (7.4–10.0 mm, N = 32). Head (Fig. 21C). Slightly narrower than thorax width; vertex brown, not raised in comparison to postocular ridge in lateral view; frons brown with apex yellow, as wide as vertex width; postpedicel as long as frons; postocular ridge brown, narrower than clypeus length; face brown; clypeus brown, bare, longer than antenna; proboscis not reaching posterior abdominal apex. Thorax (Fig. 3A). Brown with yellow markings; postpronotum yellow with posterior portion brown; scutum brown, with yellow lateral stripes, without posterior tubercles; propiesterumn yellow; anepipisterum with the anterior half yellow and the posterior half brown, without lateral tubercle; katapisterum brown, bare on the anterior third; anepimeron and katapimeron brown; anatergite brown with a wide yellow median stripe; katatergite and scutellum brown; subscutellum small, barely visible; calypter yellow, with margin yellow. Wing (Fig. 15A). Brown, without markings; M4 well sclerotized, curved, extending for half of length of cell r4+5; M5 without spur vein; M6 and CuA absent. Leg (Fig. 3A). Not elongated; forecoxa yellow; mid- and hind coxae brown; femur brown with distal apex yellow; tibia brown with dorsal face light brown; tarsus brown. Abdomen (Fig. 3A). Ovate, segments III and IV of equal width; tergite I brown with posterior margin yellow; tergites II–VI brown with posterolateral margin yellow; sternites yellow. Genitalia (Figs 28I, 31I, 33I). Epandrium with posterior margin concave; parameral sheath apex bilobate; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broadened. Variation. Proboscis sometimes exceeding posterior abdominal apex. Postpronotum colour variable, from entirely yellow or brown to a mixture of both colours. Proepisternum usually yellow, but sometimes brown. Scutellum sometimes with a narrow band on the posterior margin.

Forecoxa brown, sometimes with a little median yellow spot. Tergite I may be brown, sometimes with a short posterior yellow band. Tergites II–VI sometimes almost entirely brown, with a narrow lateral yellow margin. **Female** (Fig. 3B). Body length: 9.4–10.6 mm, wing length: 10.6–12.5 mm (N = 6). Head. Much narrower than thorax; vertex wider than in the male; frons with apex yellow or light brown, wider and longer than in the male; postocular ridge colour varying from reddish brown to dark brown, wider than in the male. Thorax. Wider than in the male, with colour extremely variable, from yellow to dark brown; postpronotum yellow or brown; anepisternum may be entirely yellow, yellow with brown markings, or brown; scutellum may be brown, yellow, or brown with posterior margin yellow; scutum sometimes with a posterior yellow spot; anepisternum yellow; katapisterum brown or yellow; anepimeron and katapimeron yellow or brown; anatergite may be yellow or brown, sometimes with a wide median yellow stripe. **Leg.** Forecoxa brown or yellow. Abdomen. Colour quite variable, from light yellow to dark brown with yellow markings; sternites yellow or brown.

The species epithet is toponymical.

**Etymology:**
The species epithet is toponymical.

**Additional material examined:**
Listed in Table S3.

**Etymology:**
The species epithet is toponymical.

**Geographical distribution (Fig. 41):**
Costa Rica (Guanacaste, Heredia, San José, Cartago, Puntarenas).

**Comments:**
Philopota costaricensis sp. nov. is only known so far from Costa Rica. This species has the highest degree of sexual dimorphism in the genus, with males usually much darker than the females.

**Philopota dissimilis sp. nov.**

(Figs 3C, 15B, 21D, 29A, 31J, 34A)

Holotype male, MZSP. Type locality: Brazil, Espírito Santo, Itarana.

**Diagnosis:**
Philopota dissimilis is very distinctive and possesses greatly elongated legs, anepisternum with lateral tubercle, and veins M₂, M₃, and CuA absent. It is most similar to *P castanea* sp. nov. as both species have vein R₄+₅ straight, extremely hunchbacked body shape, and body colour brown, but can be distinguished by the characters indicated above.

**Description:**
Holotype male (Fig. 3C). Body length: 10.7 mm (9.9–12.2 mm, *N = 12*), wing length: 17.4 mm (15.3–20.4 mm, *N = 12*). *Head.* Narrower than thorax width; vertex brown, not raised in comparison to postocular ridge in lateral view; frons brown, narrower than vertex width; postpedicel longer than frons; postocular ridge brown, wider than clypeus length; face brown; clypeus brown, bare, longer than antenna; proboscis not reaching posterior abdominal apex. *Thorax* (Fig. 3C). Brown, with scarce yellow markings; postpronotum brown with lateral margin yellow; scutum brown, without posterior tubercles; proepisternum brown; anepisternum brown, with lateral tubercle; katepisternum brown, bare on the anterior third; anepimeron and katepimeron brown; anatergite brown with a yellow median spot; katatergite and scutellum brown; subscutellum developed; calypter brown, with margin brown. *Wing* (Fig. 15B). Hyaline, with markings; R₄+₅ well sclerotized, straight, extending beyond half of length of cell r₃+₄; M₂, M₃, and CuA absent. *Leg* (Fig. 3C). Greatly elongated; coxa, femur, tibia, and tarsus brown. *Abdomen* (Fig. 3C). Conical, each segment successively narrower lateromedially than the previous one; tergite I brown with two yellow posterior spots; tergites II–VI brown with two yellow median spots; sternites brown. *Genitalia* (Figs 29A, 31J, 34A). Epandrium with posterior margin concave; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broad; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broad; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broad; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broad; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broad; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broad; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broad; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broad; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broad; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broad; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broad; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broad; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broad; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broad; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broad; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broad; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broad; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broad; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broad; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broad; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broad; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broad; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broad; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broad; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broad; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broad; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broad; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of.
Holotype male, AMNH. Type locality: Guatemala, Suchitepéquez, Variedades.

Diagnosis: Philopota flavimaculata is a distinctive species with numerous yellow markings on the body. It is similar to the Mexican species Dimacrocolus sp. nov., from which it can be distinguished by the bare clypeus and the absence of M3.

Description: Holotype male (Fig. 3D). Body length: 5.7 mm (4.6–8.0 mm, N = 9), wing length: 5.8 mm (5.0–7.4 mm, N = 9). Head (Fig. 22A). Slightly narrower than thorax width; vertex brown, not raised in comparison to postocular ridge in lateral view; frons brown with apex yellow, narrower than vertex width; postpedicel shorter than frons; postocular ridge brown, as wide as clypeus length; face brown; clypeus brown, bare, longer than antenna; proboscis reaching anterior abdominal apex without exceeding it. Thorax (Fig. 3D). Brown with yellow markings; postpronotum yellow; scutum brown, with two yellow posterior spots; with yellow lateral stripes, without posterior tubercles; proepisternum yellow; anepisternum with the anterior two thirds yellow and the posterior third brown, without lateral tubercle; katatergum brown, bare on the anterior third; anepimeron and katepimeron brown; anatergite with the median third yellow and the anterior and posterior thirds brown; katatergite brown; scutellum brown with posterior margin yellow; subscutellum small, barely visible; calypter brown, with margin brown. Wing (Fig. 15C). Brown, without markings; R4,5 well sclerotized, curved, extending for half of length of cell r2,3; M2 without spur vein; M3 and CuA absent. Leg (Fig. 3D). Not elongated; coxa brown; femur brown with distal apex yellow; tibia brown with dorsal face light brown; tarsus brown. Abdomen (Fig. 3D). Ovate, segments III and IV of equal width; tergite I brown with posterior margin yellow; tergites II–VI brown with posteromedial margin yellow; sternites yellow. Genitalia (Figs 29B, 31K, 34B). Epandrium with posterior margin concave; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broadened. Variation. Proboscis length very variable, from not reaching posterior abdominal apex to exceeding the abdominal apex. Postpronotum may be yellow or brown with anterior and posterior margins yellow. Proepisternum usually yellow, sometimes brown. Anepisternum sometimes brown with ventral and dorsal yellow spots. Spur vein of M2 may be present. Female (Fig. 4A). Body length: 8.0–9.1 mm, wing length: 8.2–8.3 mm (N = 2). Head. Much narrower than thorax; postpedicel as long as frons; proboscis not reaching posterior abdominal apex. Thorax. Wider than in the male; postpronotum brown with anterior and posterior margins yellow; proepisternum brown or yellow; anepisternum brown with ventral and dorsal yellow spots. Wing. Spur vein of M2 absent. Abdomen. Sternites brown.

Differentiated from these two species based on the presence of lateral tubercles on the posterior portion of the abdomen.

Additional material examined: Listed in Table S3.

Etymology: The species epithet is derived from the Latin flavens (feminine, singular, meaning yellow) and maculata (feminine, singular, meaning stained, spotted), in reference to the numerous yellow markings on the body of both male and female.

Geographical distribution (Fig. 40): Mexico (Hidalgo); Guatemala (Sololá, Retalhuleu, Suchitepéquez, Escuintla); El Salvador (Cuscatlán).

Comments: Philopota flavimaculata sp. nov. is only known from a few specimens collected in Mexico, Guatemala, and El Salvador. The species was sequenced and included in the phylogeny of Winton et al. (2007: 812) as Philopota sp. from Guatemala (GenBank accession numbers: AY140875, AF539906, AY144425, AY144426).

Philopota flavolateralis Brunetti
(Figs 4B–D, 15D, 22B, 29C, 31L, 34C)


Diagnosis: Philopota flavolateralis is a distinctive species characterized by the black body colour and the very hunchbacked body. The species is similar to P. tuberculata and P. grossii sp. nov. based on the presence of lateral tubercles on the posterior portion of the scutum, the raised subscutellum, and conical male abdomen. Philopota flavolateralis can be readily differentiated from these two species based on the presence of lateral yellow stripes on scutum, and the shorter length of vein R_{2+3}, which ends in the middle of cell R_{3+4}.

Redescription: Holotype male (Fig. 4B). Body length: 9.3 mm (6.4–8.7 mm, N = 9), wing length: 6.9 mm (7.4–8.2 mm, N = 9). Head (Fig. 22B). Slightly narrower than thorax width; vertex black, raised in comparison to postocular ridge in lateral view; frons black, narrower than vertex width; postpedicel as long as frons; postocular ridge black, as wide asyleus length; face black; eyeus black, pilose, and longer than antenna. Thorax (Fig. 4B). Black with yellow markings; scutum black, with yellow lateral stripes and two posterior tubercles; proepisternum black; anepisternum black, without lateral tubercle; katepisternum black, bare on the anterior third; anepimeron and katepimeron black; anatergite black with a yellow median spot; kateatergite and scutellum black; subscutellum developed; calypter pale yellow, with the ventral portion of the margin yellow and the anterior, posterior, and dorsal portions of the margin brown. Wing (Fig. 15D). Brown, with markings; R_{4+5} well sclerotized, curved, extending for half of length of cell r_{2+3}; M_{2} with spur vein; M_{3} present; CuA absent. Leg (Fig. 4B). Not elongated; coxa black; femur dark brown with distal apex yellow; tibia brown with dorsal face light brown; tarsus brown. Abdomen (Fig. 4B). Conical, each segment successively narrower lateromedially than the previous one; tergite I black with posterior margin yellow; tergites II–III black with latero posterior margin yellow; tergites IV–VI dark brown with a narrow yellow lateral margin; sternites black. Genitalia (Figs 29C, 31L, 34C). Epandrium with posterior margin concave; parameral sheath apex bilobate; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broadened. Variation. Frons usually brown, rarely dark brown with apex light brown or yellow, with width variable, narrower or as wide as vertex; proboscis not reaching posterior abdominal apex, or reaching the apex but not exceeding it; postpronotum black or black with yellow markings that vary in shape, size, and position; proepisternum black or yellow; anepisternum usually black, rarely with a median yellow spot; katepisternum usually black, rarely brown; subscutellum usually well developed, but may be less raised in some specimens; CuA frequently absent, seldom present; coxa brown or black; abdominal tergite I rarely entirely black; sternites seldom yellow. Female (Fig. 4D). Body length: 6.9–8.0 mm, wing length: 9.0–9.2 mm (N = 7). Head. Much narrower than thorax width; vertex wider than in the male; frons dark brown with apex light brown, wider than in the male; antenna shorter than frons; postocular ridge wider than in the male; proboscis length variable, from not reaching posterior or abdominal apex to exceeding it. Thorax. Brown with yellow markings, wider than in the male; postpronotum brown with posterior apex yellow; scutum brown, with or without lateral yellow stripes; calypter pale yellow or brown. Abdomen. Almost globose, much wider than in the male, brown with yellow markings; tergite I brown or brown with posterior margin yellow; tergites II–VI brown with a narrow yellow margin.


Remarks on type material: Both antennae are broken off in the holotype, but based on other specimens examined it is assumed that they are shorter than the eyeus, as the length of the antennae does not vary significantly within Philopota species. The proboscis is also broken in the holotype; thus, it is impossible.
to infer its length. The postpronotum is barely visible in the holotype because the head was broken off and was glued above the postpronotum; nevertheless, it is possible to infer that it is black with posterior portion yellow, although nothing can be said about the median and anterior portions.

**Additional material examined:** Listed in Table S3.

**Geographical distribution (Fig. 42):** Bolivia (Florida, Cochabamba); Brazil (Amazonas, Pará); Ecuador (Sucumbios); French Guiana; Peru (Loreto, Rio Morona).

**Comments:** *Philopota flavolateralis* is a relatively rare species broadly distributed in northern South America, with only a few specimens known from each locality.

**Philopota fuscofemorata sp. nov.**

*(Figs 5A, 16A, 22C, 29D, 31M, 34D)*

Holotype male, EMEC. Type locality: Mexico, Chiapas, south-east of San Cristobal de Las Casas.

**Diagnosis:** *Philopota fuscofemorata* is a rare species easily distinguished from all other *Philopota* species based on the pilose clypeus, wing markings on the male wing, presence of vein M₃, and male abdomen conical.

**Description:** Holotype male (Fig. 5A). Body length: 8.4 mm (8.4–9.4 mm, N = 2), wing length: 8.5 mm (8.5–9.7 mm, N = 2). Head (Fig. 22C). Slightly narrower than thorax width; vertex brown, raised in comparison to postocular ridge in lateral view; frons brown, narrower than vertex width; postpedicel as long as frons; postocular ridge brown, as wide as clypeus length; face brown; clypeus brown, pilose, as long as antenna; proboscis not reaching posterior abdominal apex. Thorax (Fig. 5A). Brown, with scarce yellow markings; postpronotum brown with a yellow anterior spot; scutum brown, without posterior tubercles; proepisternum brown; anepisternum brown, without lateral tubercle; katepisternum brown, bare on the anterior third; anepimeron, katepimeron, anatergite, katatergite, and scutellum brown; subscutellum small, barely visible; calypter pale yellow, with margin brown. Wing (Fig. 16A). Hyaline, with markings; R₁₋₅ well sclerotized, curved, extending for half of length of cell r₃₋₅; M₂ with spur vein; M₃ present; CuA absent. Leg (Fig. 5A). Not elongated; coxa brown; femur brown with distal apex yellow; tibia brown with dorsal face light brown; tarsus brown. Abdomen (Fig. 5A). Conical, each segment successively narrower lateromedially than the previous one; tergite I brown; tergites II–VI brown with lateral margin yellow; sternites with the anterior half brown and the posterior half yellow. Genitalia (Figs 29D, 31M, 34D). Epandrium with posterior margin concave; parameral sheath apex bilobate; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broadened. Variation. Frons may be brown with apex yellow. Postpronotum may be brown with posterior margin yellow. Scutum sometimes with lateral and posterior light brown spots. Anatergite may have a median yellow spot. Tergite I may be entirely brown or brown with posterior margin yellow. Female. Unknown.


**Etymology:** The species epithet is derived from the Latin *fuscus* (masculine, singular, meaning dark) and *femorata* (feminine, singular, meaning femora), in reference to the dark coloured femora of *P. fuscofemorata* sp. nov.

**Geographical distribution (Fig. 40):** Mexico (Chiapas).

**Comments:** *Philopota fuscofemorata* sp. nov. is a very distinctive species only known from two male specimens from Mexico.

**Philopota grossii sp. nov.**

*(Figs 5B, 16B, 22D, 29E, 31N, 34E)*

Holotype male, DZUP. Type locality: Brazil, Paraná, Piraquara, Mananciais da Serra.

**Diagnosis:** *Philopota grossii* sp. nov. is a remarkable *Philopota* species readily identified by the brown body with black markings, the two posterior tubercles on anepisternum, the male wing brown, with markings, and the presence of all three M veins. The species is similar to *P. tuberculata*, from which it can be readily distinguished by the shorter frons, the bare katepisternum, and the ovate male abdomen.

**Description:** Holotype male (Fig. 5B). Body length: 7.7 mm, wing length: 9.7 mm (N = 1). Head (Fig. 22D). Slightly narrower than thorax width; vertex brown, raised in comparison to postocular ridge in lateral view; frons brown, narrower than vertex width; postpedicel longer than frons; postocular ridge brown, as wide as clypeus length; face brown; clypeus brown, pilose, longer than antenna; proboscis reaching posterior abdominal apex without exceeding it. Thorax (Fig. 5B). Brown with black markings; postpronotum brown with posterior apex yellow; scutum brown, with two posterior tubercles; proepisternum brown; anepisternum brown, without lateral tubercle; katepisternum brown, bare on the anterior third; anepimeron and katepimeron brown; anatergite brown with a small yellow median spot; katatergite and scutellum brown; subscutellum developed; calypter brown, with margin light brown. Wing (Fig. 16B). Brown, with markings; R₁₋₅ well sclerotized, curved, extending beyond half of length of
cell r2+3; M2 with spur vein; M3 and CuA present. Leg (Fig. 5B). Not elongated; coxa brown; femur brown with distal apex yellow; tibia and tarsus brown. Abdomen (Fig. 5B). Ovate, segments III and IV of equal width; tergite I brown; tergites II–VI brown; sternites brown. Genitalia (Figs 29E, 31N, 34E). Epandrium with posterior margin concave; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus thinned. Female. Unknown.


Remarks on type material: Both the antennae are broken off in the holotype, which is the sole representative of this unusual Philopota species. For this reason it is not possible to infer the length of the antenna relative to the frons.

Etymology: This species is named in honour of Paschoal Coelho Grossi, a great coleopterist working at the Agronomy Department of the Rural Federal University of Pernambuco (UFRPE), Recife, Brazil, and collector of rare acrocerids, of which some are still to be described.

Geographical distribution (Fig. 39): Brazil (Paraná).

Comments: Philopota grossii sp. nov. is a rare Brazilian species only known from a single male specimen. This specimen was collected in Mananciais da Serra, an area still covered by pristine Atlantic rainforest, which is exclusive to Brazil. Despite the great collecting effort carried out by Brazilian entomologists in the area over a large period of time, only one specimen has been found so far.

**Philopota histrio** Erichson (Figs 5C–D, 6A, 16C, 23A, 29F, 31O, 34F)

*Philopota histrio* Erichson, 1840: 153. Lectotype male (designated here), ZMH. Type locality: ‘Brazil’ (probably Minas Gerais; see Papavero, 1971: 110). Erichson, 1840: 153 (description); Westwood, 1848: 96 (diagnosis); Walker, 1855: 341 (diagnosis); Hunter, 1900: 152 (catalogue); Gillung & Carvalho, 2009: 39 (citation).


*Philopota temperata* Walker, 1852: 196. Holotype male, BMNH. Type locality: ‘South America’. syn. nov. Walker, 1852: 196 (description); Walker, 1855: 342 (citation); Brunetti, 1926: 566 (redescription of holotype, comments).

Diagnosis: *Philopota histrio* has the highest intraspecific variation of all species in *Philopota*. Despite its high specific variation, individuals are commonly brown with numerous yellow markings. Males and females are very similar and have the same body colour and wings without markings, which is remarkable for *Philopota* species. *Philopota histrio* is very similar to *P. costaricensis* sp. nov., from which it can be distinguished easily by the spur vein of M3, the yellow posterior margin on the scutellum, and the conical abdomen in the male.

Redescription: Holotype male (Fig. 5C). Body length: 8.6 mm (6.4–10.1 mm, N = 158), wing length: 7.7 mm (6.4–8.9 mm, N = 158). Head (Fig. 23A). Slightly narrower than thorax width; vertex not raised in comparison to postocular ridge in lateral view; frons brown with apex yellow, as wide as vertex width; postpedicel as long as frons; postocular ridge brown, narrower than clypeus length; face brown; clypeus brown, bare, longer than antenna; proboscis exceeding posterior abdominal apex. Thorax (Fig. 5C). Brown with yellow markings; postpronotum yellow; scutum brown, with two yellow posterior spots, with yellow lateral stripes, without posterior tubercles; proepisternum yellow; anepisternum yellow with dorsal margin brown, without lateral tubercle; katepisternum brown, bare on the anterior third; anepimeron and katepimeron brown; anatergite brown with a yellow median stripe; katergite brown; scutellum brown with posterior margin yellow; subscutellum small, barely visible; calypter brown, with anterodorsal margin brown and posteroventral margin yellow. Wing (Fig. 16C). Brown, without markings; R4+5 well sclerotized, curved, extending for half of length of cell r2+3; M2 with spur vein; M3 absent; CuA present. Leg (Fig. 5C). Not elongated; forecoxa yellow; mid- and hind coxae brown; femur brown with distal apex yellow; tibia brown with dorsal face light brown; tarsus brown. Abdomen (Fig. 5C). Conical, each segment successively narrower lateromedially than the previous one; tergite I brown with posterior margin yellow; tergites II–IV brown with lateral posterior margin yellow; tergites V–VI brown with lateral margin yellow; sternites yellow. Genitalia (Figs 29F, 31O, 34F). Epandrium with posterior margin concave; parameral sheath apex bilobate; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus broadened. Variation. Vertex rarely slightly elevated in comparison to postocular ridge. Postpronotum colour variable, from entirely yellow, yellow with margins brown, or brown with margins yellow. Yellow posterior stripes on scutum may vary in width. Yellow band on the posterior margin of scutellum extremely variable in length and width. CuA rarely present; indeed, some specimens may have CuA in one wing, but may lack it in the other wing. Forecoxa varying from entirely yellow, yellow with brown markings to entirely brown. Tergites II–IV may be yellow with median portion brown. Female (Figs 5D, 6A). Body length: 9.3–11.0 mm, wing length: 8.6–10.9 mm (N = 31). Head. Vertex wider than in the male; frons wider, longer
and larger than in the male; antenna shorter than frons; postocular ridge wider than in the male. Thorax. Slightly wider than in the male, paler in colour. Abdomen. Almost globose, wider than in the male; tergites II–IV light brown with posterolateral margin dark yellow; tergites V–VI brown or brown with lateral margin dark yellow.

**Type material examined:** Philopota histrio Erichson. Lectotype male (designated here), ZMHB, 'Brasil. Germ.' 1239 'Type' 'histrio /Er.' Zool. Mus./Berlin'. Paratypes: male, ZMHB, 'Brasilien /coll. H. Loew' 'Coll./H. Loew/Philopota/histrio'. Erich./monogr. 153.' 'Zool. Mus./Berlin'. Philopota sobria Walker. Holotype female, BMNH, 'S. America:/ex coll./W.W. Saunders./68-4' 'Holo-/type' '5890' 'Type' 'Holotype of/Philopota/liturata./L50489'.

Additional material examined: Listed in Table S3.

**Geographical distribution** (Fig. 41): Brazil (Mato Grosso, Minas Gerais, Espírito Santo, Rio de Janeiro, São Paulo, Paraná, Santa Catarina).

**Comments:** Philopota histrio is a relatively abundant species only known so far from Brazil. When encountered in the field, these flies can be collected in very high numbers.

**PHILOPOTA LITURATA WESTWOOD**

*(FIGS 6B, C, 16D, 23B, 29G, 32A, 34G)*

*Philopota liturata* Westwood, 1848: 94. Holotype male, OUMNH. Type locality: 'Brazil'. Westwood, 1848: 94 (description); Walker, 1855: 341 (diagnosis); Hunter, 1900: 152 (catalogue); Brunetti, 1926: 564 (redescription of holotype); Gillung & Carvalho, 2009: 39 (citation).

*Philopota ovata* Westwood, 1848: 95. Holotype female, OUMNH. Type locality: 'Brazil'. *syn. nov.* Westwood, 1848: 95 (description); Walker, 1855: 341 (diagnosis); Hunter, 1900: 152 (catalogue); Brunetti, 1926: 563 (redescription of holotype, mentions that *P. liturata* might be the male of *P. ovata*); Gillung & Carvalho, 2009: 39 (citation).

**Diagnosis:** Philopota liturata is very similar to *P. conica*. Males and females of *P. liturata* have yellow markings on the thorax and abdomen, whereas females of *P. conica* are commonly brown with very few yellow markings. Additionally, *P. conica* differs from *P. liturata* by its yellow postpronotum and by the absence of both the spur of vein M₁ and of vein M₂.

**Redescription:** Holotype male (Fig. 6B). Body length: 9.0 mm (8.4–10.4 mm, N = 14), wing length: 7.0 mm (6.6–8.2 mm, N = 14). Head (Fig. 23B). Slightly narrower than thorax width; vertex brown, not raised in comparison to postocular ridge in lateral view; frons brown with apex yellow, narrower than vertex width; postpedicel shorter than frons; postocular ridge brown, as wide as clypeus length; face brown; clypeus brown, bare, longer than antenna; proboscis not reaching posterior abdominal apex. Thorax (Fig. 6B). Brown with yellow markings; postpronotum brown with anterior and posterior margins yellow; scutum brown, with yellow lateral stripes, without posterior tubercles; proepisternum yellow; anepistemum brown with yellow anterior spots; without lateral tubercle; katepistemum brown, bare on the anterior third; anepimeron and katepimeron brown; anatergite brown with a yellow median stripe; katergite and scutellum brown; subscutellum small, barely visible; calypter pale yellow, with the ventral portion of the margin yellow and the anterior, posterior, and dorsal portions of the margin brown. Wing (Fig. 16D). Brown, without markings; R₄₊₅ well sclerotized, curved, extending beyond half of length of cell r₂₊₃; M₂ with spur vein; M₁ absent; CuA present. Leg (Fig. 6B). Not elongated; coxa brown; femur brown with distal apex yellow; tibia brown with dorsal face light brown; tarsus brown. Abdomen (Fig. 6B). Conical, each segment successively narrower lateromedially than the previous one; tergite I brown with posterior margin yellow; tergites II–III brown with posterolateral margin yellow; tergites IV–VI brown with lateral margin yellow; sternites II–III with anterior third brown and posterior third yellow; remaining sternites brown. Genitalia (Figs 29G, 32A, 34G). Epandrium with posterior margin concave; parameral sheath apex bilobate; gonocoxal apodemes present, fused, apex rounded; apex of gonostylius thinned. Variation. Proboscis length extremely variable, from not reaching posterior abdominal apex to exceeding it. Postpronotum usually brown with anterior and posterior margins yellow, but seldom brown in the middle and yellow in the lateral margins. CuA present in the holotype, but absent in all other examined specimens. Female (Fig. 6C). Body length: 7.3–10.9 mm, wing length: 7.6–10.8 mm (N = 16). Head. Narrower than thorax width; vertex wider than in the male; frons longer and wider than in the male; postocular ridge wider; proboscis not reaching posterior abdominal apex. Thorax. Slightly wider than in the male; proepisternum yellow, rarely brown; calypter margin brown. Wing. With markings. Abdomen. Almost globose, wider than in the male; tergites II–VI brown with lateral margin yellow; sternites brown.

**Type material examined:** Philopota liturata Westwood. Holotype male, OUMNH, 'Brasil' 'Type/Westwood/Philopota/liturata./<153>/Tr. Ent. Soc. L./1847-9, p.94./Coll. Hope Oxon.' 'Philopota/liturata./Westwood.' 'Type Dip: 53/Philopota/liturata./Westwood/Hope Dept. Oxford'. Philopota ovata Westwood. Holotype female, OUMNH, 'Brasil' 'Type/Westwood/Philopota/ovata./Tr. Ent. Soc.'

Additional material examined: Listed in Table S3.

Geographical distribution (Fig. 40): Suriname; Venezuela (Carabobo); Colombia (Nariño); Bolivia (La Paz); Brazil (Amazonas, Pará, Minas Gerais, Espírito Santo, Rio de Janeiro, São Paulo, Paraná).

Comments: Philopota liturata is a common species that is widespread in South America. After the study of a large series of specimens of both P. liturata and P. ovata collected at the same locality, the confirmation that P. ovata Westwood, 1848, is indeed the female and a junior synonym of P. liturata Westwood, 1848, was possible. This was previously suggested by Walker (1855) and Brunetti (1926); however, neither proposed the formal synonymy as they did not possess a large series of both species to examine.

**Philopota longirostris sp. nov.**

(Figs 6D, 7A, 17A, 23C, 32B, 34H)

Holotype male, EMUS. Type locality: Panama, Gamboa.

Diagnosis: Philopota longirostris is very similar to Philopota multivenata sp. nov., based on the hyaline male wing, pilose katepisternum, and presence of vein M3. Philopota longirostris is easily distinguished from this similar species by the bare clypeus, the longer length of proboscis, the absence of markings on the male wing, and the conical male abdomen.

Description: Holotype male (Fig. 6D). Body length: 7.1 mm, wing length: 6.4 (N = 1). Head (Fig. 23C). Slightly narrower than thorax width; vertex brown, raised in comparison to postocular ridge in lateral view; frons brown with apex yellow, narrower than vertex width; postpedicel shorter than frons; postocular ridge brown, as wide as clypeus length; face brown; clypeus brown, bare, longer than antenna; proboscis exceeding posterior abdominal apex. Thorax (Fig. 6D). Brown with yellow markings; postpronotum yellow with a brown median spot and two brown lateral spots; scutum brown, with yellow lateral stripes, without posterior tubercles; proepisternum yellow; anepisternum yellow with posteroventral margin brown, without lateral tubercle; katepisternum brown, pilose on the anterior third; anepimeron and katepimeron brown; anatergite brown with a yellow median spot; katatergite and scutellum brown; subscutellum small, barely visible; calypter pale yellow, with anterodorsal margin yellow; M3 present; CuA absent. Leg (Fig. 6D). Not elongated; coxa brown; femur brown with distal apex yellow.


Remarks on type material: The epandrium of the holotype is missing, and for this reason it is not possible to infer the shape of its posterior margin. Unfortunately, the holotype is the only known male of the species.

Etymology: The species epithet is derived from the Latin longus (masculine, singular, meaning long) and rostris (feminine, singular, meaning beak), in reference to the long length of the proboscis, which exceeds the posterior abdominal apex in the male.

Geographical distribution (Fig. 40): Costa Rica (Limón); Panama (Colón, Gamboa).

Comments: Philopota longirostris sp. nov. is distributed in Central America, and is only known so far from Costa Rica and Panama.
**Philopota lugubris** Williston  
(Figs 7B–C, 12C, 17B, 23D, 29H, 32C, 34I)

*Philopota lugubris* Williston, 1901: 297. Lectotype male (designated here), BMNH. Type locality: Mexico, Guerrero, Xucumanatlan. Williston, 1901: 297 (description); Cole, 1919a: 19 (comments, diagnosis).

*Philopota dolorosa* Williston, 1901: 298. Holotype female, BMNH. Type locality: Mexico. [syn. nov.]

Williston, 1901: 298 (description); Cole, 1919a: 19 (comments, diagnosis).

**Diagnosis:** *Philopota lugubris* is very similar to *P. vitrialata* sp. nov. These two species differ in the coloration of the frons and scutellum, and in the absence of yellow spots on the posterior portion of the scutum in *P. vitrialata*.

**Redescription:** Lectotype male (Figs 7B, 12C). Body length: 6.9 mm (6.1–7.0 mm, \( N = 16 \)); wing length: 6.4 mm (5.4–6.3 mm, \( N = 16 \)). *Head* (Fig. 23D). Slightly narrower than thorax width; vertex brown, raised in comparison to postocular ridge in lateral view; frons brown with apex yellow, narrower than vertex width; postpedicel shorter than frons; postocular ridge brown, wider than clypeus length; face brown; clypeus brown, bare, longer than antenna; proboscis exceeding posterior abdominal apex.

*Thorax* (Figs 7B, 12C). Brown with yellow markings; postpronotum yellow with median margin brown; scutum brown, with yellow lateral stripes, without posterior tubercles; proepisternum brown; anepisternum brown, without lateral tubercle; katepisternum brown, pilose on the anterior third; anepimeron and katepimeron brown; anatergite brown with anterior and posterior portions yellow; vertex, frons, and postocular ridge wider than in the male; proboscis not reaching posterior abdominal apex, or reaching the apex without exceeding it; postpronotum brown, with anterior and posterior margins yellow, which vary in width and length; scutum with or without posterior yellow spots; scutellum with yellow posterior margin brown or yellow.

*Wing* (Figs 29H, 32C). Slighty narrower than thorax width; vertex pale yellow, with anterodorsal margin brown.

**Wing** (Fig. 17B). Hyaline, without markings; R₄₊₅ faintly sclerotized, narrower and posteroventral margin yellow.

**Calypter** pale yellow, with anterodorsal margin brown.

*Abdomen* (Figs 7B, 12C). Ovate, segments III and IV of equal width; tergite I brown with two yellow posterior spots; tergites II–VI brown with two yellow median spots; sternites with anterior third brown and the posterior two thirds yellow.

*Genitalia* (Figs 29H, 32C, 34I). Epandrium with posterior margin straight; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus thinned.

**Variation.** Proboscis reaching posterior abdominal apex without exceeding it, or exceeding posterior abdominal apex. Postpronotum colour variable, from brown to yellow or yellow with margins brown. Scutellum brown or brown with posterior margin yellow. Posterior yellow spots on scutum present or absent. Yellow margin of abdominal tergites variable in width.

**Female** (Fig. 7C). Body length: 6.7–7.4 mm, wing length: 7.2–7.4 mm (\( N = 3 \)). Much narrower than thorax; vertex, frons, and postocular ridge wider than in the male; proboscis not reaching posterior abdominal apex, or reaching the apex without exceeding it; postpronotum brown, with anterior and posterior margins yellow, which vary in width and length; scutum with or without posterior yellow spots; scutellum with yellow posterior margin brown or yellow.

*Type material examined:* Listed in Table S3.

**Geographical distribution (Fig. 39):** Mexico (Jalisco, Sinaloa, Guerrero).

**Comments:** *Philopota lugubris* is only known so far from Mexico. This species seems to be relatively rare, as only a few individuals are known from each locality. The availability of a relatively large series of specimens of both *P. lugubris* Williston, 1901, and *P. dolorosa* Williston, 1901, from the same locality enabled the confirmation that *P. dolorosa* is the female and a junior synonym of *P. lugubris*.

**Philopota minuta** sp. nov.  
(Figs 7D, 8A, 17C, 24A, 29I, 32D, 35A)

Holotype male, MZSP. Type locality: Brazil, Rio de Janeiro, Ilha da Marambaia.

**Diagnosis:** *Philopota minuta* is easily distinguished from all other species in the genus based on its small body size and the vein R₁ inflated at the pterostigma.

**Description:** Holotype male (Fig. 7D). Body length: 5.2 mm (4.5–6.1 mm, \( N = 108 \)), wing length: 4.5 mm (3.9–5.6 mm, \( N = 108 \)). *Head* (Fig. 24A). Slightly narrower than thorax width; vertex brown, raised in comparison to postocular ridge in lateral view; frons brown with apex yellow, narrower than vertex width;
postpedicel as long as frons; postocular ridge brown, as wide as clypeus length; face brown; clypeus brown with apex yellow, bare, longer than antenna; proboscis exceeding posterior abdominal apex. Thorax (Fig. 7D). Brown with yellow markings; postpronotum brown with posterior apex yellow; scutum brown, without posterior tubercles; proepisternum yellow; anepisternum with the median third brown and the dorsal and posterior thirds yellow, without lateral brown; katepisternum brown, bare on the anterior third; anepimeron and katepimeron brown; anategite with the median third yellow and the anterior and posterior thirds brown; katatergite and scutellum brown; subsutellum small, barely visible; calyptar brown, with anterodorsal margin brown and posterovertral margin yellow. Wing (Fig. 17C). Brown, without markings; R₁₊₅ well sclerotized, curved, extending for half of length of cell r₁₊₂; M₂ without spur vein; M₃ and CuA absent. Leg (Fig. 7D). Not elongated; coxa yellow; femur brown with distal apex yellow; tibia brown with dorsal face light brown; tarsus brown. Abdomen (Fig. 7D). Conical, each segment successively narrower lateromedially than the previous one; tergite I brown; tergites II–IV with lateroposterior portion yellow; tergites V–VI brown with lateral margin yellow; sternites yellow. Genitalia (Figs 29I, 32D, 35A). Epandrium with posterior margin concave; parameral sheath apex rounded; gonosomal apodemes present, fused, apex rounded; apex of gonostylus thinned. Variation. Clypeus usually entirely brown, sometimes with apex yellow. Scutum rarely with lateral stripes. Spur vein of M₂ rarely absent. Female (Fig. 8A). Body length: 6.3–7.4 mm, wing length: 5.3–6.3 mm (N = 38). Head. Slightly narrower than thorax; vertex wider than in the male; frons longer, wider, and more prominent than in the male; postocular ridge wider. Thorax. Slightly wider than in the male; postpronotum yellow or brown with anterior and posterior margins yellow; scutum with lateral stripes. Abdomen. Almost globose, wider than in the male; tergite I brown or brown with a narrow posterior band; tergites II–VI brown with lateral or posterior lateral margins yellow.


Additional material examined: Listed in Table S3.

Etymology: The species epithet is derived from the Latin minuta (feminine, singular, meaning small, little) in reference to the small body size of both the males and the females, which is unique within the genus.

Geographical distribution (Fig. 42): Brazil (Bahia, Minas Gerais, Rio de Janeiro, São Paulo).

Comments: Philopota minuta sp. nov. is recorded from central and south-east Brazil. Pujol-Luz (2004) described the association of P. minuta (cited as ‘Philopota sp.’) with Stachytarpheta cayennensis (Richard, 1792) (Verbenaceae) and provided information on the sexual and feeding behaviour, habitat, and abundance of the species.

**Philopota multivenata sp. nov.**

(Figs 8B, 17D, 24B, 30A, 32E, 35B)

Holotype male, KSUC. Type locality: Mexico, Morelos, leste de Cuernavaca.

Diagnosis: Philopota multivenata is a distinctive species easily identified by the non-elevated vertex, pilose clypeus and katepisternum, veins M₂, M₃, and CuA present, and male abdomen ovate. It is similar to *P. longirostris*, from which it can be distinguished by the vertex not raised in comparison to the postocular ridge in lateral view, the postpedicel as long as the frons, the pilose clypeus, and the proboscis shorter than the body length.

Description: Holotype male (Fig. 8B). Body length: 8.2 mm (8.2–9.0 mm, N = 2), wing length: 7.1 mm (7.1–7.8 mm, N = 2). Head (Fig. 24B). Slightly narrower than
thorax width; vertex brown, not raised in comparison to postocular ridge in lateral view; frons dark brown with apex light brown, narrower than vertex width; postpediceal as long as frons; postocular ridge brown, as wide as clypeus length; face brown; clypeus brown, pilose, longer than antenna; proboscis not reaching posterior abdominal apex. Thorax (Fig. 8B). Brown with yellow markings; postpronotum brown with anterior and posterior margins yellow; scutum brown, with yellow lateral stripes, without posterior tubercles; proepisternum brown; anepisternum brown with a yellow median spot, without lateral tubercle; katatergite and scutellum brown; anepimeron and katepimeron brown; anatergite brown with a wide yellow median stripe; katatergite brown; katepisternum brown, pilose on the anterior third; yellow median spot, without lateral tubercle; proepisternum brown; anepisternum brown with a lateral stripes, without posterior tubercles; anatergite brown with posterior spots, with yellow lateral stripes, without posterior tubercles; sternites brown.

Variation. Frons may be brown with apex yellow. Postpronotum may be brown with posterior margin yellow. Female. Unknown.


Etymology: The species epithet is derived from the Latin multi (masculine, singular, meaning many, several) and venata (feminine, singular, meaning vein, string), in reference to the presence of all three M veins in P. multivenata, a rare condition in Philopota species.

Geographical distribution (Fig. 41): Mexico (Morelos).

Comments: Philopota multivenata sp. nov. is only known thus far from Mexico. The species seems to be relatively rare, with a few individuals collected in each locality.

PHILOPOTA SCHLINGERI SP. NOV.
(FIGS 8C–D, 18A, 24C, 30B, 32F, 35C)

Holotype male, DZUP. Type locality: Brazil, Paraná, Balsa Nova, Rio Papagaio.

Diagnosis: Philopota schlingeri is a remarkable species characterized by the bare clypeus, male wing with or without markings, female wing with markings, and male abdomen ovate. It is similar to P. flavimaculata, from which it can be readily distinguished by the wider frons and the female wing with markings.

Description: Holotype male (Fig. 8C). Body length: 7.1 mm (6.2–7.0 mm, N = 35), wing length: 6.3 mm (5.7–6.5 mm, N = 35). Head (Fig. 24C). Narrower than thorax width; vertex brown, not raised in comparison to postocular ridge in lateral view; frons brown with apex yellow, as wide as vertex width; postpediceal shorter than frons; postocular ridge brown, narrower than clypeus length; face brown; clypeus brown, bare, longer than antenna; proboscis reaching posterior abdominal apex without exceeding it. Thorax (Fig. 8C). Brown with yellow markings; postpronotum yellow with median margin brown; scutum brown, with two yellow posterior spots, with yellow lateral stripes, without posterior tubercles; proepisternum brown; anepisternum brown with anterior portion yellow, without lateral tubercle; katatergite brown, bare on the anterior third; anepimeron and katepimeron brown; anatergite brown with a wide yellow median stripe; katatergite brown; scutellum brown with posterior margin yellow; subscutellum small, barely visible; calypter pale yellow, with margin light brown. Wing (Fig. 17D). Hyaline, with markings; R4+5 well sclerotized, curved, extending for half of length of cell r2+3; M2 with spur vein; M3 and CuA present. Leg (Fig. 8B). Not elongated; coxa brown; femur brown with distal apex yellow; tibia and tarsus brown. Abdomen (Fig. 8B). Ovate, segments III and IV of equal width; tergite I brown with posterior margin yellow; tergites II–VI brown with a yellow spot on the posterior margin; sternites brown. Genitalia (Figs 30A, 32E, 35B). Epandrium with posterior margin concave; parameral sheath apex bilobate; gonocoxal apodemes present, fused, with apex bilobate; apex of gonostylus broadened. Variation. Frons may be brown with apex yellow. Postpronotum may be brown with posterior margin yellow. Female. Unknown.


Etymology: The species epithet is derived from the Latin multi (masculine, singular, meaning many, several) and venata (feminine, singular, meaning vein, string), in reference to the presence of all three M veins in P. multivenata, a rare condition in Philopota species.

Geographical distribution (Fig. 41): Mexico (Morelos).

Comments: Philopota multivenata sp. nov. is only known thus far from Mexico. The species seems to be relatively rare, with a few individuals collected in each locality.
yellow with median portion brown, brown with anterior and posterior margins yellow, or brown with posterior apex yellow; scutum with or without posterior yellow stripes; scutellum entirely brown or brown with posterior margin yellow. Wing. Brown, with markings; vein M3 with spur vein. Abdomen. Wider than in the male; tergite I brown or brown with posterior margin yellow; tergites II–VI brown or brown with lateral margin yellow; sternites brown or brown with lateral margin yellow.


Additional material examined: Listed in Table S3.

Etymology: The specific epithet is named in honour of the late Dr Evert I. Schlinger, a foremost expert on world Acroceridae taxonomy.

Geographical distribution (Fig. 42): Brazil (Goiás, Minas Gerais, Rio de Janeiro, São Paulo, Paraná); Argentina (Tucumán).

Comments: Philopota schlingeri sp. nov. is a relatively abundant species distributed in west, southwest, and south Brazil, and in north-west Argentina. This species is highly variable intraspecifically, with the main differences occurring between Brazilian and Argentinian populations. Individuals from Brazil usually have posterior yellow spots on the scutum, as well as the male wing hyaline without markings. Argentinian specimens, by contrast, usually do not have posterior yellow spots on the scutum, and the wings are brown, with markings in both the male and the female. These differences, however, are not sufficient to separate these two disjunct populations into two different species as body colour, presence of yellow markings, and wing colour and maculation vary greatly intraspecifically in other members of the genus. For example, P. tuberculata may have hyaline or brown wings, which may have markings present or absent. In addition, the male genitalia of Brazilian and Argentinian individuals are almost identical. For these reasons both disjunct populations are grouped in the same species.

Philopota semicincta Schiner (Figs 9A, 18B, 24D, 30C, 32G, 35D)

Philopota semicincta Schiner, 1868: 144. Neotype male (designated here), CAS [holotype lost, formerly in the Naturhistorisches Museum Wien (NMW), see Pape & Thompson, 2013]. Type locality: Venezuela. Schiner, 1868: 144 (description); Hunter, 1900: 162 (catalogue).

Diagnosis: Philopota semicincta is easily distinguished from other Philopota species by the narrow vertex, which is as wide as the frons, and the ovate male abdomen, and the entirely yellow tergite I. It is most
similar to *P. amazonensis*, from which it can be distinguished by the body colour and the wider frons.

**Redescription: Neotype male** (Fig. 9A). Body length: 8.2 mm (8.2–8.6 mm, N = 3), wing length: 7.8 mm (7.8–9.3 mm, N = 3). **Head** (Fig. 24D). Slightly narrower than thorax width; vertex brown, not raised in comparison to postocular ridge in lateral view; frons brown with apex yellow, as wide as vertex width; postpedicel shorter than frons; postocular ridge brown, narrower than clypeus length; face brown; clypeus brown, bare, longer than antenna; proboscis reaching posterior abdominal apex without exceeding it. **Thorax** (Fig. 9A). Brown with yellow markings; postpronotum yellow; scutum brown, with yellow lateral stripes, without posterior tubercles; proepisternum yellow; anepisternum yellow with posterioroventral margin brown, without lateral tubercle; katepisternum brown, pilose on the anterior third; anepimeron and katepimeron brown; anatergite brown, pilose on the anterior third; antennal insertions brown; subscutellum small, barely visible; calypter pale yellow, with margin light brown. **Wing** (Fig. 18B). Brown, without markings; R4+5 well sclerotized, curved, extending for half of length of cell r2+3; M2 without spur vein; M1 absent; CuA absent. **Leg** (Fig. 9A). Not elongated; forecoxa with the anterior half yellow and the posterior half brown; mid- and hind coxae brown; femur brown with distal apex yellow; tibia brown with dorsal face light brown; tarsus brown. **Abdomen** (Fig. 9A). Ovate, segments III and IV of equal width; tergite I yellow; tergites II–VI brown with posterolateral margin yellow; sternites yellow. **Genitalia** (Figs 30C, 32G, 35D). Epandrium with posterior margin concave; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus thinned. **Variation.** Proboscis not reaching posterior abdominal apex. Anepisternum sometimes brown with a median yellow spot. Postpronotum may be yellow, yellow with margins brown, or brown. Forecoxa sometimes entirely brown. Tergites I–VI may be brown or brown with lateral margin yellow. Sternites sometimes brown in the anterior half and yellow in the posterior half. **Female.** Unknown.


**Additional material examined:** Listed in Table S3. **Geographical distribution** (Fig. 39): Costa Rica (Guanacaste, San José); Venezuela.

**Comments:** *Philopota semicincta* is distributed in Central and South America. According to Pape & Thompson (2013), the primary type of *P. semicincta* described by Schiner (1868) should be deposited in the NMW, but the specimen could not be located by its curator. It is thus assumed that the holotype is lost. *Philopota semicincta* is a rare species, of which only three individuals are known, one deposited in CAS and the other two in INBio. These three specimens were identified by Evert I. Schlinger, and they match Schiner’s original description. Owing to the difficulty of identification based only on the original description, and the absence of further drawings and taxonomic studies, the proposition of a neotype is necessary to fix this name to a name-bearing type, according to Article 75 of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999).

**PHILOPOTA TEPICENSIS SP. NOV.**

(Figs 9B, 18C, 25A, 30D, 32H, 35E)

Holotype male, LACM. Type locality: Mexico, Nayarit, Tepic.

**Diagnosis:** *Philopota tepicensis* is a conspicuous species easily differentiated by its vertex very elevated and wider than frons, pilose clypeus, and the presence of vein M3. Brown with yellow markings; frons narrower than vertex; postpedicel as long as frons; postocular ridge as wide as clypeus; clypeus pilose, longer than antenna; scutum without posterior tubercles; anepisternum without lateral tubercle; male wing brown, without markings; R1 not inflated at pterostigma; R4+5 well sclerotized, curved, extending for half of length of cell r2+3; M2 with spur vein; M3 present; CuA absent; legs not elongated; male abdomen ovate.

**Description:** Holotype male (Fig. 9B). Body length: 7.6 mm, wing length: 7.7 mm (N = 1). **Head** (Fig. 25A). Slightly narrower than thorax width; vertex brown, raised in comparison to postocular ridge in lateral view; frons brown with apex yellow, narrower than vertex width; postpedicel as long as frons; postocular ridge brown, as wide as clypeus length; face brown; clypeus brown, pilose, longer than antenna; proboscis reaching posterior abdominal apex without exceeding it. **Thorax** (Fig. 9B). Brown with yellow markings; postpronotum brown; scutum brown, with two yellow posterior spots, with yellow lateral stripes, without posterior tubercles; proepisternum brown; anepisternum brown, without lateral tubercle; katepisternum brown, bare on the anterior third; anepimeron and katepimeron brown; anatergite and katatergite brown; scutellum brown with posterior margin yellow; subscutellum small, barely visible; calypter pale yellow, with margin light brown. **Wing** (Fig. 18C). Brown, without markings; R4+5 well sclerotized, curved, extending for half of length of cell r2+3; M2 with spur vein; M3 present; CuA absent; legs not elongated; coxa brown; femur brown with distal apex yellow; tibia and tarsus brown.

**Abdomen** (Fig. 9B). Ovate, segments III and IV of equal width; tergite I brown with posterior yellow; tergites
II–VI brown with posteromedial margin yellow; sternites brown. Genitalia (Figs 30D, 32H, 35E). Epandrium with posterior margin concave; parameral sheath apex rounded; apex of gonostylus broadened. Female. Unknown.


Remarks on type material: The gonocoxite in the holotype is in very poor condition; thus, it is not possible to visualize the gonocoxal apodemes.

Schlinger/Specimen #/004253’ ‘Holotype/Holotype/tepicensis/J.P. Gillung des. 2013’.

Type material examined: Philopota tepicensis Bellardi, 1859: 77. Neotype male (designated here), USNM; [holotype lost, formerly in Museo Regionale di Scienze Naturali, Turin, Italy (MRSN)]. Type locality: Mexico, Morelos, Cuernavaca. Bellardi, 1859: 77. Neotype male (designated here), USNM, ‘Cuernavaca/54/L50489’ 'Holotype/L50489/Philopota/tepicensis/♀ Schlinger’ ‘Acroceridae/E.I. Schlinger/Specimen #/004253’ ‘Holotype/♀/Philopota tepicensis/J.P. Gillung des. 2013’.

Additional material examined: Listed in Table S3.

Geographical distribution (Fig. 39): Mexico (Morelos).

Comments: Philopota tepicensis sp. nov. is known only from a single male specimen collected in Mexico.

**Philopota truquii Bellardi**
(Figs 9C, 18D, 25B, 27C, 30E, 32I, 35F)

Philopota truquii Bellardi, 1859: 77. Neotype male (designated here), USNM; [holotype lost, formerly in Museo Regionale di Scienze Naturali, Turin, Italy (MRSN)]. Type locality: Mexico, Morelos, Cuernavaca. Bellardi, 1859: 77 (description); Cole, 1919a: 19 (comments, diagnosis); Schlinger, 1981: 575, fig. 2 (habitus), 3 (head, thorax).

Diagnosis: Philopota truquii is characterized by the male wing hyaline, without markings, the scutellum entirely brown, the vein R₄+₅ faintly sclerotized, and the ovate male abdomen. It is similar to Philopota alpina, from which it can be readily distinguished by the postpronotum brown with anterior and posterior margins yellow.

Redescription: Neotype male (Fig. 9C). Body length: 8.1 mm (7.7–9.0 mm, N = 3), wing length: 8.6 mm (7.8–9.3 mm, N = 3). Head (Fig. 25B). Narrower than thorax width; vertex brown, raised in comparison to postocular ridge in lateral view; frons dark brown with apex light brown, narrower than vertex width; postpedicel shorter than frons; postocular ridge brown, wider than clypeus length; face brown; clypeus brown, bare, longer than antenna; proboscis not reaching posterior abdominal apex. Thorax (Fig. 9C). Brown with yellow markings; postpronotum yellow with lateral and median margins brown; scutellum brown, with yellow lateral stripes, without posterior tubercles; proepisternum brown; anepisternum with the anterior half yellow and the posterior half brown, without lateral tubercle; katepisternum brown, with very sparse pilosity in the anterior third; anepimeron and katepimeron brown; anatergite yellow with a brown anterior spot; katatergite and scutellum brown; subscutellum small, barely visible; calypter yellow, with margin yellow. Wing (Fig. 18D). Hyaline, without markings; R₄+₅ faintly sclerotized, narrower and paler than other veins, curved, extending for half of length of cell r₄₅; M₂, M₃, and CuA absent. Leg (Fig. 9C). Not elongated; coxa brown; femur brown with distal apex yellow; tibia and tarsus brown. Abdomen (Fig. 9C). Oval, segments III and IV of equal width; tergite I brown with posterior margin yellow; tergites II–VI brown with posterior margin yellow; sternites with the anterior half brown and posterior half yellow. Genitalia (Figs 30E, 32I, 35F). Epandrium with posterior margin concave; parameral sheath apex rounded; gonocoxal apodemes present, fused, with apex bilobate; apex of gonostylus thinned. Variation. Proboscis length variable, from not reaching posterior abdominal apex to exceeding it. Calypter may be pale yellow. M₂ may be absent or present. Female. Unknown.

Type material examined: Philopota truquii Bellardi. Neotype male (designated here), USNM, ‘Cuernavaca/1293 (?) Mor Mex/EG Smyth’ ‘Chittenden/No 12691’ ‘Genitalia 78-6-30f./Dissection No./by E.I. Schlinger’ ‘USNM’ ‘Plesiotype/Philopota/truquii Bellardi/♀ Schlinger’ ‘Acroceridae/E.I. Schlinger/Specimen #/004270’.

Additional material examined: Listed in Table S3.

Geographical distribution (Fig. 39): Mexico (Morelos).

Comments: Philopota truquii is a relatively rare Mexican species. According to Pape & Thompson (2013), the primary type of P. truquii described by Bellardi (1859) should be deposited in the MRSN, but it was not found by the curator, Dr Guido Pagliano. Inquiries were sent to curators of other institutions, but unfortunately, the holotype was not found, and is thus presumed lost. Philopota truquii is a very rare species, of which only three male specimens from Mexico are known. These specimens are deposited in the USNM and in the AMNH, and were also identified as this species by Dr Evert Schlinger. As the original description is not sufficient to accurately identify the species and the holotype is presumed lost, a neotype for P. truquii is designated herein, according to Article 75 of the ICZN (International Commission on Zoological Nomenclature, 1999).

**Philopota tuberculata Westwood**

Philopota tuberculata Westwood, 1848: 95. Holotype male, UMO. Type locality: ‘Brazil’. Westwood, 1848: 95 (description); Walker, 1855: 341 (diagnosis); Hunter, 1900: 152 (catalogue); Brunetti, 1926: 564 (diagnosis, comments); Carrera, 1946: 174, (comments, drawing of habitus); Gillung & Carvalho, 2009: 39 (citation).

Diagnosis: Philopota tuberculata is easily identified by the yellow pollinosity on the thorax and abdomen, and the body coloration black or brown, with scarce yellow markings. This species is similar to P. flavolateralis and P. grossii sp. nov., from which it...
can be readily differentiated by the extremely hunch-backed thorax, the pilose katepisternum, and the vein R_{4+5} extending beyond half of length of cell r_{2+3}.

Redescription: Holotype male (Figs 9D, 10A). Body length: 7.1 mm (6.6–9.7 mm, N = 182), wing length: 7.1 mm (5.8–8.7 mm, N = 181). Head (Fig. 25C). Slightly narrower than thorax width; vertex black, raised in comparison to postocular ridge in lateral view; frons black with apex yellow, narrower than vertex width; postpedecel shorter than frons; postocular ridge black, as wide as clypeus length; face black, clypeus brown, pilose, longer than antenna; proboscis not reaching posterior abdominal apex. Thorax (Figs 9D, 10A). Black, with scarce yellow markings, covered by yellow pollinosity; postpronotum brown with posterior apex yellow; scutum black, with two posterior tubercles; proepisternum black; anepisternum black, without lateral tubercle; katepisternum black, pilose on the anterior third; anepimeron and katepimeron black; anatergite black with a yellow median stripe; katatergite black; scutellum dark brown; subscutellum small, barely visible; calypter yellow, with margin brown. Wing (Fig. 19A). Brown, with markings; R_{4+5} well sclerotized, curved, extending beyond half of length of cell r_{2+3}; M_{2} with spur vein; M_{3} and CuA present. Leg (Figs 9D, 10A). Not elongated; coxa brown; femur brown with distal apex yellow; tibia brown with dorsal face light brown; tarsus brown. Abdomen (Figs 9D, 10A). Conical, each segment successively narrower lateromedially than the previous one; tergite I brown; tergites II–VI brown with lateral margin yellow; sternites yellow. Genitalia (Figs 30F, 32J, 35G). Epandrium with posterior margin concave; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus thinned. Variation. Coloration of body varying from black to brown. Frons usually brown, rarely brown with distal apex yellow. Proboscis length variable, from not reaching posterior abdominal apex to exceeding it. Postpronotum usually entirely brown, sometimes brown with posterior apex yellow. Wing hyaline or brown, rarely with markings (only the holotype and another specimen have markings on the wing). Sternites sometimes brown in the anterior half and yellow in the posterior half. Female (Fig. 10C). Body length: 7.8–11.6 mm, wing length: 7.9–11.0 mm (N = 74). Head. Vertex, frons, and postocular ridge wider than in the male; proboscis not reaching posterior abdominal apex, or reaching the apex without exceeding it. Thorax. Postpronotum brown. Wing. Brown, with markings. Abdomen. Almost globose, wider than in the male. Genitalia (Fig. 37A, B). See generic description.


Additional material examined: Listed in Table S3.

Geographical distribution (Fig. 42): Brazil (Mato Grosso do Sul, Minas Gerais, Rio de Janeiro, São Paulo, Paraná, Santa Catarina, Rio Grande do Sul).

Comments: Philopota tuberculata is the most commonly represented Philopota species in collections, and is distributed in west, south-east, and south Brazil.

PHILOPOTA TURBINATA ERICHSON (Figs 10D, 11A, 19B, 25D, 30G, 32K, 35H)
Philopota turbinata Erichson, 1840: 154. Holotype male, ZMHB. Type locality: Brazil (probably state of Minas Gerais; see Papavero, 1971: 110). Erichson, 1840: 154 (description); Walker, 1855: 342 (diagnosis); Gillung & Carvalho, 2009: 39 (citation).

Diagnosis: Philopota turbinata is similar to P. conica and P. liturata, but is distinguished from these by the smaller body size, the shorter vein R_{4+5}, and male abdomen ovate.

Redescription: Holotype male (Fig. 10D). Body length: 7.2 mm (5.1–7.7 mm, N = 13), wing length: 6.4 mm (4.8–6.5 mm, N = 13). Head (Fig. 25D). Slightly narrower than thorax width; vertex brown, not raised in comparison to postocular ridge in lateral view; frons brown with apex yellow, narrower than vertex width; postpedicel as long as frons; postocular ridge brown, as wide as clypeus length; face brown; clypeus brown, bare, longer than antenna; proboscis not reaching posterior abdominal apex. Thorax (Fig. 10D). Brown with yellow markings; postpronotum brown with anterior and posterior margins yellow; scutum brown, with yellow lateral stripes, without posterior tubercles; proepisternum brown; anepisternum brown with a yellow anterior spot, without lateral tubercle; katepisternum brown, bare on the anterior third; anepimeron and katepimeron brown; anatergite brown with a yellow median spot; katatergite and scutellum brown; subscutellum small, barely visible; calypter yellow, with margin brown. Wing (Fig. 19B). Brown, without markings; R_{4+5} well sclerotized, curved, extending beyond half of length of cell r_{2+3}; M_{2} with spur vein; M_{3} and CuA absent. Leg (Fig. 10D). Not elongated; coxa brown; femur brown with distal apex yellow; tibia and tarsus brown. Abdomen (Fig. 10D). Conical, each segment successively narrower lateromedially than the previous one; tergite I brown; tergites II–III brown with posterior margin yellow; tergites IV–VI brown with lateral margin yellow; sternites brown. Genitalia (Figs 30G, 32K, 35H). Epandrium with posterior margin concave; parameral sheath apex bilobate; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus thinned. Variation.
Frons rarely entirely brown. Proboscis usually not reaching posterior abdominal apex, rarely reaching the apex without exceeding it. Tibia uniformly brown in the holotype, but usually the dorsal face is light brown. Female (Fig. 11A). Body length: 7.2 mm, wing length: 7.2 mm (N = 1). Head. Antenna shorter than frons; proboscis not reaching posterior abdominal apex. Thorax. Slightly wider than in the male; postpronotum brown with posterior apex yellow; anepisternum brown; anatergite brown with a yellow anterior spot. Wing. With markings. Leg. Tibia uniformly brown; femur brown. Abdomen. Almost globose, wider than in the male; tergites I–VI entirely brown.


Additional material examined: Listed in Table S3.

Geographical distribution (Fig. 39): Brazil (Rio de Janeiro, São Paulo, Paraná, Rio Grande do Sul).

Comments: Philopota turbinata is a relatively rare species recorded from south-east and south Brazil.

**PHILOPOTA VITRIALATA SP. NOV.**


Holotype male, CAS. Type locality: Mexico, Coahuila, north of El Tunal.

Diagnosis: Philopota vitrialata can be easily identified by the brown and narrow frons, vein R_{4,5} faintly sclerotized, and the lack of veins M2, M3, and CuA. It is similar to P. lugubris as both species have bare clypeus, male and female wing hyaline, without markings, and male abdomen ovate. Philopota vitrialata can be distinguished from P. lugubris by the frons and postpronotum coloration, and the length of the proboscis.

Description: Holotype male (Figs 11B, 13B). Body length: 6.9 mm (6.9–7.7 mm, N = 2), wing length: 6.4 mm (6.4–6.5 mm, N = 2). Head (Fig. 26A). Slightly narrower than thorax width; vertex brown, raised in comparison to postocular ridge in lateral view; frons brown, narrower than vertex width; postpedicel shorter than frons; postocular ridge brown, wider than clypeus length; face brown; clypeus brown, bare, longer than antenna; proboscis not reaching posterior abdominal apex. Thorax (Figs 11B, 13B). Brown with yellow markings; postpronotum brown with anterior and posterior margins yellow; scutum brown, with yellow lateral stripes, without posterior tubercles; proepisternum brown; anepisternum brown with dorsal and ventral yellow spots, without lateral tubercle; katepisternum brown, with very sparse pilosity on the anterior third; anepimeron and katepimeron brown; anatergite brown with anterior and posterior portions yellow; katatergite and scutellum brown; subscutellum small, barely visible; calypter pale yellow, with margin yellow. Wing (Fig. 19C).

Hyaline, without markings; R_{4,5} faintly sclerotized, narrower and paler than other veins, curved, extending for half of length of cell r_{2+3}; M2, M3, and CuA absent. Leg (Fig. 11B). Not elongated; coxa brown; femur brown with distal apex yellow; tibia and tarsus brown. Abdomen (Figs 11B, 13B). Ovate, segments III and IV of equal width; tergite I brown with two yellow posterior spots; tergites II–VI brown with posteromedial margin yellow; sternites with the anterior third brown and the posterior two thirds yellow. Genitalia (Figs 30H, 32L, 35I). Epandrium with posterior margin straight; parameral sheath apex rounded; gonocoxal apodemes present, fused, apex rounded; apex of gonostylus thinned. Variation. Proboscis sometimes exceeding posterior abdominal apex. Postpronotum colour varying from brown with posterior and anterior margins yellow to brown with lateral margins yellow. Pilosity on the anterior third of katepisternum varies in density and is sparser in the holotype than in the other specimens examined. Female (Fig. 11C). Body length: 8.5 mm, wing length: 8.7 mm (N = 1). Head. Much narrower than thorax; vertex, postocular ridge, and frons wider than in the male; proboscis exceeding posterior abdominal apex. Thorax. Wider than in the male. Wing. R_{4,5} slightly longer than in the male. Abdomen. Posterior spots of abdomen smaller than in the male; lateral margin of tergites brown.


Etymology: The species epithet is derived from the Latin vitreus (masculine, singular, meaning glassy, transparent) and alata (feminine, singular, meaning wings) in reference to the hyaline wing, which does not have markings in either the male or the female.

Geographical distribution (Fig. 41): Mexico (Coahuila).

Comments: Philopota vitrialata sp. nov. is a remarkable species only known so far from Mexico.

**PHYLOGENETIC ANALYSIS**

A total of 53 characters was explored (46 binary, seven multistate), 40 of which were based on external
Table 2. Characters and character states used in the phylogenetic analysis

<table>
<thead>
<tr>
<th>Character</th>
<th>Character states</th>
<th>Phylogenetic analysis</th>
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<tbody>
<tr>
<td>Ocelli number</td>
<td>(0) two; (1) three</td>
<td>CI: 0.5, RI: 0.5</td>
</tr>
<tr>
<td>Eye pilosity</td>
<td>(0) absent; (1) present</td>
<td>CI: 0.5, RI: 0.67</td>
</tr>
<tr>
<td>Eyes contiguity below antennae</td>
<td>(0) contiguous; (1) separate</td>
<td>CI: 0.5, RI: 0.5</td>
</tr>
<tr>
<td>Ventral portion of frons over scope and pedicel</td>
<td>(0) project; (1) not project</td>
<td>CI: 0.5, RI: 0.8</td>
</tr>
<tr>
<td>Vein R4+5 sclerotization</td>
<td>(0) faintly sclerotized, barely visible (Fig. 19C); (1) well sclerotized (Fig. 19B)</td>
<td>CI: 0.5, RI: 0.71</td>
</tr>
<tr>
<td>Vein M3</td>
<td>(0) absent (Fig. 14C); (1) present (Fig. 16B)</td>
<td>CI: 0.25, RI: 0.73</td>
</tr>
<tr>
<td>Gonocoxite ventral portion</td>
<td>(0) not covering the dorsal portion (Fig. 35B, C); (1) covering the dorsal portion (Fig. 33G)</td>
<td>CI: 0.33, RI: 0.0</td>
</tr>
<tr>
<td>Gonocoxal apodemes</td>
<td>(0) absent (Fig. 33G); (1) rounded (Fig. 33I); (2) bilobate (Fig. 35F)</td>
<td>CI: 0.4, RI: 0.0</td>
</tr>
<tr>
<td>Dorsal portion of gonocoxite</td>
<td>(0) closed (Fig. 33B–I); (1) open (Fig. 33A)</td>
<td>CI: 0.5, RI: 0.5</td>
</tr>
<tr>
<td>Distal apex of the parameral sheath</td>
<td>(0) rounded (Fig. 32C, D); (1) bilobate (Fig. 32A, B)</td>
<td>CI: 0.2, RI: 0.6</td>
</tr>
<tr>
<td>Parameral sheath apex</td>
<td>(0) without constriction (Fig. 31E–O); (1) with constriction (Fig. 31D)</td>
<td>CI: 0.5, RI: 0.5</td>
</tr>
<tr>
<td>Posterior margin of epandrium</td>
<td>(0) straight (Fig. 30H); (1) concave (Fig. 30G); (2) convex (Fig. 30I)</td>
<td>CI: 1, RI: 0.33</td>
</tr>
<tr>
<td>Cerci attachment</td>
<td>(0) to epandrium (Fig. 28E–I); (1) to subepandrial membrane (Fig. 28D)</td>
<td>CI: 1, RI: 1</td>
</tr>
<tr>
<td>Cerci surface</td>
<td>(0) smooth (Fig. 28B–I); (1) rugose (Fig. 28A)</td>
<td>CI: 1, RI: 0</td>
</tr>
<tr>
<td>Scutum with yellow dorsal stripes on the posterior portion</td>
<td>(0) absent (Fig. 12C); (1) present (Fig. 3D)</td>
<td>CI: 0.17, RI: 0.54</td>
</tr>
<tr>
<td>Scutum with yellow lateral stripes</td>
<td>(0) absent (Fig. 1C); (1) present (Fig. 1B)</td>
<td>CI: 0.33, RI: 0.43</td>
</tr>
<tr>
<td>Female wing colour</td>
<td>(0) hyaline (Fig. 9C); (1) brown (Fig. 9D)</td>
<td>CI: 1, RI: 1</td>
</tr>
<tr>
<td>Male wing colour</td>
<td>(0) hyaline (Fig. 9C); (1) brown (Fig. 9D)</td>
<td>CI: 1, RI: 1</td>
</tr>
<tr>
<td>Female wing membrane markings</td>
<td>(0) absent (Fig. 3A); (1) present (Fig. 4C)</td>
<td>CI: 0.6, RI: 0.6</td>
</tr>
<tr>
<td>Female wing membrane markings</td>
<td>(0) absent (Fig. 1B); (2) present (Fig. 1I)</td>
<td>CI: 0.5, RI: 0.78</td>
</tr>
<tr>
<td>Vein R1 inflated at pterostigma</td>
<td>(0) not inflated at pterostigma (Fig. 17C); (1) inflated at pterostigma (Fig. 17B)</td>
<td>CI: 0.53, RI: 0.0</td>
</tr>
<tr>
<td>Veins R2+3 and R4+5</td>
<td>(0) not pinulate (Fig. 17B); (1) pinulate (Fig. 17C)</td>
<td>CI: 0.5, RI: 0.77</td>
</tr>
<tr>
<td>Vein R4+5</td>
<td>(0) straight (Fig. 14B); (1) curved (Fig. 14C)</td>
<td>CI: 0.33, RI: 0.71</td>
</tr>
<tr>
<td>Vein M2</td>
<td>(0) length of vein M2; (1) extending for half of the length of cell r3+4 (Fig. 16A); (2) extending beyond half of the length of cell r3+4 (Fig. 16B)</td>
<td>CI: 0.33, RI: 0.6</td>
</tr>
<tr>
<td>Female abdomen</td>
<td>(0) globose; (1) strictly conical, each segment successively narrower lateromedially than the previous one (Fig. 27B); (2) ovate, segments III and IV of relation to the two other coxae, whereas in the remaining Philopota species they are strictly conically shaped (Fig. 27B)</td>
<td>CI: 0.43, RI: 0.73</td>
</tr>
<tr>
<td>Male abdomen</td>
<td>(0) closed (Fig. 33B–I); (1) open (Fig. 33A)</td>
<td>CI: 0.5, RI: 0.5</td>
</tr>
<tr>
<td>Male wing colour</td>
<td>(0) hyaline (Fig. 9C); (1) brown (Fig. 7D)</td>
<td>CI: 0.38, RI: 0.38</td>
</tr>
<tr>
<td>Male wing membrane markings</td>
<td>(0) absent (Fig. 7B, C, 26C); (1) present (Fig. 7B)</td>
<td>CI: 0.17, RI: 0.28</td>
</tr>
<tr>
<td>Male wing membrane markings</td>
<td>(0) absent (Fig. 12A); (1) absent (Fig. 8C, D)</td>
<td>CI: 0.25, RI: 0.83</td>
</tr>
<tr>
<td>Abdominal segment</td>
<td>(0) reduced; (1) not reaching posterior abdominal apex; (2) reaching posterior abdominal apex without exceeding it; (3) exceeding posterior abdominal apex</td>
<td>CI: 0.92, RI: 0.75</td>
</tr>
</tbody>
</table>

Abbreviations: CI = consistency index; RI = retention index; r-m = radial-medial crossvein; M2 = second posterior branch of media; M3 = third posterior branch of media.


morphology and 13 on male genitalia. All characters are unordered and non-additive, so no statements of plesiomorphic vs. apomorphic states are made. The list of characters, their states, and comments on character application are presented in Table 2. The phylogenetic matrix is presented in Table S1.

A heuristic search with equal weights resulted in a single most parsimonious cladogram (Fig. 38), which
was rooted with *Helle rufescens*. Bremer support values for each node are shown in Figure 38. The cladogram obtained (Fig. 38) has a length of 158 steps, a consistency index of 0.39, and a retention index of 0.67. The monophyly of *Philopota* was recovered with a Bremer support of 2. One synapomorphy [frons almost twice as long as wide; character 5 (0)] and two homoplastic characters [presence of pilosity on frons; character 7 (1) and male wing hyaline; character 24 (0)] support *Philopota* as a monophyletic taxon.

**DISCUSSION**

**PHYLOGENETIC ANALYSIS**

**Relationships within Philopotinae**

The monophyly of Philopotinae is supported by their autapomorphic enlarged postpronotal lobes, which are contiguous dorsomedially, forming a collar behind the head (Winterton et al., 2007). Twelve extant genera are described in Philopotinae, of which nine were included in our analysis.

DNA sequence data place *Helle* (New Zealand) and *Schlingeriella* (New Caledonia) in a clade at the base of Philopotinae, as sister to the remaining genera (Winterton et al., 2007). Because of its basal position in relation to all other genera (with the exclusion of *Schlingeriella*), *Helle* was used to root our cladogram. We did not include *Schlingeriella* in our analysis owing to a lack of material at the time; thus, we could not test the hypothesis of *Helle + Schlingeriella* forming a clade based on morphology. Both *Helle* and *Schlingeriella* are distributed in the Australasian region, and they share various morphological characters such as bare eyes; the antennae placed closer to the mouthparts at the lower part of the head; maxillary palpi present. However, these two genera differ strongly in the wing venation, as *Helle* has a complete, plesiomorphic set of wing veins and cells, whereas *Schlingeriella* has vein M₂ reduced, and lacks crossvein 2r-m, vein CuP, and cells d and bm (see Gillung & Winterton, 2011).

Hennig (1966) suggested that *Parahelle* (Madagascar), *Thyllis* (Africa and Madagascar), and *Dimacrocolus* (Madagascar) form a monophyletic clade, and this relationship is also indicated by molecular data, with *Parahelle* being strongly supported as sister to *Thyllis* (Winterton et al., 2007). These three genera are morphologically very similar, and the differences amongst them could potentially be regarded as intrageneric variation; further studies are needed to investigate whether they belong to a single genus or separate genera. Schlinger (1961, 1971, 2003) hypothesized that *Megalybus* (Chile), *Helle* (New Zealand), and *Parahelle* (Madagascar) form a monophyletic clade based on morphology and host relationships. Our results, by contrast, suggest that *Megalybus* is closely related to *Thyllis* based on the wing venation and a combination of three homoplastic characters: presence of pilosity on the pedicle [character 9 (1)], presence of a yellow band at the posterior margin of the scutellum [character 23 (1)], and presence of markings on the female wing membrane [character 27 (1)]. Future studies that include *Parahelle* as well as DNA sequence data may indicate whether *Megalybus* belongs in a clade with the Afrotropical genera *Thyllis*, *Parahelle*, and *Dimacrocolus*, or with the New World genera *Philopota* and *Terphis*.

In our analysis, the clade containing *Thyllis + Megalybus* was recovered as sister to a clade containing *Neophilopota* (Mexico), *Quasi* (Central America), *Africaterphis* (Africa), *Terphis* (South America), *Oligoneura* (Oriental and Palaearctic regions), and *Philopota* (New World). This clade is characterized by an incomplete wing venation, where M₂, M₃, M₄, CuA, and CuP may be absent or incomplete, and cells d and bm are lacking (Figs 14, 16). *Neophilopota*, *Quasi*, *Africaterphis*, and *Terphis* are grouped together in a clade defined by a combination of three homoplastic characters: clypeus height shorter than the antennae [character 12 (0)], vein R₄₊₅ curved [character 31 (1)], and the posterior margin of the epandrium straight [character 43 (0)]. *Quasi*, *Africaterphis*, and *Terphis* have reduced mouthparts, whereas *Neophilopota* has functional, elongated mouthparts that are shorter than the head height (as opposed to *Oligoneura* and *Philopota*, in which the proboscis is much longer than the head height). *Terphis* was grouped with the African genus *Africaterphis* as both genera have two ocelli [character 1 (0)], eyes contiguous below the antennae [character 3 (0)], and the male abdomen globose [character 39 (0)]. Notably, these two genera were placed as sister to the Central American genus *Quasi*, based on the bare eyes [character 2 (0)], reduced mouthparts that do not form a proboscis [character 15 (0)], and R₄₊₅ faintly sclerotized, barely visible [character 30 (0)].

The position of *Philopota* and its relationship to other philopotine genera have always been controversial. Schlinger (1961, 2003) stated that *Philopota* and *Thyllis* are closely related and placed basally within the subfamily, and suggested that the Afrotropical genus *Thyllis* gave rise to the New World genus *Philopota*. Molecular data, however, indicate that *Philopota* and *Thyllis* are not closely related, nor are they situated basally within Philopotinae (Winterton et al., 2007). Instead, these data show that *Philopota* is more closely related to the Neotropical genera *Terphis* and *Megalybus* (although *Oligoneura* was not included in the analysis). Hennig (1966) hypothesized that *Philopota* and *Terphis* comprised a monophyletic clade based on wing venation characters, stating that the reduction of wing veins shown by the two genera differs from the typical acrocercid wing type and is derived. However, Hennig's
(1966) definition of Philopota also included the Palaeartic genus Oligoneura, and likewise his definition of Terphis included the Afrotropical genus Africaterphis. Our analysis does not support the basal position of Philopota; rather it indicates that the genus is more closely related to Oligoneura based on the following characters: projection of frons over the scape and pedicel [character 4 (0)] and length of the postpronotal lobe fusion margin being equivalent to the length of the second foreleg tarsomere [character 16 (1)].

A preliminary analysis combining both morphological and DNA sequence data of Philoptotinaceae, which included the three philopotine Baltic amber genera Eulonchiella, Archaeaterphis, and Prophilopota, has been conducted as part of a broader project concerned with a total evidence phylogeny of Acroceridae (JP Gillung & SL Winterton, in prep.). In this analysis, Eulonchiella Meunier was placed as sister to Helle in a clade containing Schlingeriella + (Helle + Eulonchiella). In addition, Archaeaterphis Hauser & Winterton and Prophilopota Hennig were placed together in a clade recovered as sister to both the Afrotropical Africaterphis and the Neotropical Terphis, Neophilopota, Quasi, and Philopota. These results, however, are not definitive, and it is probable that the addition of other taxa might change some of the observed groupings. However, some of the relationships observed in our phylogenetic analysis were recovered with very strong support with respect to morphology, such as the close relationship of Philopota and Oligoneura, the clade containing Schlingeriella and Helle (and possibly the fossil genus Eulonchiella), the close relationship between Thyllis and Parahelle (and probably Dimacrocolus), and the clade containing Terphis and Africaterphis.

In our analysis, Philopota was recovered as monophyletic, and is defined by one synapomorphy [frons almost twice as long as wide; character 5 (0)] and two homoplastic characters [presence of pilosity on frons; character 7 (1) and male wing hyaline; character 24 (0)]. This clade was recovered with a Bremer support of 2.

**Relationships within Philopota**

One major clade (clade I, Fig. 38, Bremer support = 2) was recovered in Philopota, which comprises all of the species of the genus except for *P. castanea* and *P. dissimilis*. Clade I is defined by one synapomorphy and three homoplastic characters: frons as long as or longer than the postpedicel [character 6 (1)], presence of yellow lateral stripes on the scutum [character 18 (1)], presence of pilosity on the anterior half of katepisternum [character 22 (1)], and vein R_{4+5} curved [character 31 (1)]. The shape, size, and length of the frons are important characters that define Philopota, and most species in the genus have an elongated frons that is as long as or longer than the postpedicel. Contrary to this, in *P. castanea* and *P. dissimilis* (and in the other philopotine genera) the frons is less prominent and shorter than the postpedicel. The three homoplastic characters that support clade I are somewhat variable, and multiple reversions have taken place across the genus. Most species have yellow lateral stripes on the scutum [character 18 (1)], which are lacking only in *P. castanea*, *P. dissimilis*, *P. grossii*, *P. tuberculata*, and *P. minuta*. In *P. minuta* the presence or absence of the stripes is polymorphic. The presence of pilosity on the katepisternum seems to have evolved multiple times within the genus [character 22 (1)], and most species lack this trait. Vein R_{4+5} is curved in all species included in clade I [character 31 (1)], and amongst Philopota species is straight only in *P. castanea* and *P. dissimilis*.

Two reciprocally monophyletic clades were recovered within clade I: clade II containing the Mexican species *P. truquii*, *P. lugubris*, and *P. vitrialata* (Bremer support = 1) and clade III containing the remaining species (Bremer support = 3). Members of clade II have vein R_{4+5} faintly sclerotized and barely visible [character 30 (0)], a character also shared by *P. schlingeri*, in which R_{4+5} may be faintly or well sclerotized. Faint sclerotization of vein R_{4+5} (Figs 17B, 19C) is a rare state in Philopota, and only a few philopotine genera also share it. Within clade II, *P. lugubris* and *P. vitrialata* are sister taxa, sharing a straight, rather than concave, posterior epandrial margin [character 43 (0); Fig. 30H]. This state is unique within Philopota, but also occurs in some other philopotine genera (*Megalybus*, *Neophilopota*, and *Terphis*). Clade III includes most species of the genus and is distributed in Mexico and Central and South America. Two homoplastic characters define the group: male wing brown [character 24 (1)] and vein M_{2} without a spur vein [character 35 (1)], and it contains five minor clades (clades IV–VIII). Although clade III is defined in part by absence of the M_{2} spur vein (Fig. 15A), a reversal occurs in clades IV–VIII (Fig. 16B). Indeed, within clade III the spur vein is only absent in the basal grade comprised of *P. semincincta*, *P. amazonensis*, and *P. costaricensis*.

*Philopota histrio*, *P. minuta*, and *P. longirostris* comprise clade IV (Bremer support = 1), a group of species from Brazil and Central America with proboscises longer than the body length [character 15 (3)], a synapomorphy for the group. *Philopota conica* and *P. liturata* are South American species included in clade V, which is characterized by the vein R_{4+5} extending beyond half of the length of cell R_{2,3} [character 32 (2)] and was assigned with a Bremer support of 1. In most Philopota species, R_{4+5} extends for up to half of the length of cell R_{2,3} (Fig. 16C); in species of clades V and VIII, as well as in *P. dissimilis* and *P. castanea*, vein R_{4+5} extends beyond half of the length of cell R_{2,3} (Fig. 16D). Clade
VI includes *P. turbinata*, *P. schlingeri*, *P. flavimaculata*, and *P. tepicensis* and is defined by the ovate male abdomen [character 39 (2)] and has a Bremer support of 1.

The remaining two clades, VII and VIII, contain *P. fuscofemorata* and *P. multivenata*, and *P. flavolateralis*, *P. grossii*, and *P. tuberculata*, respectively. Clade VII is defined by the proboscis not reaching posterior abdominal apex [character 15 (1)] and the male wing being hyaline [character 24 (0)]. Clade VIII is defined by a synapomorphy: presence of lateral tubercles on the posterior margin of scutum [character 19 (1)]. The former clade has a Bremer support of 1, and the latter, of 3.

**CONCLUSION**

Here we revised *Philopota*, one of the most distinctive spider fly genera, and clarified the systematics of both *Philopota* and Philopotinae. As previously defined, *Philopota* included 16 species, of which seven were found to be junior synonyms by our comparative study. To the remaining nine valid species, we added 13 new, which results in a total of 22 species currently placed in *Philopota*. Thus defined, *Philopota* is the largest genus in the subfamily Philopotinae, and one of the largest genera of Acroceridae.

This is the first phylogenetic hypothesis ever proposed for the genus, and the first cladistic analysis based on morphological data for Acroceridae. Our results show that *Philopota* is monophyletic and indicate that its sister taxon is the Palearctic genus *Oligoneura*. The close relationship between these two genera is by no means unexpected, as both genera are morphologically very similar, to such an extent that they have been considered a single genus by many authors for decades. Additionally, this study provides a new framework for the classification and identification of *Philopota* using modern taxonomic tools. The identification key to the species of *Philopota* provided here is user friendly, well illustrated, and comprehensive, allowing easier and more accurate identification of the species of the genus than previously. Further collecting efforts, especially in still very poorly explored areas in Mexico, and in Central and South America will very probably result in the discovery of new species. In this context, our results will greatly facilitate species discovery and other taxonomic investigations, as well as assist other biologists and conservation specialists in decision making and planning future research on the group. Owing to the flower visiting behaviour of the species of *Philopota*, the identification key provided here will also benefit plant and insect ecologists who might come across *Philopota* spider flies. Furthermore, we expect that studies of biogeography, character evolution, behaviour, ecology, and diversification will greatly benefit from the tree of life of the Philopotinae hypothesized here.

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Figure 1. Habitus, lateral view. A, Philopota amazonensis sp. nov., paratype male. B, Philopota amazonensis sp. nov., holotype female. C, Philopota castanea sp. nov., holotype male. D, Philopota castanea sp. nov., paratype female.
Figure 5. Habitus, lateral view. A, Philopota fuscofemorata sp. nov., holotype male. B, Philopota grossii sp. nov., holotype male. C, Philopota histrio, holotype male. D, Philopota histrio, female (holotype of Philopota sobria).

Figure 11. Habitus, lateral view. A, Philopota turbinata, female. B, Philopota vitrialata sp. nov., holotype male. C, Philopota vitrialata sp. nov., paratype female.
Figure 13. Habitus, dorsal view. A, Philopota tuberculata, male. B, Philopota vitrialata sp. nov., holotype male.
Figure 14. Wings, dorsal view. A, Philopota amazonensis sp. nov., female. B, Philopota castanea sp. nov., male. C, Philopota conica, female. D, Philopota conica, male. Abbreviations: A, anal vein; CuP, posterior branch of cubitus; M₁, first posterior branch of media; M₂, second posterior branch of media; M₄, fourth posterior branch of media; R₁, anterior branch of radius; R₂+₃, second+third posterior branches of radius; R₄+₅, fourth+ fifth posterior branches of radius; Sc, subcosta; spur, spur vein of M₂. Scale bar = 1 mm.
Figure 16. Wings, dorsal view. A, *Philopota fuscofemorata* sp. nov., male. B, *Philopota grossii* sp. nov., male. C, *Philopota histrio*, male. D, *Philopota liturata*, male. Abbreviations: A, anal vein; CuA, anterior branch of cubitus; CuP, posterior branch of cubitus; M1, first posterior branch of media; M2, second posterior branch of media; M3, third posterior branch of media; M4, fourth posterior branch of media; m-m, medial crossvein; R1, anterior branch of radius; R2+3, second+third posterior branches of radius; R4+5, fourth+fifth posterior branches of radius; Sc, subcosta; spur, spur vein of M2. Scale bar = 1 mm.
Figure 18. Wings, dorsal view. A, Philopota schlingeri sp. nov., male. B, Philopota semicincta, male. C, Philopota tepicensis sp. nov., male. D, Philopota truquii, male. Scale bar = 1 mm.
Figure 20. Head, lateral view. A, *Philopota amazonensis* sp. nov., female. B, *Philopota castanea* sp. nov., male. C, *Philopota conica*, female. D, *Philopota conica*, male. Abbreviations: CL, clypeus length; clyp, clypeus; fc, face; FL, frons length; fr, frons; lab, labium; lbr, labrum; lfm, lower facial margin; ped, pedicel; pocl r, postocular ridge; postped, postpedicel; premnt, prementum; PW, postocular ridge width; scp, scape; vrt, vertex; VW, vertex width. Scale bar = 1 mm.
Figure 21. Head. A, Philopota conica, female, frontal view. B, Philopota conica, male, frontal view. C, Philopota costaricensis sp. nov., male, lateral view. D, Philopota dissimilis sp. nov., male, lateral view. Abbreviations: clyp, clypeus; CW, clypeus width; fc, face; fr, frons; lfm, lower facial margin; FW, frons width; oc tr, ocellar triangle; ped, pedicel; pocl r, postocular ridge; postped, postpedicel; scp, scape. Scale bar = 1 mm.
Figure 23. Head, lateral view. A, Philopota histrio, male. B, Philopota liturata, male. C, Philopota longirostris sp. nov., male. D, Philopota lugubris, male. Scale bar = 1 mm.
Figure 26. Head and thorax. A, *Philopota vitrialata* sp. nov., male, head, lateral view. B, *Philopota conica*, male, thorax and head, lateral view. C, *Neophilopota brevirostris*, male, thorax and head, lateral view. Abbreviations: anepst, anepisternum; cx 1, forecoxa; cx 2, middle coxa; cx 3, hind coxa; kepst, katepisternum; mr, meron; prpn lb, postpronotal lobe; prepst, proepisternum. Scale bar = 1 mm.
Figure 34. Gonocoxite and gonostylus, ventral view. A, Philopota dissimilis sp. nov. B, Philopota flavimaculata sp. nov. C, Philopota flavolateralis. D, Philopota fuscofemorata sp. nov. E, Philopota grossii sp. nov. F, Philopota histrio. G, Philopota liturata. H, Philopota longirostris sp. nov. I, Philopota lugubris. Scale bar = 1 mm.
Figure 36. Male genitalia, lateral view. A, Philopota conica. B, Oligoneura itoi. Abbreviations: aed, aedeagus; cerc, cercus; D, dorsal; d surf, dorsal surface of gonocoxite; ej apod, ejaculatory apodeme; ej proc, lateral ejaculatory process; epand, epandrium; goncx, gonocoxite; goncx apod, gonocoxal apodeme; gonst, gonostylus; mb subep, subepandrial membrane; par sh, parameral sheath; V, ventral; v surf, ventral surface of gonocoxite. Scale bar = 1 mm.
Figure 37. Female genitalia. A, Philopota tuberculata, lateral view. B, Philopota tuberculata, ventral view. Abbreviations: cerc, cercus; gen fk, furca; hyprct, hypoproct; spmth, spermatheca; st, sternite; tg, tergite. Scale bar = 1 mm.
Figure 38. Single most parsimonious cladogram showing the relationships amongst species of *Philopota* under equal weighting of the characters (158 steps, consistency index = 0.39, retention index = 0.67). Only unambiguous changes are shown. Black rectangles represent unique changes; white rectangles represent multiple changes. Bremer support values are shown in circles below branches.
Figure 39. Distribution of Philopota conica (red circles), Philopota grossii sp. nov. (blue square), Philopota lugubris (pink circles), Philopota semicincta (blue circles), Philopota truquii (yellow circles), and Philopota turbinata (green circles).
Figure 40. Distribution of *Philopota castanea* sp. nov. (blue circles), *Philopota flavimaculata* sp. nov. (pink circles), *Philopota fuscofemorata* sp. nov. (yellow circle), *Philopota liturata* (red circles), and *Philopota longirostris* sp. nov. (green circles).
Figure 41. Distribution of *Philopota amazonensis* sp. nov. (yellow circle), *Philopota costaricensis* sp. nov. (blue circles), *Philopota dissimilis* sp. nov. (blue triangles), *Philopota histrio* (red circles), *Philopota multivenata* sp. nov. (pink square), *Philopota tepicensis* sp. nov. (green circle), and *Philopota vitrialata* sp. nov. (red triangles).
Figure 42. Distribution of Philopota flavolateralis (red circles), Philopota minuta sp. nov. (pink circles), Philopota schlingeri sp. nov. (yellow circles), and Philopota tuberculata (blue circles).
REFERENCES


SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher’s web-site:

Table S1. Character matrix for the phylogenetic analysis. Missing data were scored with a question mark, ‘?’, and inapplicable data with a hyphen, ‘-‘.

Table S2. Georeferencing data for the species of \textit{Philopota}.

Table S3. Nontype material examined. EIS, Evert I. Schlinger collection database specimen accession numbers.