Instituto Nacional de Pesquisas da Amazônia – INPA
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TABANUS LINNAEUS, 1758 (DIPTERA:TABANIDAE): ANÁLISE FILOGENÉTICA COM ÊNFASE NAS ESPÉCIES NEOTROPICAIS E TAXONOMIA DO GRUPO DE ESPÉCIES RELACIONADAS À *TABANUS TRIVITTATUS* FABRICIUS

Daniel Dias Dornelas do Carmo

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Sinopse

Neste trabalho, caracteres morfológicos e dados genômicos são utilizados para melhorar nosso conhecimento acerca da história evolutiva das espécies incluídas no gênero *Tabanus*. Os resultados obtidos sustentam que o gênero não é um grupo natural e são propostos três gêneros novos para a região Neotropical, e um deles têm sua taxonomia revisada. É proposta ainda uma hipótese acerca da divergência dos gêneros novos na América do Sul.

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”In the warriors code

There's no surrender

Though his body says stop

His spirit cries, never!

Deep in our soul

A quiet ember

Know it's you against you

It's the paradox

That drives us on

It's a battle of wills

In the heat of attack

It's the passion that kills

The victory is yours alone

In the burning heart

Just about to burst

There's a quest for answers

An unquenchable thirst

In the darkest night

Rising like a spire

In the burning heart

The unmistakable fire”

Trecho da música *Burning heart* da banda *Survivor*. Trilha sonora do filme Rocky IV.

Resumo

No capítulo um foi realizada a filogenética de *Tabanus* Linnaeus. O gênero possui grande riqueza de espécies (cerca de 1350 espécies válidas) e seu status não monofilético já foi sugerido por diversos autores, apesar de nenhum método filogenético ter sido utilizado para abordar as relações do gênero com uma amostragem abrangente. *Anchored Hybrid Enrichment* foi utilizado para adquirir 193 loci para análise filogenômica de 35 espécies de *Tabanus*. Além disso, uma matriz morfológica para 88 táxons terminais foi construída a partir de caracteres internos e externos. Os conjuntos de dados moleculares e morfológicos sustentam a afilia de *Tabanus* com uma origem Neotropical para a tribo Tabanini. Com base nesses resultados, são propostos três novos gêneros endêmicos ao Neotrópico - *Cephalogongylus* **gen.n**, *Rhinoderus* **gen.n**., *Tapirotabanus* **gen. n**., - e a revalidação de um gênero - *Chelotabanus* **stat. rev.** Utilizando uma subamostra da matriz filogenômica, também foi possível estimar os tempos de divergência para o grupo *Tabanus*, que se originou durante o limite entre o Paleoceno e o Eoceno, com diversificação de alguns dos novos gêneros neotropicais com distribuição amazônica, durante o Mioceno. No capítulo dois, é revisado o grupo de espécies relacionadas a *Tabanus trivittatus*, que inclui mutucas com abdômen listrado, subcalo inflado e sem pruinosidade. São descritas cinco novas espécies elevando o número de espécies válidas de 15 para 20, quatro das quais ocorrem no Brasil: *T. albocapillus* sp. n., *T. dorsorufus* sp. n., *T. mackerrasi* sp. n., *T. macrocerus* sp. n. e uma que ocorre no Brasil, Bolívia e Peru: *T. noncallosus* sp. n. Também modificamos as chaves de Fairchild (1976) para ambos os sexos e discutimos brevemente a terminália feminina.

Abstract

Tabanus Linnaeus, 1758 (DIPTERA: TABANIDAE): Phylogenetic analysis with emphasis in Neotropical species and taxonomy of the group of species related to *Tabanus trivittatus* Fabricius.

In chapter one is employed a phylogenetic analysis of the widespread genus *Tabanus* Linnaeus. The genus possess great species richness (ca. 1350 valid species) and its non-monophyletic status has already been suggested by several authors, however, no modern phylogenetic methods have been used to address the relationships of the genus with a comprehensive sample. Anchored enrichment was used to acquire 193 loci for phylogenomic analysis of 35 *Tabanus* species. Additionally a morphological matrix for 88 terminal taxa was built from internal and external characters. Both molecular and morphological datasets sustain the aphyly of *Tabanus* with a Neotropical origin for the Tabanini tribe. Based on these results three new genera endemic to the Neotropic are proposed - *Chephalogongylus* **gen.n**, *Rhinoderus* **gen.n.**, *Tapirotabanus* **gen. n., -** and revalidate on genus - *Chelotabanus* **stat. rev.** A subsample of the phylogenomic dataset was used to estimate the divergence times for the *Tabanus* group with origin during the Paleocene/Eocene boundary, and diversification of some of the new Neotropical genera with amazonian distribution, during the Miocene. In chapter two the group of species related to *Tabanus trivittatus* which include horse flies with striped abdomens and partially bare, inflated, subcallus is revised. Five new species are described raising the number of valid species from 15 to 20, four of which occur in Brazil: *T. albocapilus* **sp. n.,** *T. dorsorufus* **sp. n.,** *T. mackerrasi* **sp. n.,** *T. macrocerus* **sp. n.** and one that occur in Brazil, Bolivia and Peru: *T. noncallosus* **sp. n.** The keys from Fairchild (1976) are modified for both sexes and the female terminalia briefly discussed.

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Introdução Geral

A família Tabanidae

Popularmente conhecidas como mutucas, as moscas da família Tabanidae são insetos de tamanho relativamente grande (4 a 25 mm), olhos com padrões de coloração complexos e tegumento com pilosidade e cor geralmente vistosos. Em comunidades rurais de todo o mundo, esses insetos são reconhecidos pela picada dolorida das fêmeas que se utilizam do sangue de vertebrados para nutrir os ovos. Apesar da presença de hematofagia, fêmeas e machos de algumas espécies são visitantes florais (Pechuman e Teskey, 1989; Johnson e Morita, 2006).

Tabanidae possui 4500 espécies válidas descritas (Pape e Thompson, 2013) distribuídas por todas as seis regiões biogeográficas. É a maior das famílias da infraordem Tabanomorpha. Tanto seu monofiletismo como o relacionamento de Tabanidae com Athericidae são bem estabelecidas por caracteres morfológicos (Woodley, 1989; Yeates, 2002; Carmo e Santos, 2011) e moleculares (Wiegmann *et al.,* 2011; Morita *et al*., 2016). São sinapomorfias da família a célula r5 englobando o ápice da asa e uma caliptra inferior muito desenvolvida (Nagatomi, 1981; Woodley, 1989; Yeates, 2002).

Mackerras (1956), usando principalmente caracteres da genitália, dividiu Tabanidae em 4 subfamílias (Figura 1) e nove tribos, classificação que por muito tempo foi a mais aceita. No entanto, a hipótese de Mackerras não deriva de uma análise filogenética formal para avaliar as relações entre os grupos.

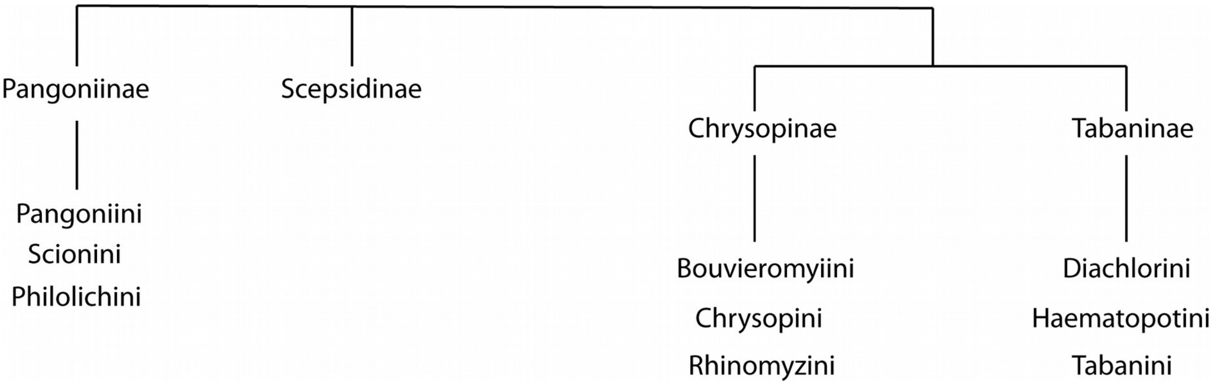

Figura 1. Subfamílias e tribos de Tabanidae, sensu Mackerras, (1956)

Uma das primeiras hipóteses filogenéticas para Tabanidae foi feita por Trojan *et al*., (1997). A análise teve como foco a subfamília Tabaninae e utilizou como terminais as tribos dessa família como previamente proposto por Mackerras, além de duas tribos adicionais (Lepidoselagini e Hematopotini). Foram levantados 9 caracteres proveniente da morfologia externa dos adultos e um caráter larval. A hipótese de Trojan mostra os Diachlorini como grupo irmão de Tabanini enquanto a tribo Haematopotini seria irmã de Heptatomini (Figura 2).

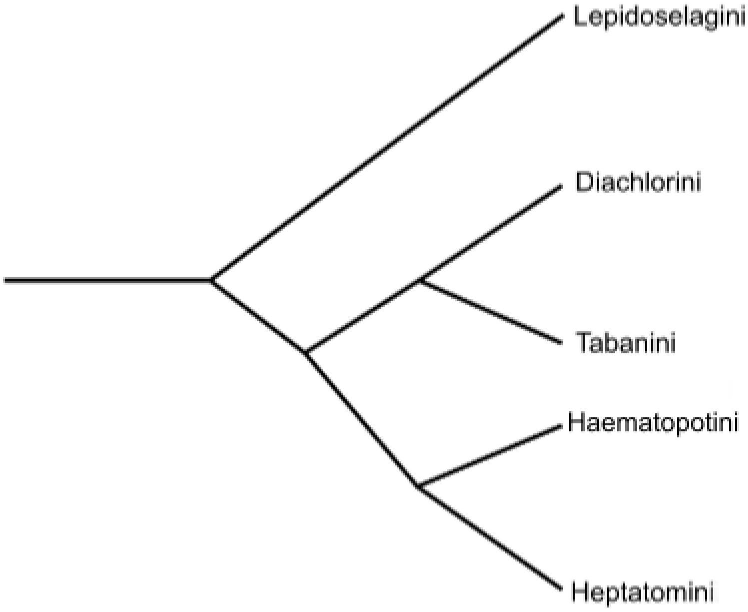

Figura 2. As relações da subfamília Tabaninae sensu Trojan (1997).

Morita *et al.* (2016) foi a primeira hipótese filogenética para Tabanidae incluindo múltiplos marcadores moleculares e ampla amostragem de táxons. Nessa hipótese, os Pangoniinae são recuperados como um grupo monofilético, irmão das demais subfamílias de Tabanidae. Já Chrysopsinae não foram recuperados como monofiléticos de forma que os Rhinomyzini foram posicionados como mais próximos de Tabaninae do que das demais tribos tradicionalmente incluídas na subfamília. A família Tabaninae é monofilética de acordo com a hipótese de Morita *et al.* (2016). Dentro da subfamília, os Diachlorini são afiléticos (*cf.* Williams e Ebach, 2017), com *Chlorotabanus* sendo grupo-irmão de Tabanini e

Haematopotini (Figure 3). Os Tabanini também aparecem como afiléticos em relação aos Hematopotini na análise dos autores. A hipótese de Morita *et al*. (2016) coloca a origem de Tabanidae no Cretáceo inferior (entre 145 - 100 milhões de anos), após a irradiação das Angiospermas (há 175 milhões de anos). Os autores discutem ainda brevemente a origem do hábito hematófago:, considerando-o plesiomórfico para Athericidae + Tabanidae, é possível que o primeiro Tabanomorpha hematófago teria surgido há 160 milhões de anos.

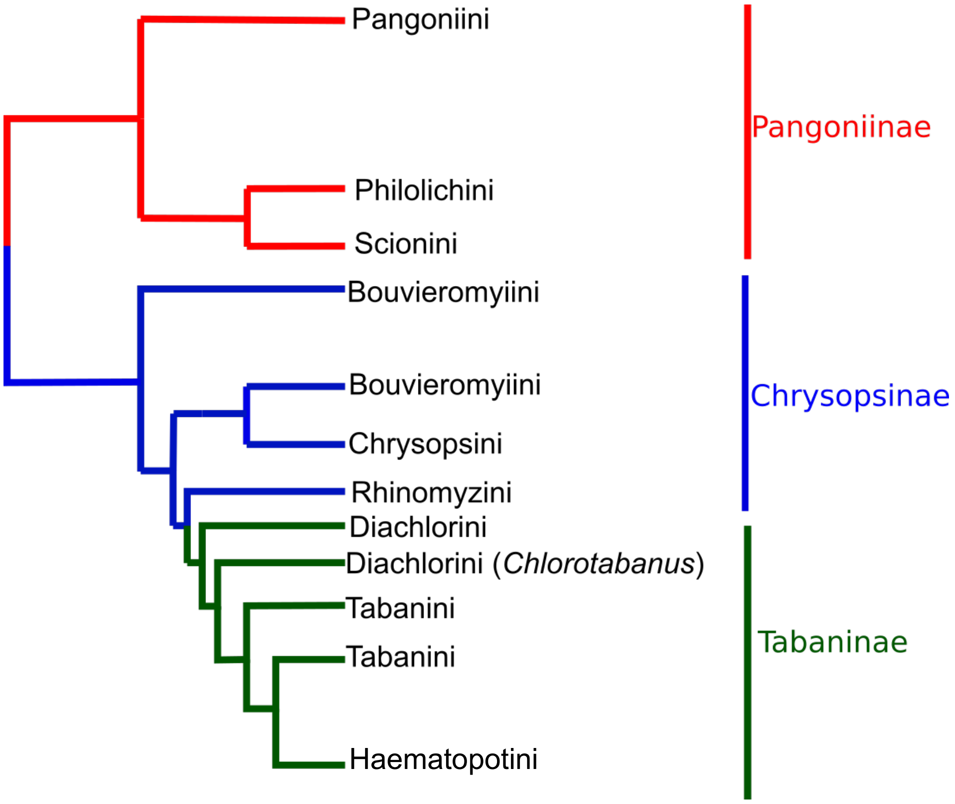

Figura 3. Cladograma esquemático representando as relações entre as subfamílias e tribos de Tabanidae sensu Morita et al. (2016).

Apesar da origem relativamente antiga, o registro fóssil e dados moleculares (Morita *et al.,* 2016) apontam para um hiato na diversificação de Tabanidae, de forma que a maior parte das subfamílias e tribos de tabanídeos hoje reconhecidas têm seu aparecimento no início do Terciário.

O gênero *Tabanus* Linnaeus

Dentre as 4500 espécies descritas para Tabanidae, cerca de 1300 foram descritas no gênero *Tabanus* Linnaeus (Pape e Thompson, 2013). Desde Linnaeus (1758), muitos espécies de Tabanidae, hoje pertencentes a outros gêneros (e.g. *Ancala* Enderlein*, Atylotus* Osten Sacken, *Agkistrocerus* Philip*, Hybomitra* Enderlein, *Therioplectes* Zeller, *Poeciloderas* Lutz), foram descritas como *Tabanus*. O gênero foi tratado como relictual (Oldroyd, 1954; Burger, 2009), ressaltando que provavelmente constitui grupo afilético (*cf.* Williams e Ebach, 2017). O grande número de espécies e a dificuldade do seu posicionamento filogenético, além de dúvidas sobre sua monofilia, tornam árdua a tarefa de determinar caracteres diagnósticos do grupo: características morfológicas utilizadas para a identificação do gênero variam conforme a região geográfica (*e.g.* Chvala *et al.*, 1972; Fairchild, 1984; Pechuman e Teskey, 1989; Coscarón e Papavero, 2009).

Assim como outros gêneros da tribo Tabanini, as espécies de *Tabanus* possuem a basicosta com número de cerdas tão denso quanto da veia costal e a labela majoritariamente membranosa. Além disso, costumam ser incluídos como caracteres diagnósticos para o gênero, a ausência de pilosidade nos olhos, a fronte relativamente estreita, a ausência de um tubérculo ocelar desenvolvido e a ausência de padrões de manchas nas asas. Entretanto, como já dito anteriormente, poucos desses caracteres são plenamente confiáveis e muitos deles possuem diversas exceções ou não são válidos para espécies de todas as regiões biogeográficas. A espécie tipo do gênero, *T. bovinus* foi descrita por Linnaeus e possuí corpo robusto, olhos sem pilosidade, e triângulos de pruína abdominais. Essa espécie possui distribuição Paleártica e compartilha características morfológicas com outras espécies muito similares, todas com a mesma distribuição.

Tabanus e o registro fóssil

Segundo Wiegmann *et al.* (2011) e Morita *et al*. (2016), a infraordem Tabanomorpha têm origem no início do Triássico, enquanto que a família Tabanidae teve sua origem no início do Cretáceo. O registro fóssil parece ser congruente com essa hipótese, de forma que os fósseis mais antigos de mutucas datam desse período (Zhang, 2012; Grimaldi, 2016).

Apesar de sua origem relativamente antiga, nenhum dos fósseis mais antigos de Tabanidae foram incluídos nas subfamílias ou tribos morfologicamente reconhecidas para Tabanidae, o que sugere que os fósseis do Cretáceo se tratam de linhagens extintas. Os primeiros fósseis de mutucas que possuem características de grupos viventes são mais recentes, do período Terciário, no Eoceno (entre 33.9 e 55. milhões de anos) (Strelow *et al*., 2013), sendo todos os fósseis desse período representantes da subfamília Chrysopsinae.

Ainda que o registro paleontológico de *Tabanus* seja escasso, alguns fósseis podem ser atribuídos ao gênero, ou ao menos à tribo Tabanini. Os fósseis mais antigos de *Tabanus* descritos na literatura são *T. vectensis* (Cockerel) (Depósito da Ilha de Wight, Reino Unido, Oligoceno), *T. statzi* Moucha (nom. nov. para *T. fulvencens* Statz) (Depósito de Rothenburg, Alemanha, Oligoceno) e *T. tremembeensis* Martins-Neto (Depósito de Tremembé, São Paulo, Brasil, Oligoceno). *T. vectensis* foi originalmente descrito por Cockerel (1920) no gênero *Chrysops;* após examinar o holótipo Stuckenberg e Oldroyd (Stuckenberg, 1975) visualizaram cerdas na basicosta, transferindo a espécie para *Tabanus.* Existem ainda fósseis de um depósito do Colorado, nos Estados Unidos (*T. parahippi* Cockerel, *T. hiparioensis* Cockerel, e *T. merychippi* Cockerel), que datam do Mioceno (23 a 5,3 milhões de anos) (Strelow *et al*., 2013).

Durrenfeldt (1968) e Grabenhorst (1985) descreveram dois fósseis do depósito de Willersshausen, na Alemanha, que datam do Plioceno superior (5,3 a 2,6 milhões de anos). Esses fósseis relativamente recentes foram identificados por ambos os autores como *T. sudeticus* Zeller. É uma espécie vivente, pertencente ao grupo de espécies relacionadas à *T. bovinus* Linnaeus, e que possui distribuição Paleártica. Os autores se basearam no formato geral do corpo e no padrão de coloração do abdômen que está preservado nos espécimes (Durrenfeldt, 1968; Grabenhorst, 1986). As características utilizadas na identificação, no entanto, são comuns a outras espécies do grupo *bovinus* (*e.g. T. bovinus* Linnaeus, *T. spodopterus* Meigen e *T. sarbazensis* Jezek). Apesar disso, o fóssil pode ao menos ser identificado como pertencente ao grupo *T. bovinus* .

Análises filogenéticas de *Tabanus*

Até o momento, poucas foram as tentativas de reconstruir hipóteses filogenéticas para o gênero *Tabanus*. El-Hassan *et al*. (2010) utilizaram métodos de distância para analisar uma matriz de 84 caracteres e 20 espécies de *Tabanus* do Egito. Nesta análise algumas espécies do gênero apresentam maior similaridade com espécies do gênero *Atylotus* do que com outros representantes de *Tabanus.*

Mais recentemente diversas análises moleculares tiveram *Tabanus* como grupo alvo (*e.g.* Cywinska *et al.* 2010; Changbunjong *et al.* 2018; Mugasa *et al*., 2018). Entretanto, nenhum desses trabalho teve como objetivo o entendimento da evolução do gênero de forma mais ampla, e sim a identificação de espécies utilizando marcadores moleculares (em especial, barcode COI) a partir de uma amostragem restrita a uma região biogeográfica (Mugasa *et al.* 2018), ou a uma única região geopolítica (Cywinska *et al*., 2010; Changbunjong *et al.,* 2018). Essas análises foram as primeiras feitas com uma amostragem considerável de espécies para o gênero; todas corroboram uma origem múltipla das espécies de *Tabanus*, com gêneros como *Atylotus* Enderlein e *Hybomitra* Enderlein inseridos como grupos irmãos de espécies tradicionalmente incluídas em *Tabanus*.

Os resultados obtidos por Morita *et al*. (2016) não são diferentes nesse sentido. Apesar da amostragem limitada de *Tabanus* incluída na análise, o gênero novamente aparece como um grupo afilético (cf. Williams & Ebach, 2017) com a inclusão de *Hybomitra, Ancala* Enderlein e *Haematopota* Meigen dentro de *Tabanus.*

Os dados obtidos na literatura reforçam o status de *Tabanus* como um agrupamento artificial e apontam para a necessidade de uma análise filogenética do gênero seguida por uma classificação atualizada que separe esse grupo em unidades taxonômicas que reflitam sua história evolutiva. Nesse contexto, a presente tese constitui importante passo para melhorar o nosso entendimento da evolução de um grupo extremamente diverso em número de espécies, correspondendo a um terço das espécies conhecidas de Tabanidae. Para tanto, foram levantados caracteres morfológicos internos e externos, e obtidas grandes quantidades de loci gênico para análise filogenômica utilizando Anchored Hybrid Enrichment.

A tese encontra-se dividida em dois capítulos. No Capítulo 1, são tratadas as relações filogenéticas dos *Tabanus* Neotropicais, propostas séries de transformação para alguns caracteres morfológicos do grupo e estimado o tempo de divergência para a origem do grupo *Tabanus* e de algumas de suas linhagens Neotropicais. É proposta também a criação de três novos gêneros monofiléticos e endêmicos à região Neotropical. No Capítulo 2, é revisada a taxonomia do grupo de espécies associadas a *T. trivittatus* Fabricius com a descrição de cinco espécies novas. Esse grupo foi suportado como monofilético nas análises realizadas e é apresentado como um novo gênero endêmico à região Neotropical.

Objetivos

A presente tese teve como objetivo geral aprofundar nosso conhecimento sobre a história evolutiva dos *Tabanus* Neotropicais, utilizando caracteres morfológicos internos e externos, dados filogenômicos e dados de distribuição das espécies. Dentro desse contexto mais amplo, também objetivou-se:

1. Recuperar as relações filogenéticas dentro e entre os grupos de espécies Neotropicais propostos para *Tabanus,* utilizando dados genômicos, além de caracteres morfológicos externos e internos;
2. Discutir caracteres morfológicos para *Tabanus* e entender a evolução desses caracteres no contexto das hipóteses filogenéticas obtidas;
3. Estudar a taxonomia do grupo de espécies associadas a *T. trivittatus* Fabricius;
4. Obter uma estimativa dos tempos de divergência para *Tabanus*
5. Modificar as chaves de Fairchild (1976) para o grupo de espécies relacionadas à *Tabanus trivittatus*
6. Realizar um breve estudo acerca da evolução da terminália feminina em *Tabanus*

Capítulo 1

Carmo, D.D.D; Wiegmann, B.M; Santos, C.M.D & Henriques, A.L. Phylogenomic and morphological analysis of *Tabanus* Linnaeus (Diptera: Tabanidae) species groups: the beginning of the end for *Tabanus* in the Neotropics. Manuscrito em preparação para a revista *Systematic Entomology*

Abstract

Tabanidae (horse flies) are the largest family of 8 families contained in the dipteran infraorder Tabanomorpha, and nearly one third of all described horse fly species are included in the genus *Tabanus* (ca 1350 valid species). This widespread genus is found in all biogeographic regions and consists of large hematophagous flies. The non-monophyly of the genus has already been suggested by several authors, however, few works used modern phylogenetic methods have been used to address phylogenetic relationships within the genus, and none of them sampling the Neotropical fauna. In this work we used anchored hybrid enrichment to acquire 193 loci for phylogenomic analysis of 35 *Tabanus* species. Additionally, a morphological matrix for 88 terminal taxa was built from internal and external characters. Both molecular and morphological datasets demonstrate the aphyly of *Tabanus* and reveal a Neotropical origin for the tribe Tabanini. Based on these results, we propose three new genera endemic to the Neotropic - *Chephalogongylus* **gen.n**, *Rhinoderus* **gen.n.,** *Tapirotabanus* **gen. n., -** and revalidate on genus - *Chelotabanus* **stat. rev.** Using a subsample of the phylogenomic dataset, also estimate the divergence times among sampled *Tabanus* group taxa and find their origin during the Paleocene/Eocene boundary with, diversification of several new Neotropical genera with Amazonian distributions during the Miocene.

Keywords: Amazon basin, Anchored Hybrid Enrichment, Divergence times, Miocene, Phylogeny, Tabanidae.

Introduction

The horse flies (Diptera: Brachycera: Tabanidae) known for their large size (4 – 25 mm), enormous colorful eyes and females with hematophagous habits, and are distributed in all biogeographic regions except the Antarctic. Currently, there are nearly 4500 valid species of Tabanidae (Pape & Thompson, 2013), with nearly one third belonging to the genus, *Tabanus* Linnaeus. These share with other genera in the tribe Tabanini, a basicosta with setae as dense as the adjoining costal vein, relatively narrow frons, bare eyes, the absence of an ocellar tubercle, a mostly membranous labella, and wings usually without spots on crossveins. However, diagnostic characters for *Tabanus* are often variable (*e.g*. Mackerras, 1971; Chvala *et al.* 1972; Pechuman & Teskey, 1989; Coscarón & Papavero, 2009), and a lack of clearly definable synapomorphies is often given as evidence against monophyly for this large group (Oldroyd, 1954; Fairchild, 1984; Burger, 2009; Morita *et al*., 2016). The aphyly (cf. Williams & Ebach, 2017) of *Tabanus* was strongly corroborated in a recent analysis - the first to evaluate the relationships of Tabanidae -, using one mitochondrial and three nuclear genes (Morita *et al*., 2016). Despite using a limited sample of the genus, the analysis corroborated the non-monophyly of *Tabanus*, with *Hybomitra* Enderlein, *Ancala* Enderlein and *Haematopota* Meigen being placed inside the genus.

In an attempt to divide *Tabanus* in more manageable taxonomic groups, the genus has been divided into several species groups (see Fairchild, 1942, 1964, 1976, 1983, 1984 - for the Neotropical region; Chvála *et al*., 1972; Hayakawa, 1980 for the Palearctic region; Oldroyd, 1954 for the Afrotropical region; Mackerras, 1971 for the Australian region; Philip, 1960, 1961, 1962; Coher, 1963; Burton, 1978; Burger & Thompson, 1981 - for the Oriental region). In fact, none of these classifications are based on formal phylogenetic analyses.

In the Neotropical region there are currently 190 valid species (Coscarón & Papavero, 2009), 56 of which assigned to species groups (Table 1). Some of those species have a restricted habitat, being arboreal or confined to specific biomes (Fairchild, 1981, 1983, 1986) while others, such as *T. occidentalis* Linnaeus, are widespread throughout the region, found from Mexico to northern Argentina.

Studies evaluating phylogenetic relationships within *Tabanus* based on a large taxon sampling are still wanting. There are few comparative morphological works available - even finding information about the genitalia of species is difficult, since genitalic characters are of limited use in species identification (Mackerras, 1971). Recently, some authors used molecular markers (usually DNA ‘barcodes’ mtCOI) to identify species of *Tabanus* (Cywinska *et al*., 2010; Mugasa *et al*., 2018; Changbunjong *et al.* 2018), and find evidence supporting multiple origins for the genus.

Fossil of *Tabanus* are relatively scarce. Given their large size, amber fossilization is unlikely; most fossils are stone compressions, where diagnostic characters are usually absent or difficult to identify. Nevertheless, the oldest fossil *Tabanus* dates from Oligocene deposits of Europe and South America (Stuckenberg, 1975; Martins-Neto, 2003; Strelow *et* al., 2013). There are also fossils from the Miocene in North America (Strelow *et al*., 2013). Durrenfeldt (1968) and Grabenhorst (1985) identified two fossil specimens from the upper Pliocene as the living species *T. sudeticus* Zeller, based on general color characters preserved in the fossil specimens. Although consistent with characters found in the *T. sudeticus*, these features also are common in other species of the *bovinus* group, and therefore the explicit identification of these fossils as *T. sudeticus* is debatable.

The present study aims to elucidate evolutionary relationships among Neotropical *Tabanus* by focusing on exemplars of species groups distributed in the region. We build a matrix using morphological characters that are traditionally used to identify groups within *Tabanus*, and also add new characters. We also investigate a phylogenomic matrix using nucleotides sequence data from genomic loci obtained by Anchored Hybrid Enrichment (AHE).

Material and Methods

Examined material

Dry specimens for morphological examination were obtained from the following collections, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto - USP (FFCLRP-USP), Florida State Collection of Arthropods (FSCA), Instituto Nacional de Pesquisas da Amazônia (INPA), Museu de Zoologia da Universidade de São Paulo (MZUSP), Museu Paraense Emílio Goeldi (MPEG) and National Museum of Natural History (NMNH) .

Ethanol preserved specimens for molecular extraction were obtained from INPA (project *Diversidade de insetos na Amazônia (Rede Bia)*), Brian Wiegmann’s laboratory at North

Carolina State University (NCSU), and the collection of the Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto - USP (FFCLRP-USP).

Morphological terminology and examination

For terminology we follow Cumming & Wood (2017). For some structures contained in sternite 8 of the horse fly female genitalia we follow the proposal of Olsufiev (1962). Frontal and divergence indexes were measured according to Fairchild (1985).

For the analysis of female terminalia, specimens were cut between the fourth and fifth segment of abdomen and transferred to a solution of KOH 10% at 40°C (40-60 minutes). The terminalia was then washed ten times with distilled water and transferred to lactic acid at the same temperature for approximately 12 hours. Esternite 8, cercus + tergites 9 and 10, and the sternite 9 were separated from the remaining abdominal segments (the terminalia was stored in glycerin). For the visualization of integument, specimens were moistened with 95 % ethanol according to Lutz (1907).

Digital photos were made using a Leica MC 205 stereozoom microscope with a camera attached and auto montage system.

Taxon sampling and identification

Depicting the phylogenetic relationships of a taxon as speciose as *Tabanus* is not a trivial task. Here, our taxon sampling focuses on the currently recognized species groups described for *Tabanus*, especially those distributed in the Neotropical region. For the morphological dataset we included representatives from all species groups proposed for the Neotropical region; for the phylogenomic dataset only the *indecisus* group was not sampled. For both analysis representatives of all other biogeographic regions were included. Specimens were identified by comparison with types and with specimens identified by specialists at collections (FSCA, INPA, USNM) when available, and also through taxonomic keys and original descriptions (Afrotropical region – Oldroyd, 1954; Australian region – Mackerras, 1971; Neotropical region - Fairchild, 1942, 1964, 1973, 1983, 1984; Palearctic region – Chvála *et al.*, 1972; Oriental region – Philip, 1960, 1961). We marked as *cf.* the species not conclusively identified. Two species from the Oriental region could not be determined to the species level, so we kept the identification at the species group level.

Morphological sampling

We sampled 88 terminal taxa for the morphological matrix (Appendix I and II), including 77 representatives of *Tabanus*. As outgroups, two species of Diachlorini and 11 species of seven other genera of Tabanini (*Ancala, Agkistrocerus, Atylotus, Glaucopis, Hybomitra, Phorcotabanus* and *Poeciloderas*) were included. A list of the number of species per group included in the morphological matrix is found in Table 1.

Table 1. *Tabanus* species groups included in both analysis

Region	Species groups	Species sampled in the morphologic analysis	Species sampled in the phylogenomic analysis
Afrotropical	*marmorosus* group	*marmorosus* Surcouf, 1909	none
	ruficrus group	*ruficrus* Palisot de Beauvois, 1807	none
	Plain group	none	none
	sufis group	*sufis* Jaennicke, 1867	*taeniatus* Macquart, 1834
Australian	*innotabilis* group	*parvicallosus* Ricardo, 1914	*parvicallosus* Ricardo, 1914
Nearctic	*occidentalis* group	*lineola* Fabricius, 1794	*subsimilis* Bellardi, 1859
	Not included in any group	*atratus* Fabricius, 1775	none
Neotropical	*bigoti* group	*bigoti* Bellardi, 1859	*hirtitibia* Walker, 1850
		hirtitibia Walker, 1850	
		thiemeanus (Enderlein, 1925)	*thiemeanus* (Enderlein, 1925)
	fortis group	*aaptus* Fairchild, 1984	*fortis* Fairchild, 1961
		fortis Fairchild, 1961	
	indecisus group	*indecisus* (Bigot, 1862)	Not included
	nebulosus group	*glaucus* Meigen, 1820	*glaucus* Meigen, 1820
		importunus Wiedemann, 1828	*importunus* Wiedemann, 1828

		nebulosus De Geer, 1776	*nebulosus* De Geer, 1776
		ornativentris Kroeber, 1929	
	occidentalis group	*kwatta* Fairchild, 1983	Not included
		occidentalis Linnaeus, 1758	
		triangulum Wiedemann, 1828	
		vittiger Thomson, 1869	
		wilkersoni Fairchild, 1983	
		wokei Fairchild, 1983	
	oculus group	*albocirculus* Hine, 1907	*albocirculus* Hine, 1907
		antarcticus Linnaeus, 1758	*antarcticus* Linnaeus, 1758
		defilippii Bellardi, 1859	*defilippii* Bellardi, 1859
		oculus Walker, 1848	*oulus* Walker, 1848
		pseudoculus Fairchild, 1942	
		polyphemus Fairchild, 1958	
		unipunctatus (Bigot, 1892)	
	pellucidus group	*amazonensis* (Barreto, 1949)	*amazonensis* (Barreto, 1949)
		angustifrons Macquart, 1848	*angustifrons* Macquart, 1848
			crassicornis Wiedemann, 1828
			fuscus Wiedemann, 1819
		nematocallus Fairchild, 1984	*nematocallus* Fairchild, 1984
		pellucidus Fabricius,	*pellucidus* Fabricius,

		1805	1805
	trivittatus group	*argentivittatus* Fairchild, 1976	*callosus* Macquart, 1848
		callosus Macquart, 1848	*sextriangulus* Gorayeb & Rafael, 1984
		enanus Fairchild, 1942	*trivittatus* Fabricius, 1805
		isis Fairchild, 1976	
		palpalis Brèthes, 1910	
		picicallosus Fairchild, 1951	
		platycerus Fairchild, 1971	
		restrepoensis Fairchild 1942	
		schadei Fairchild, 1976	
		sextriangulus Gorayeb & Rafael, 1984	
		tristichus Fairchild, 1976	
		trivittatus Fabricius, 1805	
		unistriatus Hine, 1906	
	xenorhynchus group	*piceiventris* Rondani, 1848	*piceiventris* Rondani, 1848
		sannio Fairchild, 1956	*xenorhynchus* Fairchild, 1947
		xenorhynchus Fairchild, 1947	
	not included in any group	*acer* Brèthes, 1910	*amapaensis* Fairchild, 1961
		amapaensis Fairchild, 1961	*vestitus* Wiedemann, 1819
		claripennis (Bigot, 1892)	
		duckei Fairchild, 1984	
		fuscofasciatus Macquart, 1838	
		humboldti Fairchild,	

		1984	
		vestitus Wiedemann, 1819	
Oriental	*striatus* group	*partitus* Walker, 1857	No species included
		striatus Fabricius, 1787	
		triceps Thunberg, 1827	
	Not included in any group	*ceylonicus* Schiner, 1868	No species included
		exoticus Ricardo, 1913	
		bakeri Philip, 1959	
Palearctic	*bovinus* group	*bovinus* Linnaeus, 1758	*bovinus* Linnaeus, 1758
		sarbazensis Jezek, 1990	*sudeticus* Zeeler, 1842
		spodopterus Meigen, 1820	
		sudeticus Zeeler, 1842	
	bromius group	*bromius* Linnaeus, 1758	Not included
		maculicornis Zetterstedt, 1842	
		tergestinus Egger, 1859	
	Chrysurus group	No species included	chrysurus Loew, 1858
	cordiger group	*cordiger* Meigen, 1820	No species included
	glaucopis group	*glaucopis* Meigen, 1820	No species included
	nemoralis group	*nemoralis* Meigen, 1820	No species included
	quatuornatatus group	*quatuornotatus* Meigen, 1820	No species included
	iyoensis group	*humilis* Coquillet, 1898	No species included
		iyoensis Shiraki, 1918	
		triceps Thunberg, 1827	

Genomic sampling

For the phylogenomic data collection using AHE, we used 44 terminal taxa. Of these, 35 are representatives of *Tabanus*, included as ingroup. As outgroups we used three Diachlorini species and four species from other Tabanini genera (*Agkistrocerus*, *Ancala*, *Hybomitra* and *Poeciloderas*). A list of the number of species per group included in the phylogenomic analysis may be found in Table 1.

Character selection and coding

For the morphological analysis, we scored characters used in horse fly taxonomic literature (Fairchild, 1942; Oldroyd, 1954; Chvála *et al.*, 1972; Fairchild, 1976, 1983, 1984), and included several new characters, especially from female terminalia. In general, we avoided coding characters from integument color and wing spots due to the high level of variation (resulting in low phylogenetic signal). However, some characters of clearly contrasting integumental patterns (for example, in tibia) and the presence of integumental vestiture or spots were included due to its importance for the taxonomy of *Tabanus*. Only independent characters were included in the matrix; when biological dependence was verified, the characters were merged or excluded.

Most characters were coded as non-additive (Fitch optimization). There are only three additive characters (15, 32 and 36) in the matrix, coded in such a way when the exam of structures supported such hypothesis. Additivity was considered justifiable when there were at least some level of dependence between two different states of a character or when there were clear similarity or hierarchy between character states (Wilkinson, 1992; Slowinski, 1993) or when suggested by previous authors.

Some traits found in specimens we studied have shown at least some degree of polymorphism. In those cases, the two or more states observed were coded for that species. When the level of polymorphism was high, or present in a great number of species, we excluded such characters.

The use of continuous traits has long been debated in phylogenetic analysis (Felsenstein, 1988; Thiele, 1993; Rae, 1995, 1998; Garcia-Cruz & Sosa, 2006). Discretization has been a popular way of treating such traits in Tabanidae systematics (*e.g*. Trojan *et al*., 1997; Fang *et al*., 1999; El-Hassan, 2013). Goloboff *et al*., (2006) proposed a method to deal with continuous characters without discretization. Implemented in TNT (Goloboff *et al*., 2008), the method allows ranges to be included directly in the morphological matrix, which are then analysed as additive characters. Here, the frontal and divergence indexes, respectively, the ratio of the frons height by the width of frons base and the ratio between the vertex and frons base, are important features for the taxonomy of *Tabanus*. After measuring specimens, we included those characters in the matrix as continuous. For the parsimony analysis including continuous characters, we used the software TNT (Goloboff *et al*., 2008). As the frontal index is dependent on the shape of frontal callus (character 1), both characters were included alternatively in the matrix.

DNA extractions

Genomic DNA was obtained for the 45 terminal taxa using the QIAGEN DNeasy kit (QIAGEN, Valencia, United States) following the manufacturers protocol. Some modifications to the standard extraction protocol included: tissues were left incubating overnight (at 56°C) and the volume of buffer AE was set at 54µL instead of 200. In bigger horse flies with robust bodies, tissue were obtained from the thorax, in smaller specimens we used the whole body. If a specimen was rare or difficult to acquire, tissue was obtained from the right hind leg only. Vouchers are deposited in the research collections of (INPA, Manaus, Amazonas) and (NCSU, Raleigh, NC).

Anchored Hybrid Enrichment data collection

For data capture and sequencing we used Anchored Hybrid Enrichment (AHE) described by Lemmon *et al*., (2012), and following the protocol of Young *et al*., (2012) in the Wiegmann laboratory in North Carolina State University (NCSU). These methods use a set of Diptera-specific probes designed to target highly conserved regions of orthologous genes, flanked by more variable regions. The broad spectrum of sequence variability and conservation allows for probe utility to address both shallow and deep phylogenetic questions (Lemmon *et al*., 2012).

To check the quantity and quality of the initial DNA extraction we took a Qubit reading with the DNA sample concentrations. Only samples with more than 10 ng/µL were used for target capturing and sequencing. When the sample concentration was low, we performed whole genome amplification to obtain adequate starting DNA concentration using the Repli-G enzyme and kit (Qiagen, Valencia, USA). Repli-G amplification was carried out following manufacturer instructions. Starting high molecular weight DNAs were then sonicated, to break those fragments into smaller fragments used for exon capture using the AHE probes. Captured loci for each taxon were each given a unique taxon index, were pooled, and included in an Illumina library for single-read NextGen sequencing on a Illumina 2500 in the NCSU Genomic Sciences Laboratory.

Alignment and orthology search

We used the 1kite phylogenomic analysis pipeline (Misof *et al*., 2014; 1kite.org) installed on the NCSU Bioinformatics Research Center computing cluster at North Carolina State University. We filtered our captured loci to include only Diptera single-copy orthologs using the program Orthograph (Petersen *et al*., 2017). This program uses a best reciprocal hit search strategy employing profile hidden Markov models to match nucleotide sequences with from a reference set of fly ortholog alignments constructed from sequences found in the OrthoDB database of orthologous gene models (Petersen *et al*., 2017; Gillung *et al*., 2018).

Each taxon specific set of captured loci were then subjected to a decontamination step to remove non-fly sequences identified among the top 25 hits when subject to NCBI BLAST search against the nucleotide sequence database. This important step removes contaminating microbial, fungal and human sequences that may have been co-amplified in the Repli-G process. Matches with non insect sequences were excluded, while insect sequences matches were kept. We also paid special attention to matches containing only nematodes and some hymenopterans since those are recognized parasites of horse flies.

Sequences were aligned using the multisequence alignment strategy in the program Mafft (Katoh & Standley, 2013). Alignment of nucleotide sequences provides a hypothesis of positional homology for each site in a nucleotide sequence. Therefore, this is a crucial step in phylogenetic analysis and suboptimal or misaligned sequences can lead to incorrect phylogenetic hypotheses. Alignment quality was assessed for each locus using the sequence-based outlier assessment procedure described in Misof *et al*., (2014). Outliers were realigned if possible, and excluded if not. Another common problem with automated construction of multiple sequence alignments from large phylogenomic dataset is possibility of random alignments caused by non-homologous sharing of similar sequence motifs. When this ocurs, regions of the alignment can be put together by random similarity instead of by sequence orthology which is derived from common descent (Misof & Misof, 2009). We identified random similarity in our dataset using the quantitative alignment assessment tool, Aliscore (Misof & Misof, 2009).

Finally we merge all retained and refined alignments in a concatenated supermatrix, using FASConCAT-G (Kück & Longo, 2014). Our supermatrix is comprised by 193 loci with 102138 sites.

Substitution models and partitioning

For substitution model selection and partitioning scheme we used Partitionfinder2 (Lanfear *et al.*, 2016) installed on the Cipres Phylogenetic Web Portal (Cipres.org). We defined datablocks by gene and used rcluster (Lanfear *et al.*, 2014) as the search algorithm. Given the size of our dataset, rcluster max had to be reduced from the default 1000 to 100. We set rcluster percentage at 10, and minsubset at 50. Partitionfinder2 retrieved 45 different partitions with three different models, GTR, GTR + I and GTR + I + G.

Phylogenetic analysis

Since the advent of molecular phylogenetic analysis and the use of statistical approaches for finding phylogenetic trees, there is a long debate concerning the best optimality criteria for phylogenetic analysis. Parsimony has already been shown to be inconsistent in some cases (Felsenstein, 1978; Huelsenbeck, 1997), but debate among phylogeneticists concerning selection of the ‘best’ optimality criteria for tree estimation continues to raise important questions about the validity and necessity of key process assumptions. This is specially true for morphological datasets where character variation is more difficult to parameterize and model (Steel & Penny, 2000; Wright & Hillis, 2014; O’Reilly *et al.*, 2017; Congreve & Lamsdell, 2016; Brown *et al.*, 2017; Puttick *et al.*, 2017a; Puttick *et al.*, 2017b; Goloboff *et al.*, 2018; O’Reilly *et al.*, 2018; Puttick *et al.*, 2018). We analysed our datasets with two optimality criteria each. The resulting trees were later edited and visualized using FigTree 1.4.3.

Phylogenomic analysis

For this analysis we used two different criteria of optimality, Maximum likelihood and Bayesian inference. Bayesian analyses were run in MrBayes 2.2.6 (Ronquist *et al*., 2012) available on the CIPRES web portal. The analyses were carried out with two simultaneous runs, each with eight chains. Each run contained 50 million generations of the mcmc chain, with trees sampled every 10000 generations and a burnin cutoff set at 25 percent. In all cases, chains reached convergence, and standard deviation of the sampled splits was observed to be 0.0012

Maximum likelihood analyses were run in RAxML-HPC2 available at the CIPRES web portal. For each ML run, a rapid bootstrap analysis (Stamatakis *et al*., 2008) was used with 1000 replicates and the GTRGAMMAI model of nucleotide substitution.

Morphological analysis

After numerical scoring, we constructed our character matrix using Winclada (Nixon, 2002). We analyzed the matrix using parsimony under both equal and implied character weighting schemes through TNT (Goloboff *et al*., 2008), and Bayesian inference using the Markov Model proposed by Lewis (2001) and implemented in MRbayes (Ronquist *et al*., 2012)). To deal with the several possible concavity values from implied weighting we used a sensitivity analysis as proposed by Mirande (2009). The parameters of the script described in Mirande (2009) were kept at default values, and therefore, were selected k values that assign to an average character fits of 50, 54, 58, 62, 66, 70, 74, 78, 82, 86 and 90% of the fit of a perfectly hierarchic character.

For all the parsimony analyses we used the following conditions: random seed was set at 0, with 5000 replications and 10 trees retained per replication using TBR as swapping algorithm. For Bayesian inference, we used the standard discrete model available in Mr.Bayes 3.2.6 (Ronquist *et al*., 2012). The analysis runned with two simultaneous chains allowed to run for 10 million generations. Trees were sampled every 1000 generations with a burnin cutoff set at 25 percent. Additive characters were assigned using the ctype command.

Divergence time estimation

Divergence times for *Tabanus* lineages were estimated using the program BEAST2 (Bouchaert *et al*., 2014), included on the CIPRES web portal. Given the large size of our phylogenomic dataset (ca.100 Kb), we created a subsample selecting only the sequences with more than 10.000 parsimony informative sites. With this reduced, but highly informative dataset, we used Partitionfinder2 with the same parameters described above, resulting in 19 partitions with the same models found for the complete dataset. This reduced dataset was also subjected to phylogenetic analysis using maximum likelihood (RaxML) and Bayesian Inference (MrBayes) using the same parameters listed above. The topologies obtained, were identical to those obtained with the full dataset.

The reduced dataset partitioned by gene was used in the Bayesian divergence times analysis. This analysis was run with 150 million generations, sampled every 15 thousand generations. The substitution models were unlinked, and the tree models were linked. We used a relaxed clock with lognormal distribution.

For divergence times estimation, Benton & Donoghue (2006) suggest the use of a hard minimum age provided by the fossil evidence, and a soft maximum given by the absence of fossils from underlying deposits. The hard minimum is absolute (i.e., the clade cannot be younger than the age of the oldest fossil), while the soft maximum is not (i.e., the clade can be older). Here, we calibrated the relaxed clock using three fossils with a lognormal distribution each, with a hard minimum (M parameter in BEAST2) and a soft maximum (offset parameter) with 95% confidence interval (S parameter).

The oldest known Tabanini-like fossil, *Tabanus vectensis* (Cockerel), was used as a calibration point at the basal-most node comprising the split between the outgroup and the ingroup. The hard minimum was 21 MYA and the soft maximum 34 MYA (M = 21; Offset = 34). Based on Diachlorini fossils from Dominican Republic, we used a calibration point placed on the earlies not among the outgroups, with a hard minimum of 7 MYA and a soft maximum of 23 MYA (M = 7; Offset = 23). The third calibration point was placed in the divergence between *T. sudeticus* and *T. bovinus* based on the fossil from the *bovinus* group from the Pliocene (M = 2.7; Offset = 2.6). For all the three calibration points, the option *mean in real space* was selected.

Results

Phylogenomic analysis

In both the maximum likelihood and Bayesian inference analysis, the monophyly of *Tabanus* is not supported. Hence, we may consider the genus an aphyletic group (cf., Williams & Ebach, 2017), with only and all of the Tabanini genera sampled to be those firmly placeable within the genus (Fig. 1). Most clades in the topology of Figure 1 are well supported, especially with Bayesian inference, with posterior probabilities in several of them being above 0.9. The *Tabanus* group is shown to have originated in the Neotropical region and may be divided into four clades here labeled Clade A, B, C and D. Clade A, formed only by Neotropical species, is the sister group of clades ((B C) D). Clade B is comprised by species which occurs in several biogeographic regions, along with clade C, while clade D is comprised solely by Neotropical species.

Clade A of Figure 1 comprises 12 Neotropical species. The species of the *trivittatus* species group (Fairchild, 1976; Carmo & Henriques, 2019) is monophyletic with strong posterior probability (PP) support of 1.0. The *oculus* groups is aphyletic, with the Central American species *T. albocirculus* Hine as sister-group of the very similar South American *T. antarcticus* Fabricius. *T. oculus* Walker is more closely related to the *trivittatus* group, but with relatively low support (PP = 0.8). *T. defilippii* Bellardi is placed with the *pellucidus* and *nebulosus* groups in clade D.

T. fortis Fairchild (*fortis* group) is the sister group of the two species of the *bigoti* group (*T. hirtitibia* Walker and *T. thiemeanus* (Enderlein)), included in the analysis. This clade is sister group of *T. vestitus* Wiedemann + *T. amapaensis* Fairchild.

The Palearctic *bovinus* group (*T. sudeticus* Zeller + *T. bovinus* Linnaeus) is monophyletic and sister-group of the East Asian distributed *T. chrysurus* Loew. Clade B is the sister group of clade C, a clade comprised by species of *Tabanus* from Afrotropical, Palearctic, Oriental and Australian regions, and also from other genera of Tabanini.

At clade D the genus *Poeciloderas* Lutz is sister group of *T. subsimilis* Bellardi the only representative of the *occidentalis* species group in our genomic dataset. The clade formed by both species is sister group to a clade comprised by representatives of the Neotropical groups *xenorhynchus*, *ocullus*, *nebulosus* and *pellucidus*. *T. unimacula* Kröeber (*xenorhynchus* group) is the sister group of two reciprocally monophyletic clades formed by the groups *pellucidus, nebulosus* and one species each of groups *xenorhynchus* and *oculus*. The species included by Fairchild (1984) in the *pellucidus* group, are shown to be monophyletic with the inclusion of *T. humboldti* Fairchild, originally assigned to no group (Fairchild, 1984). The *nebulosus* group is shown monophyletic with the inclusion of *T. piceiventris* Rondani, originally from the *xenorhynchus* group and *T. discus* (*pellucidus* group).

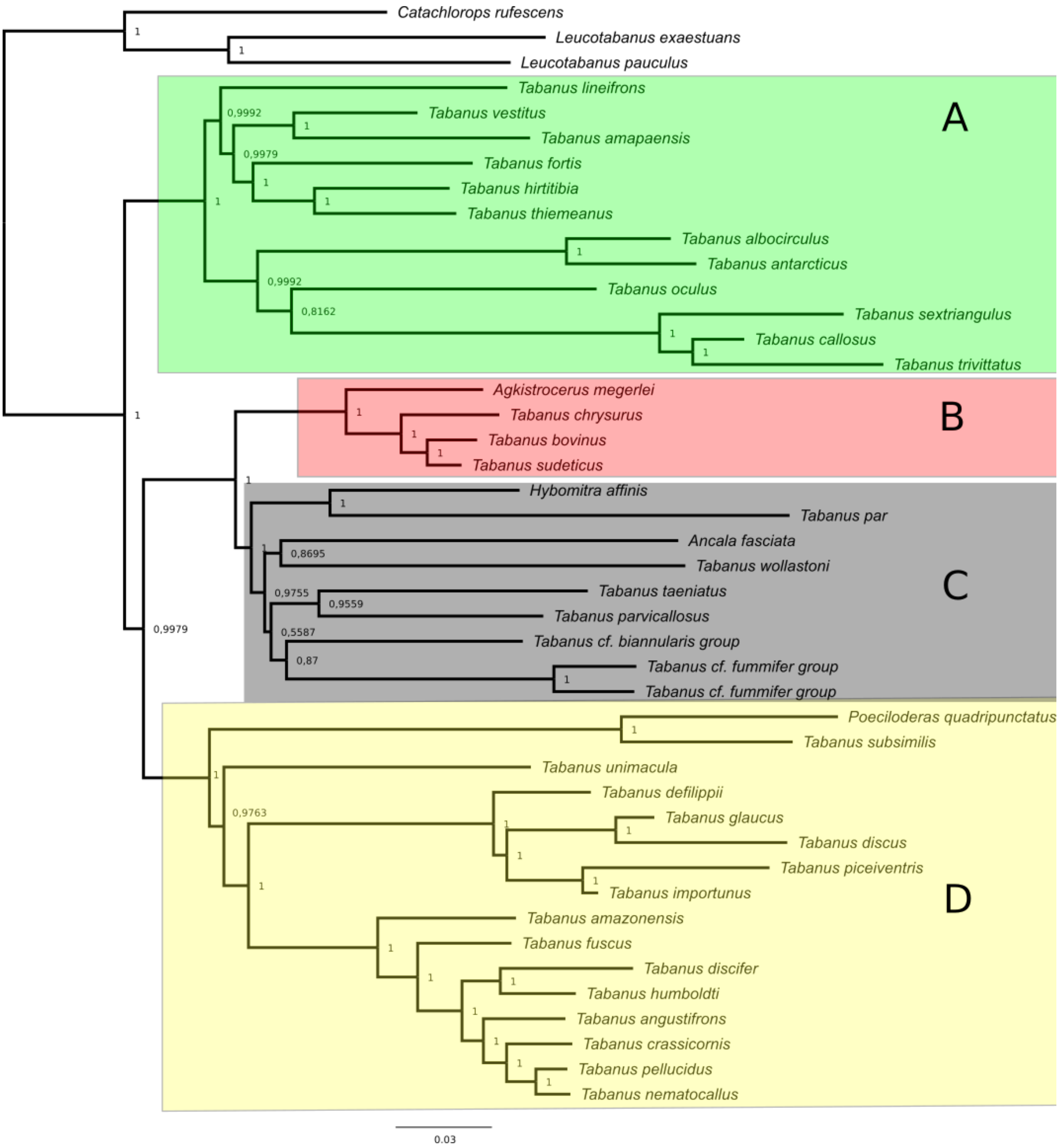

Figure 1. Phylogenomic hypothesis using Bayesian inference of the data obtained through Anchored Hybrid Enrichment for 37Tabanus species. Numbers at nodes are posterior probabilities. Letters represent clades discussed in the text.

Morphological analysis

Phylogenetic relationships of Tabanus

Morphological matrix with discrete characters only

The cladograms obtained under differing optimality criteria are presented in Figs. 2 - 4. The strict consensus of the parsimony analysis under equal weights is the most resolved (Fig. 2) but some clades were recovered under all the criteria utilized (Figs. 2 - 4).

In the strict consensus of Fig. 2 *Agkistrocerus megerlei* is supported as sister group of all other Tabanini genera included in our analysis. As in the previous analysis (Fig.1), *Tabanus* is non monophyletic, and may be considered an as aphyletic group with the inclusion of *Atylotus*, *Hybomitra*, *Poeciloderas*, *Glaucops* and *Ancala* into the genus. The origin of the *Tabanus* group is Neotropical, with the species of the *pellucidus* group along with *T. defilippii* (*oculus* group), and *T. humboldti* (Fig. 2; Clade A) being the sister group of all other *Tabanus* species. The monophyly of the *pellucidus* group is also supported under Bayesian inference (Fig. 4 clade D) but without the inclusion of *T. defilippii*.

Clade B is comprised largely of Neotropical species (Fig. 2 clade B) and *T. bigoti* is the sister group of all the other species within this clade, which has three Neotropical lineages (Clades C, D and E). Clade C is comprised by two Neotropical species not included in any group (*T. amapaensis* and *T. vestitus*) and part of the species included in the *oculus* group (*T. antarcticus*, *T. albocirculus*, *T. oculus* and *T. pseudocolus*).

In clade E, *T. piceiventris* - originally included by Fairchild (1984) in the *xenorhynchus* group - is the sister group of the species of the *nebulosus* group (*T. lutzi, T. nebulosus, T. nebulosus ornativentris, T. importunus* and *T. glaucus*) and one species of the *indecisus* group (*T. indecisus*). At clade D, the *xenorhynchus* group (*T. xenorhynchus* and *T. sannio*) is supported as monophyletic with the exclusion of *T. piceiventris*, and sister group to a group of Oriental distribution, the *striatus* group (*T. triceps, T. partitus* and *T. striatus*), also supported as monophyletic in our analysis. *T. unipunctatus* and *T. polyphemus* (*oculus* group in part) are also in this clade and are the sister group of the remaining species. The monophyly of the *xenorhynchus*, *nebulosus* and *striatus* groups is supported in all optimality criteria employed (Fig. 2 clades A, C and D; Fig. 3 clades E, H and K).

The *bigoti* group (clade G; (*T. hirtitibia* + *T. thiemeanus*)) is supported as monophyletic with the exclusion of *T. bigoti.* In clade H the monophyly of the *bovinus* group is supported, with the inclusion of *T. atratus* (not assigned to any group; Nearctic) and *Poeciloderas quadripunctatus*. In this clade is included *T. bovinus,* the type species of *Tabanus* and thus this is a *Tabanus* stricto sensu group. This group is at least partially supported in all other optimality criteria analysed (Fig. 3 clade F; Fig. 4 clade B).

Clade J is formed by species of the outgroup Tabanini included in the analysis. *Glaucops* is supported as a subgroup of *Hybomitra*, a result recovered in all optimality criteria analysed, however, the position of *Glaucops* varies, with *Hybomitra* being monophyletic in the implied weighting analysis (Fig. 3, clade H).

T. glaucopis (*glaucopis* group) is supported as the sister group of the *T. quatuornotatus* group (Fig. 2, clade K). Both groups have Palearctic distribution and similar morphological features (Chvála *et al.*, 1972).

Within clade F the Palearctic species of *Tabanus* are rendered aphyletic with relation to a clade formed by two reciprocally monophyletic Neotropical groups, the *occidentalis* and *trivittatus* group (Fig. 2, clade I). The monophyly of both groups was recovered with all optimality criteria, but the sister group relationship between them was not recovered with Bayesian inference (Fig. 3, clades I; Fig. 4 clades F and I). These two Neotropical groups correspond to Neotropical species with striped abdomens and both groups are seem to include phylogenetically cryptic species with striking morphological similarities.

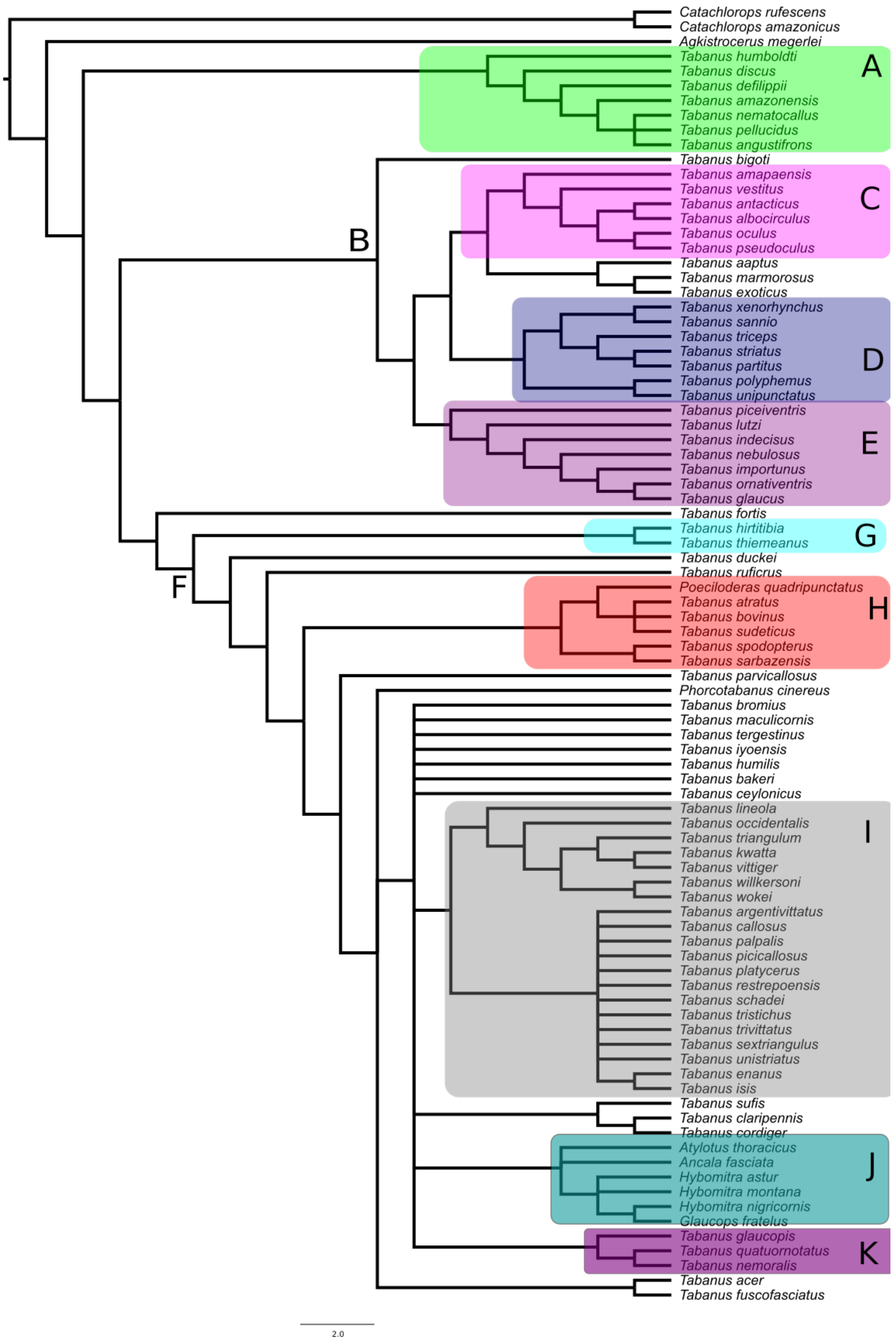

Figure 2. Strict consensus of the 40 most parsimonious trees resulting from the analysis of the morphological matrix under equal weights with discrete character only. Clades and color boxes represent clades discussed in the text. Clades A, F and J are comprised by Neotropical species, clade K is Palearctic, other clades has species from several regions.

Figure 3. Strict consensus between different k values (K = 5.1, 6.0, 7.0, 8.4, 9.9, 11.9, 14.5, 18.2, 23.3, 31.5 and 46.1) resulting from the analysis of the morphological matrix under implied weights with sensibility analysis as proposed by Mirande (2009).

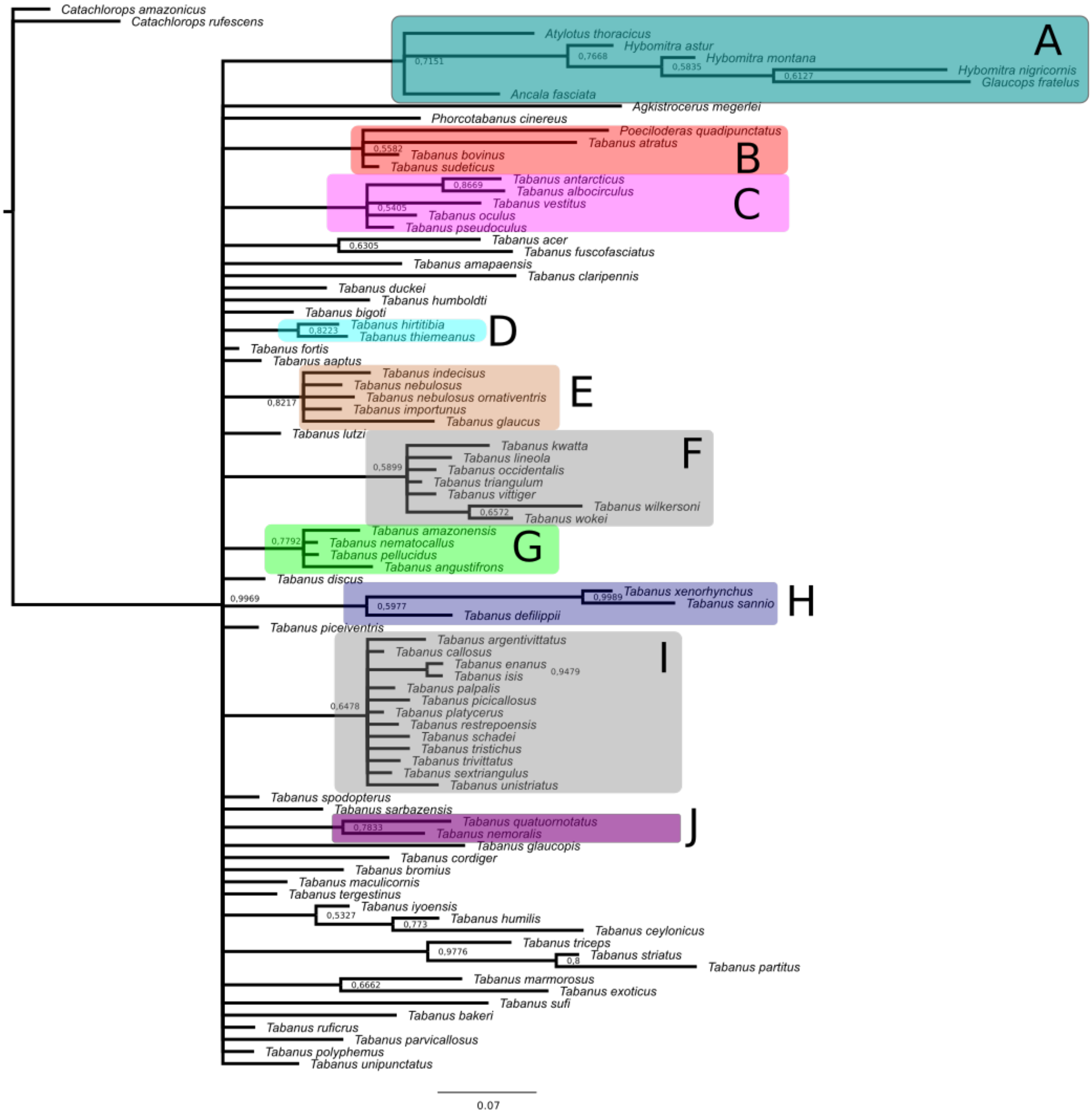

Figure 4.Phylogram obtained through Bayesian inference analysis of the morphological matrix. Numbers at clades are posterior probabilities. Letters and color boxes represent clades discussed at text. Colors were also used to match clades of figures 2 and 3.

Morphological matrix with continuous and discrete characters

Proportions between structures are often employed in horse fly taxonomy. In *Tabanus*, the frontal and divergence index are pivotal to identifying species and species groups (Fairchild, 1976, 1983, 1984). We included both characters in our matrix. The frontal index (*i.e.* the ratio between frons height and width of the base) present dependency with the shape of the subcallus in our morphological matrix, since it is not possible the existence of a large callus on a very narrow frons. Therefore, both characters had to be included alternatively in the analysis.

When the divergence index (the ratio between vertex and base of frons) is included in the analysis, he phylogeny presents more resolution, and the position of some taxa is altered (Fig. 5). Once again, a Neotropical origin of *Tabanus* is recovered; however, *T. piceiventris* is supported in the first divergence of *Tabanus* species. The *nebulosus* group is recovered as monophyletic (Fig. 5 clade E) and sister group to the other Tabanini species. Clade B is comprised only by Neotropical species, and the *oculus* group is monophyletic, with the exclusion of *T. defilippii* and inclusion of two Neotropical species not included in any group (*T. amapaensis* + *T. vestitus*) (Fig. 6, clade C). Clade C is sister group to a clade formed by the *bigoti* group, which is not monophyletic, and clade G (*T. thiemeanus* + *T. hirtitibia*) is more closely related to clade A formed by species of the *fortis* (*T. fortis*), *pellucidus* (*T. discus, T. amazonensis, T. nematocallus*, *T. pellucidus* and *T. angustifrons*), *oculus* (*T. defilippii*) and *xenorhynchus* (*xenorhynchus* and *sannio*). *T. humboldti* is a sister group of clade comprised by the *oculus* and *xenorhynchus* group (*T.humboldti* (*T. defilippii* (*T. xenorhynchus* + *T. sannio*). The *pellucidus* and *xenorhynchus* groups (except *T. piceiventris*) is once again recovered as a natural group.

The resolution of clade F is greatly improved with the addition of the continuous characters - the monophyletic *striatus* group are also included here. The *Tabanus* stricto sensu group is supported with the inclusion of *A. megerlei* (Fig. 5, clade H). The monophyly of the *glaucopis* and *quatuornotatus* groups is also supported (Fig.5, clade J) as well as the Neotropical *occidentalis* and *trivittatus* groups (Fig. 5, clade I).

When the frontal index (character 56) is also included in the analysis substituting the shape of the frontal callus (character 1), the *Tabanus* stricto sensu group is supported as sister group the *occidentalis* + *trivittatus* clade (Fig. 6, clade I). Also, *T. piceiventris* is included in the *nebulosus* group (Fig. 6, clade E).

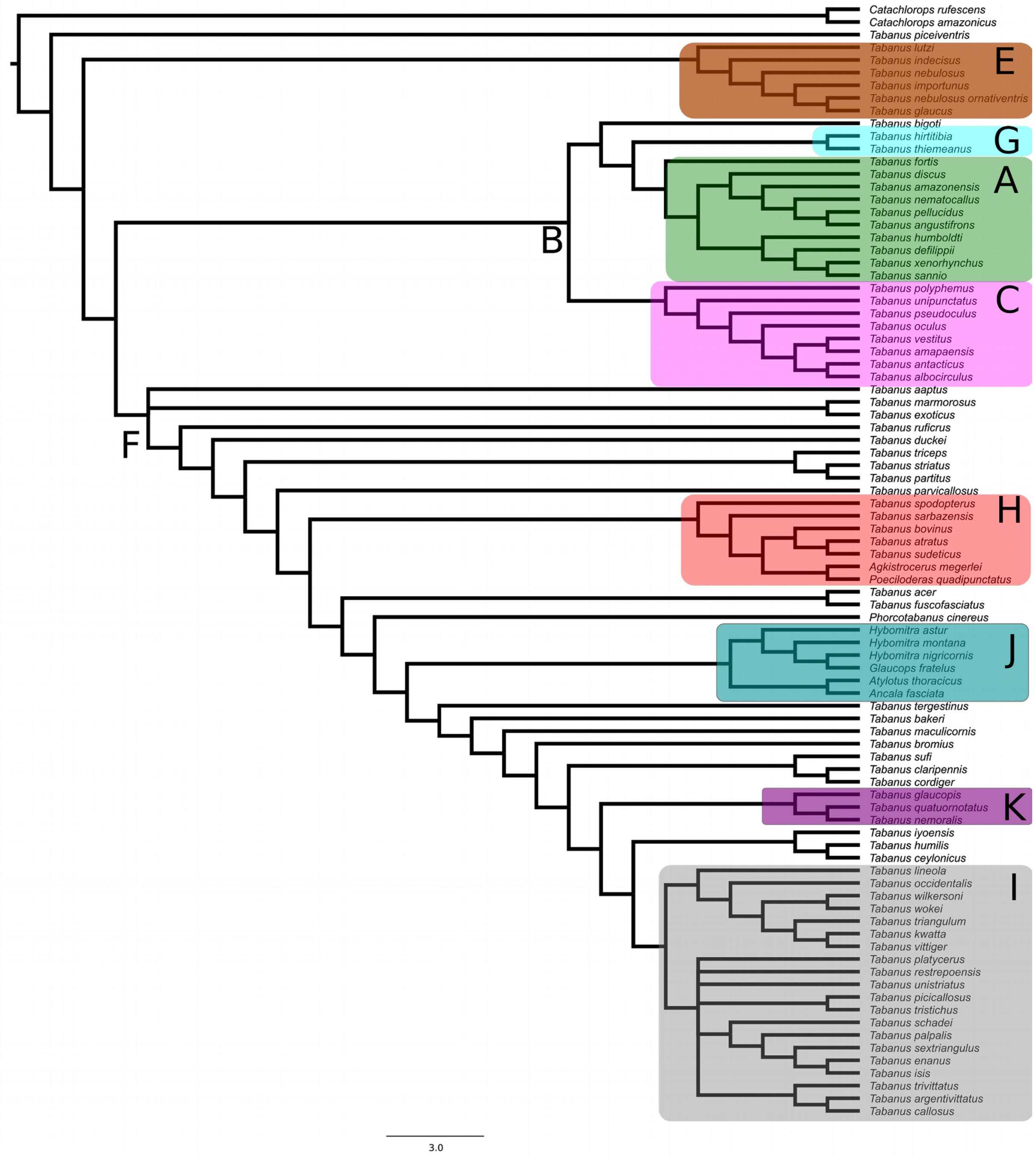

Figure 5. Strict consensus of the 10 most parsimonious tree analysed under equal weights with the divergence index coded as a continuous character. Letters and color boxes represent clades discussed at the text.

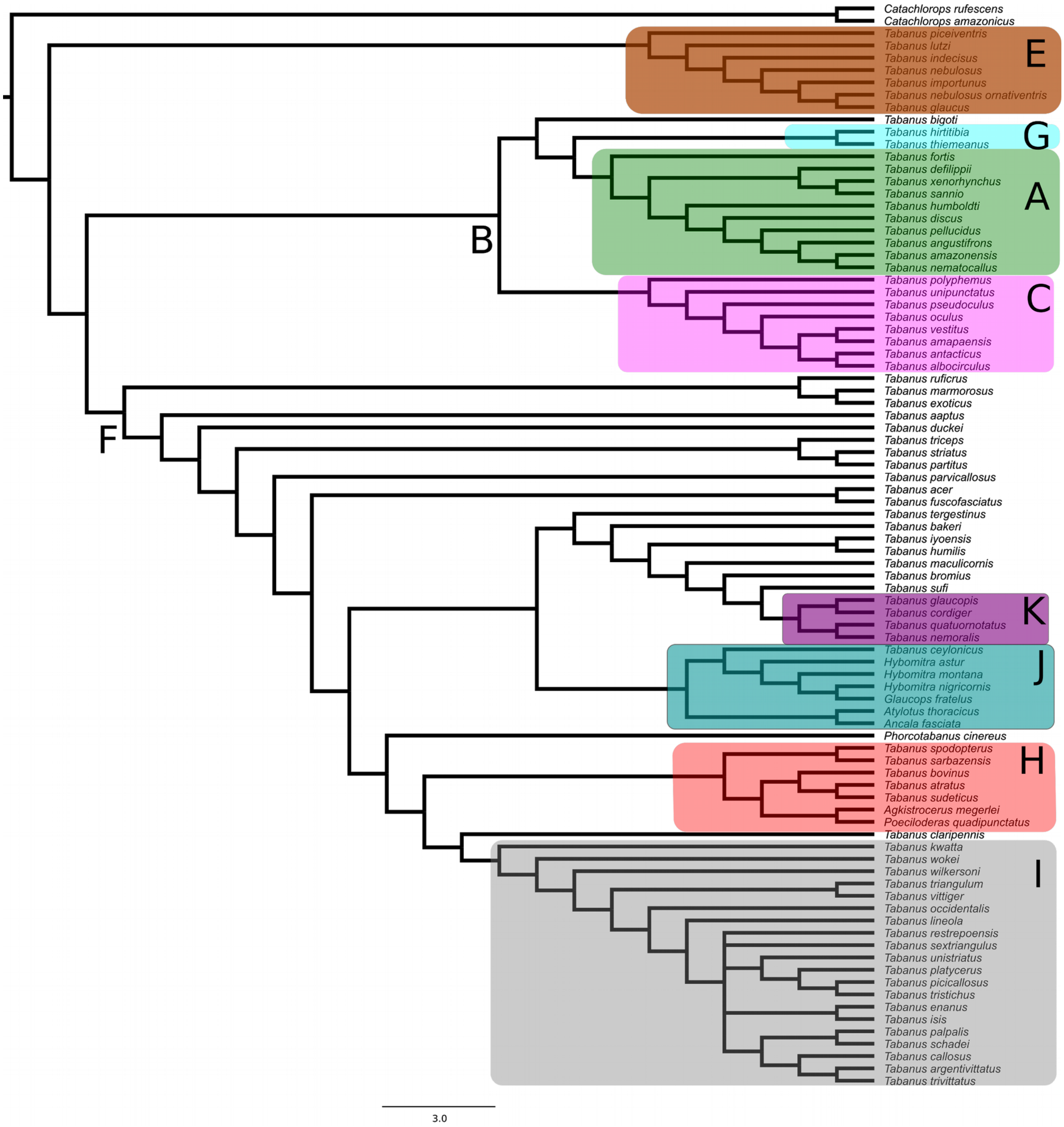

Figure 6. Strict consensus of the 10 most parsimonious trees analyzed under equal weights with both the frontal and divergence index included as continuous characters (character 1 was removed to avoid character dependence). Letters and color boxes represent clades discussed at the text.

Character list

Discrete characters

1 - Frontal callus shape. Fitch optimization. Length (L) = 18; Consistency index = 16; Retention index (RI) = 66. Fig. 7.

0 longitudinal ovoid
1 claviform
2 transversal ovoid
3 rectangular

Frontal characters are commonly used in Tabanidae taxonomy (*e.g.* Fairchild, 1976; Fairchild, 1983; Fairchild, 1985; Henriques & Krolow, 2010; Carmo & Henriques 2018). The shape of the callus is used both to delimit species groups (*e.g.* Chvála *et al*., 1972 - *quatuornotatus* group; Fairchild 1983 - *occidentalis* group), and also to identify species (*e.g.* Fairchild, 1976, 1983). The shape of the frontal callus variates considerably in the *Tabanus* group, and the character states seems to follow the width of the frons, which indicate dependence between the two structures. In the cladogram of Figs. 61 the state 1 is shown as the plesiomorphic condition, with modifications to other states in several groups.

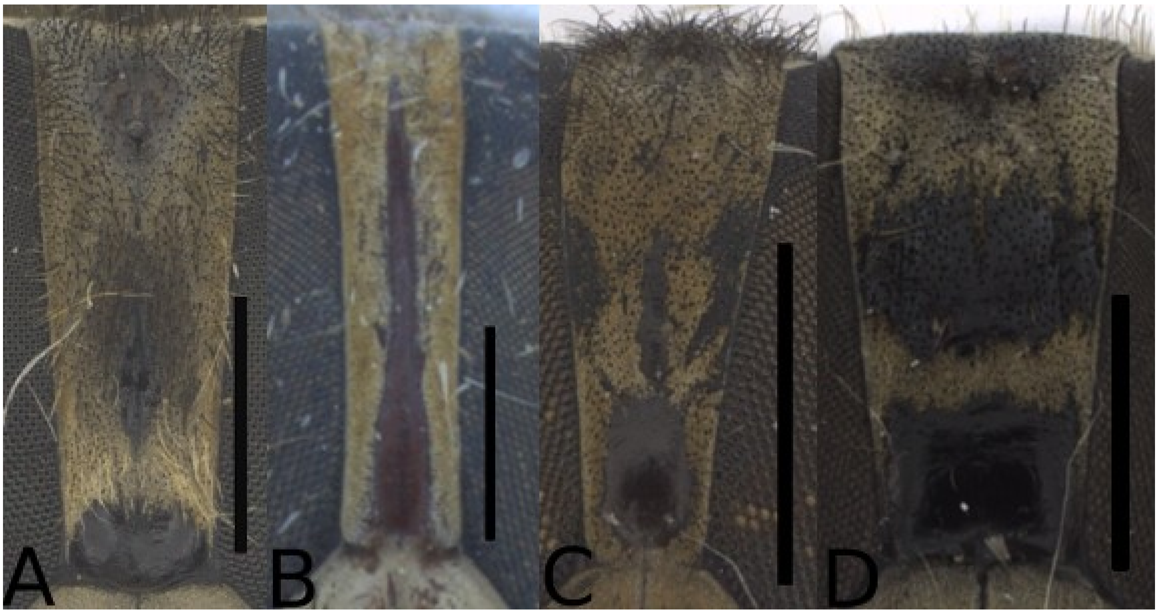

Figure 7. States of character 1. A. State 0 - *Hybomitra montana*. B. State 1 – *Tabanus nebulosus*. C. State 2 - *T. occidentalis.* D. State 3 - *T. cordiger.* Scale bars = 1mm.

2 - Longitudinal pruinescent bands at gena. Fitch optimization. L = 9; CI = 11; RI = 77. Fig. 8.

0 absent
1 present

This character has been used especially to identify species and species groups of Palearctic *Tabanus* (Chvála *et al.*, 1972). The pruinescent stripes at gena are present in species of the *trivittatus* and *occidentalis* species groups.

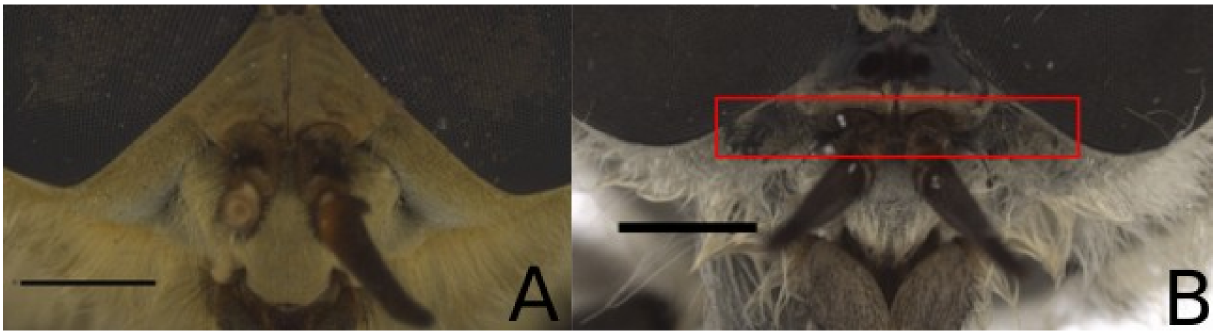

Figure 8. States of character 2. A. State 0 - *Tabanus bigoti.* B. State 1 - *T. glaucopis.* Scale bars = 1 mm.

3- Second palpus segment. Fitch optimization. L = 7; CI = 28; RI = 86. Fig. 9

0 flat (width dimension very reduced, given to the palpus the aspect of a flat disc at frontal view)
1 weakly inflated laterally (with a moderate swelling at base, but without globular aspect)
2 strongly inflated laterally (with a strong globular aspect at base)

When defining the groups of larger *Tabanus* in the Neotropical region, Fairchild (1976) used the laterally flateened palpus as diagnostic feature for species of the *xenorhynchus* group. During character coding, we found at least three states for this character. The second segment of palpus ranges from flat to very inflated, with an intermediate state between the two extremes.

4 -

Figure 9. States of character 3. A. State 0 - *Tabanus sannio* B. State 1 - *T. bigoti* C. State 2 - *T. cicur*. Scale bars = 1mm.

4-Second palpus segment length. Fitch optimization. L = 3; CI = 33; RI = 33. Fig. 10.

0 long, greater than labella
1 short, shorter than labella

In the dichotomous key of Fairchild (1984), the second segment of palpus shorter than the length of the stylets is a trait used to identify some species of the *nebulosus* group. Despite being a useful identification tool, Fairchild's comparison is not adequate as an hypothesis of homology since this feature is dependent of the length of the proboscis, which could lead to error in some species with long proboscis (as *Tabanus nebulosus*; see Character 20. Fig. 18B). Therefore, during character coding, we choose to compare the length of the palpus with the labellum.

Figure 10. *S*tates of character 4. A. State 0 - *Tabanus sannio.* B. State 1 - *T. importunus.* Scale bars = 1 mm.

5 - Ocellar tubercle. Fitch optimization. L = 4; CI = 25; RI = 50. Fig. 11

0 very reduced or absent
1 pronounced

The absence of a ocellar tubercle is a trait commonly used to the identification of *Tabanus* in taxonomic revisions and keys (*e.g.* Oldroyd, 1954; Chvála *et al.*, 1972; Pechuman & Teskey, 1989; Burger, 2009; Coscarón & Papavero, 2009). Our results point out to the loss of the ocellar tubercle in the root of the Tabanini tribe, with two independent reversals later.

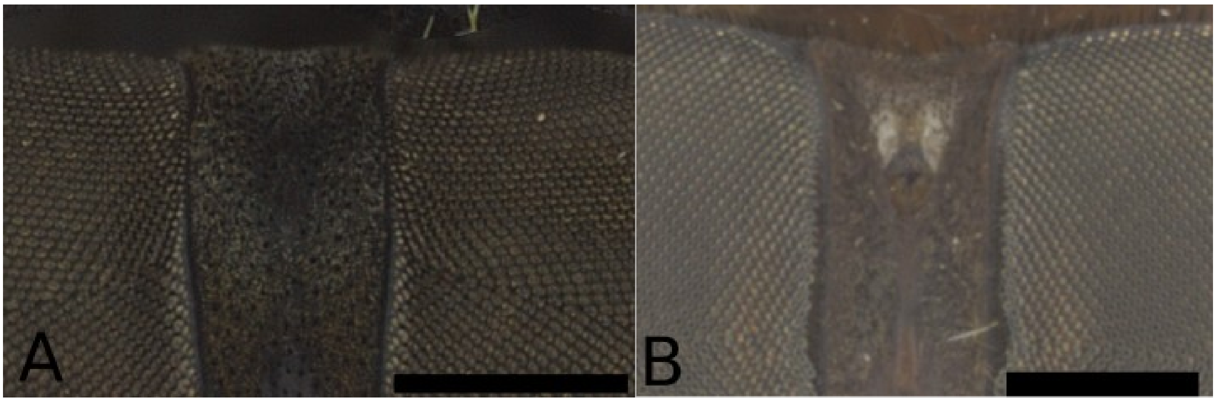

Figure 11. States of character 5. A. State 0 - *Catachlorops rufescens. B. Tabanus trivittatus.* Scale bars = 0.5 mm.

6 - Compound eye. Fitch optimization. L = 5; CI = 20; RI = 33. Fig. 12

0 pilose
1 bare

Another character used in *Tabanus* identification, this character is highly variable among horse flies. Our results shows that the pilosity of the eye appears independently at least four times in the Tabanini tribe.

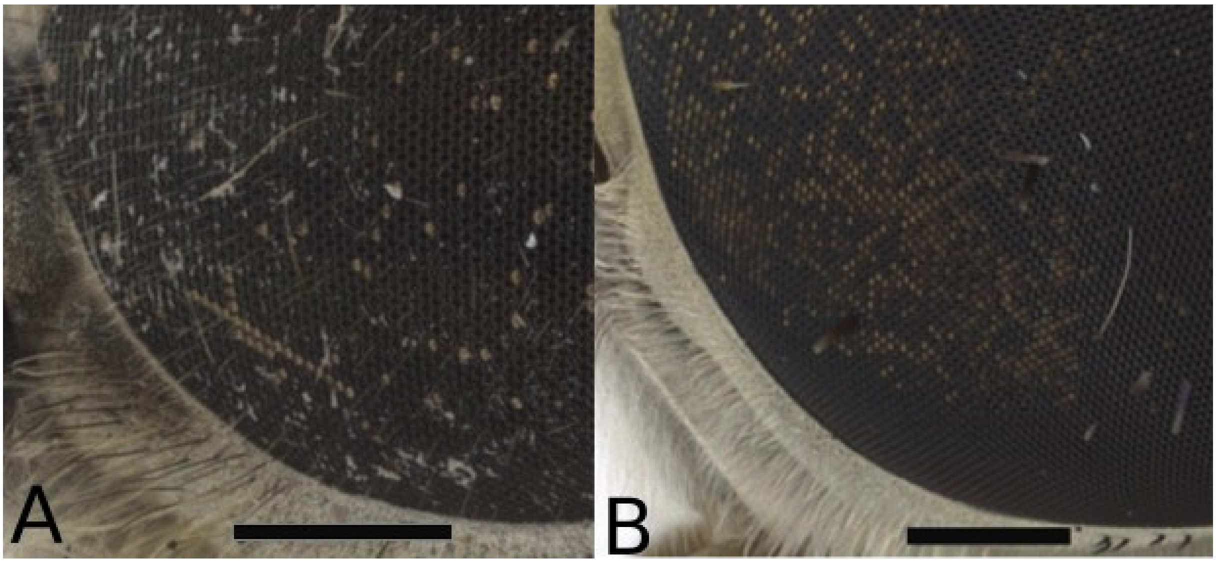

Figure 12. States of character 6. A. State 0 - *Tabanus quatuornotatus.* B. State 1 - *T. angustifrons.* Scale bars = 1 mm.

7 - Shape of the eye. Fitch optimization. L = 11; CI = 27; RI = 57. Fig. 13.

0 width greater than heigth, circular at lateral margin
1 width greater than length, lateral margin dislocated ventrally
2 width greater than length
3 width greater than heigth, elliptical at lateral margin

The eyes strongly expanded laterally is used by Fairchild (1983) as diagnostic characteristic of the *occidentalis* group. Examining both the ingroup and the outgroup taxa included in this analysis, we found four character states for this character. Our results support the opinion of Fairchild, as 7(3) shown as a synapomorphy of the *occidentalis* group (Fig. 61).

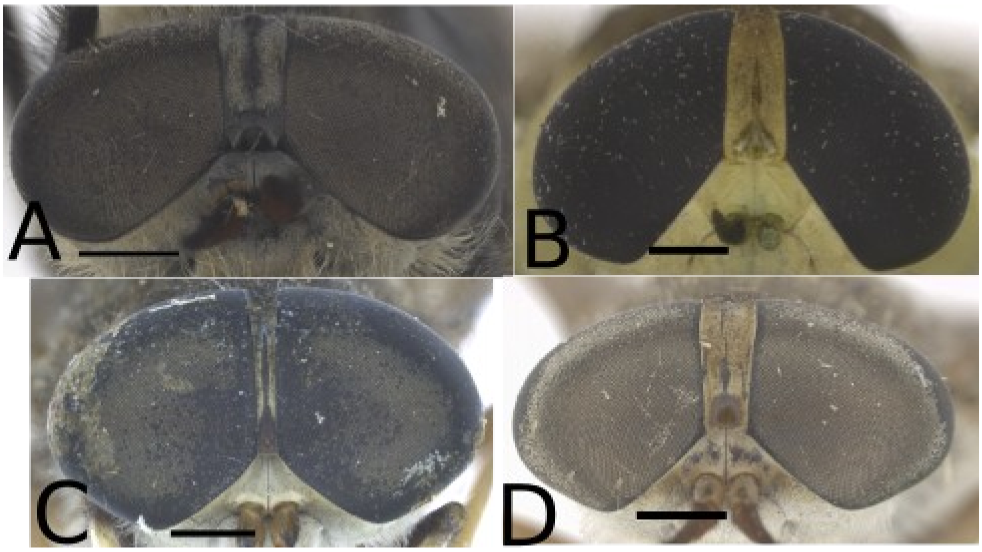

Figure 13. States of character 7. A. State 0 - *Hybomitra astur*. B. State 1 - *Ancala fasciata*. C. State 2 - *T. albocirculus*. D. State 3 - *T. triangulum*. Scale bars = 1 mm.

8 - Median callus length. Fitch optimization. L = 10; CI = 10; RI = 77. Fig. 14.

0 surpassing ⅔ of the frons hight

1 not surpassing ⅔ of the frons hight

A long median callus, ending more closely to the vertex, is the plesiomorphic condition, while the shorter median callus appeared several times in the groups here analyzed.

Figure 14. States of characters 8 and 9. A. State 0 - *Tabanus hirtitibia. B. State 1 - T. tergestinus.* Scale bars = 1 mm.

9 - Basal and median callus. Fitch optimization. L = 7; CI = 14; RI = 33; Fig. 14.

0 fused

1 separated

Several authors used this character to identify *Tabanus* species (*e.g.* Chvála *et al*., 1972; Coscarón, 1979; Fairchild, 1983). The character is considerably variable, and polymorphism was observed in one species, *T. lineola*.

10 - Limits between median and frontal callus. Fitch optimization; L = 7; CI = 14; RI = 50; Fig. 15.

0 clearly discernible
1 indistinct

While in some species analyzed the subcallus and median callus are easily separated by a constriction, in others the limits between both structures are barely discernible. Both states of this characters occur with multiple forms of callus (Character 1; Figure 61) which discards dependency between both characters.

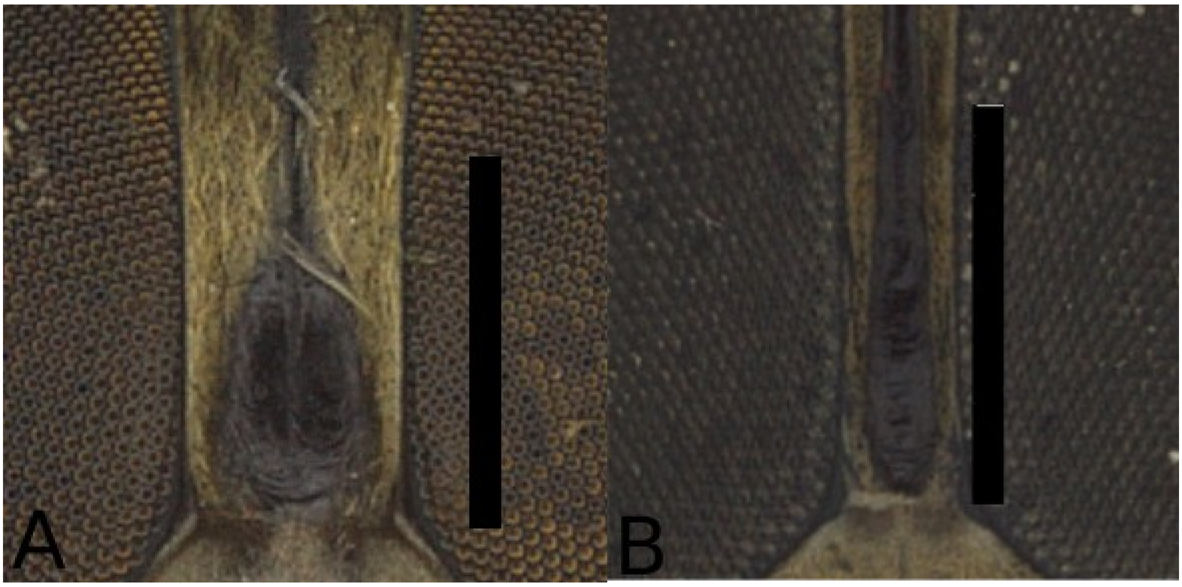

Figure 15. States of character 10. A. State 0 - *Tabanus spodopterus.* B. State 1 - *T. nematocallus.* Scale bars = 1 mm

11 - Subcallus surface (lateral view). Fitch optimization. L = 5; CI = 40; RI = 82. Fig. 16.

0 whole shining
1 whole pruinose
2 with pruinose stripes limited to ventral and dorsal edges

A bare and shiny subcallus, separated from the frons and the antennae by pruinose stripes, is a diagnostic feature for the *trivittatus* group in the Neotropical region (Fairchild, 1976; Carmo & Henriques, 2019). Examining the specimens included in this analysis, we found three states for this character. The pruinose condition is shown to be plesiomorphic, while the shiny subcallus with two pruinose stripes is an unambiguous synapomorphy of the *trivittatus* group (Fig. 61).

Figure 16. States of character 11. A. State 0 - *Tabanus atratus*. B. State 1 - *T. sarbazensis*. C. State 2 - *T. tristichus*. Scale bars = 0.5 mm.

12 - Subcallus shape I. Fitch optimization. L = 8; CI = 12; RI = 73. Fig. 17.

0 flat
1 globose

Another diagnostic character and synapomorphy of the *trivittatus* group, despite the independent origins (e.g., in the Palearctic *quatuornotatus* and *glaucopis* groups). The globose subcallus is usually seen when the structure is bare and shiny (character 11; Fig. 10A, B); however, the subcallus is inflated and pruinose in several species (*T. nemoralis; T. maculicornis*, *T. bromius*) which indicate independence between the characters 11 and 12.

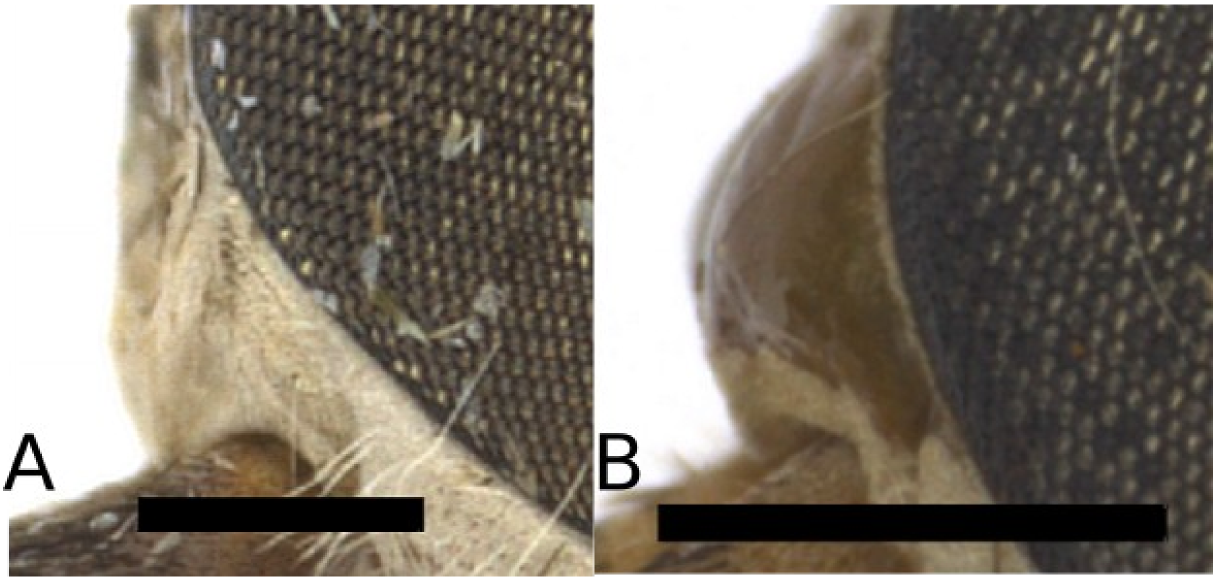

Figure 17. States of character 12. **A.** State 0 - *Tabanus amazonensis*. **B**. State 1 - *T. schadei*. Scale bars = 0.5 mm.

13 - Subcallus shape II. Fitch optimization. L = 12; CI = 8; RI = 72. Fig. 18.

0 transversal

1 triangular

This character corresponds to the dimension of the subcallus. The character is a very homoplastic, however, it supports some clades (Fig. 61). The triangular state is synapomorphy of a clade comprised by several Palearctic (*cordiger*, *bromius*, *iyoensis*, *quatuornotatus*, *humilis* groups), Afrotropical (*sufis* group) and Neotropical species (*occidentalis* and *trivittatus* groups) (Fig. 61).

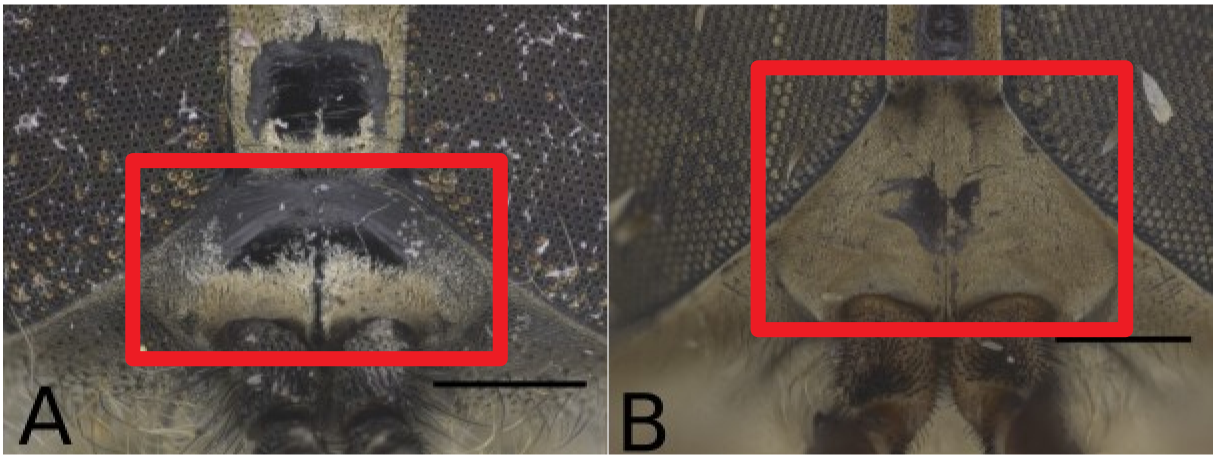

Figure 18. States of character 13. **A**. State 0 - *Tabanus piceiventris.* **B**. State 1 - *T. quatuornotatus.* Scale bars = 0.5 mm

14 - Postpedicel. Fitch optimization. L = 3; CI = 33; RI = 33. Fig. 19.

0 length greater than height
1 length and height with similar proportions

The postpedicel length is usually employed in the identification of some *Tabanus* species (Fairchild, 1976; Carmo & Henriques, 2019). In this analysis, the character is a synapomorphy of *T. isis* + *T. enanus*, independently originating in *T. willkersoni* and *T. bromius* (Fig. 61). Measurements were made between the greatest length and hight of the postpedicel.

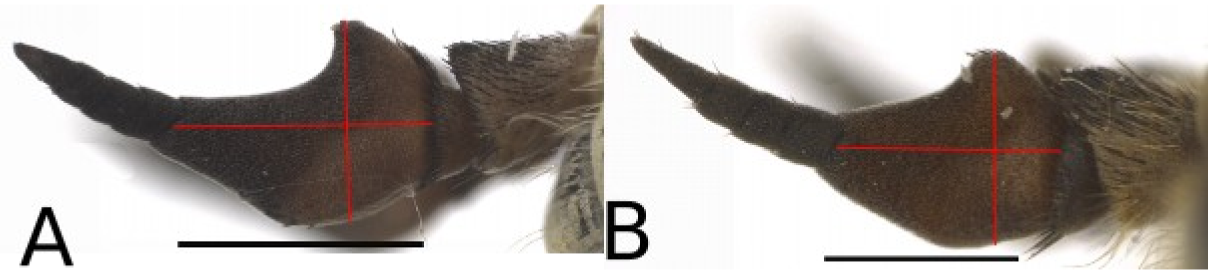

Figure 19. States of character 14. **A**. State 0 - *Tabanus sudeticus*. **B**. State 1 - *T. bromius*. Scale bars = 0.5 mm.

15 - Dorsal elevation of the postpedicel. Farris optimization. L = 13; CI = 23; RI = 82. Fig. 20.

0 with a slight elevation of the plate
1 with a spine, 90° angle with the plate
2 with a short hook, shorter than postpedicel
3 with a long hook, as long as postpedicel

Lutz (1913), Enderlein (1922) and Borgmeier (1934) used the presence of a long tooth at the postpedicel to propose groups of sugneric rank within the Neotropical *Tabanus* (respectively *Chelotabanus* Lutz, *Chelommia* Enderlein and *Alliomma* Borgmeier). The species of each of these subgenera are variable, but all of them included species of the *bigoti*, *pellucidus* and *nebulosus* groups. Fairchild (1964: 179) comments about the possible hierarchical nature of this character, stating that a "...tendency to develop a long antennal tooth has been expressed within this group of narrow front Neotropical *Tabanus*...”. To reflect the hierarchical nature of the character, we choose to code it as additive. The state 3 is plesiomorphic, present in the Diachlorini outgroups included, with a later independent origin or a reversal in a clade formed by *T. hirtitibia* and *T. thiemeanus*, while states 1 and 0 seem to have appeared several times (Fig. 61).

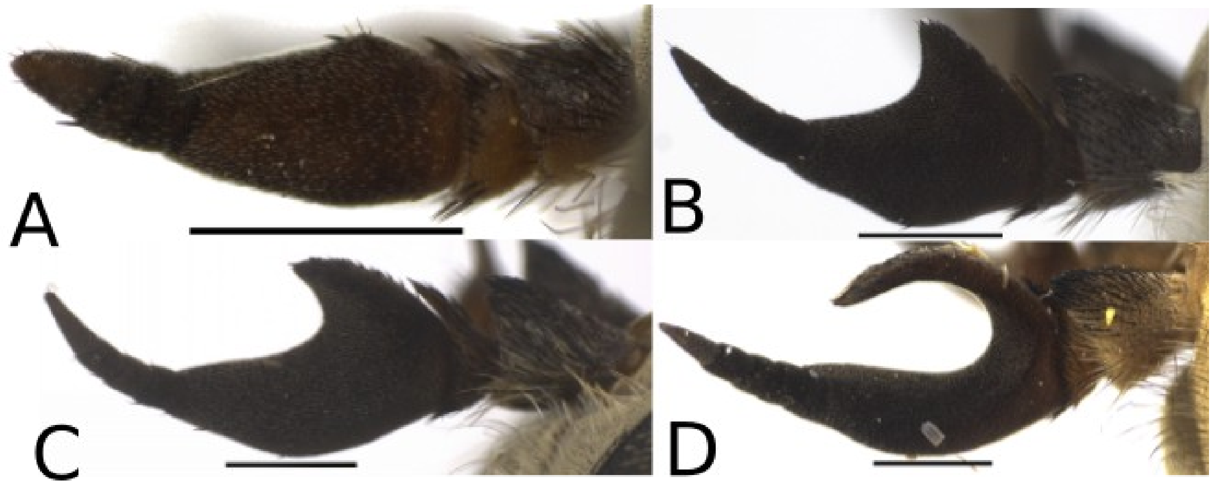

Figure 20. States of character 15. **A**. State 0 - *Glaucopis fratelus.* **B.** State 1 - *Tabanus angustifrons.* **C.** State 2 - *T. nematocallus.* **D.** State 3 - *T. hirtitibia.*

16 -Scape shape. Fitch optimization. L = 9; CI = 11; RI = 38. Fig. 21.

0 as long as height
1 longer than heigth

Character state 1 is synapomorphy for a clade comprised by the Tabanini genera *Ancala*, *Atylotus*, *Hybomitra* and *Glaucops*, with independent origins in several species included in the present analysis. Measurements were between the greatest length and the hight of the middle of the scape. We avoid to use the measurements of the apex of the structure to avoid distortions caused by the presence of a expansion of the scape.

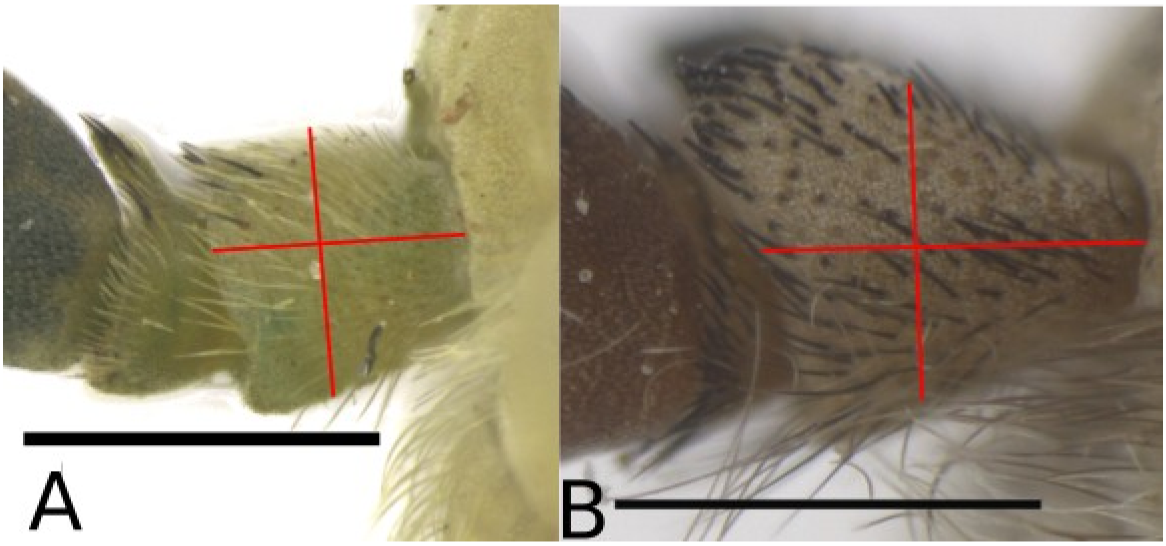

Figure 21. States of characters 16 and 17. **A**. State 0 - *Ancala fasciata.* **B.** State 1 - *T. triangulum.* Scale bars = 0.5 mm.

17 - Dorso-apical expansion of the scape over the pedicel. Fitch optimization. L = 12; CI = 8; RI = 50. Fig. 21

0 absent or vestigial

1 pronounced

Another diagnostic characters for the groups *bigoti*, *nebulosus* and *pellucidus* (Fairchild, 1964), in our analysis it is highly homoplastic. We suspected this character could be dependent of the previous one. However, state (0) is also observed when the scape is short (for instance, in *T. bovinus* and *T. sudeticus*), which is an evidence of independence between both characters.

18 - Postpedicel ventral sinuosity. Fitch optimization. L = 10; CI = 10; RI = 72. Fig. 22.

0 absent

1 present

This character refers to the shape of the ventral surface of the postpedicel, which may present a prominent sinuosity or said sinuosity can be completely absent. The character has high variability, but state 0 is apomorphic for several groups.

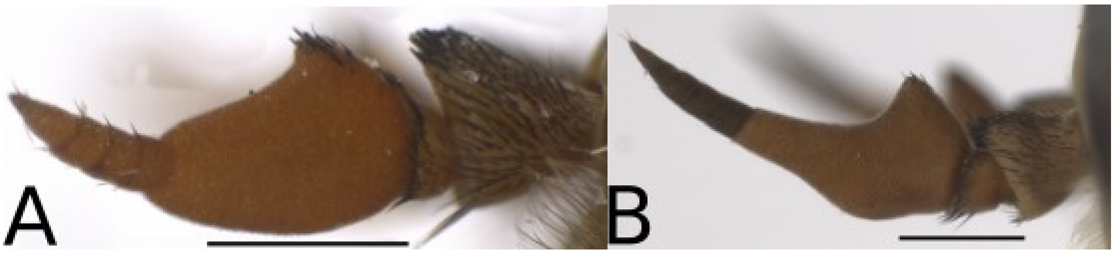

Figure 22. States of character 18. **A**. State 0 - *Tabanus argentivittatus. **B.*** State 1 - *T. lutzi.* Scale bars = 0.5 mm.

19 - Length of antennal style. Fitch optimization. L = 17; CI = 11; RI = 50. Fig. 23

0 shorter than half of the postpedicel length

1 half of the postpedicel length

2 very long, slightly surpassing the length as postpedicel

This character is used to identify some *Tabanus* species, including the very similar *T. trivittatus* and *T. callosus*. Carmo & Henriques (2018) already mentioned the variation of the length of the antennal style in the referred species. The character was coded as polymorphic for *T. trivittatus*. At first glance, it may appear to have dependency between characters 19 and 14 (Fig. 19). However, the two structures seems to be variating independently since our analysis shows no obvious correlation between both characters.

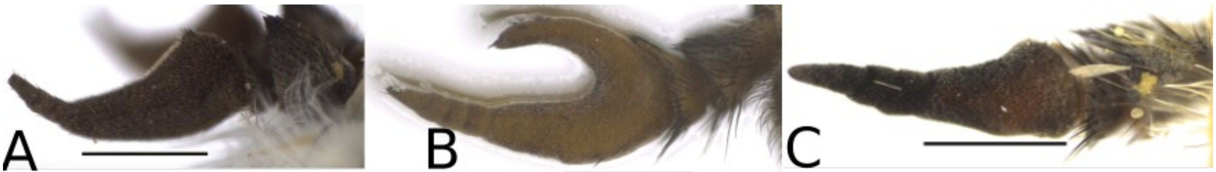

Figure 23. States of character 18. **A.** State 0 - *Catachlorops rufescens.* **B.** State 1 - *Phorcotabanus cinereus.* **C.** State 2 - *Hybomitra nigricornis.*

20 - Proboscis. Fitch optimization. L = 17; CI = 11; RI = 50. Fig. 24.

0 much shorter than head height

1 as long as head height

A proboscis nearly as long as the head height is one of the features Fairchild (1984) proposes as diagnostic for the *xenorhynchus* group. We observed that the state (1) is also present in other *Tabanus*, especially in some species of the *nebulosus* group (*T. nebulosus, T. nebulosus ornativentris* and *T. glaucus*). In *T. piceiventris,* traditionally included in the *xenorhynchus* group, both states are present - the character is coded as polymorphic in our matrix. Our data support this character as a synapomorphy of the *xenorhynchus* group, excluding *T. piceiventris* (Fig. 61) .

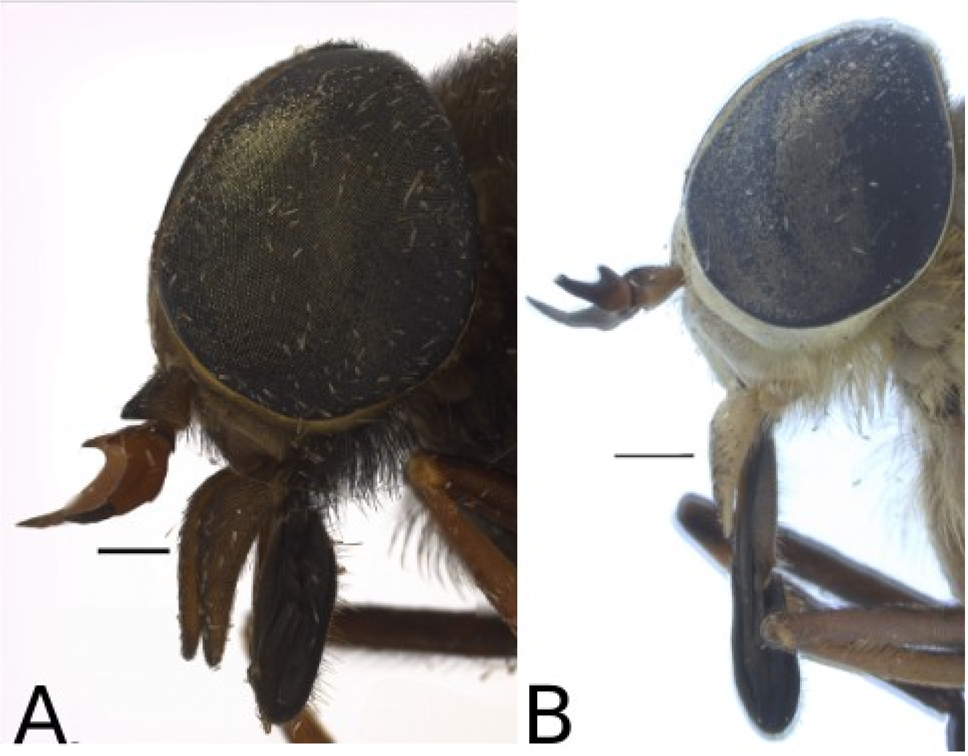

Figure 24. States of character 20. A. State 0 - Tabanus fortis. *B. State 1 - T. nebulosus.* Scale bars = 0.5.

21 - Clypeus. Fitch optimization. L = 1; CI = 100; RI = 100. Fig. 25

0 retracted
1 protracted

We observed a protracted clypeus in species of the *xenorhynchus* group. The protracted condition contributes to the proboscis to be even longer, however, dependence between characters 19 and 20 has been discarded based in the retracted condition absent in some long proboscid species (as *T. nebulosus*). This character is an unambiguous synapomorphy of the *xenorhynchus* group excluding *T. piceiventris* (Fig. 61).

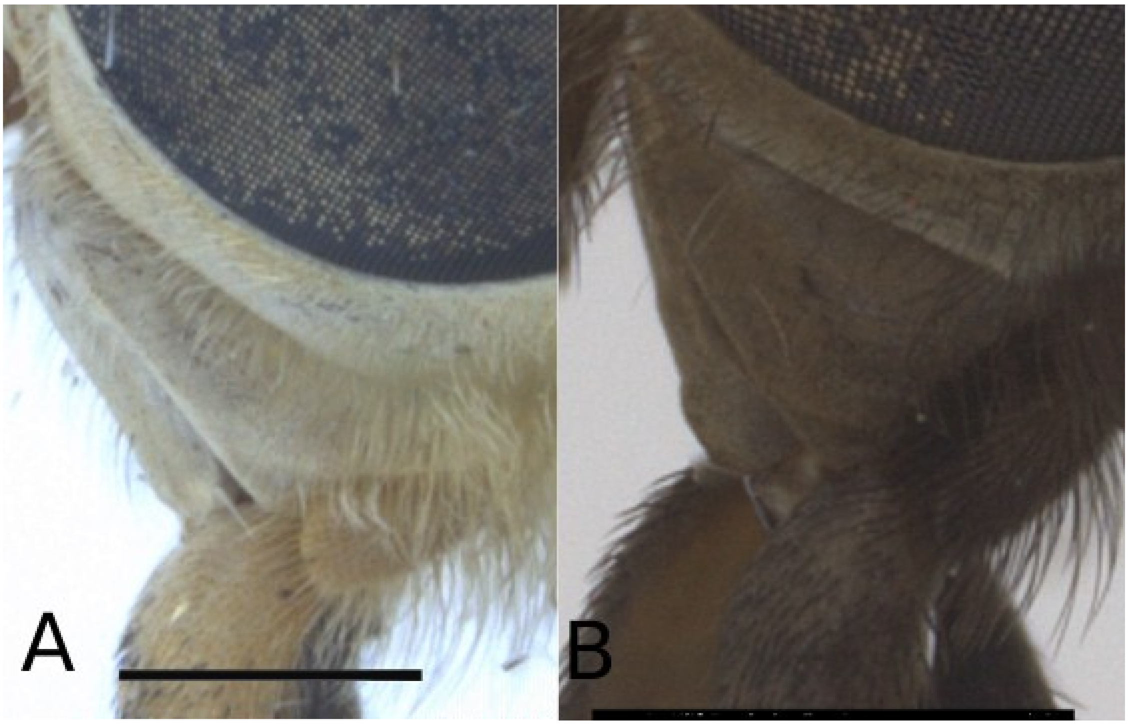

Figure 25. States of character 21. **A**. State 0 - *Tabanus nebulosus.* **B**. State 1 - *T. xenorhynchus.* Scale bars = 1 mm.

22 - Basal callus. Fitch optimization. L = 12; CI = 8; RI = 38. Fig. 26

0 not touching the eyes margins
1 touching the eyes margins

This character was used by Chvála *et al.* (1972) and Coscarón (1979) in dichotomous keys for the *Tabanus* of Europe and Argentina, respectively. In our analysis, the callus not touching the eye margins is a plesiomorphic condition, with the state 1 being apomorphic for several groups (Figs. 61).

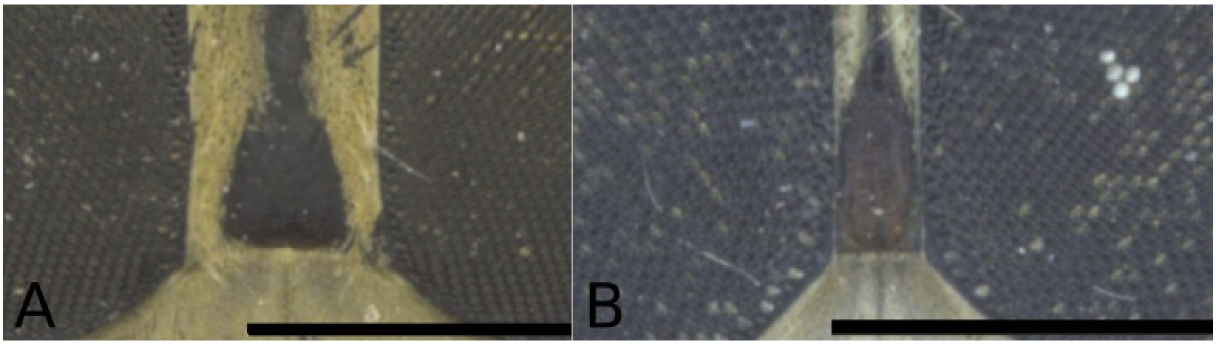

Figure 26. States of character 22. **A.** State 0 - *Tabanus bovinus.* **B.** State 1 - T. albocirculus. Scale bars = 1 mm.

23 - Median callus shape. Fitch optimization. L = 7; CI = 14; RI = 33. Fig. 27.

0 narrow
1 broad

This is an important diagnostic character for the Palearctic and Australian species of *Tabanus*. In the Neotropical species included in the present analysis, however, only the narrow condition is present. Our hypothesis show that the broad condition of the median callus appeared three times, and it is a synapomorphy of a clade formed by the groups *quatuornotatus* and *glaucopis*, with some independent origin in other taxons

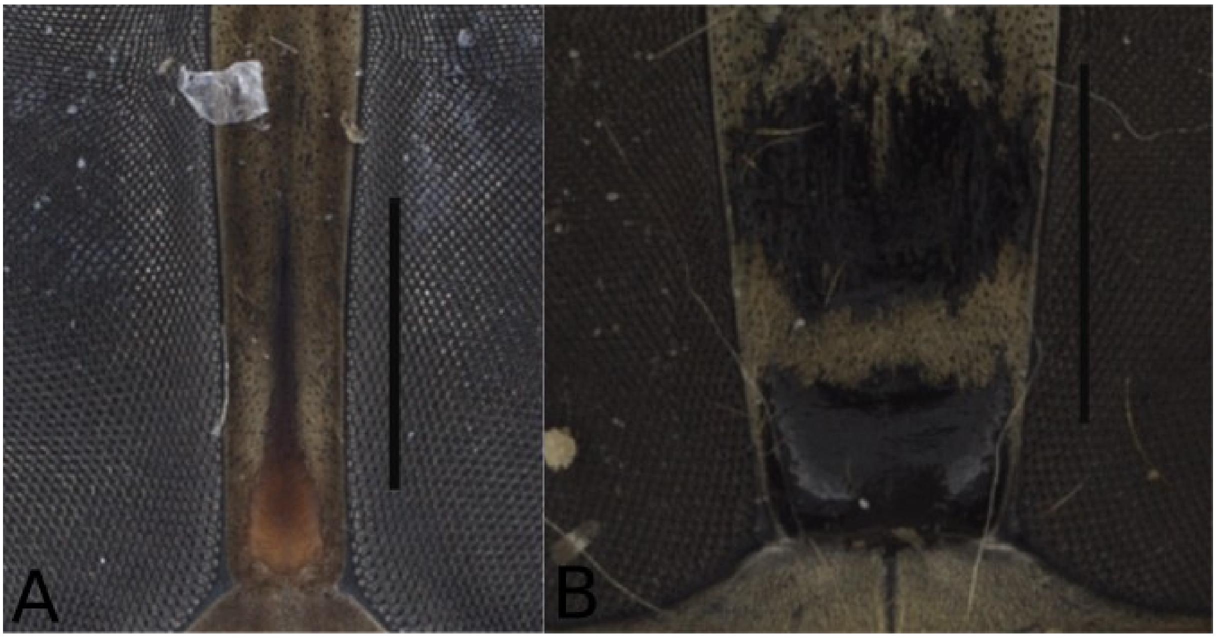

Figure 27. States of character 23. **A.** State 0 - *Tabanus parvicallosus.* **B.** State 1 - *T. cordiger.* Scale bars = 1 mm.

24 -Head dorsal margin. Fitch optimization. L = 12; CI = 8; RI = 89. Fig. 28.

0 strongly angled
1 nearly straight

The shape of the occiput in *Tabanus* is rather variable; however, it supports some groups in our analysis (*e.g pellucidus*, *xenorhynchus* and *bovinus*). The state 1 plesiomorphic to the Tabanini tribe.

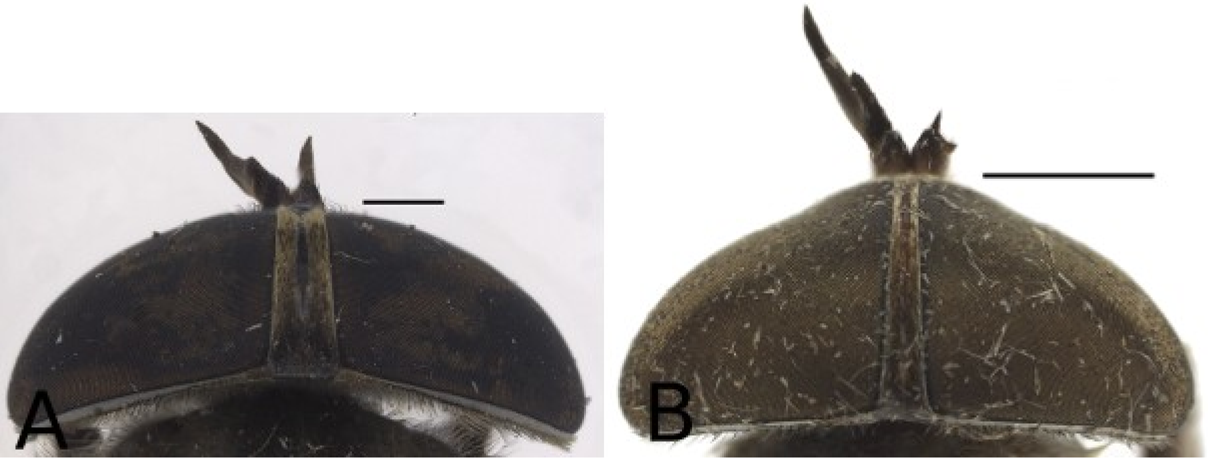

Figure 28. *S*tates of character 24. **A.** State 0 - *Tabanus spodopterus.* **B.** State 1 - *T. amazonensis.* Scale bars - A = 1 mm; B = 2 mm.

25 - Eye bands. Fitch optimization. L = 6; CI = 16; RI = 84. Fig. 29.

0 absent
1 present

Several species of Tabanidae possess eyes with different coloration patterns. This is an important taxonomic feature used as a diagnostic for species groups, as the Neotropical *occidentalis* and *trivittatus* (Fairchild, 1976, 1983), the Afrotropical *sufis* (Oldroyd, 1954), and the Palearctic *quatuornotatus* and *nemoralis* (Chvála *et al*., 1972). The eye color is not caused by pigmentation but by morphological differences in the cristaline, which produces the colors by diffraction (Oliveira Castro, 1937). Unfortunately, upon death, accumulated fat on these structures impairs the passage of light and, therefore, the color patterns may only be seen in live or ethanol-preserved specimens. Sometimes it is possible to see the eye pattern of specimens by hidrating it or using some sort of solvent solution.

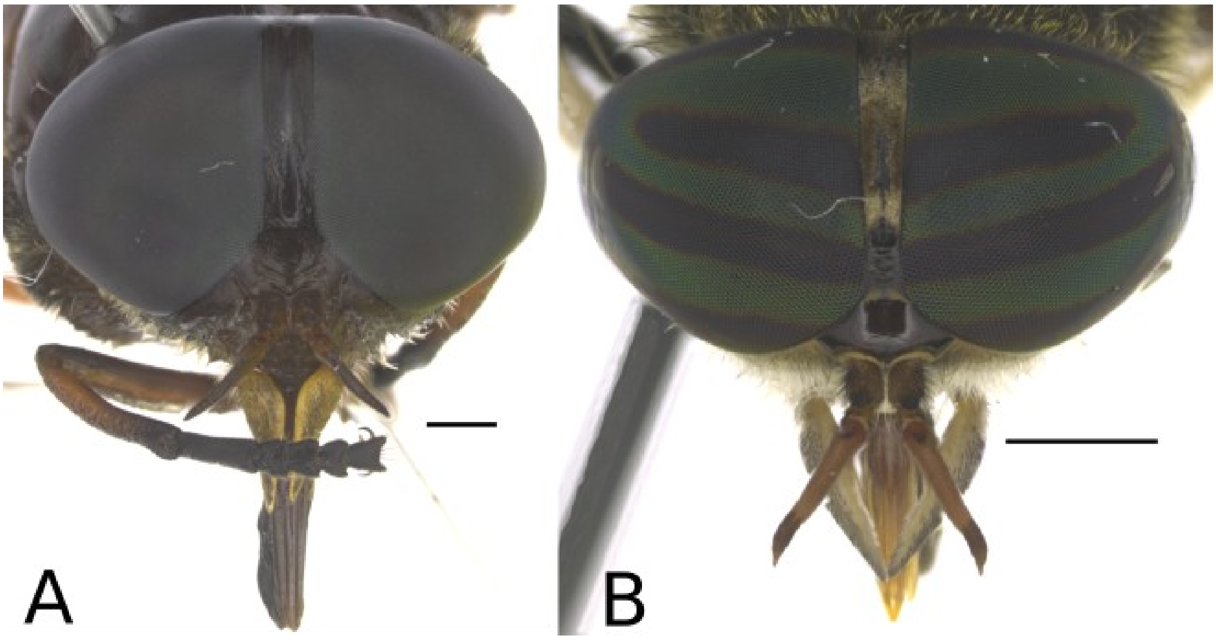

Figure 29. States of character 24. **A.** State 0 - *Tabanus nebulosus*. **B.** State 1 - *T. trivittatus*. Photos taken from specimens preserved in ethanol. Scale bars = 1 mm.

26 - Number of eye bands. Fitch optimization. L = 9; CI = 33; RI = 64. Fig. 30.

0 one
1 two
2 three
3 four

Several different eye patterns may be seen in Tabanidae. In *Tabanus,* these patterns vary from one to four stripes, with Neotropical species having only two or three stripes. Eyes with two stripes is the plesiomorphic condition in our analysis. The state 2 - eye with three bands - supports the relationship of the Neotropical *occidentalis* and *trivittatus* groups with the Palearctic Tabanini species.

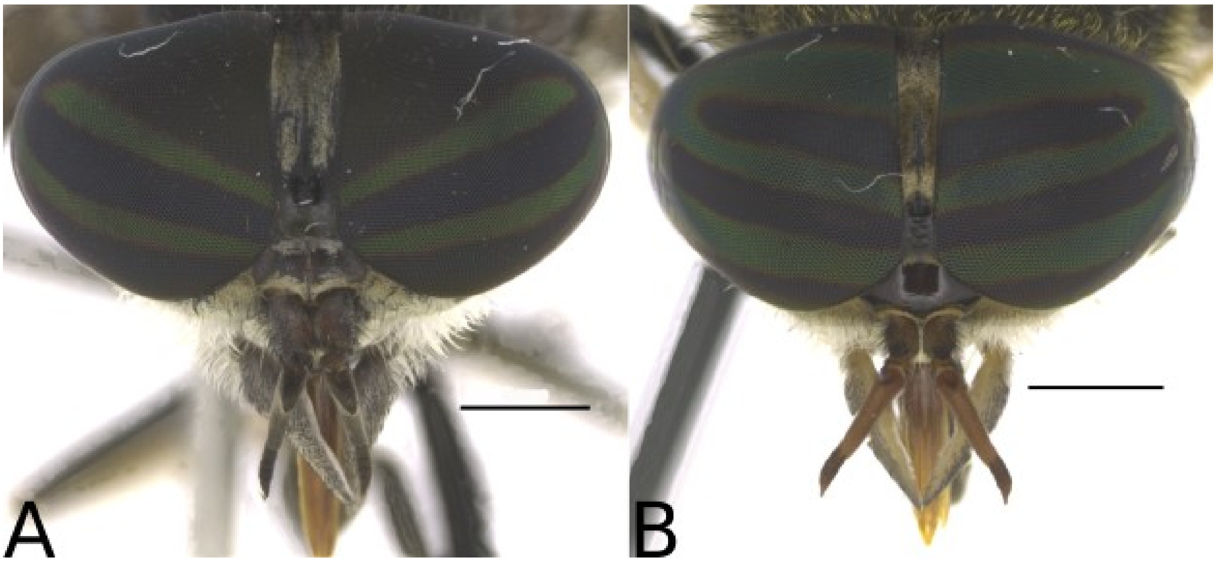

Figure 30. Some states of character 26. **A.** State 1 -*Poeciloderas quadripunctatus*. **B.** State 2 - *Tabanus trivittatus*. Photos taken from specimens preserved in ethanol Scale bars = 1mm.

27 - Basicosta. Fitch optimization. L = 4; CI = 50; RI = 50. Fig. 31

0 bare

1 with setae as dense as in costal vein

2 with sparse setae

The basicosta strongly setulose was used by Mackerras (1954) to define the Tabanini tribe. However, according to Mackerras himself, some species of Tabanini possess only few setae at basicosta (or no setae at all). The state 2, basicosta with sparse setae, is seen in the Palearctic groups *glaucopis* and *quatuornotatus* and in the Afrotropical *sufis*. *T. quatuornotatus* presents some variation, ranging from no setae to three or four setae, while *T. glaucopis* and *T. nemoralis* possess few sparse setae. *T. quatuornotatus* was coded with state 0. Chvála *et al*. (1972) recommended that the *quatuornotatus* group, which has hairy eyes, should be included within *Tabanus* as a subgenus.

Figure 31. States of character 27. **A.** State 0 - *Catachlorops amazonicus.* **B**. State 1 - *Tabanus piceiventris.* **C.** State 2 - *T. nemoralis.* Scale bars = 0,5 mm.

28 - Sulcus at costal vein. Fitch optimization. L = 10; CI = 10; RI = 71. Fig. 32

0 absent
1 present

In the dichotomous key for the groups of *Tabanus* of the Ethiopian (Afrotropical) region, the presence of a bare sulcus at the coastal vein is part of the couplet 6, describing diagnostic features of the *ruficrus* group, probably an artificial one (Oldroyd, 1954). We found the sulcus at costa vein in several species of *Tabanus*. Although variable, the character supports several groups in our analysis, being other character to support the relationship between the *occidentalis* and *trivittatus* group with the group formed by the Palearctic species of *Tabanus*.

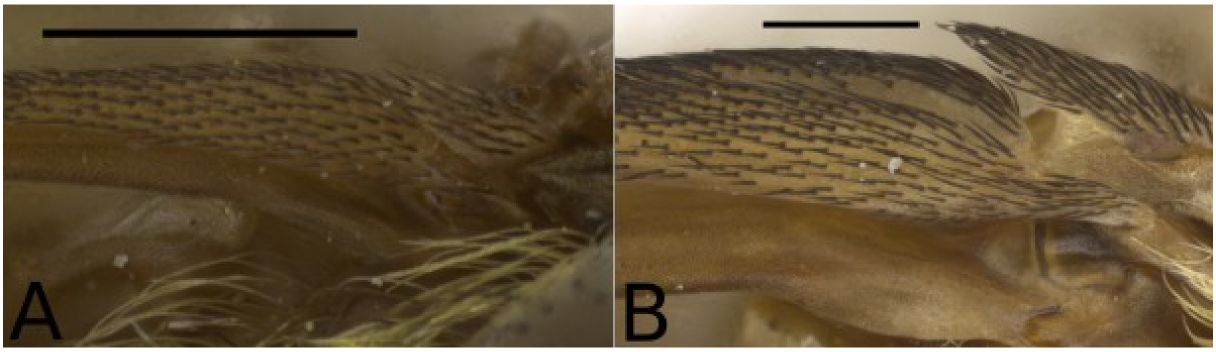

Figure 32. States of character 28. **A.** State 0 - *Tabanus unistriatus.* **B.** State 1 - *T. bigoti.* Scale bars = 0.5 mm.

29 - Appendix at R4. Fitch optimization. L = 8; CI = 12; RI = 50. Fig. 33.

0 absent
1 present

The presence of an appendix at R4 is a trait distributed in the whole Tabanidae. It is usually used in identification keys (*e.g.* Oldroyd, 1954; Chvála *et al*., 1972; Fairchild, 1984). As expected, the character is very homoplastic (CI = 12). However, it is a synapomorphy of a clade formed by some species of the *oculus* group, the species *T. vestitus* and *T. amapaensis* (both Neotropical and not included in any group of species), *T. aaptus* (*fortis* groups), *T. marmorosus* (Afrotropical, *marmorosus*-group) and *T. exoticus* (Oriental, not included in any group of species).

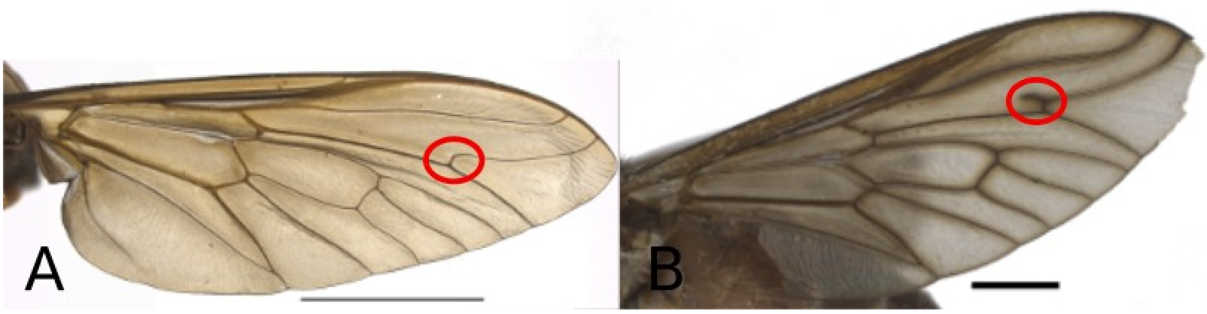

Figure 33. States of character 30. **A.** State 0 - *Tabanus fortis.* **B.** State 1 - *T. antarcticus.* Scale bars - A = 5 mm; B = 2 mm.

31 - Extension of appendix at R4. Fitch optimization. L = 4; CI = 25; RI = 50. Fig. 34

0 short (shorter than the confluence between R4 and R5)

1 long (greater than the confluence between R4 and R5)

The appendix at R4 ranges from a short, small appendix, to a long appendix (in the Tabanini). This is synapomorphy for part of the *oculus* group ((*T. antarcticus* + *T. albocirculus*) + (*T. oculus* + *T. pseudoculus*)), with two independent origins in *T. sufis* and *T. exoticus*.

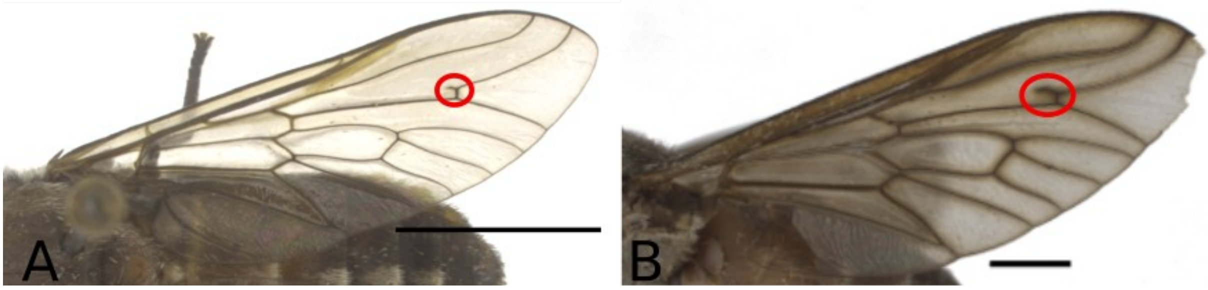

Figure 34. States of character 30. **A.** State 0 - *Tabanus amapaensis.* **B.** State 1 - *T. antarcticus.* Scale bars - A = 5 mm; B = 2 mm.

31 - Relative position of veins R5 and M1. Farris optimization. L = 14; CI = 14; RI = 55. Fig. 35.

0 parallel to each other

1 converging towards the wing margin
2 fused before the wing margin

Another character used in identification keys for species of *Tabanus*, especially in the Neotropical region (Fairchild, 1984). The character is polymorphic in two of the species included in our analysis. In *T. albocirculus*, the three states are present, while in *T. nematocallus*, states 1 and 2 may be present in the same specimen. We considered the existence of both states 1 and 2 the same specimens of *T. nematocallus* as evidence of hierarchy between these character states, and therefore, we code it as additive.

Figure 35. Sates of character 31. **A.** State 0 - *Tabanus xenorhynchus.* **B.** State 1 - *T. bovinus.* **C.** State 2 - *Poeciloderas quadripunctatus.* Scale bars = 5 mm.

32 - Vein M1. Fitch optimization. L = 6; CI = 16; RI =20. Fig. 36.

0 curved
1 without apparent curvature

The vein M1 may be curved (state 0) or be near straight. The character state 0 supports a clade formed by species of the *bovinus* group with *P. quadripunctatus* and *T. atratus*.

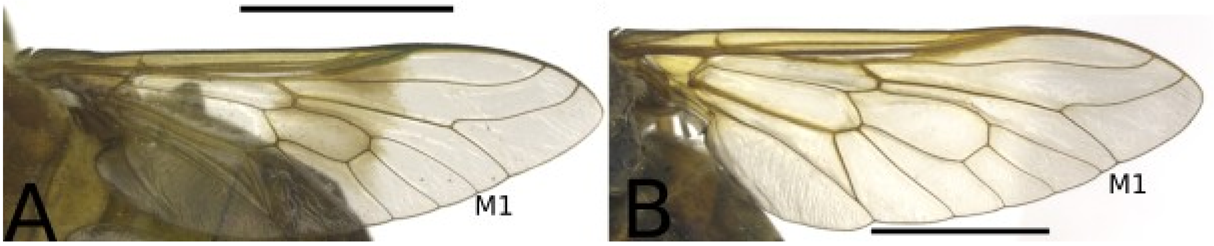

Figure 36. States of character 32. **A.** State 0 - *Ancala fasciata.* **B**. *State 1 - T. bovinus.* Scale bars = 5 mm.

33 - Vein M2 and M3. Fitch optimization. L = 15; CI = 6; RI = 63. Fig. 37.

0 with a sinuosity
1 straight

This highly variable character (CI = 6) is a synapomorphy of the *trivittatus* group, with independent origins in several other clades and terminals.

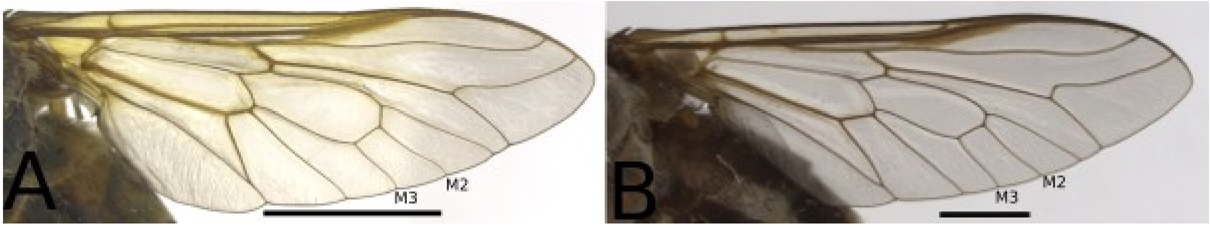

Figure 37. States of character 33. **A.** State 0 - *Tabanus bovinus.* **B**. State 1 - *T. triceps.* Scale bars - A = 5 mm; B = 2 mm.

34 - Scutellum. Fitch optimization. L = 11; CI = 9; RI = 47. Fig. 38.

0 two times wider than long
1 more than two times wider than long

The state 0 is plesiomorphic in our analysis with a reversion in the clade formed by the groups *occidentalis* and *trivittatus*.

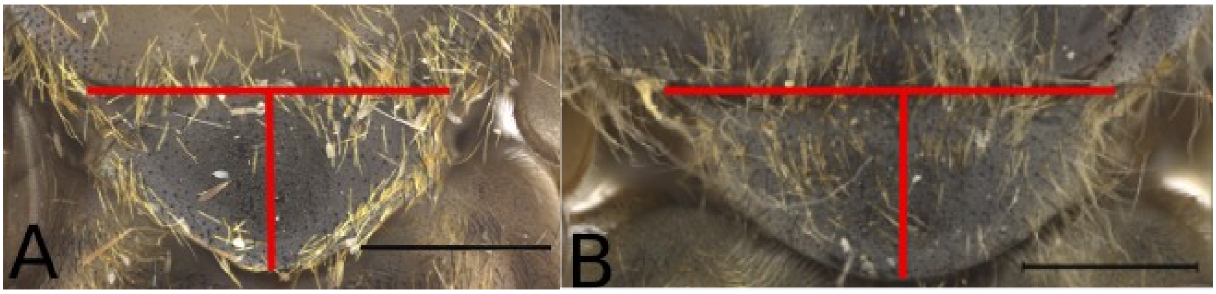

Figure 38. States of character 34. **A.** State 0 - *Tabanus trivittatus. B.* State 1 - *T. bromius.* Scale bars = 1 mm.

35 - Black pruinescent circle at scutellum and prescutellum. Farris optimization. L = 11; CI = 9; RI = 47. Fig. 39.

0 absent
1 incomplete
2 complete

This character is used as diagnostic for several groups of Neotropical *Tabanus*. Fairchild (1984) included the presence of a well marked black pilose prescutelar spot (state 1 in the present analysis) in the couplet 16 of his key, leading to species of the *nebulosus* group. State

2 was used to define the genera *Lophotabanus* Szilady and *Bellardia* Rondani. Both genera are synonymized with *Tabanus* and correspond to the species of the *oculus* group.

States 1 and 2 seem to have some dependency. Both in literature and in our own observations, the presence of a spot in the scutellum is always followed by the presence of a spot in the prescutellum. Hence, we coded this character as an additive multistate character. The incomplete state is supported as a synapomorphy of species of the *nebulosus* and *pellucidus* group. State 2 has three independent origins.

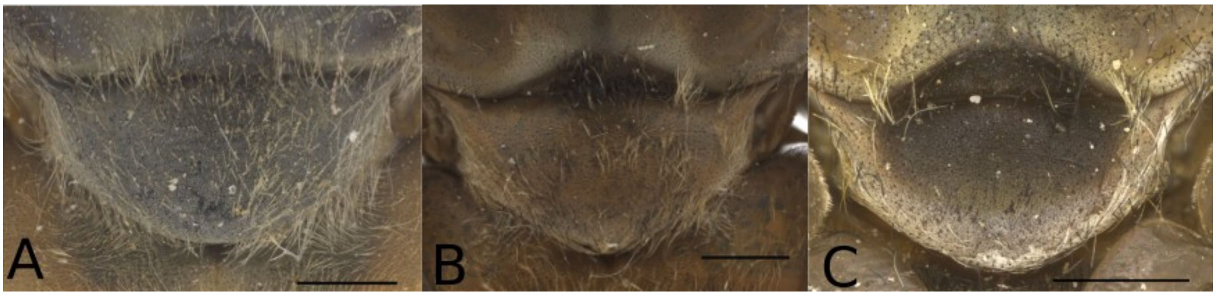

Figure 39. States of character 35. **A.** State 0 - *Tabanus sarbazensi.* **B.** State 1 - *T. lutzi.* **C.** State 2 - *T. albocirculus.* Scale bars = 1 mm.

36 - Fringe of conspicuous hairs at the margin of scutellum. Fitch optimization. L = 9; CI = 22; RI = 72. Fig. 40.

0 absent
1 present

This character was observed in some species of the *xenorhynchus* and *oculus* groups. The *oculus* group is aphyletic in our analysis and, therefore, the character is homoplastic.

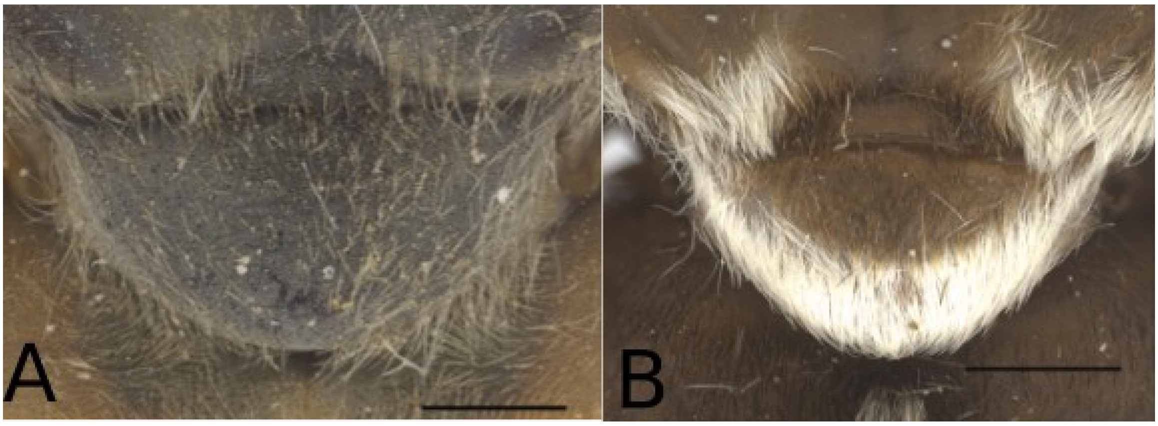

Figure 40. States of character 36. **A.** State 0 - *Tabanus sarbazensis.* **B.** State 1 - *T. xenorhynchus.* Scale bars = 1 mm.

37 - Anterior tibia integument. Fitch optimization. L = 15; CI = 6; RI = 53. Fig. 41.

0 monocolor
1 bicolor

This is an important character in the taxonomy of Neotropical *Tabanus*. Fairchild states that a clearly bicolored tibia is present in the majority of the species of the *occidentalis* group. In our analysis, the monocolor tibia is plesiomorphic with seven independent modifications to the bicolored state.

Figure 41. States of character 37. **A.** State 0 - *Tabanus piceiventris.* **B.** State 1 - *T. callosus.* Scale bars = 0.5 mm.

38 - Fringe of setae at hind tibia. Fitch optimization. L = 10; CI = 10; RI = 64. Fig. 42.

0 with sparse setae
1 with dense setae

A more or less differentiated fringe of setae was observed in all the terminal taxa studied. However, the aforementioned fringe varies on the sizes of the setae and their number. The setae may be sparse and discernible from other macrotrichia of the tibia, sometimes by color (state 0) or forming a clear differentiated fringe with dense setae. Fairchild (1964) pointed the fringe of dense hairs at the posterior tibia as a diagnostic of the genus *Chelotabanus* (*pellucidus*, *nebulosus* and *bigoti* groups). We also observed the fringe in several *Tabanus* of other biogeographic regions. The absence of a dense fringe of hairs is synapomorphy of the *trivittatus* group (Fig. 61).

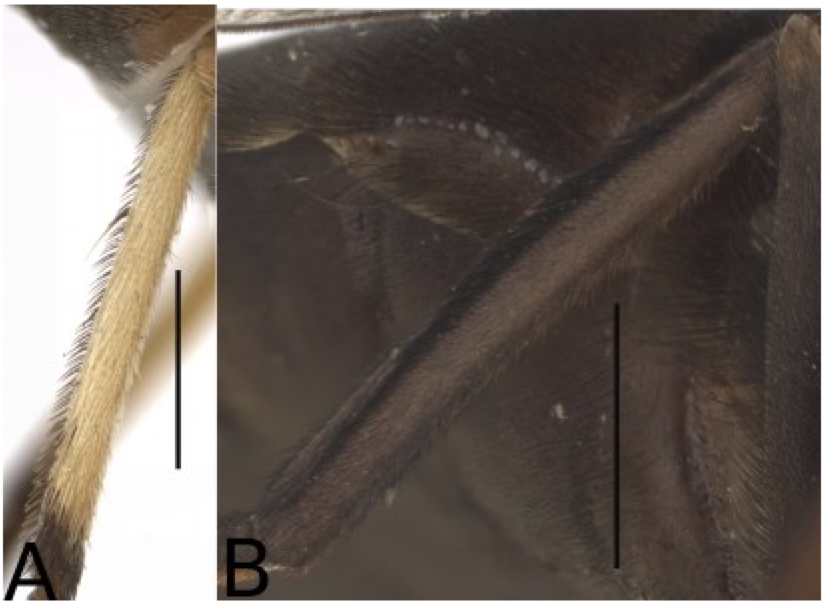

Figure 42. States of character 38. **A.** State 0 - *Tabanus argentivittatus.* **B.** State 1 - *T. ruficrus.* Scale bars - A = 1 mm; B = 2 mm.

39 - Fifth tarsomere. Fitch optimization. L = 23; CI = 4; RI = 46. Fig. 43.

0 clearly longer than wide
1 as long as wide

A variable character with multiple independent origins in our phylogenetic hypothesis. It is synapomorphy of a clade formed by three species of the *pellucidus* group (*T. angustifrons*, *T. pellucidus* and *T. nematocallus*), with some independent origins.

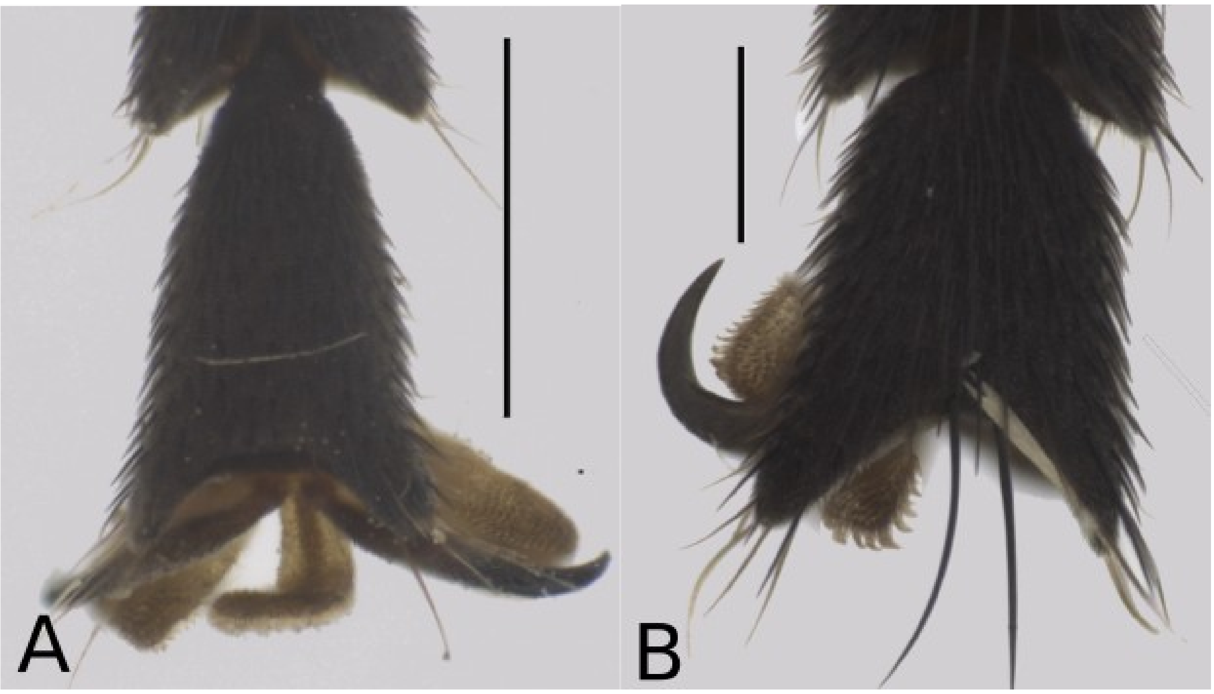

Figure 43. Sates of character 39. A. State 0 - *Tabanus maculicornis.* **B.** State 1 - *Hybomitra astur.* Scale bars = 0.5 mm.

40 - Dorsomedial integumental pattern at sternites. Fitch optimization. L = 12; CI = 8; RI = 56. Fig. 44.

0 absent
1 present

Some species of *Tabanus* present a stripe medially at the abdomen, which may or may not be covered by a pattern of pruinosity (character 38). The presence of stripe is synapomorphy of the *occidentalis* group, with other independent origins. For visualizing the pattern of pruinosity is often necessary to moisten or to rub the pruine of the specimen to see the underlain integumental pattern. Both the *occidentalis* and *trivittatus* groups are promptly known by having white to yellow stripes at their abdomens. However, upon moistening or friction, the pattern of *trivittatus* appears only by pruinescence, while the *occidentalis* group possess a real integumental stripe.

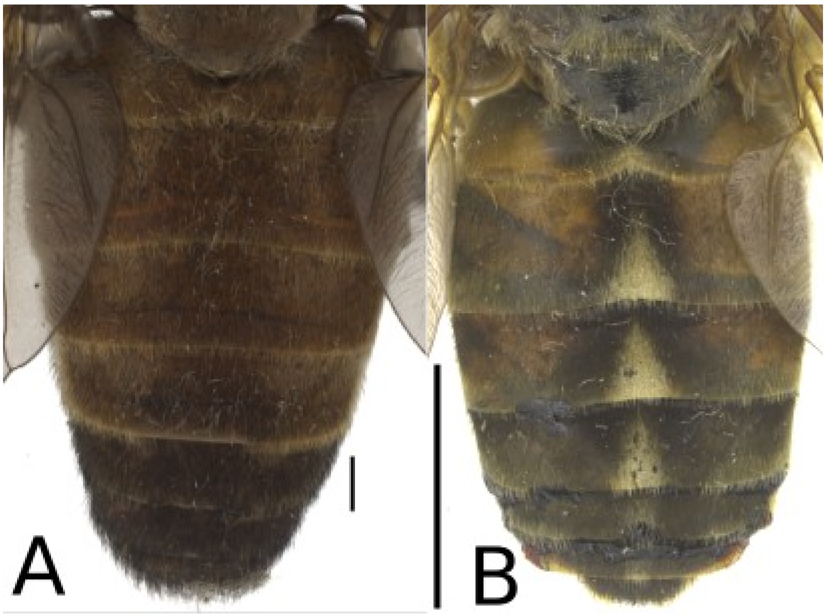

Figure 44. States of character 40. **A.** State 1 - *Tabanus lutzi.* **B.** State 0 - *T. bovinus.* Scale bars - A = 1 mm; B = 5 mm.

41 - Dorsomedial vestiture pattern at tergites. Fitch optimization. L = 12; CI =8; RI = 56. Fig. 45.

0 absent

1 present

This character is related to the pruinescence pattern which may cover the integumental stripe. Here, we have observed species with both a integumental and pruinose stripes, and also species without an integumental stripe but with an pruinose stripe, which discards the possibility of dependence between this character and the characters 40 and 42.

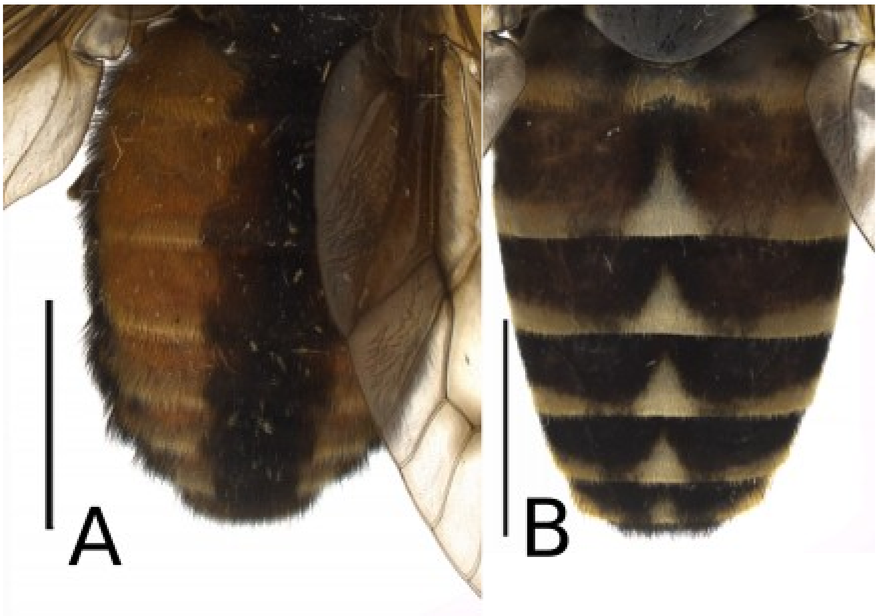

Figure 45. States of character 41. **A.** State 0 - *Agkistrocerus megerlei.* **B.** State 1 - *Tabanus sudeticus.* Scale bars = 5 mm.

42 - Type of integumental dorsomedial abdominal pattern. Fitch optimization. L = 3; CI = 33; RI = 83. Fig. 46.

0 dark and very broad stripe
1 light and narrow stripe (only visible by moistening the specimen)

We generally avoided using color features during character coding. However, we decided to include the present character, since the integumental black stripe is also broad and usually with different form than the light stripe, and the structure were not considered to be homologous.

Figure 46. States of character 42. A. State 0 - *Tabanus tergestinus.* **B.** State 1 - *T. kwatta. Scale bars* - A = 5 mm; B = 2 mm.

43 - Type of abdominal dorsomedial vestiture pattern. Fitch optimization. L = 10; CI = 30; RI = 84. Fig. 47.

0 composed by incipient small triangles

1 composed by conspicuous triangles

2 composed by a stripe

3 composed by asymmetrical white pillose spots

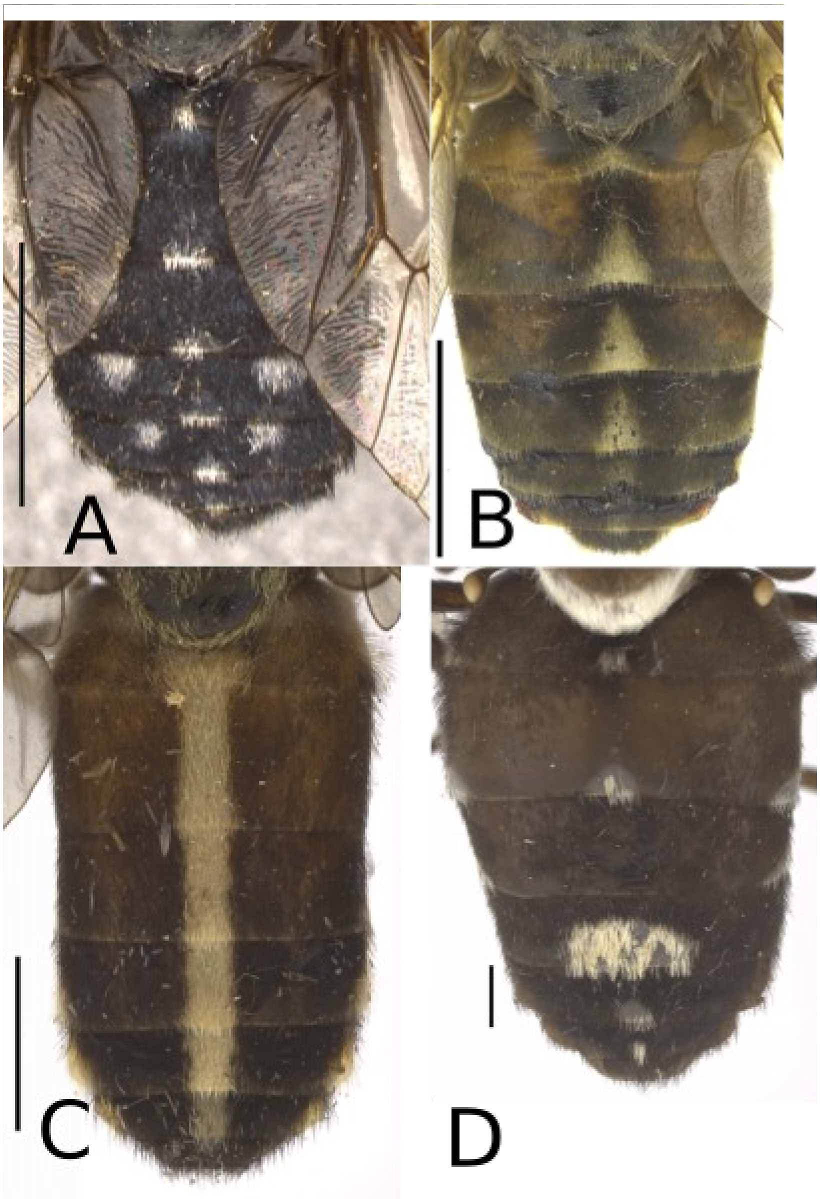

Figure 47. States of character 43. **A.** State 0 - *Tabanus angustifrons.* **B.** State 1 - *T. bovinus.* **C.** State 2 - *T. argentivittatus.* **D.** State 2 - *T. xenorhynchus.* Scale bars - A-C = 5 mm; D = 2 mm.

This is a very important character since the abdominal patterns are crucial to the identification of several *Tabanus* groups, especially the ones with striped abdomens (*occidentalis* group (Neotropical), *trivittatus* group (Neotropical) and *striatus* group (Oriental). This character refers to the vestiture pattern (pruinescence and pillosity) and not the integument color (character 38).

Character states 0 and 1 were coded as different states, because both condition are morphologically different. The triangles as defined in state 0 are comprised only by hairs, eventually with a single thin layer of pruinesce, while the triangles as defined in character state 1 have hairs and thick pruinescence. State 0 is easily lost, especially in ethanol-preserved specimens, while the triangles as defined in state 1 may resist even to clarification with caustic agents as KOH. In our analysis, the character state 2 is a synapomorphy of the clade formed by the *occidentalis* and *trivittatus* groups, with independent origins at the *striatus* group. Character state 3 is a synapomorphy of the *xenorhynchus* group (excluding *T. piceiventris*) with an independent origin in the Afrotropical species *T. marmorosus* (Fig. 61).

44 - Dorsolateral abdominal vestiture pattern. Fitch optimization. L = 11; CI = 9; RI = 69. Fig. 48
0 absent
1 present

A dorsolateral abdominal vestiture pattern appeared and disappeared several times in the evolution of *Tabanus*. The reversion of this character in species of the *trivittatus* group sustain its independence with the presence of a middorsal abdominal stripe. The character is a synapomorphy of the clade *occidentalis* + *trivittatus*, and of a clade with some species of the *pellucidus* group (*T. amazonensis* + (*T. pellucidus, T. angustifrons, T. nematocallus*) (Fig. 61).

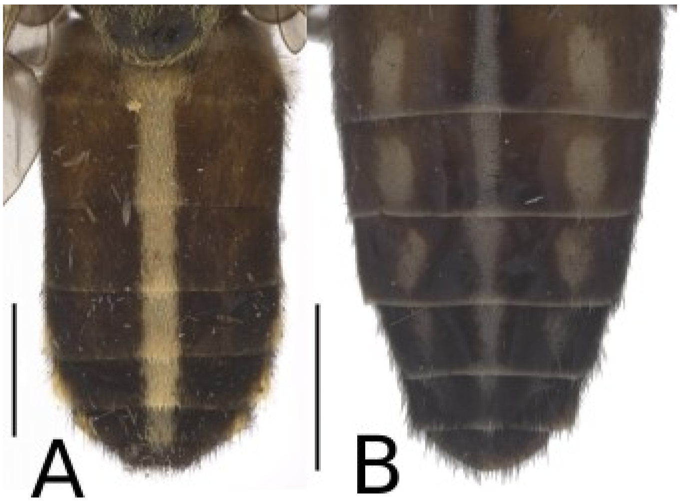

Figure 48. States of character 44. **A.** State 0 - *Tabanus argentivittatus.* **B.** State 1 - *T. sextriangulus.* Scale bars = 2 mm.

45 - Dorsolateral abdominal vestiture pattern. Fitch optimization. L = 11; CI = 9; RI = 69. Fig. 49.

0 with a pattern of pillose discrete spots or triangles
1 with a pruinose stripe

As found with the mid-dorsal abdominal stripe, the dorsolateral stripe may be formed by a thick pruinescent layer or a thin pruinescent layer. Similar the former case formation of a complete or incomplete stripe can be scored for most taxa.

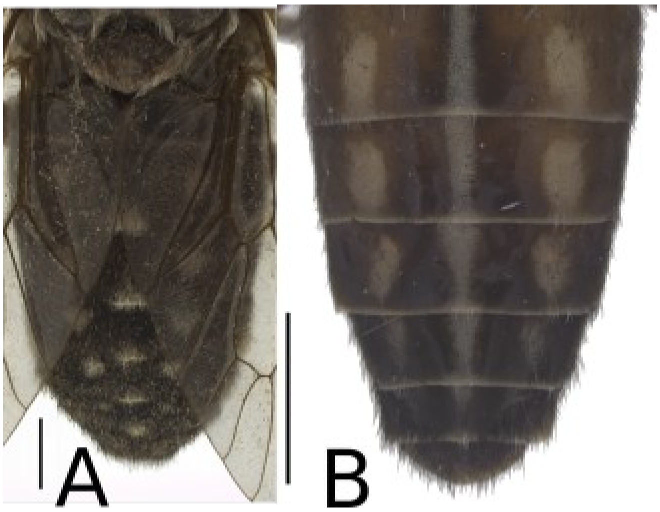

Figure 49. States of character 45. A. State 0 - *Tabanus amazonensis.* **B.** State 1 - *T. sextriangulus.* Scale bars = 2 mm.

46 - Pruinose stripe at lateral of abdominal tergites. Fitch optimization. L = 8; CI = 12; RI = 78. Fig. 50.

0 absent
1 present

This is a diagnostic feature for the *trivittatus* group (Fairchild, 1976; Carmo & Henriques, 2019). The feature is shown to be a synapomorphy for the *occidentalis* + *trivittatus* groups, an internal clade of the *pellucidus* group (*T. amazonensis* + (*T. pellucidus, T. nematocallus* and *T. angustifrons*), and also of the *striatus* group (Fig. 61), with some other independent origins. The state 1 is present in species without a complete prunescent stripe at the abdomen (as *T. amazonensis* and *T. nematocallus*). Multiple origins are evidence against dependency between character 46 and character 41.

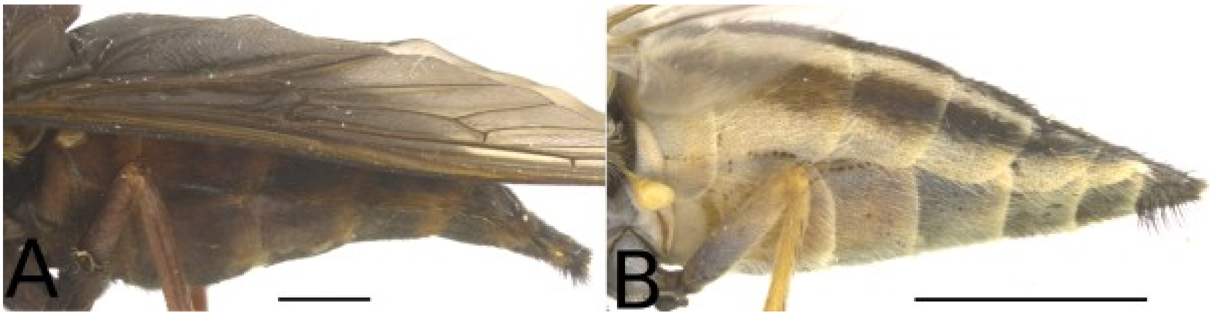

Figure 50. States of character 46. **A.** State 0 - *Tabanus fortis*. **B.** State 1 - *T. palpalis.* Scale bars = 2 mm.

47 - Pruinose bands at abdominal sternites. Fitch optimization. L = 14; CI = 7; RI = 35. Fig. 51.

0 absent
1 present

The presence of a band at the abdominal sternites is used to identify species of *Tabanus*, including those of the *trivittatus* group (Fairchild, 1976; Carmo & Henriques, 2019). This character is highly variable, with multiple independent origins throughout the genus.

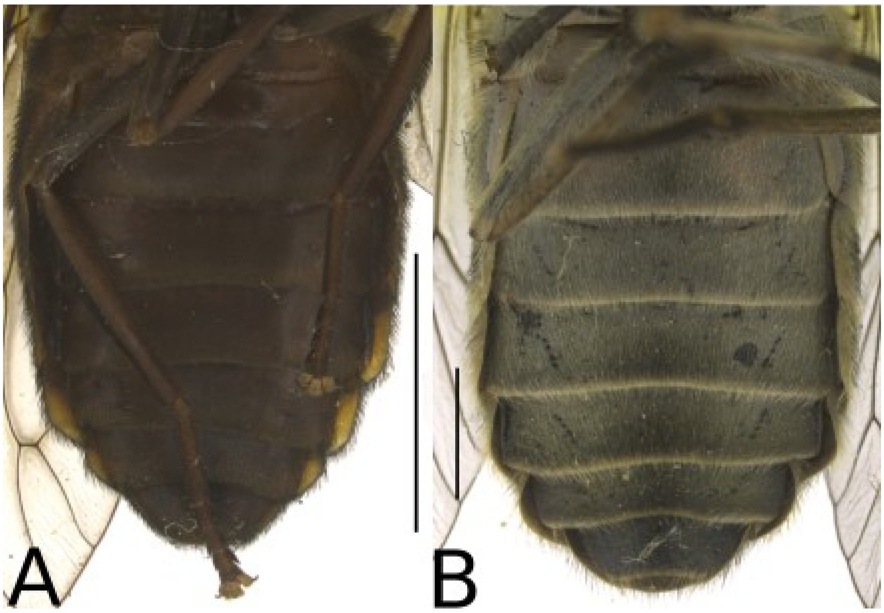

Figure 51. States of character 47. **A.** State 0 - *Tabanus ruficrus.* **B.** State 1 - *T. bromius.* Scale bars: A = 5 mm; B = 2 mm.

48 - Bands at the abdominal tergites. Fitch optimization; L = 3; CI = 33; RI = 71. Fig. 52.

0 absent
1 present

The band at the abdominal sternites is present in few species of *Tabanus*, including some species of the *iyoensis* and *bovinus* group. In the Neotropical region, this band is found in *T. vestitus* and in some species of the *oculus* group.

Figure 52. States of character 48. **A.** State 0 - *Tabanus nematocallus.* **B.** State 1 - *T. humilis.* Scale bars = 2 mm.

49 -Hypoginial valves. Fitch optimization. L = 3; CI = 33; RI = 71. Fig. 53.

0 globose
1 acuminated

Hypoginial valves globose, is the plesiomorphic condition, while the modification for an acuminated margin happens several times throughout our phylogenetic hypothesis. State 1 is synapomorphy of the *pellucidus* group (Fig. 61).

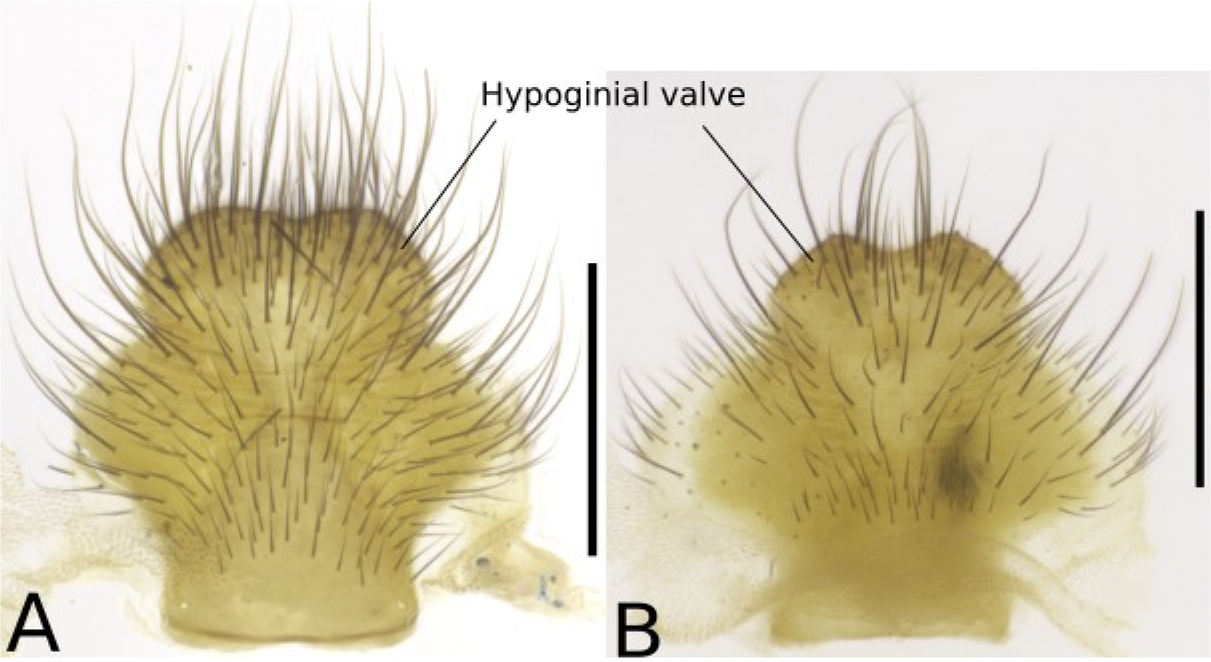

Figure 53. States of character 49. A. State 0 - *Tabanus vestitus*. ***B.*** *State 1 - T. humboldti.* Scale bars = 0.5 mm.

50 - Hypoginial valves. Fitch optimization. L = 12; CI = 8; RI = 42. Fig. 54.

0 reduced
1 pronounced

The reduced condition was observed in three species included in this analysis, *T. sufis, T. partitus* and *T. striatus*. In the reduced condition, the lobes of the structure are not discernible and the valve occupies a small portion of the sternite. Our analysis show that this character had two independent origins (Fig. 61)

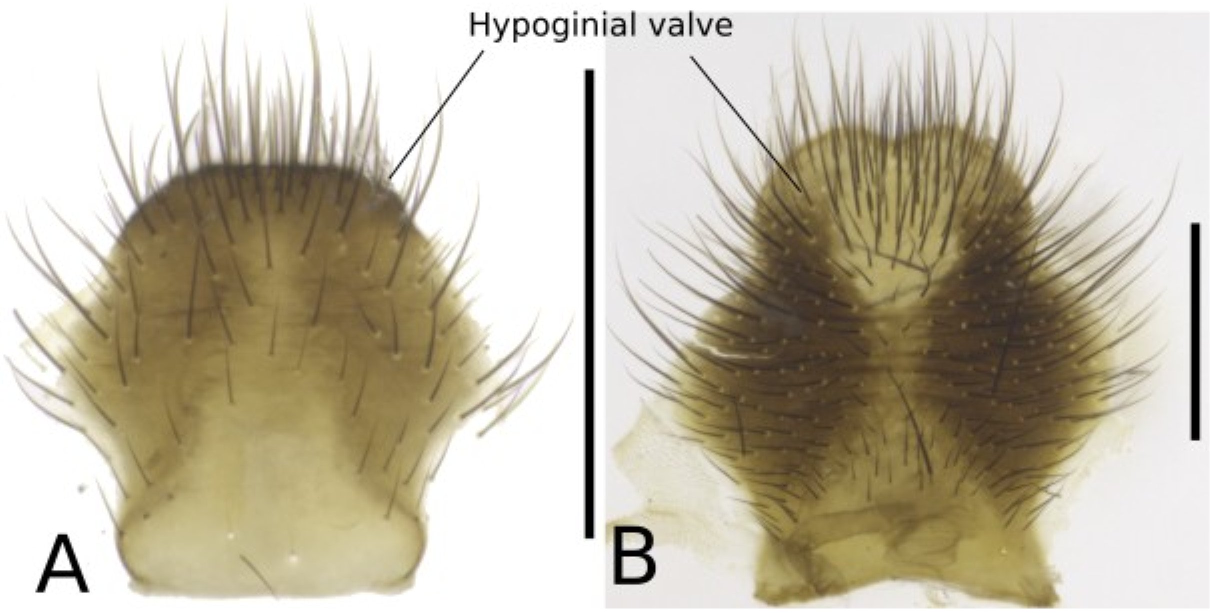

Figure 54. States of character 50. A. State 0 - *Tabanus sufis.* **B.** State 1 - *T. exoticus.* Scale bars = 0.5 mm.

51 - Position of the lateral lobes of sternite 8. Fitch optimization. L = 6; CI = 16; RI = 28. Fig. 55.

0 located at the anterior portion of the sternite
1 located at the posterior portion of the sternite

While in some species the lateral lobes of the sternite 8 are more close to the basal lobe (anterior), in other species it is close to the hypoginial valves (posterior). State 1 is synapomorphy of the *trivittatus* group, with reversals at *T. unistriatus* , *T. restrepoensis* and *T. tristichus* (Fig. 61).

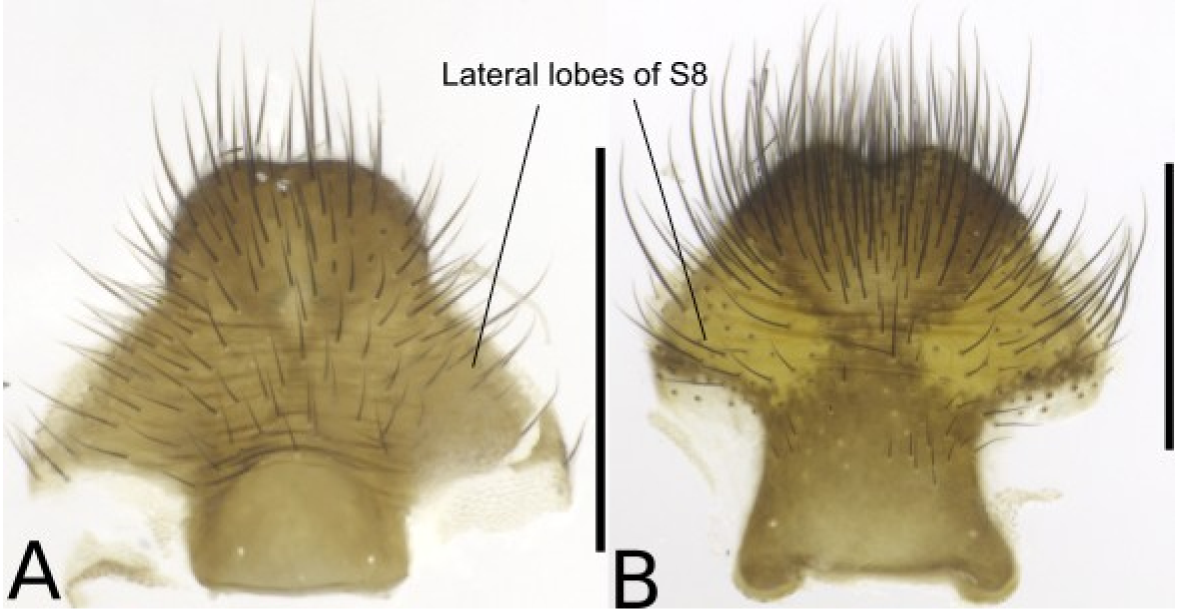

Figure 55. States of character 51. **A.** State 0 - *Tabanus callosus.* **B.** State 1 - *T. parvicallosus.* Scale bars = 0.5 mm.

52 - Pigmentation of lateral lobes of sternite 9. Fitch optimization. L = 11; CI = 9; RI = 41. Fig. 56.

0 absent
1 present

A strong pigmentation in the lateral lobes of the sternite 8 (state 1) was observed in all the Palearctic specimens of *Tabanus* and *Hybomitra* herein studied, regardless of the size of the specimen. In the Neotropical species, the pigmentation was only observed in *T. acer*. Olsufjev (1962, p. 527) and Chvála *et al*. (1972, p. 227, Fig. 65) have already observed this condition, as evidenced by their illustrations, but they did not present any further comments concerning its phylogenetic signal or taxonomic utility. This character appears in clade F (Fig. 2, Fig. 61), majorly formed by Palearctic species, with a further reversion at the clade comprised by the Neotropical *occidentalis* and *trivittatus* group.

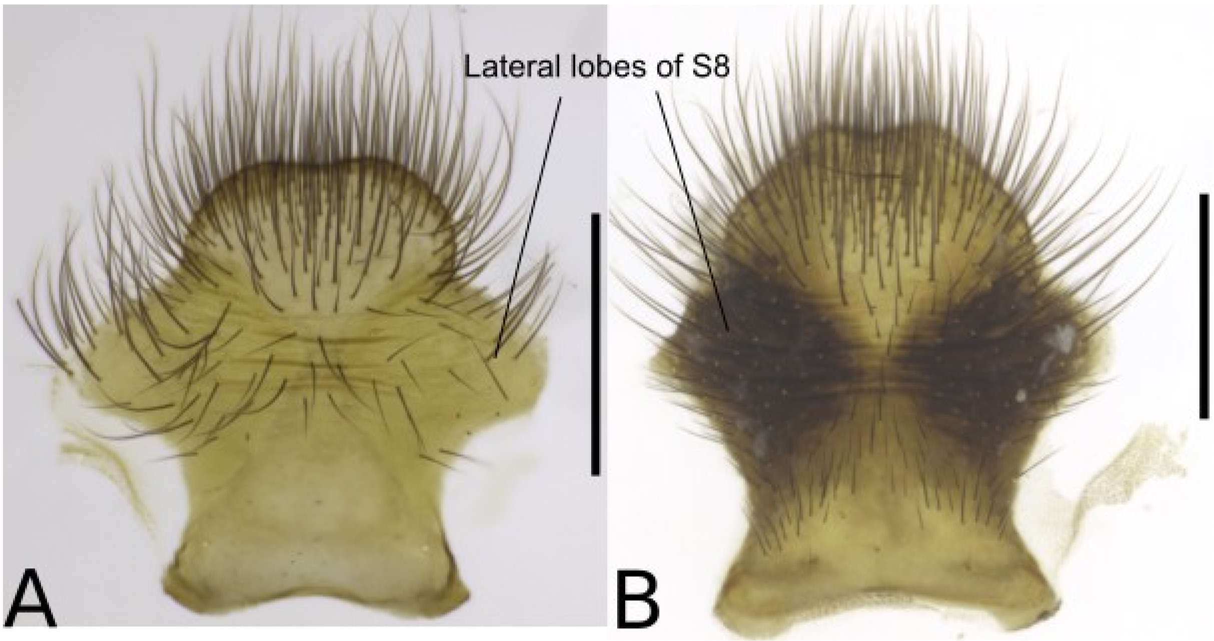

Figure 56. States of character 52. **A.** State 0 - *Tabanus indecisus.* **B.** State 1 - *T. sudeticus.* Scale bars = 0.5 mm.

53 - Globular convexity at the basal lobe of sternite 8. Fitch optimization. L = 5; CI = 20; RI = 75. Fig. 57.

0 absent
1 present

The presence of a globular convexity at the basal lobe of the sternite 8 was observed by Carmo & Henriques (2018) in a taxonomic review of the *T. trivittatus* species group. In our phylogenetic analysis this character has five independent origins, being a synapomorphy for two clades, the one comprised by species of the *trivittatus* group, and the other by some species of the *oculus* group (*T. albocirculus, T. anctarticus, T. oculus* and *T. pseudoculus*) and the species *T. amapaensis* and *T. vestitus* (Fig. 61).

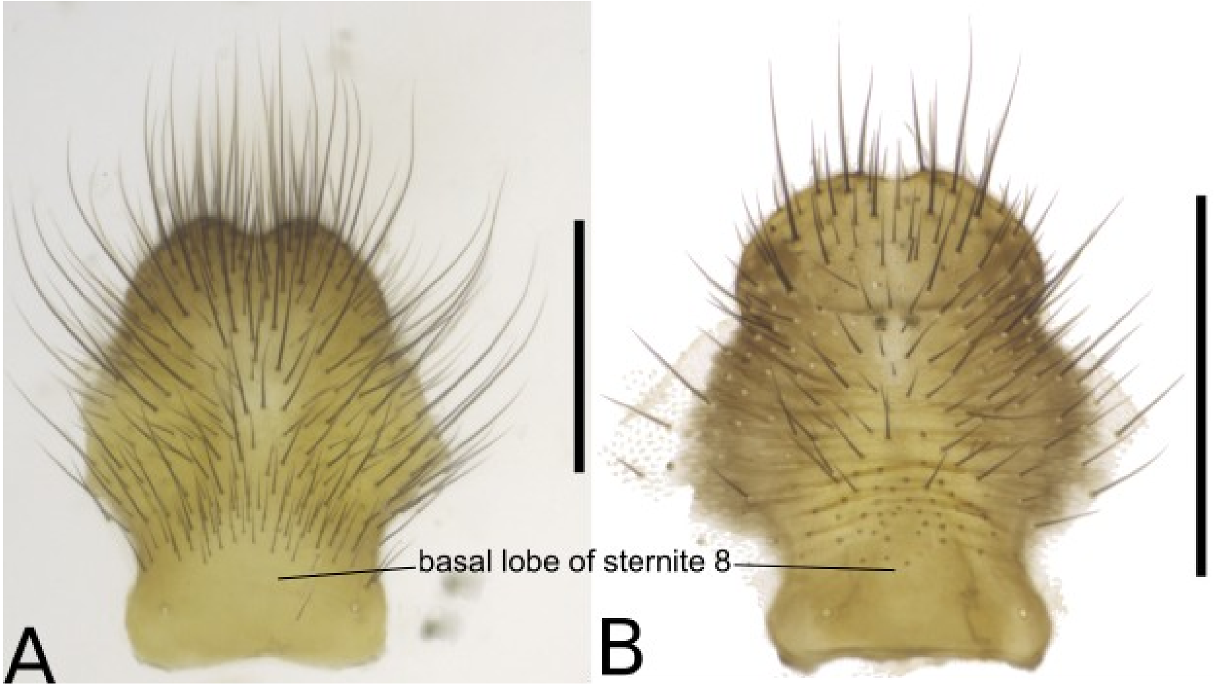

Figure 57. States of character 53. **A.** State 0 - *Tabanus pellucidus.* **B.** State 1 - *T. tristichus.* Scale bars = 0.5 mm.

54 - Lateral lobes of sternite 8 apex. Fitch optimization. L = 5; CI = 20; RI = 63. Fig. 58.

0 V shaped (forming an angle greater than 90°)
1 L shaped (forming a 90°)

In some of the studied specimens, the apex of the lateral lobes of the sternite 8 are basally dislocated giving the structure an L shape. This character appears three times in our analysis, as a synapomorphy of the *trivittatus* group, at *T. bakeri*, and at the clade *T. striatus* + *T. partitus* (Fig. 61). *T. partitus* and *T. striatus* possess the apex dislocated basally and the lateral lobes are positioned closer to the hypogynial valves, which discards the dependence between this character and character 51.

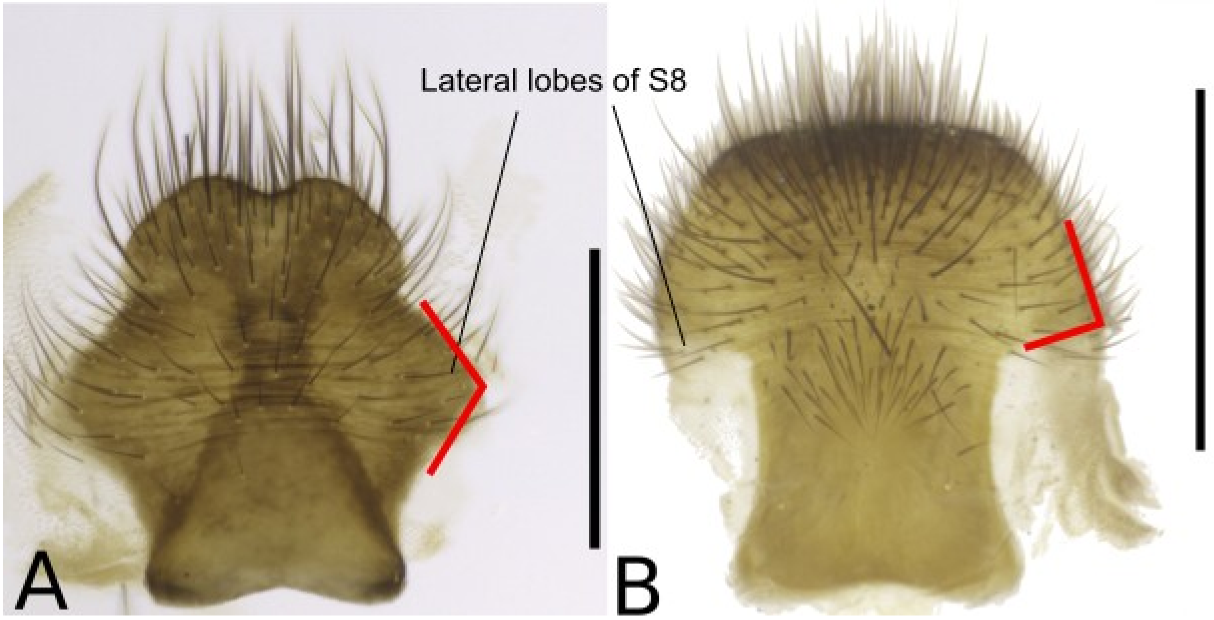

Figure 58. States of character 54. **A.** State 0 - *Tabanus fuscofasciatus.* **B.** State 1 - *T. partitus.* Scale bars = 1 mm.

Continuous characters.

Character 55. Divergence Index. Fig. 59.
Range: 0.7 to 2.8

Characters 55 is commonly used in the identification of species fo Tabanidae. The frons of the flies in the Tabanini tribe may be divergent at base, parallel or convergent at base, with several intermediate states between those extremes.

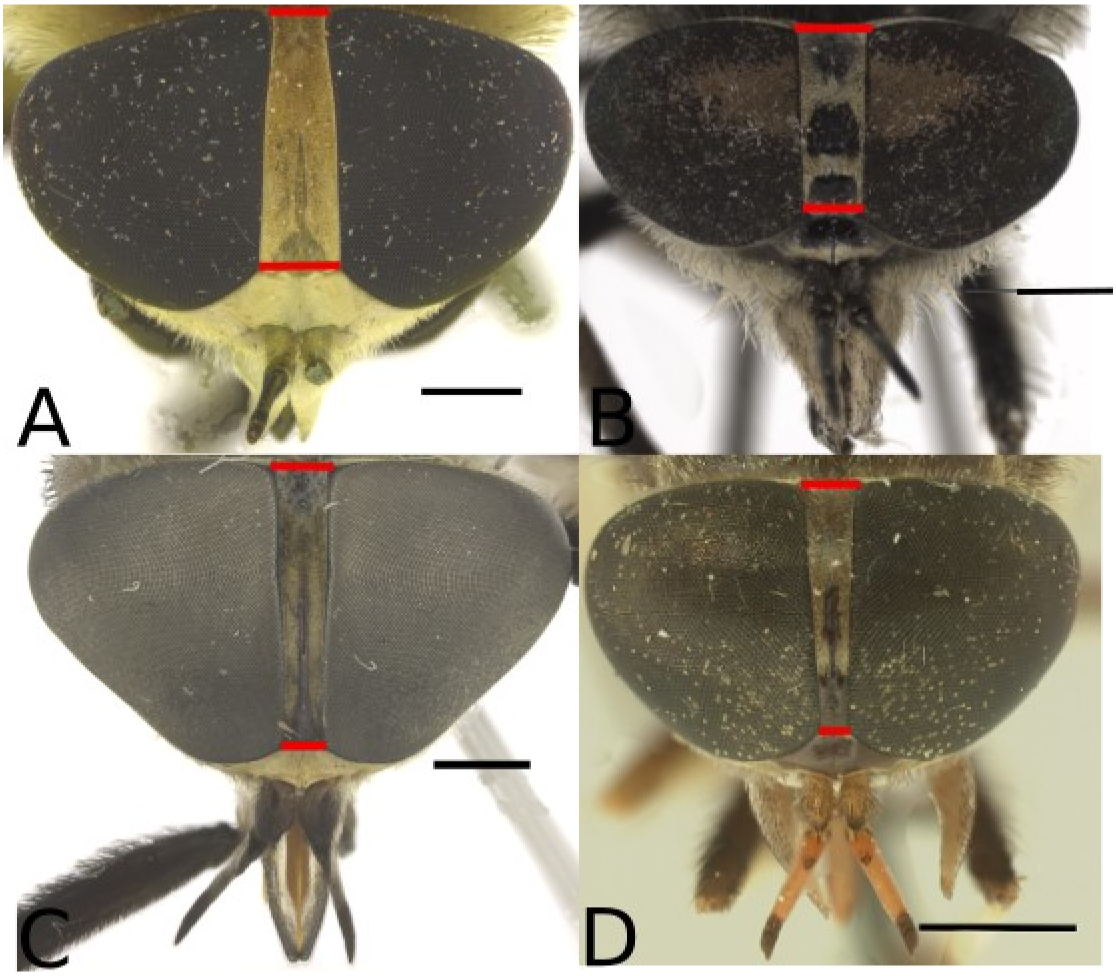

Figure 59. Measurements and some states of character 55. **A.** *Ancala fasciata* - 0.72. **B.** *Tabanus quatuornotatus* - 1.27. **C.** *T. vestitus* - 1.63. **D.** *T. unistriatus* - 2.8. Scale bars = 1 mm.

Character 56. Frontal Index. Fig. 60

Range: 2.2 to 11.6

Another measurement character used to Tabanini identification. A narrow frons is one of the character usually attributed to the genus *Tabanus*. However, examining the world tabanid fauna, it is possible to find several exceptions, as *T. sufis* (Fig. 60A).

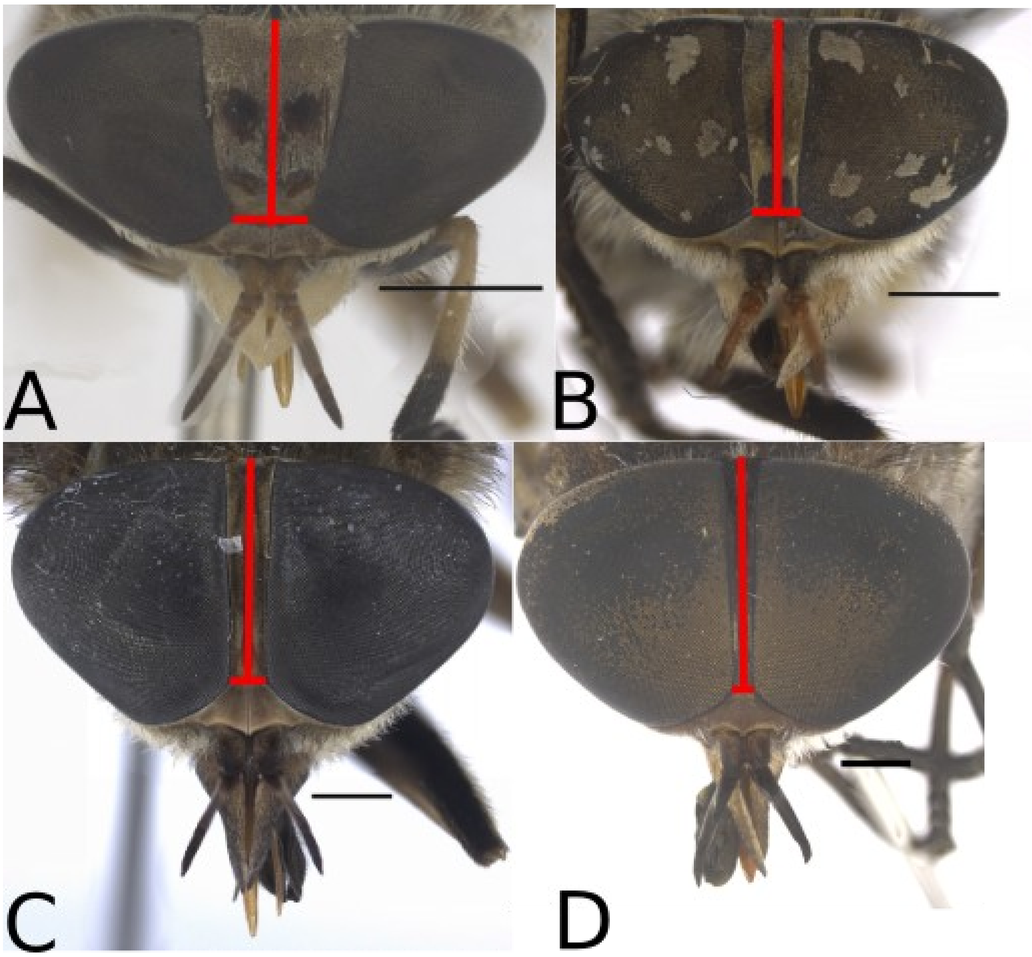

Figure 60. Measures and some character states of character 56. **A.** *Tabanus sufis* - 2.8. **B.** *T. maculicornis* - 4.6. **C.** *T. parvicallosus* - 5.6. **D**. *T. pellucidus* - 11.6. Scale bars = 1 mm.

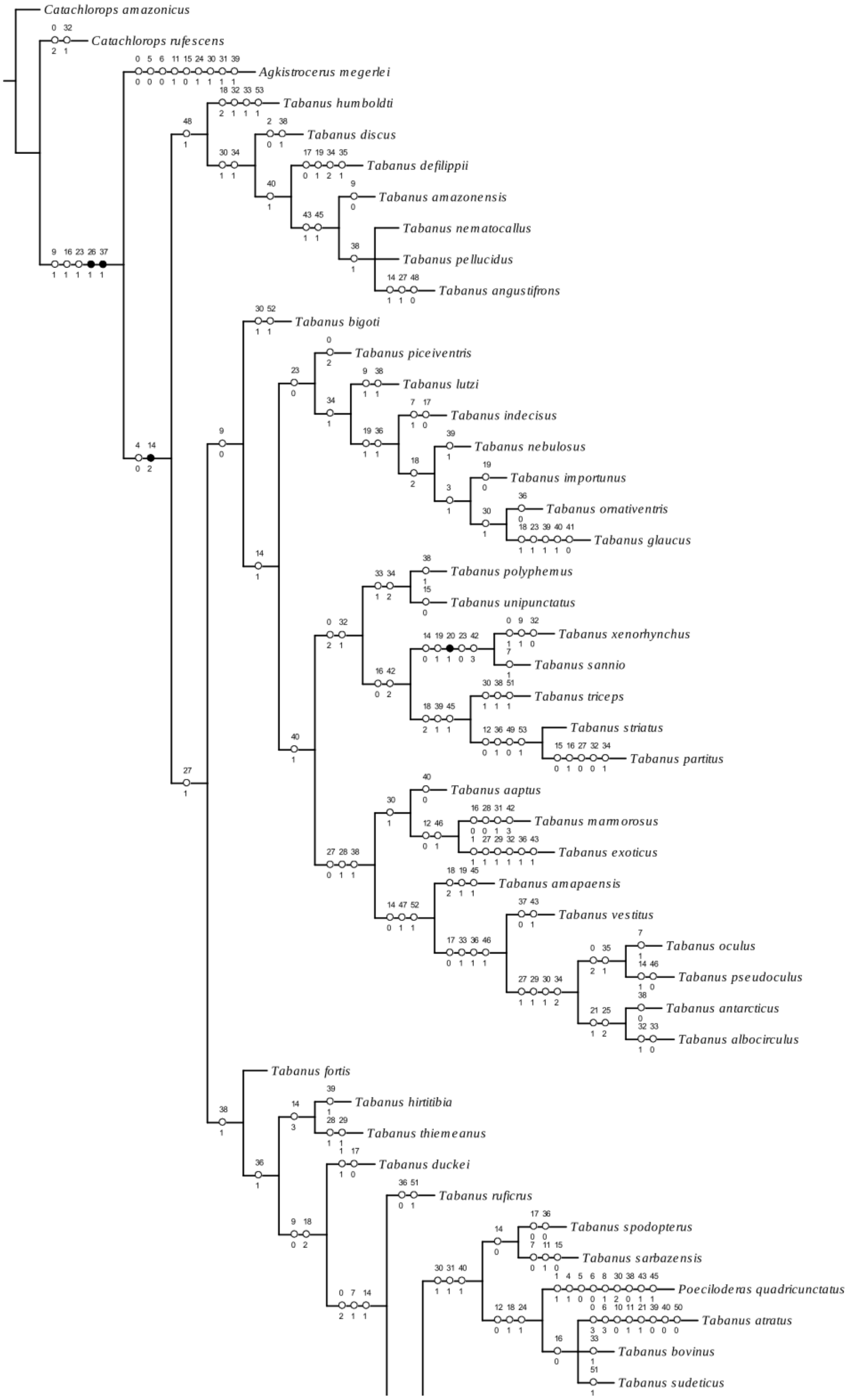

Figure 61. (cont) Strict consensus of the 40 most parsimonious trees analyzed under equal weights, with only discrete character included and character transformations plotted. Optimization was unambiguous. White circles represent homoplastic transformations, black circles represent uncontradicted transformations. Numbers above circles are character numbers, numbers below are character states.

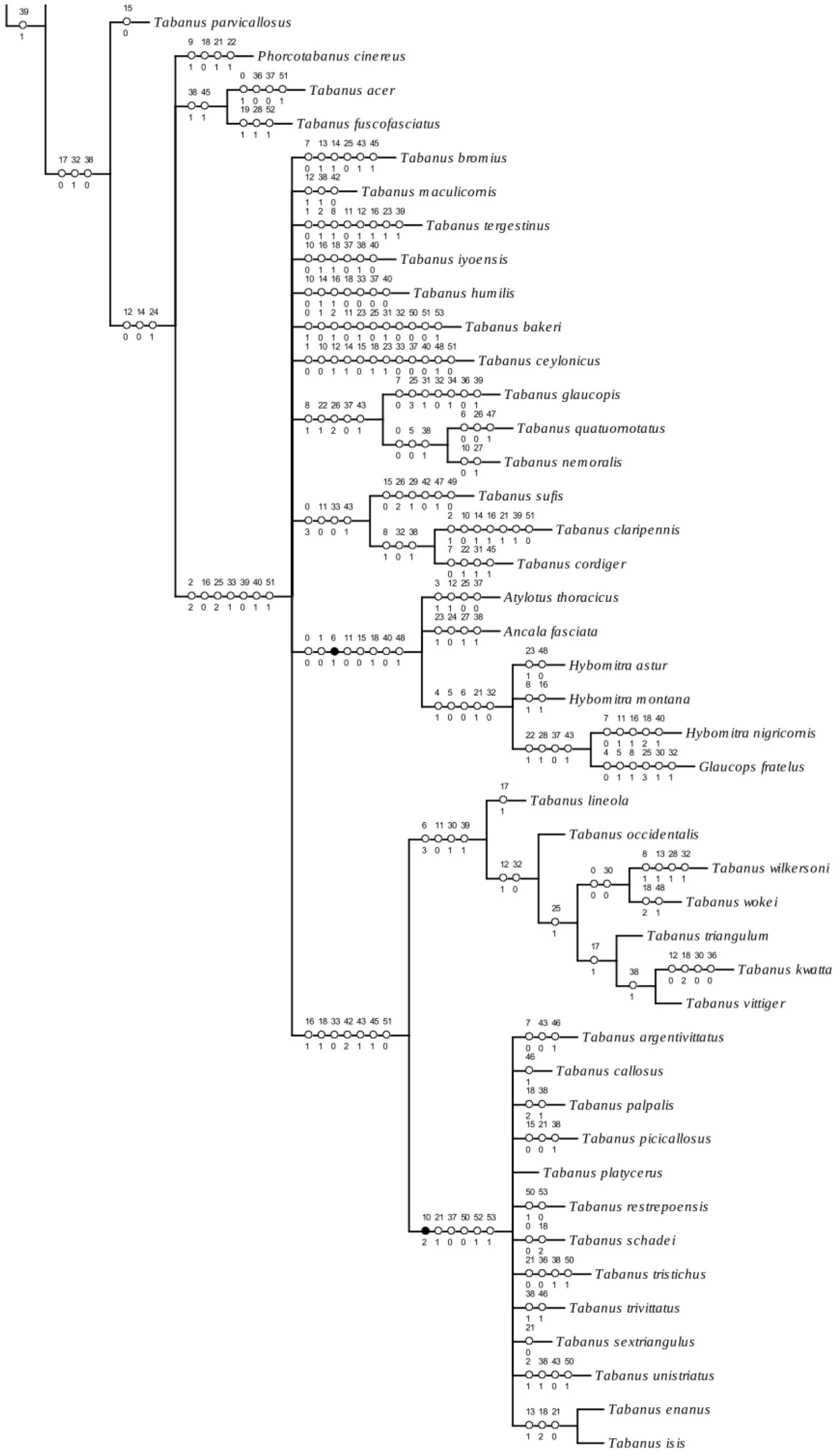

Figure 61. (cont) Strict consensus of the 40 most parsimonious trees analyzed under equal weights, with only discrete character included and character transformations plotted. Optimization was unambiguous. White circles represent homoplastic transformations, black circles represent uncontradicted transformations. Numbers above circles are character numbers, numbers below are character states.

A revised classification of Tabanus

Tabanus stricto sensu

Both our phylogenomic and morphologic datasets support the aphyly of *Tabanus* (Figs. 1 - 6), with most outgroup Tabanini species included *Tabanus*. The Palearctic species related to the *bovinus* group are more close related to other genera of Tabanini than to the Neotropical species of *Tabanus*. Our results support a new concept for *Tabanus* stricto sensu comprising species of the *bovinus* and *chrysurus* groups, both with Palearctic distribution (Fig. 1 - genomic data), and the Nearctic *T. atratus*. These are species with large bodies, unbanded and unpilose eyes.

Our morphologic data supports the inclusion of the Neotropical *P. quadripunctatus* in the group *Tabanus* s.s. This result, however, is based on highly variable characters (12(0); 18(1) and 25(1); Fig. 61), and is not supported by the genomic data. Also, the implied weighting and the Bayesian inference analyses do not support the inclusion of *Poeciloderas* in the *Tabanus* s.s. Alternatively, the genomic dataset presents *Poeciloderas* as the sister-group of *T. subsimilis* (from the *occidentalis* group). Further evidence is necessary to determine the position and status of the genus *Poeciloderas*.

The genomic dataset and the morphological analysis with continuous characters also includes *Agkistrocerus megerlei* in *Tabanus* s.s.. According to our topology based on molecular data, *A. megerlei* is the sister group of *Tabanus* (Fig. 1; clade B). Since we examined only one species of the genus *Agkistrocerus* and the genomic dataset supports a monophyletic grouping of Palearctic *Tabanus*, we chose to retain the generic status of *Agkistrocerus*, not synonymizing it with *Tabanus* until further evidence become available.

New Neotropical genera of Tabanini

Both genomic and morphological datasets support the monophyly of several Neotropical linneages of species originally included into *Tabanus* (Fig. 1 - 6). Based on this evidence, we propose four new genera, endemic to the Neotropical region.

Cephalogongylus Carmo & Henriques **gen. n.**

Type species: *Tabanus trivittatus* Fabricius, 1805

Diagnosis: Subcallus inflated, bare and shiny, pruinescent areas limited to dorsal and ventral portions. Sternites with one to three white to yellow dorsal and one lateral pruinescent and pillose stripes. Fringe of setae at hind tibia undeveloped, basal lobe of sternite 8 with a convex elevation, lateral lobes of sternite 8 located anteriorly.

Species included: *Cephalogongylus albocapillus* (Carmo & Henriques 2018), *C.aniptus* (Fairchild 1976), *C. argentrivittatus* (Fairchild 1976), *C. argentivittatus huallagensis* (Fairchild 1976), *C. callosus* (*Macquart* 1848), *C. dorsorufus* (Carmo & Henriques 2018), *C. enanus* (Fairchild 1942), *C. isis* (Fairchild 1976), *C. mackerrasi* (Henriques & Carmo 2018), *C. macrocerus* (Henriques & Carmo 2018), *C. noncallosus* (Carmo & Henriques, 2019) *C. palpalis* (Brèthes 1910), *C. picicallosus* (Fairchild 1976), *C. platycerus* (Fairchild 1976) *C. restrepoensis* (Fairchild 1942), *C. rhizonshine* (Philip 1954), *C. schadei* (Fairchild 1976), *C. sextriangulus* (Gorayeb & Rafael, 1984) *C. tristichus* (Fairchild 1976), *C. trivittatus* (Fabricius 1805) and *C. unistriatus* (Hine 1906).

This genus includes species originally placed in the *trivittatus* species group revised by Fairchild, 1976 and Carmo & Henriques, 2019. The monophyly of the group is strongly supported in our genomic (Fig. 1, Clade A; PP = 1) and in all morphological analyses (Figs. 2 - 6 Clade I). In the morphological analysis this genus is supported by five homoplastic and one unambiguous synapomorphies, 22(1) subcallus touching the eye margins character state, 38(0) fringe of hairs at posterior tibia reduced, 51(0) lateral lobes of sternite 8 localized close to the basal lobe, 53(0) a globular convexity at the basal lobe of sternite 8, 54(0) the lateral lobes of sternite 8 "V" shaped, 11(0) subcallus bare and shiny with pruinescent areas limited only to the ventral and dorsal edges of the callus (Fig. 61).

The morphological datasets support the species of the *occidentalis* group as the sister group of *Cephalogongylus*, a result not supported by the phylogenomic data in which the *oculus* group is aphyletic, with moderate support (Fig 1, Clade A. PP = 0.8). The *occidentalis* group is sustained as the sister group of *Cephalogongylus* only by homoplastic transformations, including the presence of dorsal abdominal stripes. Given the variation in the position of the genus, we decided not to include the species of *occidentalis* into *Cephalogongylus*. This is a Neotropical genus distributed from northern Mexico to Argentina.

Etymology. From greek *Cephalo* = head, *gongylus* = globe. In reference to the globose and bare subcallus.

Chelotabanus Lutz 1913 **rev. stat.**

Diagnosis. Brown to black species. Eyes unbanded. Legs unicolored. Very narrow frons (F.I. usually > 10). Cell r5 open, narrowed or closed. Postpedicel with a prominent dorsal tooth. Tergites generally with white pillose small triangles. Hypoginial valves usually globose.

Type-species. *Tabanus fuscus* Wiedemann 1819.

Species included. *Chelotabanus amazonensis* (Barretto, 1949), *Ch. angustifrons* (Macquart, 1848), *Ch. crassicornis* (Wiedemann, 1821), *Ch. discifer* (Walker, 1850), *Ch. discus* (Wiedemann, 1828) *Ch. fuscus* (Wiedemann, 1819), *Ch. humboldti* (Fairchild, 1984), *Ch. nematocallus* (Fairchild, 1984), *Ch. pellucidus* (Fabricius, 1805) and *Ch. xuthopogon* (Fairchild, 1984).

Lutz (1913) included *Chelotabanus* into a key of the subfamily Tabaninae, without designating a type-species, and based on generic characters (as the length of the entire specimen and of the abdomen). Later, Bequaert (1924) designated *T. fuscus* Wiedemann as the genus type-species. Fairchild (1951) stated that the species included by Lutz into *Chelotabanus* were *T. fuscus* Wiedemann, *T. glaucus* Wiedemann (as *T. cinerarius*) and *T. aurora* Macquart. According to Fairchild (1951), Lutz would also include *T. aurora* into another genus, *Odontotabanus* Lutz, which comprises some species later included into the *nebulosus* group (Fairchild 1984).

Our definition of the *Chelotabanus* differs from the one originally proposed by Lutz and includes species described by Fairchild as belonging to the *pellucidus* group along with *T. humboldti*. *Chelotabanus* was recovered in our genomic dataset with strong support (Fig. 1 pp = 1). In the morphological datasets, the genus is not considered monophyletic in the implied weights analysis, and in the Bayesian inference analysis, in which *Ch. humboldti* is positioned outside the group composed by the other species of *Chelotabanus* (Fig. 3 and 4). The characters supporting the monophyly of *Chelotabanus* in the morphological analysis are the accuminated shape of the hypogynial valves 50 (1), and the narrow frons (Character 57 (F.I. > 10). Our phylogenomic dataset does not support the inclusion of *T. discus* (included by Fairchild in the *pellucidus* group) into *Chelotabanus* and, instead, this species is more closely related to members of the *nebulosus* group. However, the inclusion of *T. discus* in *Chelotabanus* is supported by the morphological data (Fig.2) and the species is morphologically very different from those associated with *T. nebulosus* and therefore , we decided to keep *T. discus* as *incertae sedis* for now. Almost all the species in this genus are endemic to the Amazon basin, with only *Ch. fuscus* with distribution in the Atlantic forest of Brazil.

Rhinoderus Carmo **gen. n.**

Type-species. *Tabanus basilaris* Kröber 1931

Diagnosis. Proboscis nearly as long as the head height. Clypeus protracted ventrally, resembling a beak. Palpus flat. Contrastingly patterned wings and body.

Species included. *Rhinoderus basilaris* (Kröber 1931), *R. sannio* (Fairchild 1956), *R. subviolaceus* (Fairchild 1961), *R. unimacula* (Kröber 1934) and *R. xenorhynchus* (Fairchild 1947).

This genus is formed by species included by Fairchild into the *xenorhynchus* group, with the exception of *T. piceiventris*. The monophyly of *Rhinoderus* was recovered in all morphological analysis, being the only clade with maximum support in the morphological analysis with Bayesian inference (Fig. 3, clade H. PP = 1). The morphological analysis strongly supports the monophyly of *Rhinoderus*, which presents conspicuous diagnostic characters:a very long proboscis (state 1 of character 20), protracted clypeus (state 1 of character 21), and contrasting white pillose triangles at the tergites (state 3 of character 43). Several species of *Rhinoderus* are known to be arboreal (Fairchild, 1984) and the genus is not abundant in collections. *Rhinoderus* is distributed from Guatemala to the Atlantic Forest, in Brazil.

Etymology. From greek *Rhino* = nose, beak, and *deros* = long. The name refers to the long proboscis, uncommon in the Tabanini tribe.

Tapirotabanus Carmo **gen. n.**

Type species. *Tabanus nebulosus* Degeer 1776.

Diagnosis. Frons moderately narrowed (F.I. between 4.7 and 8), convergent to slightly divergent bellow (D.I. between 0.9 and 1.7). Callus usually clavate. Prominent black spot at the prescutelum (never at scutellum), usually surrounded by white hairs. Proboscis sometimes as long as head height or the palpus very short.

Species included. *Tapirotabanus comosus* (Stone, 1944), *Tap. corpulentus* (Brèthes, 1910), *Tap. glaucus* (Wiedemann, 1819), *Tap. guyanensis* (Macquart, 1846), *Tap. importunus* (Wiedemann, 1828), *Tap. indecisus* (Bigot, 1892), *Tap. lutzi* (Kröber 1934). *Tap. nebulosus* (DeGeer, 1776), *Tap. nebulosus ornativentris* (Kröber, 1929), *Tap. olivaceiventris* (Macquart, 1847), *Tap. piceiventris* (Rondani, 1848).

This genus is composed largely by the species included by Fairchild (1984) into the *nebulosus* species group. The genus has high support in the phylogenomic dataset (Fig. 1, Clade D. PP = 1). In the morphological dataset, *Tapirotabanus* is supported in all the different optimality criteria employed. *Tapirotabanus* is supported by a homoplasious character state, the angle of the occiput (state 0 of character 24), and by the presence of an incomplete scutellar circle (state 1 of character 34), which is absent only in *T. piceiventris*. Other characters present in *Tapirotabanus*, as the long proboscis - 20(1) - and the short palpi - 4(0) - are highly homoplastic.

Our genomic dataset supports the inclusion of *T. discus* and *T. defilippii* into *Tapirotabanus* (Fig. 1). However, the inclusion of this species in *Tapirotabanus* was not recovered in our morphological datasets since both species are very distinct morphologically from the other species included in *Tapirotabanus*, and therefore we decided not to include this species in the genus.

Etymology. From latim *Tapirus* = tapir, *tabanus* = fly. The name is given to honor the way some Traditional Amazonian communities refer to large horse flies, '*mutuca'* (brazilian portuguese word for horse fly) '*anta'* (brazilian portuguese for tapir).

Monophyletic lineages of Tabanus not elevated to generic rank

The occidentalis group

The *occidentalis* group (*lineola* sensu Philip and Fairchild) is composed by Neotropical and Nearctic species, with *T. occidentalis* possessing broad distribution in the Neotropical region, from northern Mexico to southern Argentina. The species are very similar, and there are few external or internal characters that effectively differentiate between species, which makes the stable resolution of thetaxonomy of the group an arduous task. In our morphological dataset the species of this group are recovered as related to *Cephalogongylus* gen. n. being aphyletic to the genus in some scenarios (Fig. 2 – 6). Unfortunately, in our genomics dataset we have been able to sequence data for only one species of this group, the Nearctic, *T. subsimilis*. Nevertheless the genomic data supports this species as the sister group to the Neotropical genus *Poeciloderas* with strong support (Fig. 1. PP = 1), an hypothesis that must be further investigated. Given the differences in molecular and morphological hypotheses, and the possibility of the relationship with *Poeciloderas* we decided not to change the status of those species, until further evidence is available.

The. oculus group

The subgenus *Lophotabanus* Szilady, (1926), included several species with black spot at the scutellum and prescutelum. Later, Fairchild, (1942) redefined the subgenus to include only species with a complete black circle at the scutellum, and synonymized *Lophotabanus* with *Bellardia* Rondani a name found by Strand, (1928) to be preoccupied. Strand, then, create the name *Bellaria* Strand to allocate the species of the subgenus. The great morphological variation found in the species included in *Bellaria* and the difficulty in delimiting subgeneric groups within *Tabanus* made Fairchild, (1969) abandon the subgeneric group altogether and also stating that the *oculus* group was probably an artificial agroupment.

In our analysis the *oculus* group is recovered as aphyletic in most cases, and one subgroup is constantly recovered monophyletic, the group formed by *T. oculus*, *T. albocirculus*, *T. antarcticus* and *T. pseudoculus*. In the phylogenomic dataset this group is aphyletic (only *T. oculus, T. albocirculus* and *T. antarcticus* were included) to *Cephalogongylus* gen. n. (Fig. 1), however, with only moderate support (PP = 0.8) and the group could be monophyletic. In the phylogenomic analysis, *T. defilippii* is included in a clade within *Tapirotabanus* gen. n. In the implied weighting analysis, or when continuous characters are included, the *oculus* group is monophyletic, with the inclusion of *T. vestitus* and *T. amapaensis*, which lack the black circle at the scutellum.

We refrain from name this taxa at this moment, first because of the variation at the position of several species between the different hypothesis obtained and also the morphologic dissimilarity of those species with the clades they are included (as *T. defilippii* within *Tapirotabanus* (Fig.1) and *T. polyphemus* and *T. unipunctatus* with the *Rhinoderus* (Fig. 3, Clade D)). Given our results, we are convinced of the monophyly of at least (*T. oculus, T. antarcticus*, *T. pseudoculus*, *T. albocirculus*), however, it may be premature to name this groupement at this point.

T<u>he bigoti group</u>

In all our analysis *T. hirtitibia* and *T. thiemeanus* are shown to be sister groups, and this clade has high support in the phylogenomic analysis (Fig. 1. PP = 1). Fairchild (1964) included the species he thought related to *T. bigoti* in the subgenus *Chelotabanus* Lutz, an groupment not recovered in any of our analysis and abandoned in subsequent works by Fairchild himself. Later (Fairchild, 1984) in the list of species excluded from his work of larger *Tabanus* of eastern South America, he add a brief comment to the species *T. hirtitibia*, *T. thiemeanus*, *T. surifer* Fairchild and *T. weyrauchi* Barreto, that those species are related to *T. bigoti*. Our morphological analysis did not retrieved the relationship between *T. bigoti* and the clade formed by *T. hirtitibia* and *T. thiemeanus* (Figs. 2 – 6). The *bigoti* group, as other groups of *Tabanus* has been proposed only on taxonomical grounds, and the characters of the group are highly variable, with polymorphism being observed in the species. The sister group relation of *T. hirtitibia* and *T. thiemeanus* is sustained by one synapomorphy, the very long tooth of the antennae, with nearly the same size as the postpedicel, a character also shared by *T. weyrauchi* and *T. surifer*. At least part of the species originally included in the *bigoti* group might constitute a monophyletic group, which may be given generic status, however, the inclusion of more taxa is necessary in further analysis.

The quatuornotatus and glaucopis groups

These are two Palearctic groups of *Tabanus* which possess similar traits as the pillose eyes 6(0), and only sparse few setae at the basicosta 28(2). Chvála *et al.*, (1972) suspected that those two groups were related, and that at least the *quatuornotatus* group should be subgenerically separated from the other species within *Tabanus*. Our morphological dataset offers support for the hypothesis of Chvála *et al*., (1972), however the low taxon sampling of both groups included here, our sparse knowledge of the Palearctic fauna and the absence of molecular evidence, lead us to take a more cautionary approach with these taxa and refrain from making any new generic assingments.

The striatus group.

This group was revised by Burger & Thompson (1981) and includes three Oriental species with striped abdomens (*T. striatus*, *T. partitus* and *T. triceps*). Our morphologic results supports this group as monophyletic with three homoplastic transformations, the antennal style nearly as long as postpedicel 19(2), and the presence of stripes at abdominal tergites 41(1) and 47(1).

We decided to keep this group in *Tabanus* since our sample of the Oriental region is low, and the knowledge of horse flies in the region still needs great taxonomic effort. Consequently, no classificatory changes will be made before more deeply sampled phylogenetic and taxonomic studies of the fauna can proceed.

Origin and Distribution of the Tabanus group

Our divergence times estimation analysis places the split between the tribes Diachlorini and Tabanini between the end of the Paleocene and the beginning of the Eocene (50 - 55 MYA) (Fig. 63), a result congruent with the hypotheses obtained by Lessard *et al.,* (2013) and Morita *et al.,* (2016). The modern clades of Tabanini begin their radiation between the mid Eocene and early Oligocene (50 - 30 MYA). The *Tabanus* stricto sensu (*A. megerlei* (*T. chrysurus* (*T. sudeticus* + *T. bovinus*) diverges between the mid Oligocene and the mid Miocene (27 - 12 MYA), while the split between *T. bovinus* and *T. sudeticus* is at the Pliocene.

The randomness of dispersion events (*i.e.* the transposition of a barrier by a group of organisms) and the consequent difficulty to infer such hypothesis, lead, for a preference of vicariance events in biogeographic reconstructions. In a vicariance event, the origin of a barrier, isolate individuals of the same population causing speciation In this context, a Mesozoic distribution, evoking the breaking up o Gondwana is usually the favored explanation for organisms with worldwide distribution, such as *Tabanus* and the family Tabanini. Our phylogenetic analysis suggests a much younger origin for Tabanini, in the

Palaeogene, which is congruent with previous phylogenetic analysis of Tabanidae. A similar pattern may also be observed in other insect groups widespread distributed, such as muscid flies (Haseyama *et al*., 2015) and bumble bees (Hines, 2008).

The divergence times estimation supports an Neotropical origin for the Tabanini group, between the end of the Paleocene and the beginning of the Eocene. In such scenario, the lineage which gave origin to the Tabanini currently distributed through other zoogeographical regions (Afrotropical, Australian, Palearctic and Oriental regions) diverged from the Neotropical fauna in the interval of the early to mid Eocene (53 - 42 MY). During this time, Antarctica was still connected to South America, and the weather was warm and humid, very similar to what is found today in the Atlantic Forest, as evidenced by subtropical plant fossils (Le Roux, 2012). The favorable weather, corresponding with the flourishing diversity of flowering plants (Le Roux, 2012) and ungulate vertebrate hosts (Gelfo *et al*., 2015) in the Antarctic continent possibly allowed Tabanini horse flies to colonize the continent with later dispersal to Australia and then to other regions. Mackerras (1971) comments on the morphological similarities between Australian and Oriental *Tabanus* fauna, with at least *T. serus* Walker being found in both Australia, Indonesia and Papua New Guinea. This, associated with the high flight capabilities of horse flies, indicate that colonization of the Oriental region through Australia may have occurred. During the mid of the Eocene (~41 MA), the subtropical weather in Antarctica was replaced by a more temperate one (Le Roux, 2012) as evidenced by fossil plants. This climate change coincides with the age of the separation of the non Neotropical clade from Neotropical fauna, and could be a driver of extinction and speciation. The separation of Antarctica from both Australia (~35 MYA) and South America (35 - 30 MYA) (Mcloughlin, 2001) and the consequent cooling of Antarctica (McLoughlin, 2001; Le Roux, 2012) would have caused further extinctions and isolated populations from South America and Australia, possibly leading diversification of both Neotropical and non Neotropical clades (Fig. 62).

Alternatively, both biological (Ezcurra & Agnolín, 2012) and geological data (Kastens *et al*., 1998; Markwick & Valdez, 2004) suggests a reconnection between Africa and South America, during the Eocene by the existence of a chain of large volcanic islands. Such islands would allow the colonization of other biogeographical regions by the Tabanini flies, with isolation of populations of different regions when the islands disappeared at the end of the Eocene

(Ezcurra & Agnolín, 2012). An amalgam of both hypothesis could also explain the diversification of tribe.

Cladogenesis of most Neotropical lineages of Tabanini started between the Eocene (55.8 - 33.9 MYA) and the Oligocene (33.9 - 23 MYA), with increased diversification and appearance of most Amazonian modern clades starting in the Miocene (23 - 5.3 MYA) until the end of the Pliocene (5.3 - 2.6 MYA). *Rhinoderus* gen. n. diverge from the reciprocally monophyletic *Tapirotabanus* gen. n. and *Chelotabanus* stat. n. between the early Eocene, and mid Oligocene. *Ch. amazonensis* diverge from the remaining species of *Chelotabanus* between the early Oligocene and mid Miocene, while most species of the genus diverge during the Miocene with recent species *Ch. pellucidus* and *Ch. nematocallus* splitting between the end of the Miocene and end of the Pliocene. *Tapirotabanus* is more recent, and cladogenesis and diversification happened in the Miocene, with the divergence between *Tap. piceiventris* and *Tap. importunus* in the Miocene/Pliocene boundary. *Cephalogongylus* gen. n. diverged entirely during the Miocene, along with *T. hirtitibia* and *T. thiemeanus*. During the beginning of the Oligocene, the region that today comprises Amazonia was connected to the Andes and southern South America in the so-called “Pan-Amazonia”. At the same time the rise in the sea level caused marine transgressions through the Llanos basin (present Venezuela). With the beginning of the Miocene (~23 MYA) there is the beginning of mountain building in Central and North Andes, at the same time that climatic changes contributed to the formation of the Pebas System, a system of shallow lakes and swamps (Wesselingh & Salo, 2006; Hoorn *et al.*, 2010). There was intense orogeny in the region, at the same time that the Pebas system isolated populations from the Andean region and the Guyana shield. Those phenomena are pointed as responsible for the diversification of several animal groups such as mollusks (Wesselingh & Salo, 2006), geckos (Gamble *et al.*, 2008), killifish (Bragança & Costa, 2018), armadillos, anteaters and sloths (Delsuc *et al.*, 2004). The changing of Amazonia from the Pebas lacustrine system to a fluvial one at the end of the Miocene and through the Pliocene, create new lowlands habitats that could be colonized by the formed species. Most horse flies have habitat preferences due to restricted larval habits (Fairchild, 1981) and therefore the formation of the Pebas system, in association with the intense orogeny in the region could have acted as vicariant events, which may have contributed to the diversification of Tabanini during the Miocene.

T. antarcticus and *T. albocirculus* are two very similar species from the *oculus* group. Color characters and the morphology of the male are the only characters used to identify the species, and specimens of *T. albocirculus* found at south of Central America are more paler and therefore similar to *T. antarcticus* specimens (Fairchild, 1986). In our hypothesis, the divergence of both species is synchronous with intense orogeny in Central and North Andes (Hoorn *et al.*, 2010), and is tempting to point this as responsible for divergence of both species.

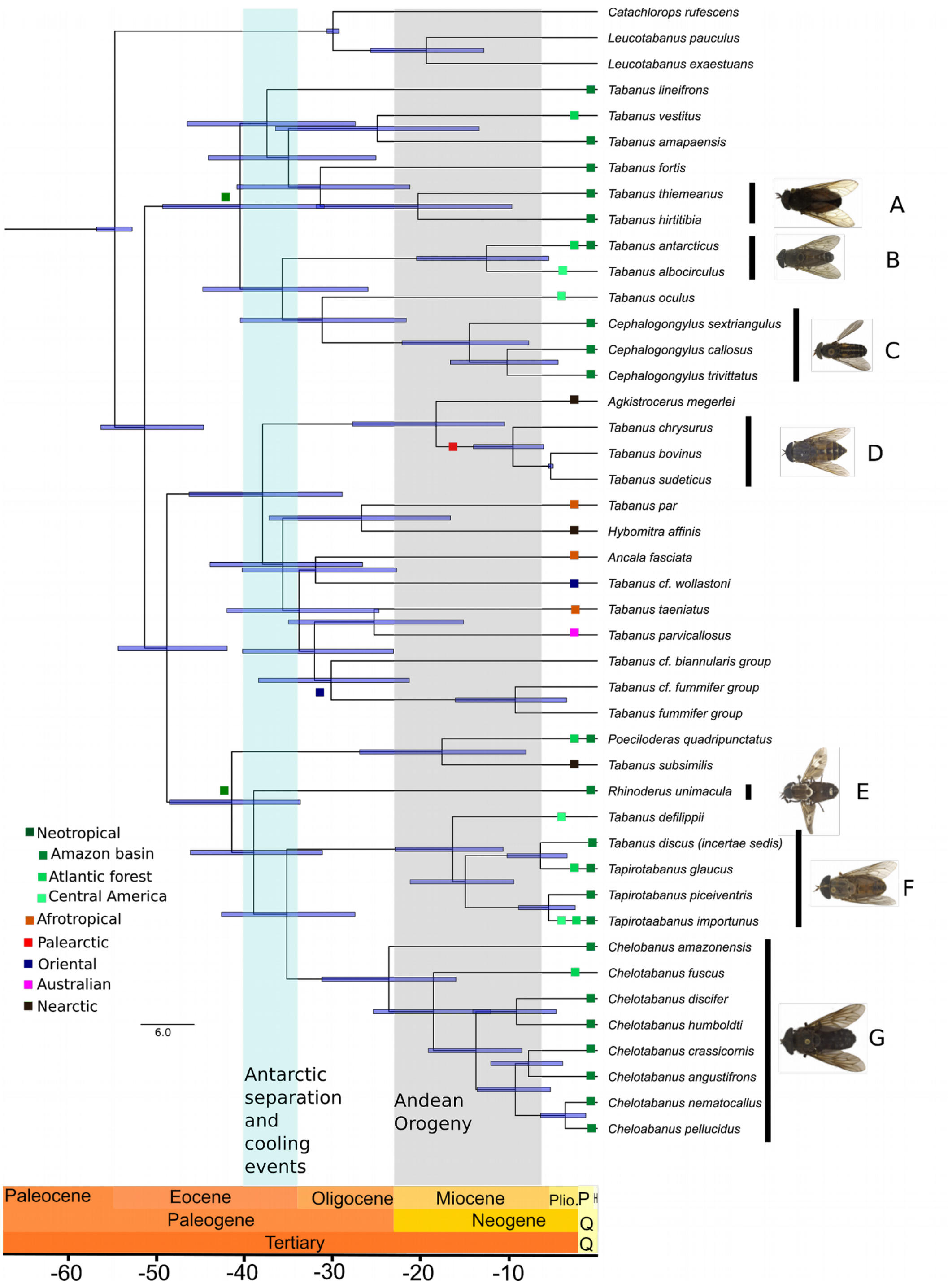

Figure 62. Divergence times estimation of the Tabanus group using BEAST2. Blue bars at nodes represent the height 95% HPD intervals. Scale bars are in million years. Photos are of *Tabanus* species groups discussed in the text and new Neotropical genera described. **A.** *Tabanus bigoti* group. **B.** *T. oculus* group (part). **C.** *Cephalogongylus* gen. n. **D.** *Tabanus* stricto sensu. **E.** *Rhinoderus* gen.n. **F.** *Tapirotabanus* gen.n. **G.** *Chelotabanus* Lutz stat. rev. Blue vertical shade represent Antarctic separation and climatic changes. Grey vertical shade represent Andean orogeny events and change from the lacustrine Pebas system to a fluvial system at Amazon basin.

Conclusions

This is the first attempt to resolve the complex phylogenetic diversity of *Tabanus* and associated species of Tabanini using phylogenetic methods with a broader representation of sampled species. Despite differences in our resulting trees, especially among the basal nodes, and in the internal relationships found by morphological and phylogenomic datasets, most groups-level clades were supported in both analysis (*e.g. Cephalogongylys* gen. n, *Chelotabanus* gen. n, *Tapirotabanus* gen.n). Morrphological based clades had stability were nearly all recovered under both of the optimality criteria employed. The non-monophyly of *Tabanus* and the evidence that the true genus is probably Holarctic in its distribution open new interesting lines for both future phylogenetic and taxonomic research. Analysis with *Tabanus* should continue to be undertaken in the years to come, focusing on species of other zoogeographical regions and even expanding the Neotropical sampling. The increasing facility to obtain nucleotide phylogenomic and transcriptomic data undoubtedly will greatly improve our capability of understanding the evolution of *Tabanus* and other complex groups, however, the results presented here shows that despite being highly variable, morphological characters posses phylogenetic signal and the use of such characters in conjunction with modern molecular techniques is probably the most robust way of true disentangling the history of organisms in its three dimensions, form, time and space.

Finally the discovery of Oligocene/Miocene origins for the new genera with Amazonian distribution described in this work adds to the expanding list of diverse groups (as killifish, mammals and mollusks) which share a similar biogeographic history. Divergence times estimation and biogeographical information for insects unfortunately remains relatively scarce for many organisms found in the Amazonian region. Future research using horse flies or other insect groups as models will be invaluable for increasing our evolutionary understanding of South American fauna.

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Capítulo 2

Carmo, D.D.D. & Henriques, A.L.Taxonomy of *Tabanus-trivittatus* species group (Diptera: Tabanidae) with the description of five new species. Manuscrito aceito para publicação no periódico Zootaxa

Taxonomy of *Tabanus trivittatus* species-group (Diptera: Tabanidae), with the descriptions of five new species

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Abstract

The group of species related to *Tabanus trivittatus* include horse flies with striped abdomens and partially bare, inflated, subcallus. Herein we describe five new species and raise the number of valid species from 15 to 20, four of which occur in Brazil: *T. albocapilus* **sp. n.,** *T. dorsorufus* **sp. n.,** *T. mackerrasi* **sp. n.,** *T. macrocerus* **sp. n.** and one that occur in Brazil, Bolivia and Peru: *T. noncallosus* **sp. n.** We also modified the keys from Fairchild (1976) for both sexes and briefly discuss the female genitalia.

Key words: horse flies, Neotropics, new taxa, Tabanini

Introduction

Tabanus Linnaeus, the most species rich genus in the Tabanidae family, includes nearly 1350 (Pape & Tompson 2013) valid species, comprising nearly one third of all horse fly species distributed in all biogeographic regions. However, there is still much work to be done concerning the genus taxonomy and systematics, and for long it has been suspected that the genus is not monophyletic (*e.g.* Oldroyd 1959; Burger 2009).

Historically recognized as a difficult taxon (Oldroyd 1954; Fairchild 1976; 1984; Morita *et al*. 2016), a great number of Tabanini genera used to be *Tabanus* (*e.g. Agkistrocerus* Philip, *Atylotus* Osten Sacken, *Hybomitra* Enderlein, *Poeciloderas* Lutz*, Therioplectes* Zeller). Several authors attempted to address the *Tabanus* problem and a majority of species are divided into species groups (see Oldroyd (1954) for Afrotropical region; Chvála *et al.* (1972) for Palearctic region; Mackerras (1971) for Australian region and Fairchild (1942, 1964, 1976, 1983, 1984 for Neotropical region), despite the fact that no phylogenetic studies address the validity of such groups.

The *Tabanus trivittatus* species-group contains 15 valid species and one subspecies, ranging from Mexico to Argentina. This species-group was revised by Fairchild (1976), and includes Neotropical *Tabanus* with striped abdomens, three green eye bands (only visible in living specimens), frons divergent above and at least partially bare, shiny, inflated subcallus, lateral of abdominal tergites pale with pale hairs, a globular convexity at the base of sternite 8 and lateral lobes located at the medial and anterior portion of the plate. The morphology of the species is quite uniform and both molecular and morphological evidence supports it as a natural group inside the genus (D.D.D. Carmo, unpublished data).

Herein, we present a study of *Tabanus trivittatus* and related species, describing five new species, of which four occur in Brazil and one occurs in Brazil, Bolivia and Peru.

Material & Methods

Terminology follows Cumming & Wood (2017). We received specimens deposited in the following collections – Coleção de Entomologia da Universidade Federal do Tocantins (CEUFT), Museu de Zoologia da Universidade de São Paulo (MZUSP), Instituto Nacional de Pesquisas da Amazônia (INPA) and Museu Paraense Emilio Goeldi (MPEG). The collections of the Florida State Collection of Arthropods (FSCA) and National Museum of Natural History (USNM) were visited by the first author. The American Museum of Natural History (AMNH) was visited by the second author. Primary types were examined for two species, *T. schadei* Fairchild and *T. sextriangulus* Gorayeb & Rafael. The holotype of *T. argentivittatus* huallagensis Fairchild, T. *platycerus* Fairchild and *T. picicallosus* Fairchild was observed through photos available at the database of the Harvard Museum of Comparative Zoology. We examined the paratypes of *T. aniptus* Fairchild*, T. argentivittatus* Fairchild, *T. picicallosus* Fairchild, *T. tristichus* Fairchild.

We macerated the genitalia in KOH 10%, neutralized with acetic acid, and stored them in glycerin. To visualize the integument we moistened the specimen with a drop of ethanol 95%, as described in Lutz (1907).

We elaborated maps using the software QuantumGiz (Quantum Giz development team). Geographic coordinates were obtained from the literature, available under the synonymy list of each species, or directly from labels of specimens. Geographic coordinates were used when available, when not, we approximate the coordinates to the smallest political level.

Results

Key for females of *Tabanus trivittatus* species-group. Adapted from Fairchild (1976)

1 Subcallus largely pruinescent, bare areas reduced to patches above each antennal base, separated by a median pruinescent stripe (Fig. 10C). Abdomen acutely pointed. All coxae, fore femur and at least bases of remaining femora black. Antennal style contrastingly black, postpedicel yellow, but slightly longer than style, its dorsal angle rounded. Abdomen pale haired beneath, unbanded, the dorsal mid stripe of a series connected slender triangles, dorsolateral stripes broader. Pacific coast of Panama (Fig. 33) ………………………………. *enanus*

- Subcallus extensively bare, without pruinescent mid stripe (Figs. 1C, 5C, 7C, 9C, 11C). Abdomen not regularly pointed 2

2 Abdomen with conspicuous color contrast, first two or three tergites brownish yellow with yellow hairs, the remainder dark brown with black hairs (Fig. 3A). Fore femur brown, mid and hind femora with brownish yellow integument, frequently infuscated at the base, never whole black. Subcallus relatively flattened (Fig. 3D). Abdomen unbanded ventrally. Frons clearly divergent. South Panama to Northwestern Colombia (Fig. 33) ……. *aniptus*

- Abdomen without contrast, if present, not evident. A different combination of characters ……………... 3

3 Frons broad, height four times the basal width (Fig. 21C). Scutum with sides, including notopleuron, posterior portion, scutellum and a pair of dorsolateral integumental stripes, pale (Figure 21A). Legs yellow except tip of fore tibia. Antenna wholly yellow orange. Abdomen wholly pale-haired beneath, the dorsal mid stripe narrow and continuous, the dorsolateral stripes a series of separate oval patches (Fig. 21A). Paraguay, Brazil (Mato Grosso do Sul) (Fig. 36) ………………………………………. *schadei*

- Frons narrow at least six times as high as basal width. Scutum uniformly colored, no more than notopleuron and scutellum paler …………………………….. 4

4 Abdomen black or dark brown with a single prominent continuous pale median stripe from first to sixth tergite (Fig. 5A and 27A), very rarely with faint indications of dorsolateral pale stripes on tergite 1 or tergites 1 and 2. Wings distinctly brownish especially along fore border and apex. All coxae and femora mostly black. Abdomen distinctly banded ventrally ………. 5

- Abdomen with evident dorsolateral stripes at least to tergite 3 (Figs. 7A, 10A, 11A, 12A) .. 7

5 Smaller species, generally less than 10 mm long. Antenna with style darker, generally black and contrasting, or postpedicel partly or wholly dusky (Fig. 27D). Wings less dark. Guatemala to western Colombia and Ecuador?Peru (Fig. 34) …………….. *unistriatus*

- Larger species, generally over 10 mm in length. Antenna wholly reddish orange. Wing intensely smoky, cell r1 and r2+3 almost black ..…………………….…………….. 6

6 All femora black. Brazil (Acre and Amazonas), eastern Peru and Ecuador (Fig. 34) .. *argentivittatus*

- All femora yellow, at most with the hind femur dusky. Peru (Huánuco) (Fig. 34) …. *argentivittatus huallagensis*

7 Notopleuron dark, concolorous with scutum (better visualized with integument moistening or scraping) ………………….……………….... 8

- Notopleuron paler than adjacent scutum (better visualized with integument moistening or scraping) ……………………….………. 12

8 Postpedicel long, nearly or longer than twice the length of antennal style (Fig. 25D). Dorsal tooth close to postpedicel base ....…..………...…… 9
- Postpedicel shorter, sometimes nearly as long as high. Style length obviously longer than half postpedicel length (Figs. 7D, 14D and 16D) ………..................................... 10

9 All coxae and femora black (Fig. 25C). Colombia, Venezuela, Guyana, Surinam, French Guiana, Brazil (Amazon region) (Fig. 34), Peru, Bolivia ……………………………………….. *trivittatus*
- All coxae, mid and hind femora yellow (Fig. 12C) Northern Brazil (Pará, Maranhão) (Fig. 34) ….. *mackerrasi* sp.n.

10 All coxae and femora black or dark brown. Wings light gray (Fig. 7B). Eastern Colombia and Peru, southern Venezuela, Guyana, Brazil (Amazon basin) (Fig. 31) ……….………..... *callosus*
- Mid and hind femora brownish yellow or dusky only at the base, never all black. Coxae variable. Wings weakly to strongly infuscated …………………………….. 11

11 Femora yellow (Figure 16B). Callus black, clearly inflated in lateral view (Fig. 16D). Wings strongly infuscated. Eastern Peru, Brazil (Acre) (Fig. 31) ……..…....…. *picicallosus*
- Fore femur black, mid and hind femora blackish at the base, yellow at apex (Fig. 14B). Callus light brown, slightly inflated in lateral view (Fig. 14D). Wings only weakly infuscated at radial cells. Eastern Peru and Bolivia, Brazil (Acre) (Fig. 34) ….. *noncallosus* sp.n.

12(7) Postpedicel long and slender (Fig. 13D), similar to *T. trivittatus*, nearly or longer than twice the length of the antennal style. Dorsal tooth close to postpedicel base. Northern Brazil (Pará, Maranhão) (Fig. 36) ………………………………. *macrocerus* sp. n.
- Postpedicel short and stout (Figs. 9D, 11D and 18D). Style nearly the same length as postpedicel, sometimes longer. Dorsal tooth dislocated toward middle of postpedicel …… 13

13 All coxae integument mainly yellow. Fore femur yellow to brownish yellow, remaining femora wholly pale (Fig. 11B) ……………………………………………………….. 14
- At least fore coxa darker than the remainder. Fore femur brown to black, remaining femora at least blackish at the base or darker than tibiae ….……… 18

14 Fore tibia obscurely bicolored, basal half to 2/3 yellow with pale hairs, remaining1/3 yellow to brownish yellow with black hairs. Fore femur mainly pale haired ……….. 15
- Fore tibia clearly bicolored, basal half to 2/3 yellow or white, the remaining 1/3 black and black haired (Fig. 18B). Fore femur mainly black haired ………………. 16

15 Frons twice as wide at vertex than at the base (Fig. 11A). Postpedicel nearly as long as high (Fig. 11D). Dorsolateral stripes even to tergite 3, interrupted from 4 to 6. Peru and Bolivia (east of Andes) (Fig. 31)……….. *isis*
- Frons less convergent (Fig. 24A). Postpedicel longer than high (Fig. 24D). Dorsolateral stripes continuous to tergite 5, sometimes 6. Coast of Suriname, French Guiana and Brazil (Pará) (Fig. 35)…………………………………… *tristichus*

16 Integument of scutum red to reddish brown. Fore femur mainly pale haired, black haired only on anterior region. Middorsal stripe a slender series of connected triangles. Dorsolateral a series of disconnected patches from tergite 1-6 (Fig. 9A). (Mato Grosso, Rondônia, Mato Grosso do Sul, Tocantins and Federal District) (Fig. 35) ………………... *dorsorufus* sp.n.
- Integument of scutum darker. Fore femur mainly black haired. Middorsal abdominal stripe broad and more even. Dorsolateral abdominal stripes variable (Figs. 1A, 18A) ……….. 17

17 Dorsolateral abdominal stripes a series of disconnected patches. Frons narrower (F.I. 8.4) (Fig. 1A). Northwestern Brazil (Acre, Rondônia) (Fig. 32) …………….. *albocapillus* sp. n.
- All Abdominal stripes even, yellow (Fig. 18A). Frons broader (F.I. 6.4). Eastern Colombia, Peru and Bolivia, Brazil and northern Argentina (Fig. 35) …………….. *restrepoensis*

18(13) Postpedicel nearly as long as high (Fig. 19D). Pruinescence at dorsal area of subcallus (Fig. 19C) more extensive than other species except, *T. enanus*. Dorsolateral stripes extending into tergite 5 (Fig. 19A). Mexico (Nayarit, Jalisco, Morelos) (Fig. 33) …...….. *rhizonshine*

- Postpedicel clearly longer than high (Figs. 15D, 17D and 22D). Pruinescence of dorsal area on subcallus not so extensive (Fig. 15C). Dorsolateral abdominal stripes variable ..……... 19

19 Frons broad (Frontal index less than 6.0), strongly divergent above, more than twice as wide at vertex than at base (Fig. 15C). Abdominal stripes even (Fig. 15A). Argentina (Salta, Catamarca, Misiones), Brazilian Cerrado (Tocantins, Mato Grosso, Goiás, São Paulo) and Paraguay (Villarica, Cerro Pelado) (Fig. 32) ....……………. *palpalis*

- Frons narrower and less divergent. Middorsal abdominal stripe a series of connected triangles. Dorsolateral disconnected …………………………………………………. 20

20 Dorsolateral stripes reaching tergite 5, sometimes 6 (Fig. 22A). Wings always glass clear. Amazon basin (Fig. 32) ....…. *sextriangulus*

- Dorsolateral stripes reaching tergite 4 (Fig. 17A). Wings glass clear or lightly infuscated. Panama to western Ecuador (Fig. 33) ...……….................................. *platycerus*

Key to known males of *Tabanus trivittatus* species-group. Adapted from Fairchild (1976)

1 Ventral half (inflated portion) of subcallus wholly bare and shiny (Figs. 6C and 8C) ……. 2

- At least ventral half of subcallus pruinescent (Figs. 2C, 20C, 26C and 28C) ……………… 5

2 Middorsal abdominal stripe very broad (Fig. 6A). Dorsolateral barely visible … *argentivittatus*

- Middorsal abdominal stripe not so broad. Dorsolateral obviously evident ………. 3

3 All femora black, strongly contrasting with yellow tibiae (Fig. 8B) …. *callosus*

- At least mid and hind femora yellow, not contrasting with the yellow and yellow haired tibiae …………………………………………………………….……... 4

4 Dorsolateral abdominal stripes a series of oval patches …………………………… *schadei*

- Dorsolateral abdominal stripes continuous …………………………………... *restrepoensis*

5 Area of large facets of the eye distinctly pilose ………………………..………. 6

- Area of large facets of the eye bare ……………………………………………. 7

6 Postpedicel long and slender (Fig. 26D). Abdomen banded ventrally ………………………………………………………………………. *trivittatus*

- Postpedicel short and broad. Abdomen unbanded ventrally ………………….. *palpalis*

7 Subcallus with a dorsal triangular shiny area (Fig. 2C) ………………… *albocapillus* sp.n.

- Subcallus entirely pruinescent, without shiny area (Figs. 20C and 28C) ………………. 8

8 Middorsal abdominal stripe broad and even, dorsolateral stripes faint or absent. Occiptal band of small facets very narrow ……………………………….. *unistriatus*

- Middorsal abdominal stripe narrower than the well-marked dorsolateral stripes. Occipital band of small facets wide ………………………………………………. *rhizonshine*

Tabanus albocapillus **sp. n. Carmo & Henriques**

(Figures 1A–D, 2A–D, 32)

Diagnosis. Frons strongly divergent, twice as wide at vertex than at base. Postpedicel short, sometimes as high as long, with same size or shorter than style. Notopleuron paler than adjacent scutum. Abdominal mid stripe broad, a series of connected triangles through tergite 6, lateral stripes broad and interrupted through tergite 5 or 6. Sternites banded, black pilose on anterior margins, white pilose on posterior margins. Subcallus brown, not markedly inflated on lateral view.

Holotype female. Length 12.4 mm, wing 9 mm. Eyes bare. Frons pruinescent white, narrow and strongly divergent above (Frontal index (F.I). 8.4, divergence index (D.I.) 2.3). Callus brown, higher than wide. Median callus brown, surrounded by dark pruinescence and hairs. Subcallus only slightly inflated, light brown. Clypeus and gena pale gray and white pilose, except for golden pruinescent spots dorsally. First antennal segment pale yellow, covered with black pilosity, pedicel and postpedicel orange, the style dusky. Palpus pruinescent white,

white pilose at basal third, the remainder black pilose. Proboscis black, covered with pale pruinescence.

Scutum and scutellum with black integument, contrasting light brown at lateral portion including notopleuron and supra-alar area, covered with abundant decumbent golden hairs and sparse erect black hairs. Pleuron with black integument covered with gray pruinescence, and white hairs, except for yellow area on dorsal portion of anepisternum and katepisternum with a tuft of pale yellow hairs. All coxae with yellow integument, gray pruinescence and white hairs, except extreme apex of fore coxa, darker with black hairs. Fore femur brownish with black hairs, mid and posterior tibiae yellow covered with gray pruinescence and white hairs. Fore tibia bicolored, basal half yellowish with pale pilosity, the apical half darker with black hairs, mid and hind tibiae yellow with white hairs except for black hairs at apex of mid tibia and fringe of black hairs at hind tibia. All tarsi brown, with black hairs. Wings hyaline, stigma yellowish.

Abdomen brown with black hairs, yellow hairs and pruinescence on tergites lateral margins. Middorsal stripe broad, continuous through segment 6, yellow and yellow pilose. Dorsolateral discontinuous through segment five, faint indications at 6, yellow and yellow pilose. Sternites with brown integument, black median integumental stripe. Sternites 1 and 2 predominantly with black hairs, 3-5 banded, black hairs basally and white hairs on second half, the remainder with black hairs.

Male. As in female, except for holopticism, superior 2/3 with enlarged omatidia. Scutum covered with white long hairs. Sternites with white hairs and no black medial stripe.

Comments. The species differs from *T. restrepoensis, T. tristichus* and *T. isis* by the darkest legs and interrupted dorsolateral stripes. From *T. dorsorufus* sp.n. it differs by having a narrower frons and darker integument.

Type Material. Holotype female: BRASIL, AC[*Acre*], Senador Guiomard, 10°04′28″S; 67°37′00″W, 23.viii.2016, na luz[in the light], AA. Agudelo, DMM. Mendes, FF. Xavier., JA. Rafael [leg.] (INPA); paratypes: BRASIL, AC[*Acre*], Senador Guiomard, Fazenda Experimental Catuaba, UFAC, 10°04′28″S, 67°37′00″W, 6-24.xi.2013, Armadilha Malaise, J. T. Camara [leg.] (f# INPA); *Rondônia*, Porto Velho, AHE Jirau – Rio Madeira, S 9°35′54.4″; W 65°2′53.7″, Malaise, 4 camp., T6 e T8, 09-20.ix.2010, R.R. Silva & E.Z. Albuquerque [leg.] (f# MZUSP); same data as holotype (2 m# INPA).

Etymology. From Latin, *albo* (white) + *capillus* (hair). In reference to the abundant white hairs in the whole male body and in the female, especially in the gena, pleuron and legs.

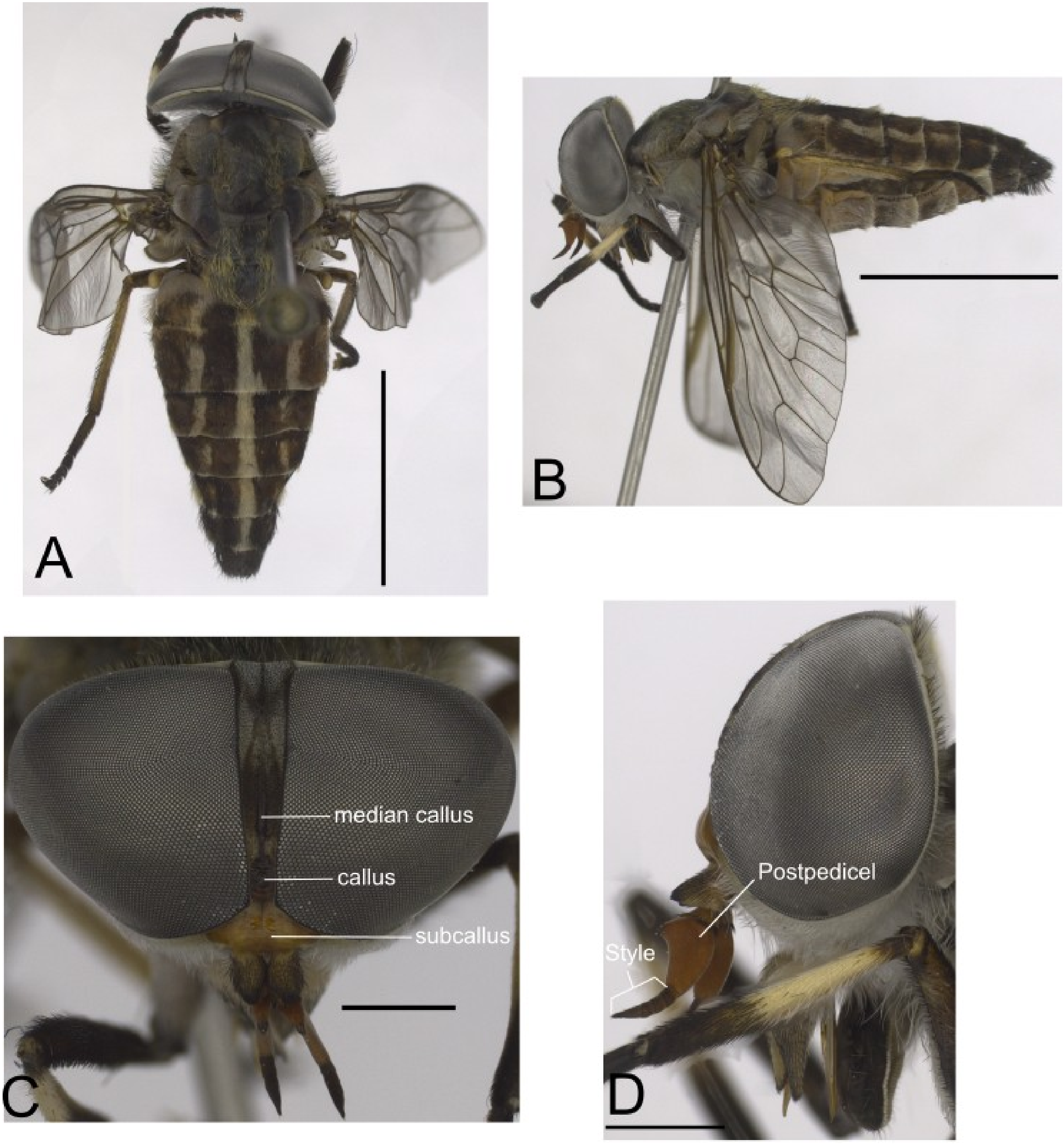


Figure 1. *Tabanus albocapillus sp. n.* Holotype female. A. Dorsal habitus. B. Lateral habitus. C. Head, anterior view. D. Head, lateral view. Scale bars. A, B. 5 mm. C, D. 1 mm.

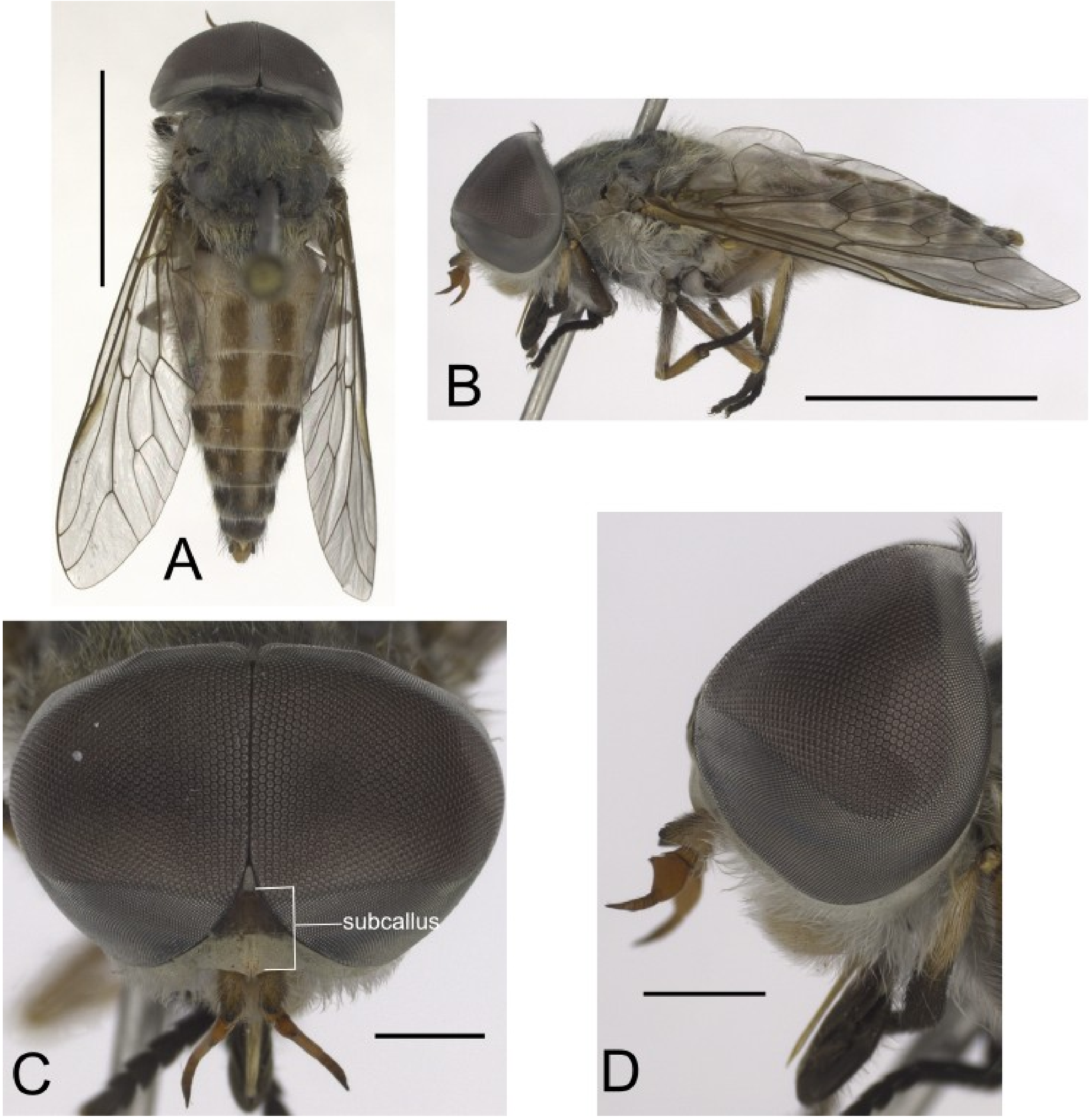


Figure 2. *Tabanus albocapillus* sp. n. Paratype male. A. Dorsal habitus. B. Lateral habitus. C. Head, anterior view. D. Head, lateral view. Scale bars. A, B. 5 mm. C, D. 1 mm.

Tabanus aniptus Fairchild

(Figures 3A–E, 4A–D, 33)

Tabanus aniptus Fairchild, 1976: 242, fig. 1; Wilkerson, 1979: 365 (Colombia spp.); Fairchild, 1986: 110 (Panama spp.); Fairchild & Burger, 1994: 131 (cat.); Coscarón & Papavero, 2009: 124 (cat.); Wolff & Miranda-Esquivel, 2016: 280 (cat.).

Tabanus trivittatus Fabricius of Fairchild, 1961: 31 (Costa Rica spp., misident.); of Lee *et al*., 1969: 455 (Raposo river spp., misident.); of Wolff & Miranda-Esquivel, 2016: 287 (cat., in part).

Diagnosis. Light brown with contrasting abdominal color pattern, the first two or three segments yellowish brown, the remainder, black. Frons narrow and divergent above (F.I. 9-11, D.I. 2.4). Wings lightly brownish tinted, darker at c, sc, r1 and r2+3. Abdominal stripes fainted. Notopleuron brown, concolour with scutum, sometimes slightly paler. Fore femur brown, mid and hind femora yellowish brown.

Comments. This species range from Nicaragua to Colombia, west of the Andes. Wilkerson (1979) mentions a specimen from Ecuador, however, does not provide any further details about the locality for the specimen. This species may be easily identified by the contrasting pattern of the abdomen.

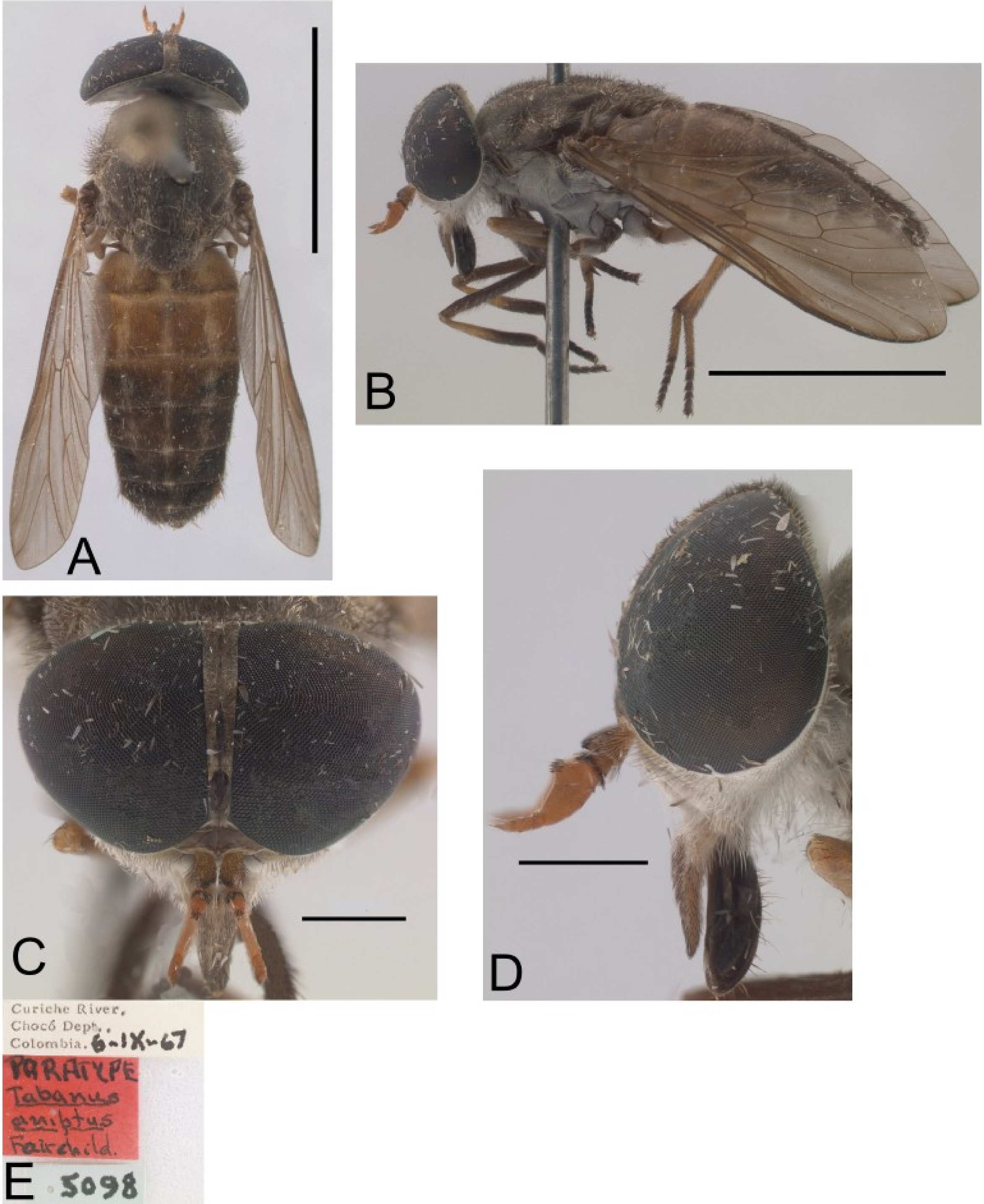


Figure 3. *Tabanus aniptus.* Paratype female. A. Dorsal habitus. B. Lateral habitus. C. Head, anterior view. D. Head, lateral view. Scale bars. A, B.1 mm. C, D. mm. E. Labels. Scale bars. A, B. 5 mm. C, D. 1 mm. Photos obtained by courtesy of FSCA.

Material examined. Paratype female (FSCA), labels as in figure 3E; COLOMBIA, *Cauca,* Guapi, Altitude 10 M. Tropical Rain Forest. Neted R. Wilkerson V – 10 -76 (m# FSCA).

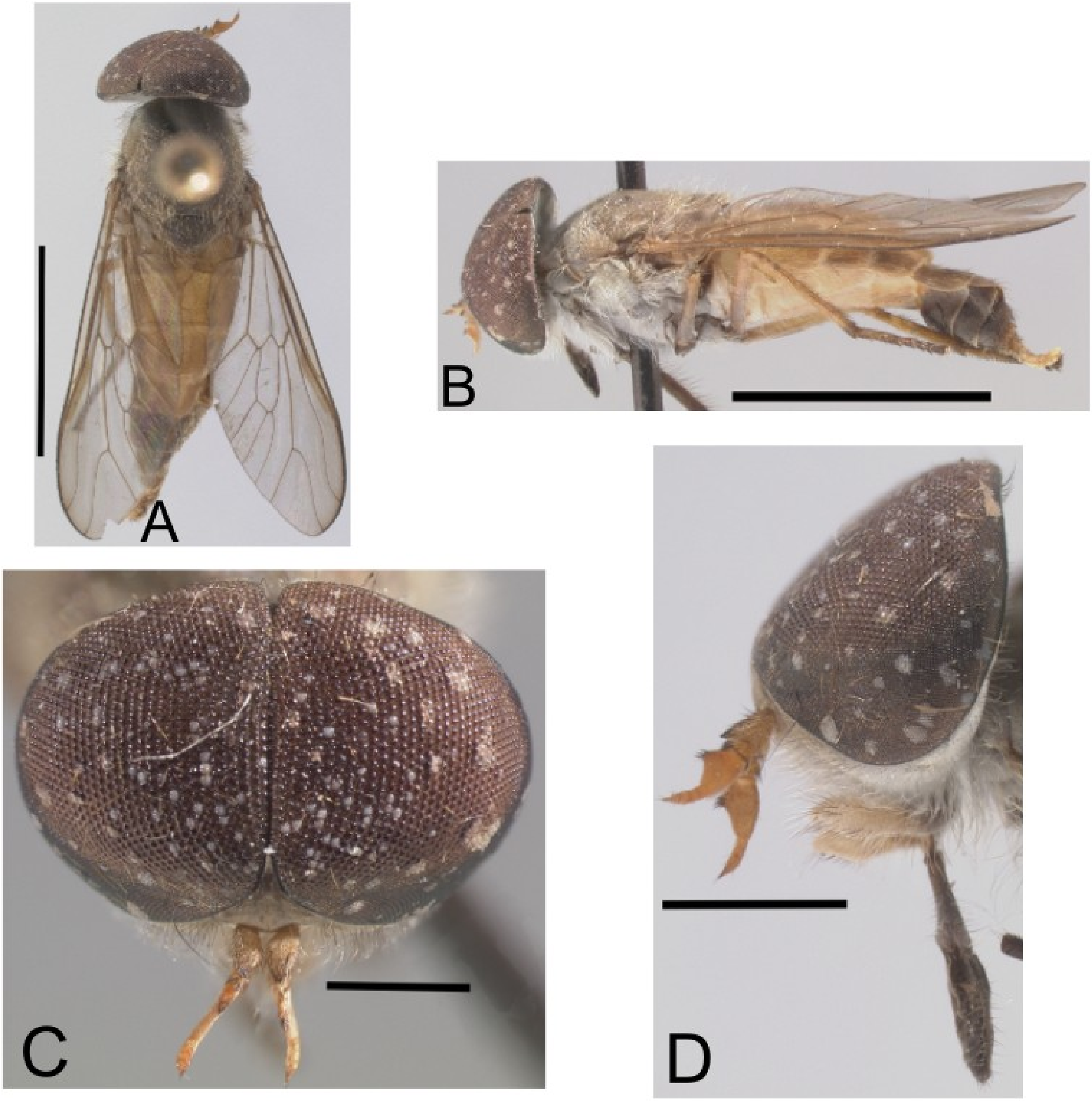


Figure 4. *Tabanus aniptus.* Male. A. Dorsal habitus. B. Lateral habitus. C. Head, anterior view. D. Head, lateral view. Scale bars. A, B.1 mm. C, D. mm. Scale bars. A, B. 5 mm. C, D. 1 mm. Photos obtained by courtesy of FSCA

Tabanus argentivittatus **Fairchild**

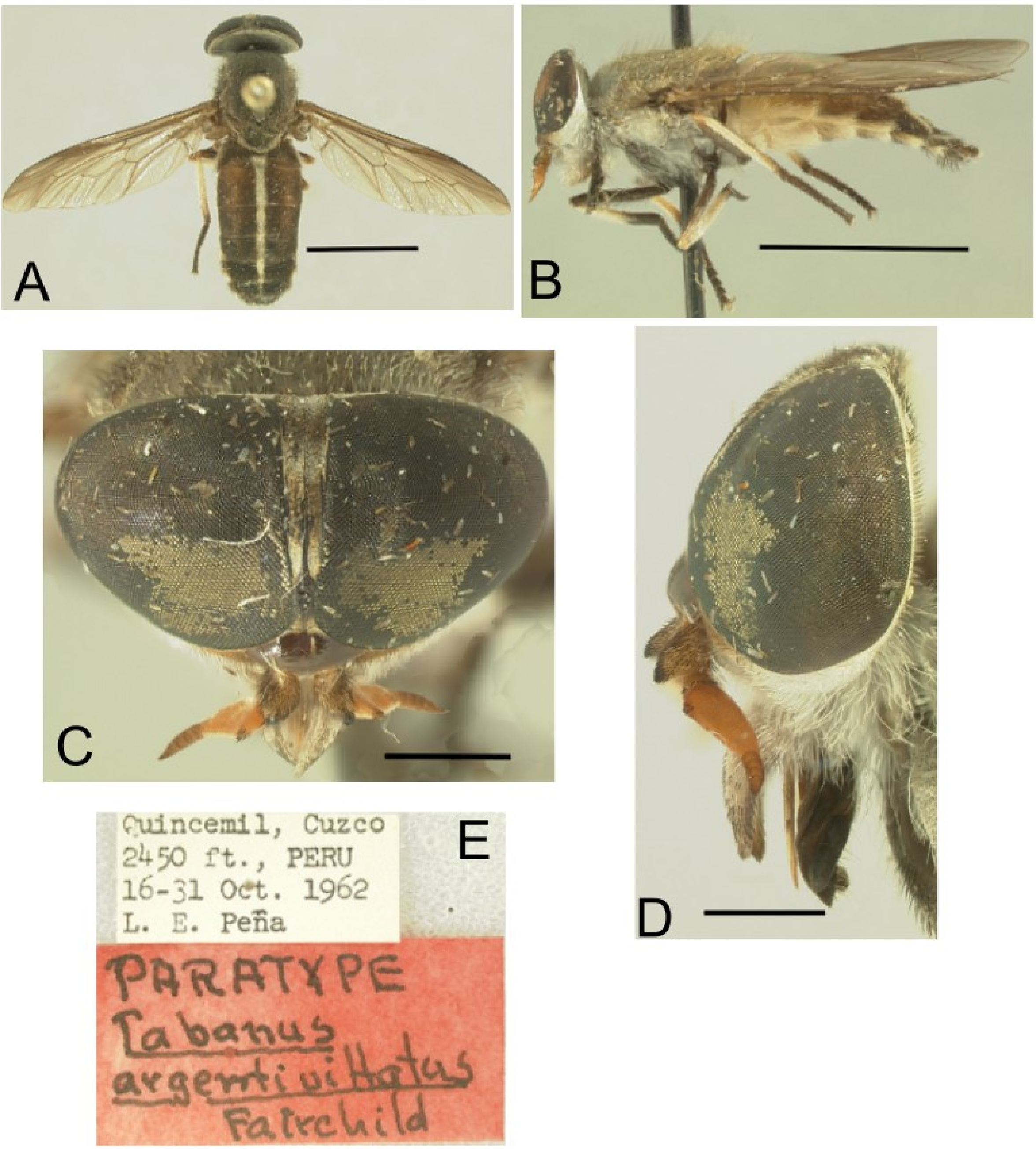
(Figures 5A–E, 6A–D, 34)

Tabanus argentivittatus Fairchild, 1976: 244, fig. 2; Wilkerson & Fairchild, 1985: 51 (Peru spp.); Henriques & Gorayeb, 1993: 19 (MPEG spp.); Fairchild & Burger, 1994: 131 (cat.); Henriques, 1997: 88 (INPA spp.); Coscarón & Papavero, 2009: 124 (cat.); Cárdenas *et al*., 2009: 527 and appendix 4: 17 (Ecuador spp., in part).

Diagnosis. Species with a single prominent dorsal stripe from tergites 1-6 and with the anterior half of wing conspicuously brown tinted. All coxae and femora black. Notopleuron dark, concolorous with scutum. Frons not markedly divergent (D.I. 1.75). Subcallus inflated at lateral view.

Comments. See under *T. unistriatus*.

Material examined. Paratype female (FSCA), labels as in figure 5E; BRASIL, *Amazonas*, Coari (11 f# INPA); Benjamin Constant, (f# INPA) PERU, *Madre de Dios,* Rio Tambopata (f# INPA).



Quincemil, Cuzco
2450 ft., PERU
16-31 Oct. 1962
L. E. Peña

PARATYPE
Tabanus
argentivittatus
Fairchild

Figure 5. *Tabanus argentivittatus.* Paratype female. A. Dorsal habitus. B. Lateral habitus. C. Head, anterior view. D. Head, lateral view E. Labels. Scale bars. A, B. 5 mm. C, D. 1 mm. Photos obtained by courtesy of FSCA

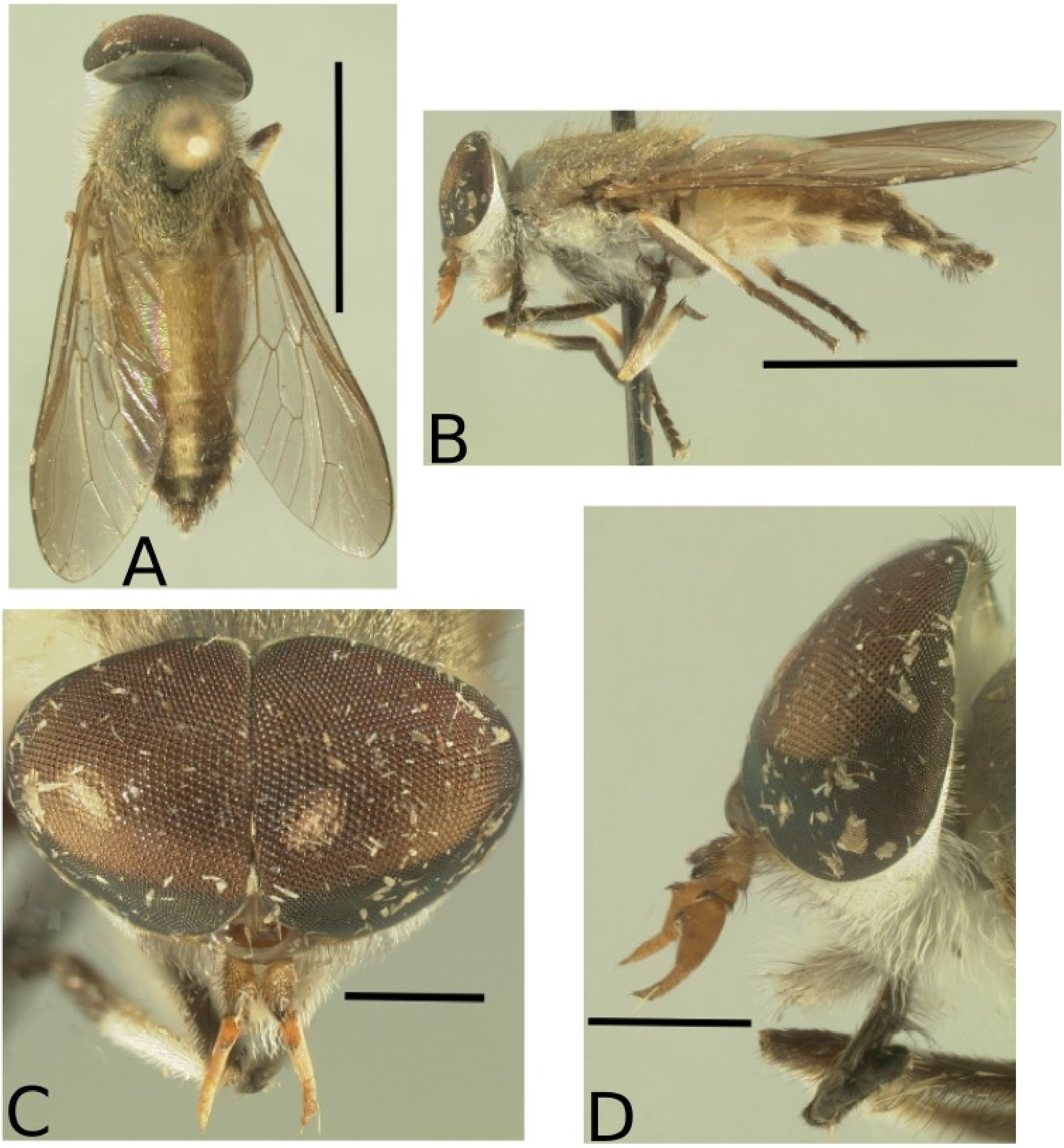


Figure 6. *Tabanus argentivittatus.* Male. A. Dorsal habitus. B. Lateral habitus. C. Head, anterior view. D. Head, lateral view. Scale bars. A, B.5 mm. C, D. 1 mm. Photos obtained by courtesy of FSCA.

Tabanus argentivittatus huallagensis Fairchild

(Figure 34)

Tabanus argentivittatus huallagensis Fairchild, 1976: 245, fig. 3; Wilkerson & Fairchild, 1985: 51 (Peru spp.); Fairchild & Burger, 1994: 131 (cat.); Coscarón & Papavero, 2009: 124 (cat.).

Diagnosis. As *T. argentivittatus*, but a pale form. Fore coxae and femora black, the remainder brownish yellow.

Comments. To the present moment, it may be differentiated from *T. argentivittatus* by the general color of the body and geographic distribution, since both morphotypes have not been collected in the same area. The only register of *T. argentivittatus huallagensis* is the type-material and being restricted to valleys from Peru in Huánuco. Holotype was examined through photos, available at the MCZ database.

Tabanus callosus **Macquart**

(Figures 7A–D, 8A–D, 31)

Tabanus callosus Macquart, 1848: 171 (1848: 11); Walker, 1854: 200 (BMNH spp.; Hunter, 1901: 140 (cat.); Kertész, 1908: 232 (cat.); Kröber, 1933: 342 (taxonomy), 1934: 292 (cat.); Fairchild, 1942b: 162, pl. 1, fig. 4 (taxonomy), 1956: 12 (syn.); Barretto, 1957: 86 (Guiana spp.); Philip, 1960: 82 (Peru spp.); Fairchild, 1970: 840 (French Guiana spp.), 1971: 103 (cat.; as syn. of *trivittatus* Fabricius, 1805), 1976: 246, fig. 4 (rev.); Moucha, 1976: 97, 148 (cat.; as syn. of *trivittatus* Fabricius, 1805); Wilkerson & Fairchild, 1985: 51 (Peru spp.); Rafael *et al.*, 1991: 361 (Roraima spp.); Henriques & Gorayeb, 1993: 19 (MPEG spp.); Fairchild & Burger, 1994: 132 (cat.); Henriques, 1997: 88 (INPA spp.); Henriques & Rafael, 1999: 215 (distr.); Henriques, 2004: 148 (habitat); Coscarón & Papavero, 2009: 125 (cat.); Wolff & Miranda-Esquivel, 2016: 280 (cat.); Henriques, 2016: 178 (AMNH spp.); Krolow *et al.*, 2017: 104 (French Guiana spp.).

Diagnosis. Style subequal to postpedicel, never less than half its length. Scutum and scutellum blackish with grey pruinescence, notopleuron concolorous with scutum and with long black hairs. All coxae and femora black, the former with gray pruinescence Abdomen with three abdominal stripes, the middorsal reaching tergite 6, dorsolateral reaching tergite 4, sometimes with faint indications at 5. Abdomen clearly banded ventrally.

Comments. This species has great resemblance with *T. trivittatus*. Both species show a uniform morphology and similar body sizes (*T. trivittatus* ranges from 9 to 16 mm, while *T. callosus* ranges from 8 to 14 mm). The major difference between the species is the antennae, where, the postpedicel (basal plate) in *T. callosus* is short and in *T. trivittatus* the postpedicel is long, usually twice the style length. In addition, the postpedicel tooth angle is closer to the base in *T. trivittatus.* Some specimens of *T. callosus* seem to possess intermediate states between the two species. There is also great variation between the two in regards to sternite 8 of female genitalia (Fig. 29 A–F). We also observed morphological difference in the males. The male postpedicel of *T. callosus* is shorter than *T. trivittatus* (Figs. 8D and 26D). In addition, the subcallus is bare and inflated at ventral region in the male of *T. callosus* (Fig. 8C, D)*,* but pruinescent and flat in the male of *T. trivittatus* (Fig. 26C, D). The differences observed in the males corroborate the hypothesis that these are two different species.

Material examined. Large series of INPA and MPEG collections with records distributed through the Amazon Basin. BRASIL, *Amazonas* BR 119, km. 275; Coari; Novo Airão; Parque Nacional do Jaú (50 f# and 6 m# INPA); *Amazonas,* São Gabriel da Cachoeira; Barcelos, Manaus; *Roraima*, Ilha de Maraca; *Rondônia*, Ouro Preto do Oeste. COLOMBIA, *Vaupes* (43 f# MPEG).

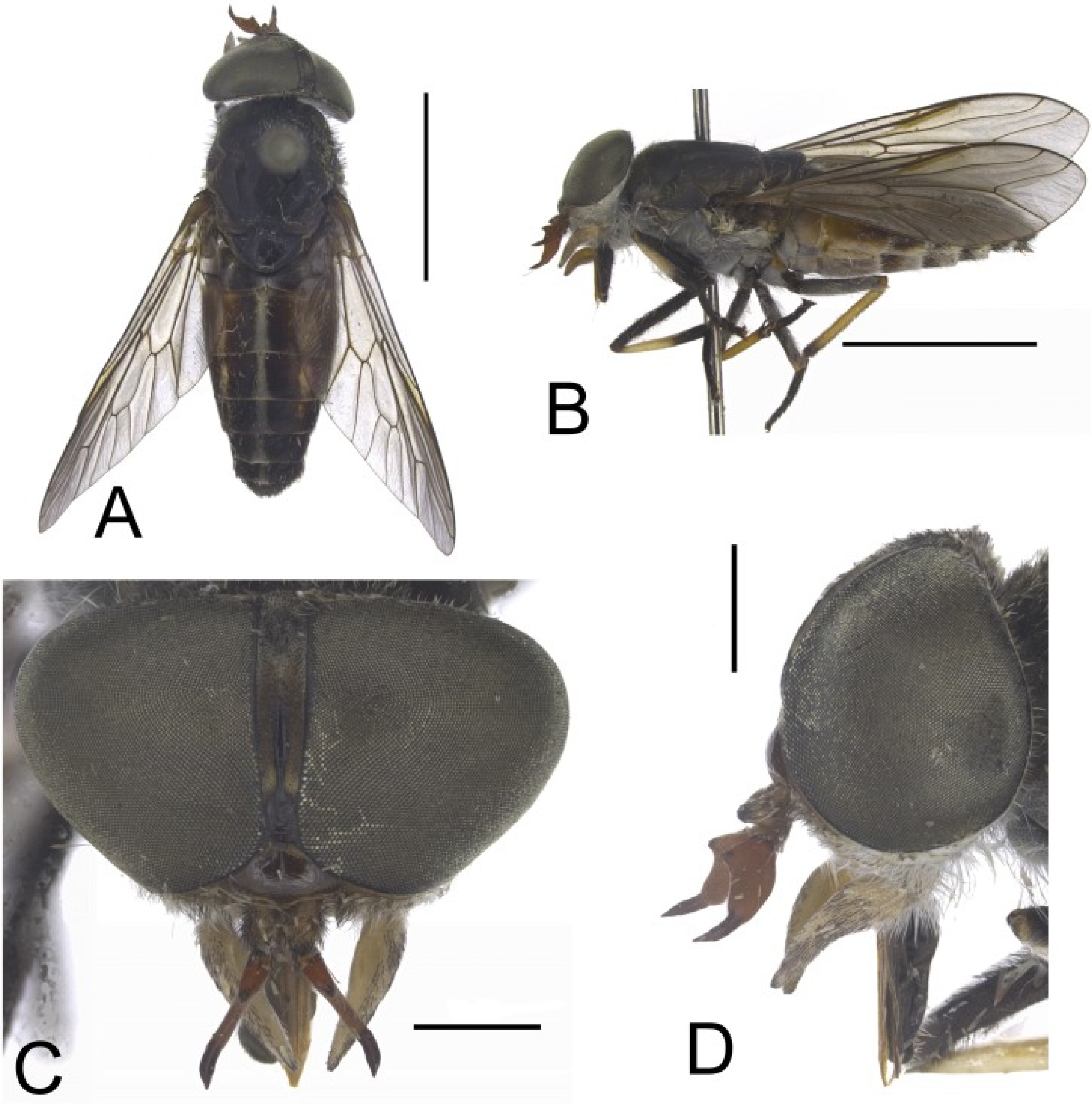


Figure 7. *Tabanus callosus.* Female. A. Dorsal habitus. B. Lateral habitus. C. Head, anterior view. D. Head, lateral view. Scale bars. A, B. 5 mm. C, D. 1 mm.

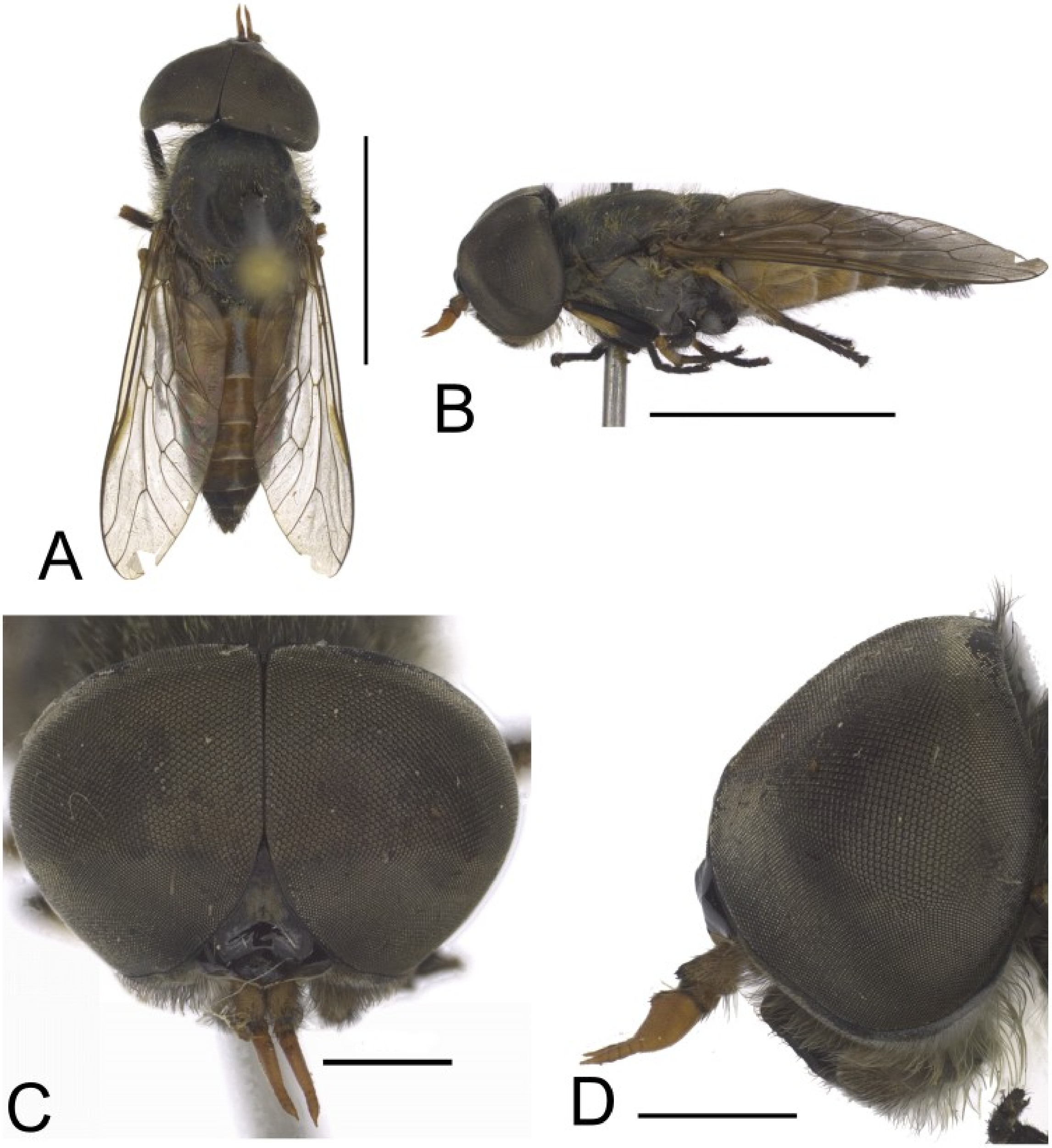


Figure 8. *Tabanus callosus.* Male. A. Dorsal habitus. B. Lateral habitus. C. Head, anterior view. D. Head, lateral view. Scale bars. A, B. 5 mm. C, D. 1 mm.

Tabanus dorsorufus **sp. n. Carmo & Henriques**

(Figures 9A–D, 35)

Diagnosis. A reddish-brown species with postpedicel nearly as long as high. Notopleuron integument paler than adjacent scutum. All coxae, mid and hind femora yellow with gray pruinescence. First tibia clearly bicolored, last third black. Abdominal middorsal stripe a series of yellow connected triangles. Dorsolateral stripes a series of disconnected dashes on tergites 1-6.

Holotype female. Length 11 mm, wing 9 mm. Eyes bare. Frons yellow pruinescent, divergent above, F.I. 6.3, D.I. 1.9. Frontal callus brown, higher than wide. Subcallus light brown, weakly inflated. Median callus slender, surrounded by dark pruinosity and hairs. Clypeus and gena with gray pruinescence and white hairs. First antennal segment pale brown, white haired, dark hairs above; second and third segments orange, tip of style slightly darker. Palpus with yellowish integument and white hairs, black hairs on distal portion. Proboscis black, yellowish pruinescent.

Scutum reddish with vestiges of gray pruinescence and black hairs. Scutellum red with brown anterior area. Notopleuron paler, light brown, with black hairs on lower half and gold on upper half. Integument of katepisternum concolorous with scutum, anepisternum darker, both with white hairs. All coxae with integument yellow, gray pruinescence and white hairs. Fore femur dark brown, with black hairs dorsally and white hairs and pale pruinescence ventrally. Fore tibia strongly bicolored with basal 2/3 yellow with white hairs, the remainder black and black haired. Fore tarsus blackish with black hairs, fringe of pale hairs at first tarsomere, ventrally. Mid and hind femora yellow with white hairs and gray pruinescence. Mid tibia yellow with white hairs, black hairs at apex. Hind tibia yellow with white hairs, fringed. Mid and hind tarsi brown with black hairs. Wing glass clear, stigma yellow.

Abdomen light brown, darkening to the apex. Median stripe a series of connected triangles of pale pruinescence and hairs on tergites 1-6. Dorsolateral a series of disconnected dashes from tergites 1-6. Sides of tergites paler and white haired. Abdomen unbanded ventrally and with white hairs, except for black hairs on sternites 6 and 7.

Male. Unknown.

Comments. The new species differs from *T. restrepoensis, T. tristichus* and *T. isis* by the discontinuous dorsolateral stripes and the middorsal stripe a row of narrow connected triangles. It also differs from the latter two by the strong bicolored fore tibia, and from *T. tristichus* by the more divergent frons. The holotype was fixed in ethanol, which caused the loss of some vestiture.

The paratype series shows variations in the postpedicel format (from nearly as high as long to longer than high) and style collor (from orange to black).

Type material. Holotype female: BRASIL, MT [*Mato Grosso*], Chap[ada] dos Guimarães, P [Parque]. N [Nacional]. Chapada dos Guimarães, S 15°24′37.2″; W 055°50′10.4″, Malaise 19 – Trilha do Véu da Noiva, 03-04.ix.2011, Lamas, C.J.E. & eq. [leg] (MZUSP); paratypes: same data as holotype (3 f# MZUSP), *Mato Grosso do Sul*, Rio Verde, S 18°09′39.4″; W 54°09′02,4″, Malaise 38, 14-30.x.2012, Lamas, Nihei & equipe [leg] (f# MZUSP), *Mato Grosso,* Aquidauana, Reserva Ecológica UEMS, Veg. Fechada Flor[esta] Est. Decidual S 20°25′59.0*;* W 55°39′20.8″, Malaise 07, 26.viii-11.ix.2012 Lamas, Nihei & eq. col; *Tocantins,* Peixe, vii.2011, Malaise, M.A. Bragança [leg] (3 f# CEUFT), *Distrito Federal*, Fazenda Água Limpa, UNB, 2003 (4 f# INPA, f# FSCA, f# BMNH); *Rondônia,* Ouro Preto do Oeste, [Handwritten] Linha 212 Lot 36 Gleba 21-B 3 a 5.ix.1986 Armadilha Suspensa [canopy trap] F.F. Ramos [Leg.] (2f# MPEG); same locality 31.viii.1986 (f# MPEG).

Material examined. Same data as holotype (12 f# MZUSP). *Distrito Federal*, Fazenda Água Limpa (8 f# INPA).

Etymology. From Latin, *dorsum* (back) + *rufus* (red).

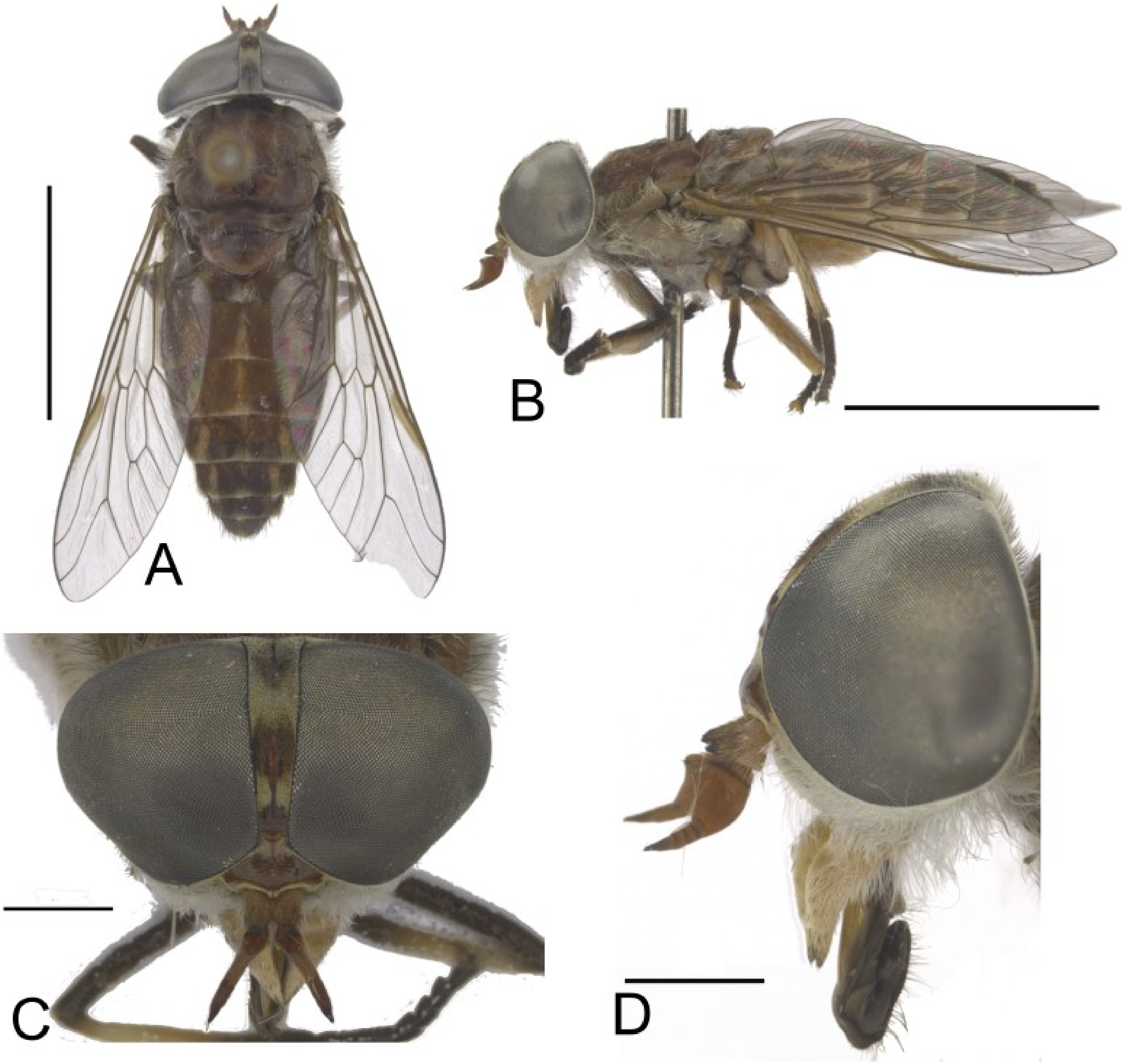


Figure 9. *Tabanus dorsorufus* sp. n. Holotype female. A. Dorsal habitus. B. Lateral habitus. C. Head, anterior view. D. Head, lateral view. Scale bars. A, B.5 mm. C, D. 1 mm.

Tabanus enanus Fairchild

(Figures 10A–D, 33)

Tabanus enanus Fairchild, 1942b: 157, pl. l, fig. 8; Fairchild, 1971: 93 (cat.), 1976: 248, fig. 5 (rev.); Moucha, 1976: 104 (cat.); Fairchild, 1986: 113 (Panama spp.); Henriques & Gorayeb, 1993: 19 (MPEG spp.); Fairchild & Burger, 1994: 136 (cat.); Henriques, 1997: 88 (INPA spp.); Coscarón & Papavero, 2009: 129 (cat.).

Diagnosis. Postpedicel oval, nearly as high as long; subcallus covered with pruinescence, except for small bare area. Middorsal abdominal stripe narrow, a series of connected triangles, visible through tergite 5; dorsolateral wider and disconnected, visible through segment 5. Subcallus only slightly inflated at lateral view. First femur black, mid and hind infuscated at base, the remainder yellow.

Material examined. Panama, *Darien*, Santa Fé, 8-III-64. (f# INPA).

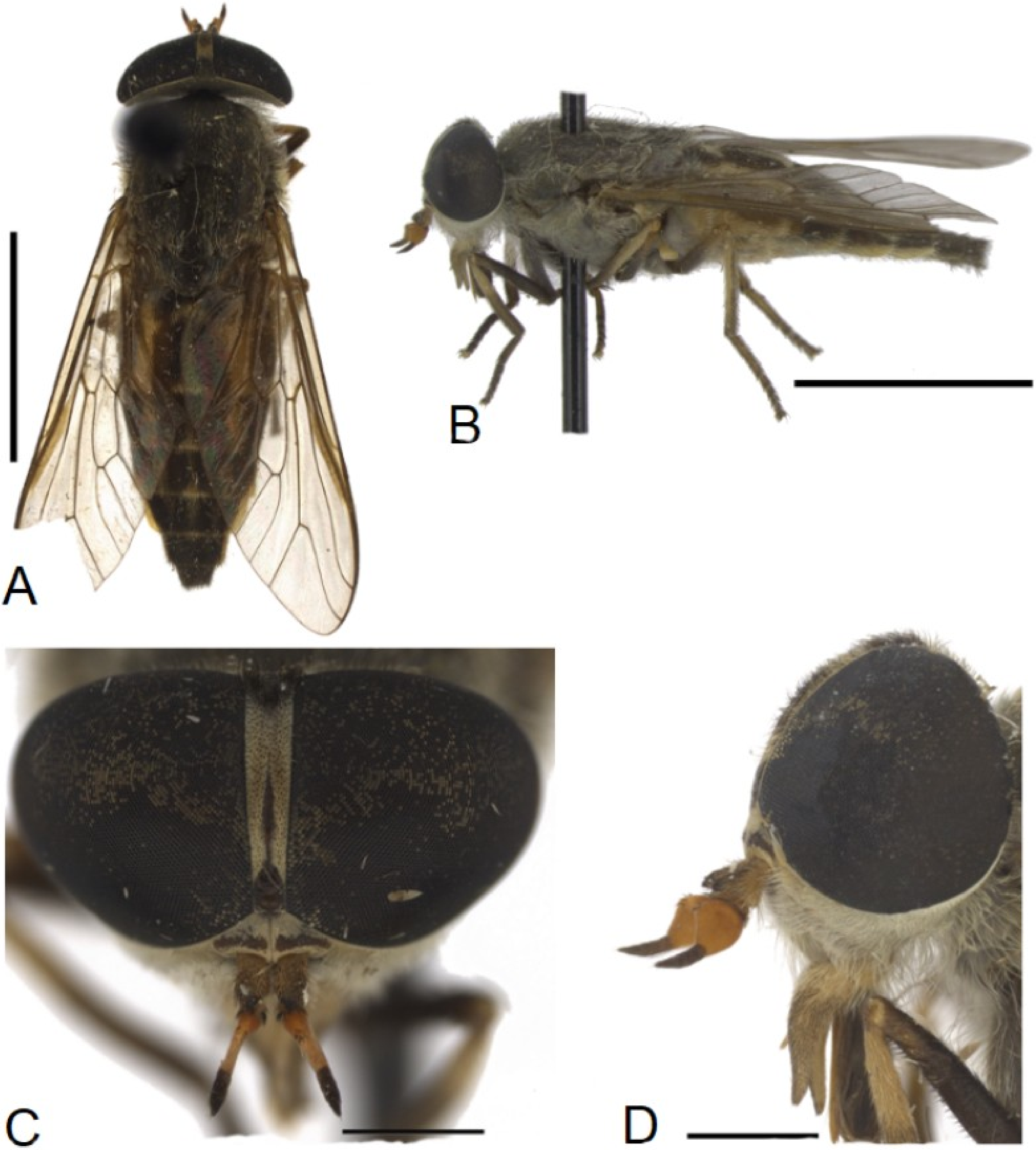


Figure 10. *Tabanus enanus.* Female. A. Dorsal habitus. B. Lateral habitus. C. Head, anterior view. D. Head, lateral view. Scale bars. A, B. 5 mm. C, D. 1 mm.

Tabanus isis Fairchild

(Figures 11A–D, 31)

Tabanus isis Fairchild, 1976: 249, fig. 6; Wilkerson & Fairchild, 1985: 51 (Peru spp.); Fairchild & Burger, 1994: 140 (cat.); Chainey, *et al*., 1994: 335 (Bolivia spp.); Coscarón & Papavero, 2009: 133 (cat.).

Diagnosis. Postpedicel as high as long. Frons not markedly divergent above (D.I. 1.8). Notopleuron paler than adjacent scutum. All legs yellow, fore tibia weakly bicolored. Middorsal stripe a series of continuous triangles. Dorsolateral abdominal stripes broad, continuous to tergite 3, interrupted through tergite 6.

Comments. Fairchild (1976) described this species and pointed out to the resemblance with *T. restrepoensis* and *T. tristichus*. *T. isis* may be differentiated from the both species by darker integument of the scutum and abdomen; middorsal stripe narrow and irregular. From *T. restrepoensis* by fore tibia weakly bicolored. From *T. tristichus,* which also has weakly bicolored fore tibia, by the more divergent frons and ecological habits, since *T. tristichus* seems to be restricted to coastal areas.

Material examined. BOLIVIA, *Cochabamba*, Villa Tunari, Hotel Los Tucanes 16°58.392’S 65°23.793’W 320 m 4-6.IX.2000 M. Hauser (f# INPA).

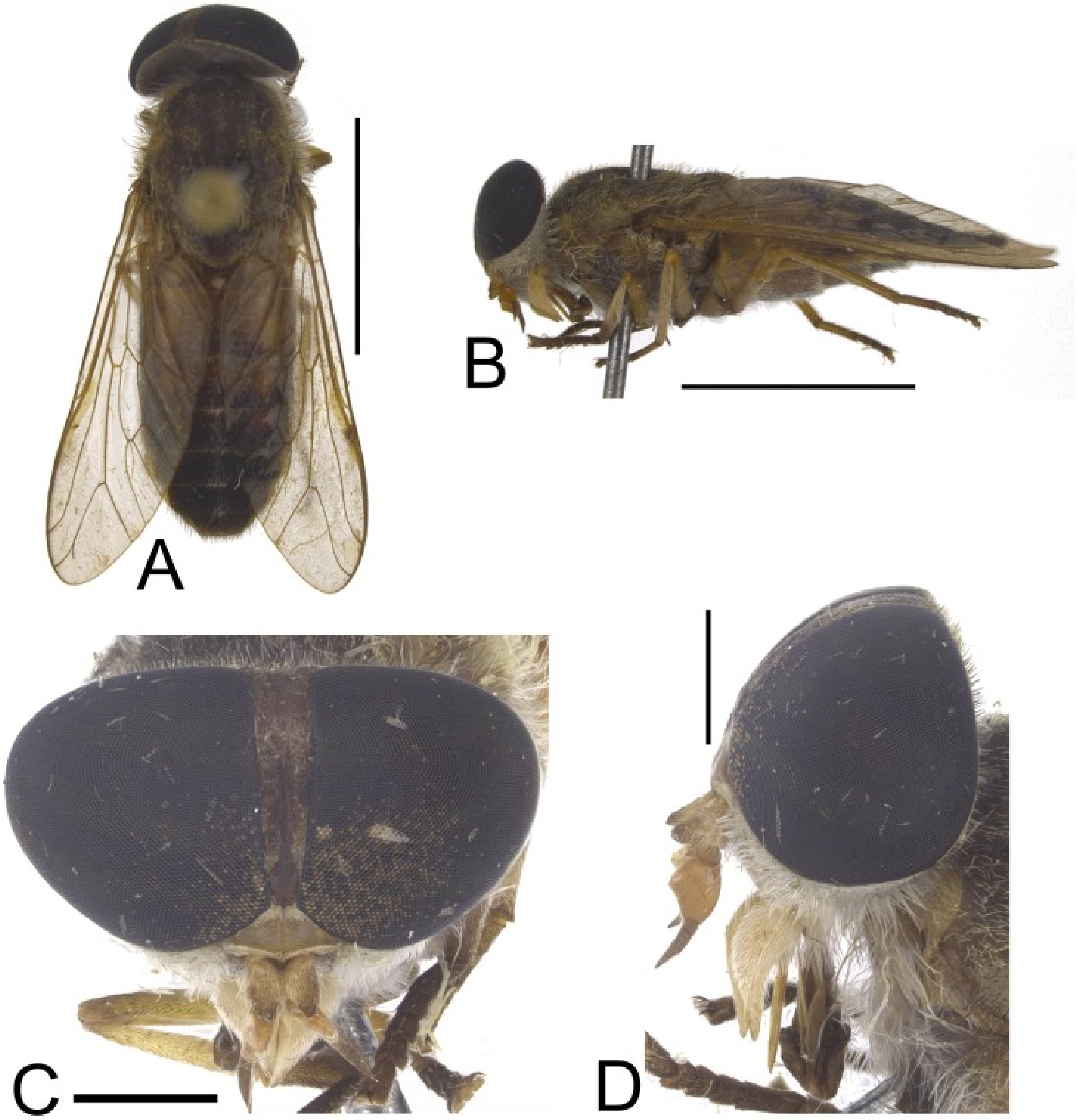


Figure 11. *Tabanus isis.* Female. A. Dorsal habitus. B. Lateral habitus. C. Head, anterior view. D. Head, lateral view. Scale bars. A, B. 5 mm. C, D. 1 mm.

Tabanus mackerrasi sp. n. Henriques & Carmo

(Figures 12A–D, 36)

Diagnosis. Postpedicel long, about two times the style length. Notopleuron integument dark, concolorous with adjacent scutum. Fore coxa and femur dark-brown, remaining coxae and femora with yellow integument, sometimes infuscated at base. Abdominal middorsal stripe a series of connected yellow triangles. Dorsolateral stripes a series of disconnected dashes on tergites 1-4, sometimes barely visible on tergite 5. Abdomen weakly banded ventrally.

Holotype female. Length 11 mm, wing 9 mm. Eyes bare. Frons pruinescent yellow, divergent above, F.I. 6.6, D.I. 1.8. Callus brown, higher than wide. Median callus black surrounded by dark pruinosity and hairs. Subcallus inflated, light brown. Clypeus and gena pale gray with yellowish hairs, except for brownish pruinescence and hairs near antennal base. First and second antennal segments yellowish brown, third segment orange. Second segment of palpus pale yellow with black hairs, except for white hairs at base. Proboscis black, dark gray pruinescent.

Scutum and scutellum grayish brown pruinescent, recumbent golden hairs and somewhat erect black hairs mixed, integument black, except supra-alar area brown. Notopleuron concolorous with scutum, paler at center, covered with mixed black and golden hairs. Pleuron integument black, gray pruinescent with yellow hairs, except anepimeron and upper surface of katepisternum with integument yellowish brown. First coxa dark brown, remaining predominantly yellow with some black areas. Fore femur dark brown with black hairs. Fore tibia strongly bicolored, basal 2/3 white with white hairs, the remainder blackish with black hairs. Fore tarsus blackish with black hairs, brown hairs ventrally. Mid and hind femora integument yellowish with yellow hairs, infuscated with brown pruinescence on basal 2/3. Mid tibia yellowish with white hairs except for black hairs at apical region. Hind tibia yellowish with white hairs except by fringe of black hairs on ventral surface. Mid and hind tarsi yellowish brown, covered with dark pruinosity and black hairs. Wings lightly infuscated on r1 and r2+3, stigma yellowish.

Abdomen brown, darkening toward apex. Middorsal stripe a series of continuous yellowish pruinescent, yellow haired triangles on tergites 1-6. Dorsolateral stripes a series of disconnected yellowish pruinescent dashes on tergites 1-4, faint at 5. Sternites 1-3 pale brown, remainder darker, largely covered with white hairs, black hairs at bases of sternites 3-6, wholly black on 7.

Male. Unknown

Comments. This species is very similar to *T. trivittatus* and *T. macrocerus* sp. n., separated from the former by the somewhat paler integument, mid and hind coxae and femora. Additionally, *T. mackerrasi* is separated from *T. macrocerus* sp. n. by the dark notopleuron, concolorous with adjacent scutum, some specimens of *T. mackerrasi* also have a black integumental stripe ventrally at the abdomen, however this character is variable. Despite of using only one character, we decided to propose these as two species, since the character in question, the pattern of coloration of the notopleuron with relation to the notum, is a character traditionally used to delimitate species in the *trivittatus* group (Fairchild 1976; Gorayeb & Rafael 1983), being a crucial character in the key. Further evidence may show this three species, to be the same taxon or a complex of several species.

Type material. Holotype female: BRASIL, *Maranhão*, Alto Turiaçu, Aldeia Gurupiuna, 19 a 22.II.90, Helder Queiros Coletor. Armadilha 1,6m suspensa (MPEG); paratypes: same data as holotype (3 f# MPEG), BRAZIL, *Pará*, Município Benevides, PA-408 km 06, 10-XI-1980, R. B. Neto (f# INPA f# MZUSP); same locality as holotype, 16.19.II.90 (f# INPA); BRASIL, Serra Norte, Manganês, 22-X-1984, 14:30 às 14 h cavalo [horse] MPEG DIP 12005349 (f# MZUSP).

Etimology. We named this species in honor of the late Australian entomologist Ian Murray Mackerras, in recognition of his great contribution to the classification and morphology of horse flies.

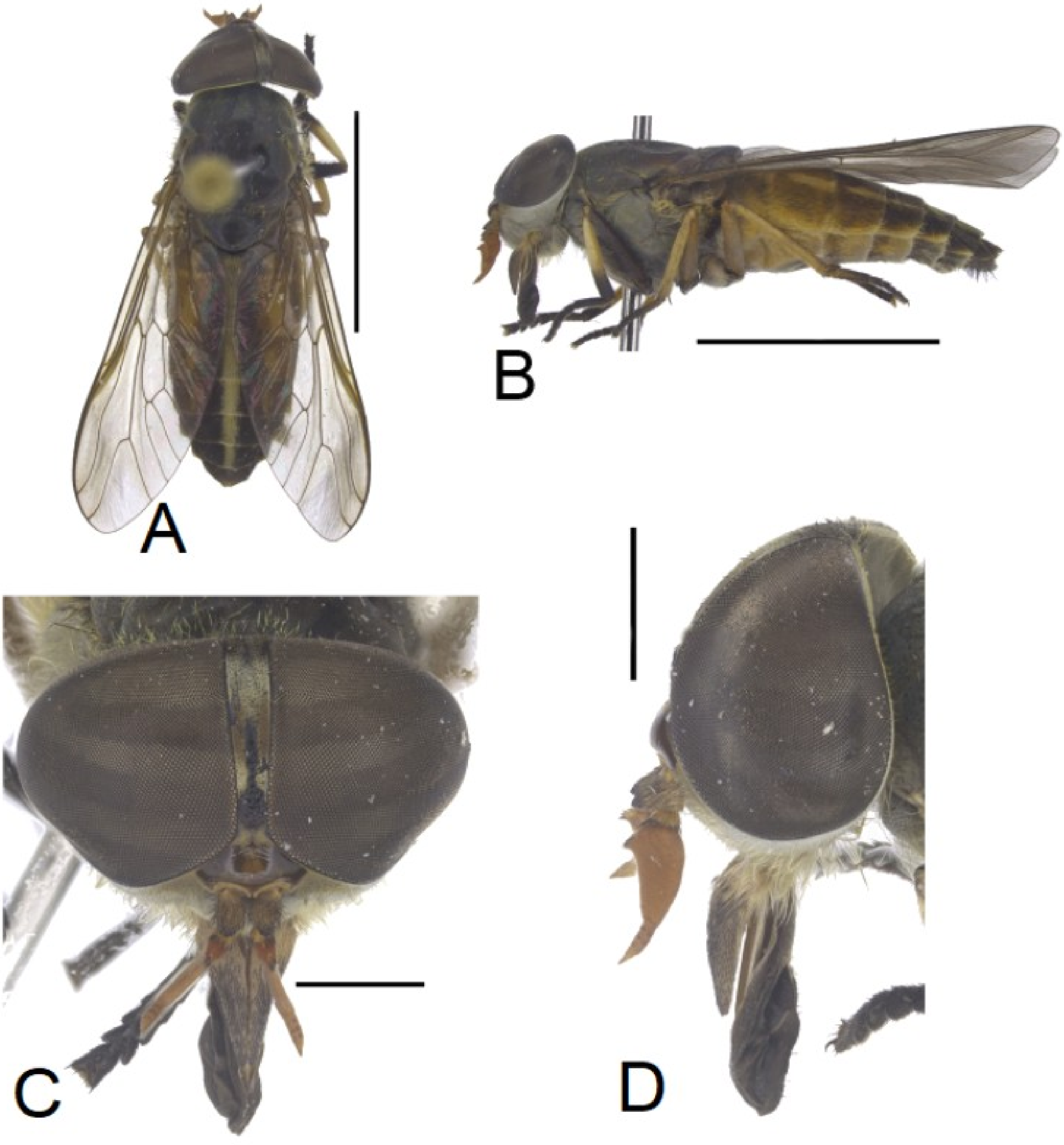


Figure 12. *Tabanus mackerrasi* sp. n. Holotype female. A. Dorsal habitus. B. Lateral habitus. C. Head, anterior view. D. Head, lateral view. Scale bars. A, B. 5 mm. C, D. 1 mm.

Tabanus macrocerus sp. n. Henriques & Carmo

(Figures 13A–D, 36)

Diagnosis. A brownish species with postpedicel long, about two times the style length. Notopleuron integument paler than adjacent scutum. All coxae, mid and hind femora yellowish. Abdominal median dorsal stripe a series of yellow connected triangles, sometimes apparently even. Dorsolateral stripes a series of disconnected dashes on tergites 1-4, sometimes barely visible on tergite 5. Abdomen ventrally banded and without a median black stripe, if present, inconspicuous and not reaching the sternite margin.

Holotype female. Length 9.2 mm, wing 7.9 mm. Eyes bare. Frons pruinescent yellow, divergent above, F.I. 7.5, D.I. 1.96. Callus brown, higher than wide. Median callus black surrounded by dark pruinescence and hairs. Subcallus inflated, dark brown, paler in middle. Clypeus and gena pale gray with white hairs, except for brownish pruinescence and hairs on upper gena near antennal base. First antennal segment pale brown, dark pruinescent above, second and third segments wholly orange, pale pruinescent, the style only slightly darker. Palpus with yellowish integument, gray pruinescence and black hairs, white hairs on basal half, mainly on anterior and posterior margins. Proboscis black, dark gray pruinescent.

Scutum and scutellum grayish brown pruinescent, recumbent golden hairs and somewhat erect black hairs mixed, integument black, except supra-alar area brown. Notopleuron paler, brown with golden hairs on upper half and black on bottom half. Pleuron with black integument, largely yellowish pruinescent and white hairs, except upper surface of katepisternum with yellowish integument and anepisternum largely with yellowish hairs. All coxae with integument yellowish and white hairs. Fore femur blackish with black hairs. Fore tibia heavy bicolored, the basal 2/3 white with white hairs, the remainder blackish with black hairs. Fore tarsus blackish with black hairs. Mid and hind femora yellowish with white hairs, mid femur with black hairs on anterior border. Mid tibia yellowish with white hairs, black hairs at apex. Hind tibia yellowish with white hairs, black hairs at posterior border and apex.

Mid and hind tarsi brown with black hairs. Wing lightly infuscated on r_1 and r_{2+3} cells with brown veins, stigma yellowish.

Abdomen brown, darkening to the apex. Median stripe a series of continuous yellowish triangles of pruinescence and hairs on tergites 1-6. Dorsolateral stripes a series of disconnected yellowish pruinescent dashes on tergites 1-4, barely visible on tergite 5. On the second tergite, the dash is largest and prominent. Sides of tergites paler and white haired. Sternites pale brown largely white hairs, but black hairs on anterior margin of sternites 3-5, more abundant on sternite 6 and wholly on sternite 7. Anterior border of sternites 2-6 whitish pruinescent.

Male. Unknown.

Type material. All collected by J. Rafael & J. Vidal. Holotype female: BRASIL, *Pará*, Novo Repartimento, Vicinal 45, 04°21′51″S, 50°01′49″W, 27.xi.2001, biting in horse (INPA); paratypes: same data of the holotype (f# INPA, 2 f# FSCA, 2 f# MPEG, 2 f# CEUFT); *idem*, 29.xi.2001 (f# MZUSP), Novo Repartimento, Vicinal 08, 04°26′42″S 49°54′25″W,28.xi.2001, Tucuruí, Faz. do Senador, 03°59′48″S, 49°45′03″W, 30.xi.2001, biting in horse (2 f# INPA); Jacundá, Porto Novo, 30.xi.2001, biting in horse (f# INPA), *Maranhão*, São Pedro da Água Branca, 04°59′05″S, 48°08′03″W, 07.xii.2001, malaise trap (f# CZMA).

Etymology. From Greek, *makros* (large) + *keros* (horn, relative to antenna).

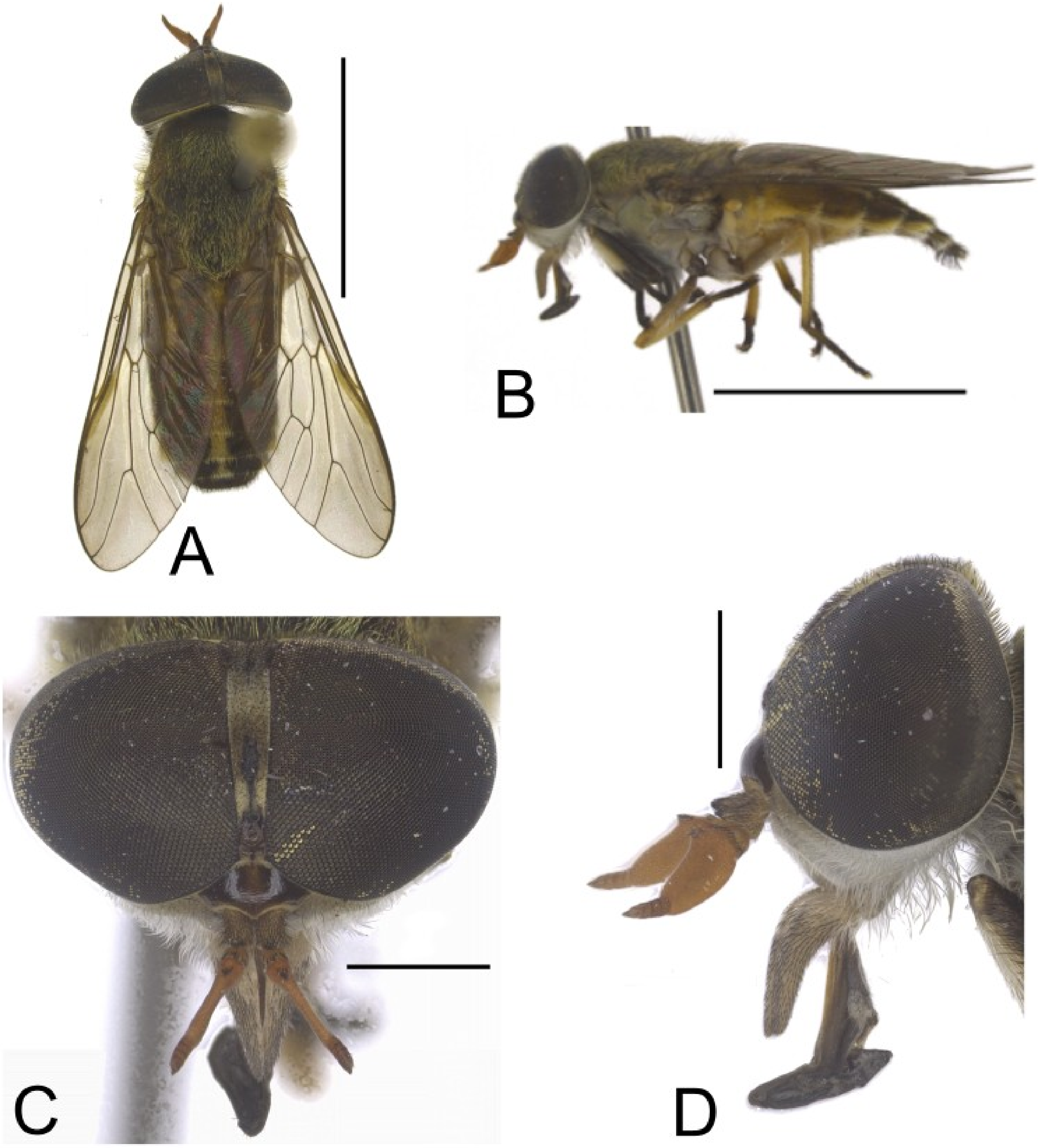


Figure 13. *Tabanus macrocerus* sp. n. Holotype female. A. Dorsal habitus. B. Lateral habitus. C. Head, anterior view. D. Head, lateral view. Scale bars. A, B. 5 mm. C, D. 1 mm.

Tabanus noncallosus sp. n. Carmo & Henriques

(Figures 14A–E, 34)

Diagnosis. A brownish species with subcallus light brown and only slightly inflated. Notopleuron concolorous with scutum. Frons not markedly divergent above (D.I. 1.7) All coxae and fore femur black. Mid and hind femora blackish at base, and yellow at apical half. Mid and hind tibia yellow. Wings brown tinted especially on costal and radial cells.

Holotype female. Length 10.5 mm Wings 8.4 mm. Frons pruinescent yellow, golden near median callus apex, slightly divergent above F.I. 6.3, D.I. 1.7. Frontal callus brown, rounded, higher than wide. Median callus dark brown, slender and connected to callus. Subcallus light brown, slightly inflated. Clypeus and gena pruinescent white with white hairs. Both yellow with black hairs. Postpedicel clearly longer than high, dorsal tooth with black hairs at apex. Style greater than half postpedicel length. Palpus slightly inflated at base, light brown covered with yellow pruinescence and mixed black and white hairs.

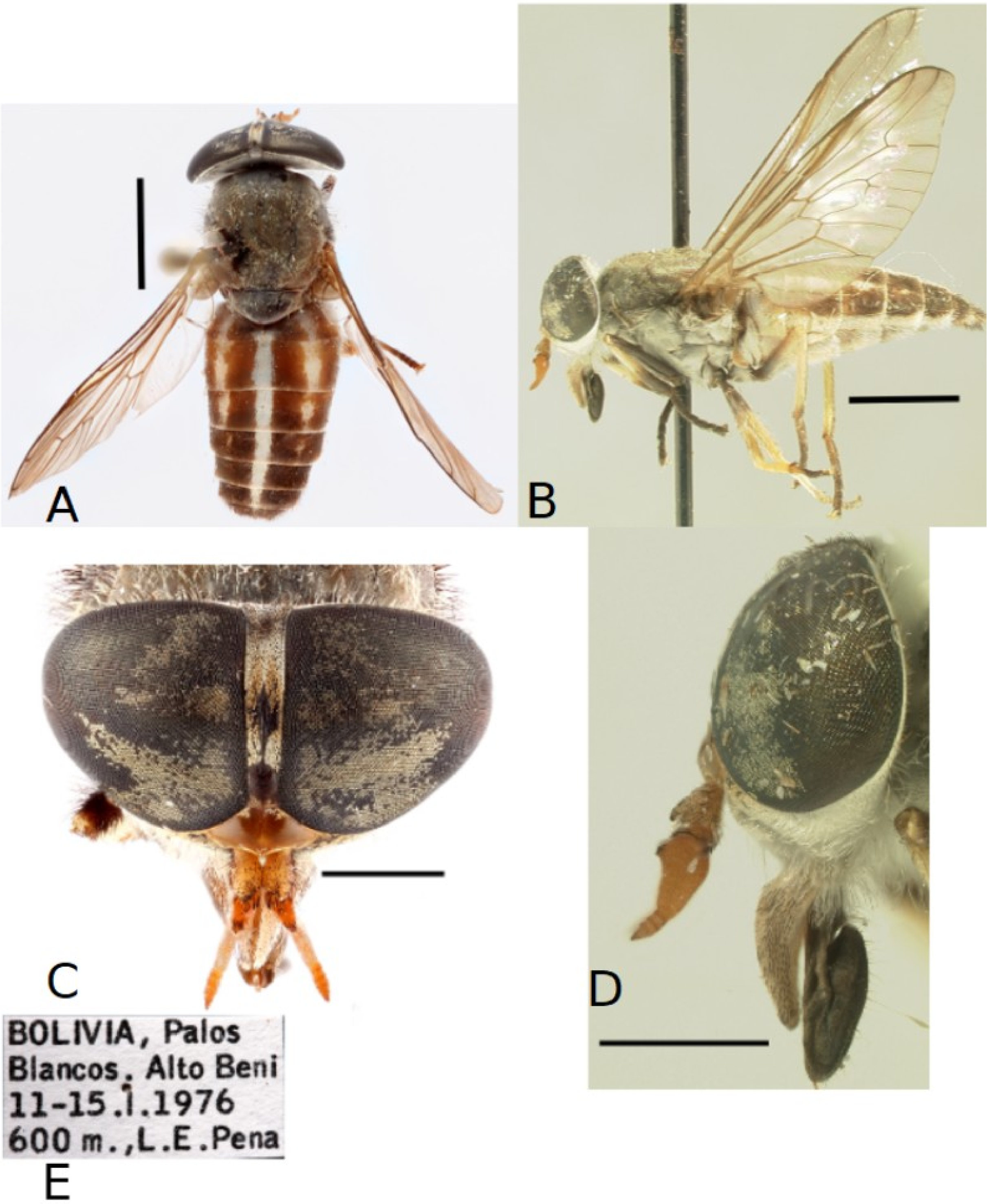
Scutum and scutellum integument blackish except for brown supra-alar region, black erect hairs mixed with recumbent golden hairs. Notopleuron dark, concolourous with scutum with long black hairs. Pleuron integument dark brown, pruinescent gray with white hairs. Fore femur and all coxae black. Mid femora blackish at basal third, yellow at the remainder. Hind femur blackish infuscated basally, the remainder yellow. Fore tibia bicolored, basal half yellow with yellow hairs, apical half brown with black hairs. Mid and hind tibia yellow with yellow and black hairs, hind tibia with comb of erect black hairs ventrally. Fore tarsus dark brown with black hairs. Mid and hind tarsi brownish yellow with black hairs. Wings lightly brownish tinted at r1 and r2+3. Costal cell hyaline. Stigma yellow.

Abdomen brown, black pilose. Mid stripe broad, pruinescent white, reaching tergite 6. Dorsolateral broad, interrupted through tergite 3, faint indications at 4. Sides of tergites 1-5 with pale pilosity and pruinescence. Abdominal sternites pruinescent black, black haired, medial stripe. Sides of sternites 1-4 light brown with pale hairs, black with black hairs at the remainder. Posterior margin of sternites with narrow white pruinescent band.

Comments. This species possess intermediary characteristics between *T. callosus* and *T. picicallosus*. It differs from both by having a less pronounced subcallus. It also differs from the former by the paler femora. From the latter, it differs by the black coxae and wings less infuscated.

Type material. Holotype female: BOLIVIA, [*La Paz*], Palos Blancos, Alto Beni, 11-15.I.1976, 600m., L.E.Pena [leg] (FSCA); paratypes: PERU, *Madre de Dios*, Rio Tambopata Res, 30 km (air) SW Puerto Maldonado, 290m, 20-31-X-1982. R. Wilkerson [leg] (f# FSCA), BRASIL, *Acre*, Parque Nacional da Serra do Divisor, Sítio 5, Norte, 7°27′32″S, 73°46′28″W, 14/XI/1996, E.F. Morato, leg. (f# INPA).

Etymology. From Latin, *non* (no) + *callosus*, by the similarity with this species.



BOLIVIA, Palos
Blancos, Alto Beni
11-15.I.1976
600 m.,L.E.Pena

Figure 14. *Tabanus noncallosus* sp. n. Holotype female. A. Dorsal habitus. B. Lateral habitus. C. Head, anterior view D. Head, lateral view. Scale bars. A, B. 3 mm. C, D. 1 mm. Photos obtained by courtesy of FSCA.

Tabanus palpalis **Brèthes**

(Figures 15 A–D, 29B, 32)

Tabanus palpalis Brèthes, 1910: 477; Brèthes, 1921: 54 (Argentina spp.); Coscarón, 1967: 127 (Argentina spp.); Fairchild, 1971: 98 (cat.), 1976: 250, fig. 7 (rev.); Moucha, 1976: 129 (cat.); Coscarón, 1979: 276, figs. 7C-H (taxonomy); Henriques & Gorayeb, 1993: 19 (MPEG spp.); Fairchild & Burger, 1994: 145 (cat.); Henriques, 1997: 88 (INPA spp.); Chainey, *et al*., 1994: 336 (Bolivia spp.); Barros & Gorayeb, 1996: 548 (Pantanal spp.); Barros, 2001: 919, 920 (seasonality Pantanal spp.); Coscarón & Papavero, 2009: 138 (cat.); Lima *et al*., 2015: 7 (Tocantins spp.); Krolow & Henriques, 2017: 4 (Mato Grosso do Sul spp.).

Tabanus callosus Macquart, of Brèthes, 1907: 284 (cat., misident.).

Tabanus trivittatus Fabricius, of Wulp, 1881: 160 (Argentina record, misident.) of Brèthes, 1907: 285.

Tabanus lucidecallosus Fairchild, 1942b: 163, pl. l, fig. l; Bequaert & Renjifo-Salcedo, 1946: 79 (Colombia spp.).

Diagnosis. Postpedicel of antenna nearly the same length of style. Subcallus brown, only slightly inflated in lateral view. Frons clearly divergent above, about as twice as wide at vertex than at base. Notopleuron with integument lighter than adjacent scutum. Femora black or at least basally infuscated. Middorsal stripe even through tergite 6. Dorsolateral slightly irregular through tergite 4.

Comments. A series from Barra dos Bugres, Mato Grosso, has the fore coxa yellow. These specimens may be difficult to be identified with the keys provided here. We consider this character not enough to characterize a new taxon since the color of coxae is known to vary within the same species of the group. This is probably just a paler form of *T. palpalis.*

Material examined. BRASIL, *Tocantins*, Araguacema; *Pará*, Conceição do Araguaia (16 f# INPA); *São Paulo***,** Cássia dos Coqueiros, Cajuru (13 f# MZUSP, 8 f# INPA); *São Paulo*, Araçatuba, Fazenda Jacarecatinga (7 f# MZUSP), Guatapará (3 f# MZUSP); PARAGUAY, *San Pedro*, Carumbé (2 f# MZUSP).

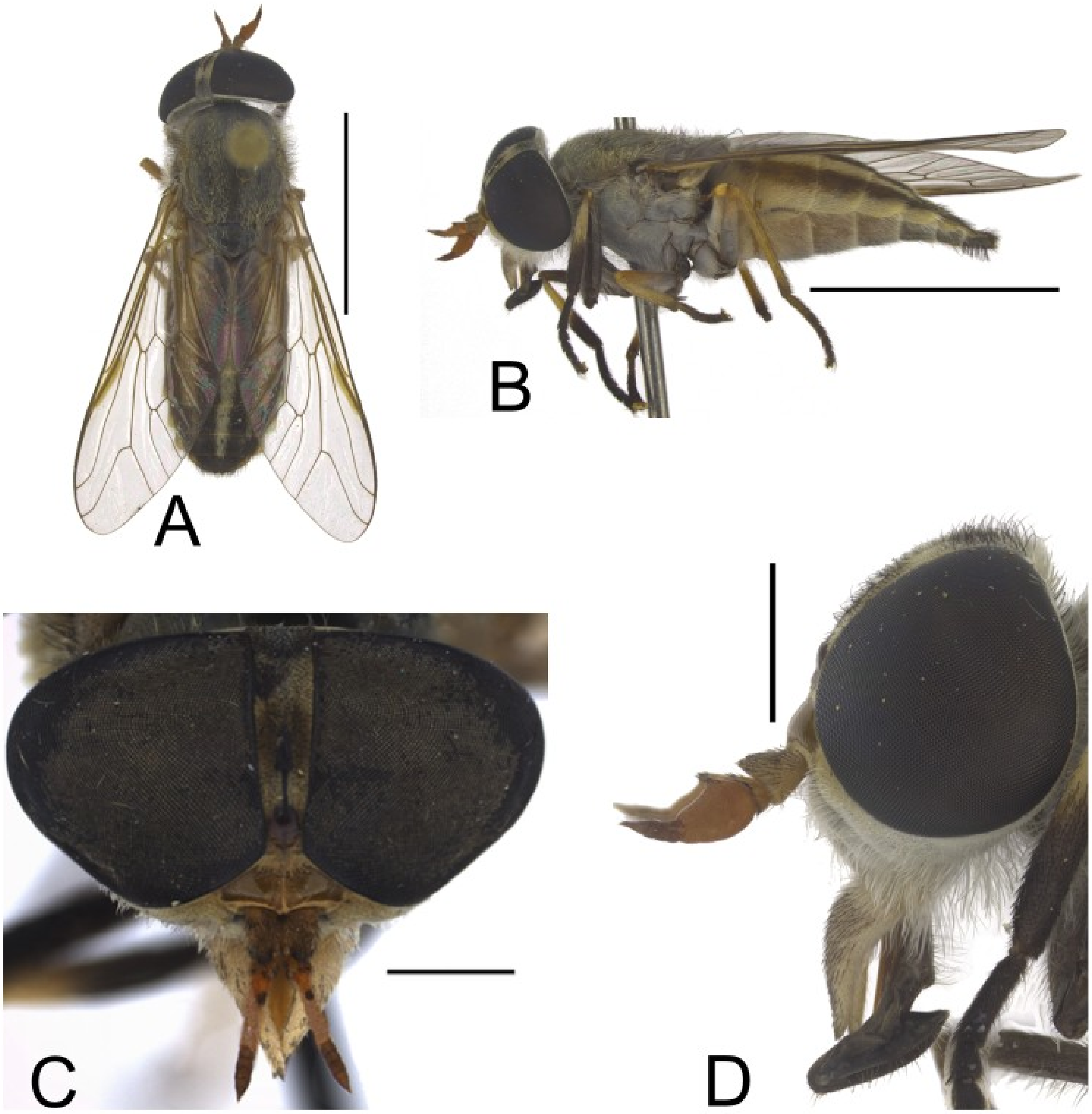


Figure 15. *Tabanus palpalis.* Female. A. Dorsal habitus. B. Lateral habitus. C. Head, anterior view. D. Head, lateral view. Scale bars. A, B. 5 mm. C, D. 1 mm.

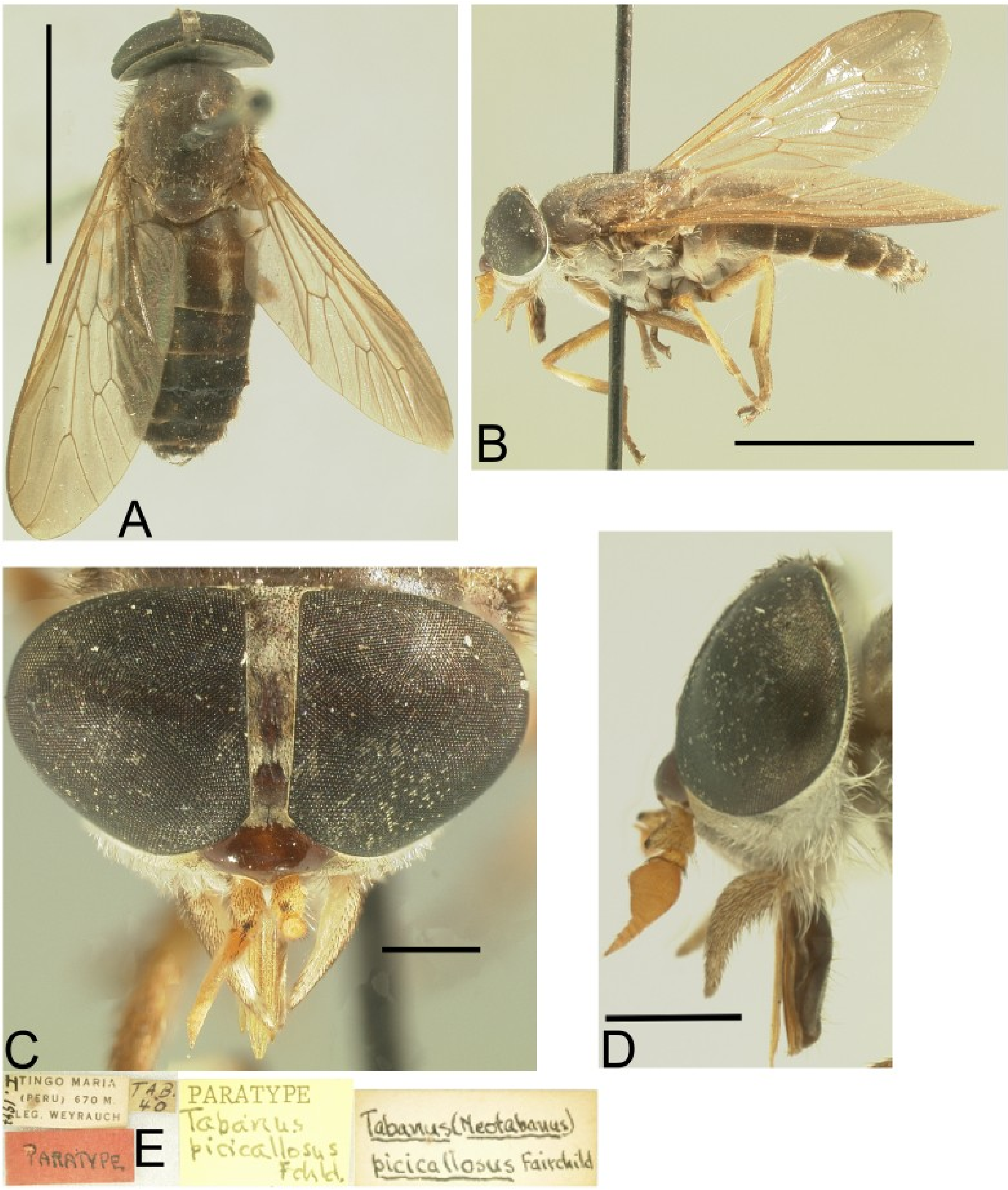
Tabanus picicallosus **Fairchild**

(Figures 16A–E, 31)

Tabanus picicallosus Fairchild, 1951: 458, figs. 9, 9a; Fairchild, 1971: 99 (cat.), 1976: 251, fig. 8 (rev.); Moucha, 1976: 131 (cat.); Wilkerson & Fairchild, 1985: 51 (Peru spp.); Henriques & Gorayeb, 1993: 19 (MPEG spp.); Fairchild & Burger, 1994: 146 (cat.); Coscarón & Papavero, 2009: 139 (cat.).

Diagnosis. Subcallus black, strongly inflated in lateral view. Femora pale yellow. Wings strongly tinted. Notopleuron concolorous with adjacent scutum. Dorsolateral stripes reaching segment 4, mid dorsal stripe reaching tergite 6. Frons not markedly divergent (D.I. 1.7).

Material examined. Paratype female (FSCA), labels as Fig. 11E; BRAZIL, *Acre***,** Rio Branco; M. Thaumaturgo, Rio Tejo (2 f# MPEG). Holotype examined through photos available at the MCZ database.



H
TINGO MARIA
(PERU) 670 M.
LEG. WEYRAUCH

TAB.
40

PARATYPE

PARATYPE
Tabanus
picicallosus
Fchld.

Tabanus (Neotabanus)
picicallosus Fairchild

Figure 16.*Tabanus picicallosus*. Paratype female. A. Dorsal habitus. B. Lateral habitus. C. Head, anterior view. D. Head, lateral view. E. Labels. Scale bars. A, B. 5 mm. C, D. 1 mm. Photos obtained by courtesy of FSCA.

Tabanus platycerus Fairchild

(Figures 17A–E, 33)

Tabanus platycerus Fairchild, 1976: 251, fig. 9; Fairchild, 1986: 119 (Panama spp.); Henriques & Gorayeb, 1993: 19 (MPEG spp., in part); Fairchild & Burger,1994: 146 (cat.); Henriques, 1997: 88 (INPA spp., in part); Coscarón & Papavero, 2009: 139 (cat.).

Diagnosis. Notopleuron integument lighter than adjacent scutum. All coxae, mid and hind femora brownish yellow, pruinescent gray, white haired, hind coxae sometimes with black areas. Middorsal abdominal stripe a series of slender connected triangles through tergite 6; dorsolateral disconnected through tergite 4.

Comments. Fairchild (1976) described this species based on specimens from Costa Rica and Panama. Since then, this species has been registered east of the Andes, by Henriques and Gorayeb (1993; Brazil), Cárdenas & Vieira (2005; Ecuador), Cárdenas (2009; Ecuador) and Henriques (2016; Venezuela). We also examined several specimens from the Amazon Basin at the INPA and Museu Goeldi collections identified as *T. platycerus.* All specimens from the collections had lateral abdominal stripes present beyond segment four, reaching the fifth segment and sometimes with vestiges on the sixth, a character not seen in the type series of *T. platycerus,* but present in the very similar *T. sextriangulus*. We believe that this might be the case for all species registers east of the Andes, therefore *T. platycerus* distribution is restricted to Central America, while citations above refers to *T. sextriangulus*.

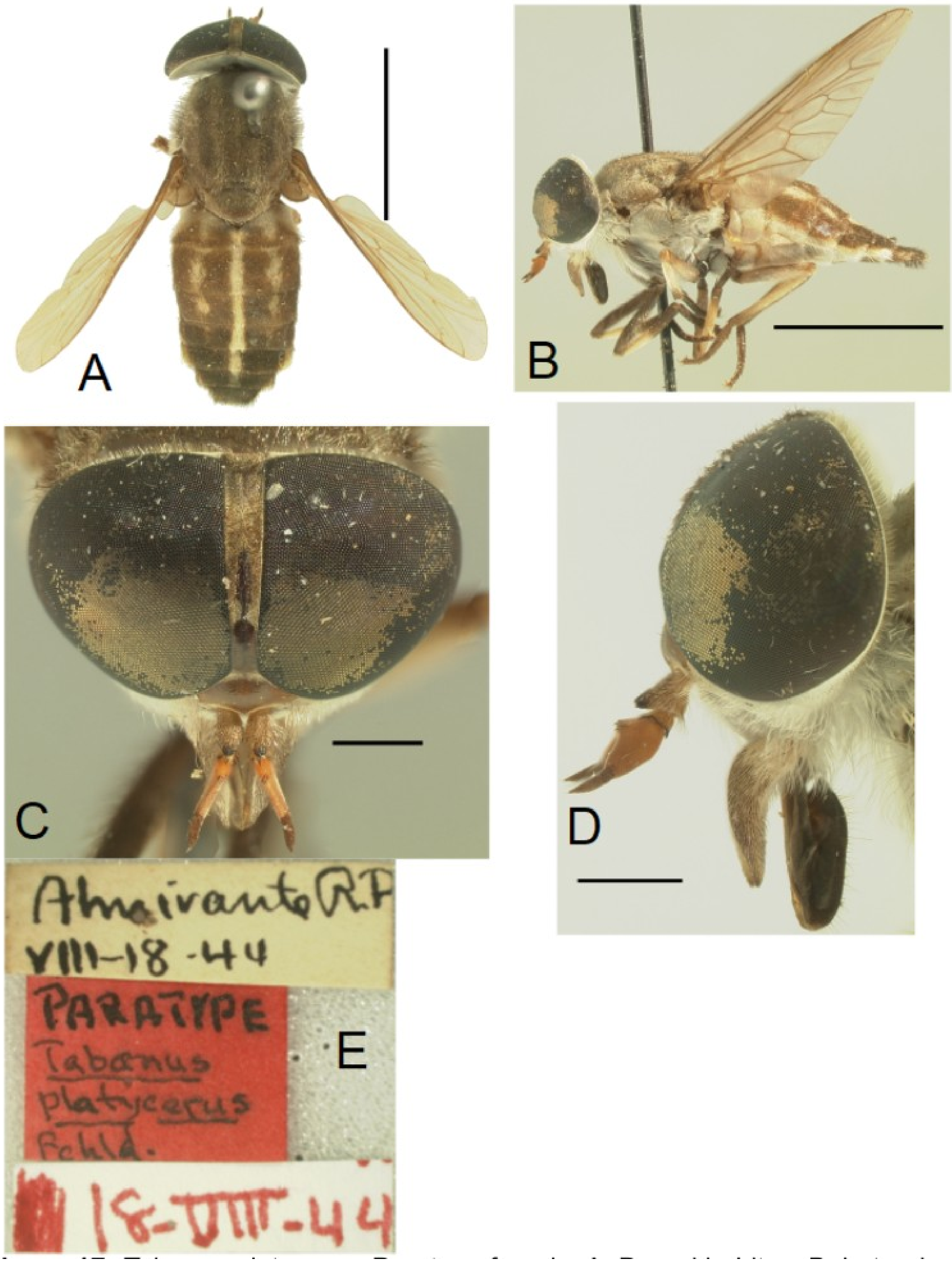


Figure 17. *Tabanus platycerus.* Paratype female. A. Dorsal habitus. B. Lateral habitus. C. Head, anterior view. D. Head, lateral view. E. Labels. Scale bars. A, B. 5 mm. C, D. 1 mm. Photos obtained by courtesy of FSCA.

Material examined. Paratypes, label as fig. 17 E (5 f# FSCA). PANAMA, *Bocas del Toro* (f# INPA 2 f# MPEG). Holotype examined by photos, available at the MCZ database.

Tabanus restrepoensis **Fairchild**

(Figures 18A–D, 35)

Tabanus restrepoensis Fairchild, 1942b: 163; Bequaert & Renjifo-Salcedo, 1946: 78 (Colombia spp.); Barretto, 1957: 87 (Guyana spp.); Fairchild, 1971: 101 (cat.), 1976: 253, fig. 10 (rev.); Moucha, 1976: 135 (cat.); Wilkerson & Fairchild, 1985: 51 (Peru spp.); Henriques & Gorayeb, 1993: 19 (MPEG spp.); Fairchild & Burger, 1994: 148 (cat.); Henriques, 1997: 88 (INPA spp.); Cárdenas & Vieira, 2005: 155 (Ecuador spp.); Coscarón & Papavero, 2009: 141 (cat.); Wolff & Miranda-Esquivel, 2016: 285 (cat.).

Diagnosis. Frons divergent (D.I. > 2). All coxae and femora yellow. Notopleuron integument paler than adjacent scutum. Middorsal abdominal stripe even through tergite 6. Dorsolateral even and continuous through tergite 4 or 5. Subcallus dark brown to black, not conspicuously inflated under lateral view.

Comments. Fairchild (1976) already highlighted the resemblance of this species to *T. tristichus*, but differentiated them both by the more divergent frons of *T. restrepoensis*, broader antennae, palpus more inflated basally and broader abdominal stripe in *T. tristichus.* After examining specimens at the collections studied, we have seen that the antenna and palpus characters are very variable and not very useful to separate the two species. We decided to keep them separated, by the divergent frons, strongly bicolored tibia of *T. restrepoensis* and geographic distribution, *T. tristichus* is restricted to areas with coastal influence.

Material examined. BRAZIL, *Pará*, Conceição do Araguaia (6 f# INPA); *Tocantins,* Araguacema (F # INPA); PERU, *Madre de Dios*, Rio Tambopata (f# INPA); BRAZIL, *Acre,* Serra do Divisor (5 f# MPEG).

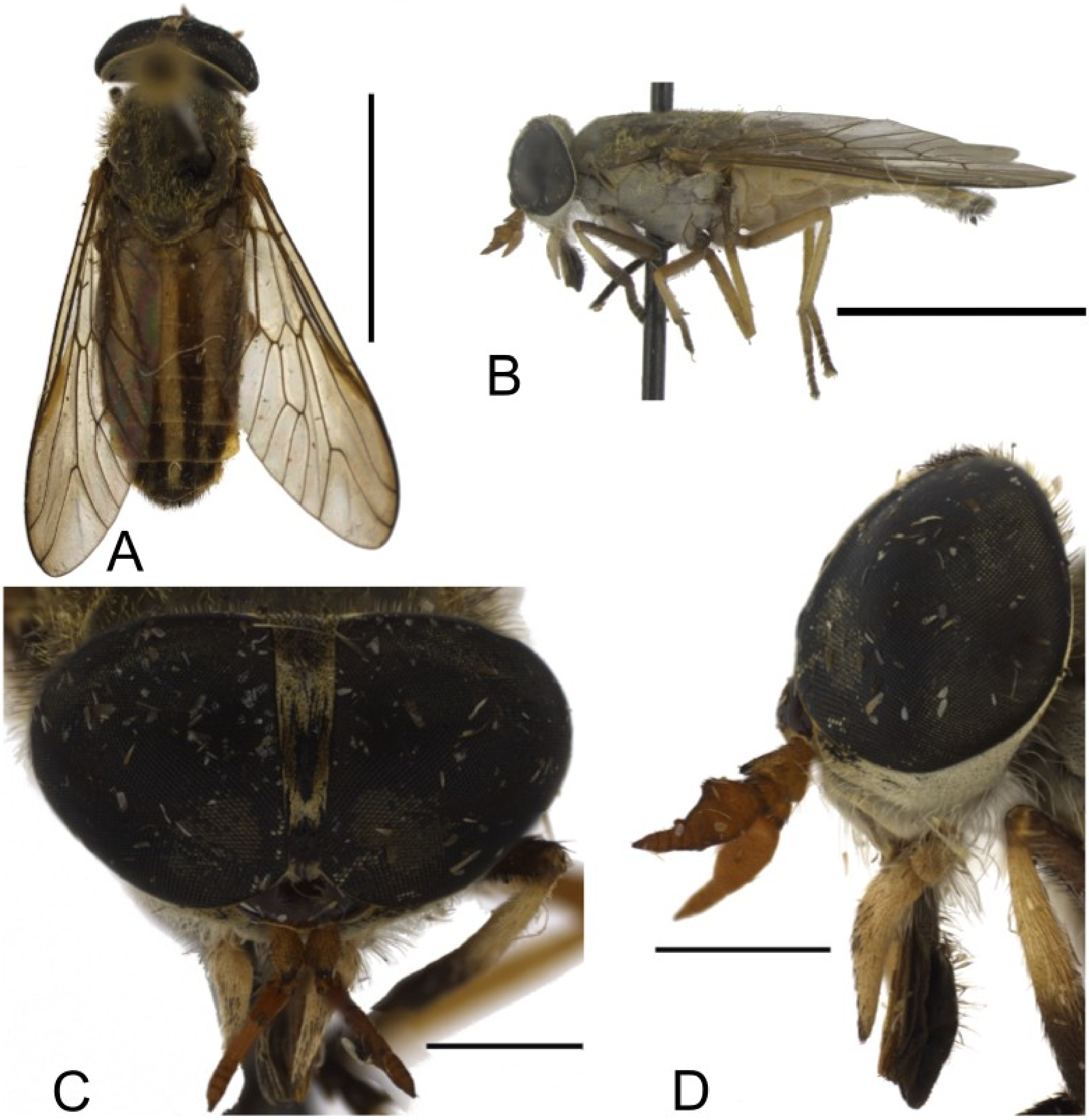


Figure 18. *Tabanus restrepoensis*. Female. A. Dorsal habitus. B. Lateral habitus. C. Head, anterior view. D. Head, lateral view. Scale bars. A, B. 5 mm. C, D. 1 mm.

***Tabanus rhizonshine* Philip**

(Figures 19A–D, 20A–D, 33)

Tabanus rhizonshine Philip, 1954: 13, fig. 15; Fairchild, 1971: 101 (cat.), 1976: 254, fig. 11 (rev.); Moucha, 1976: 135 (cat.); Arnaud, 1985: 150 (Philip spp.); Fairchild & Burger, 1994: 148 (cat.); Coscarón & Papavero, 2009: 141 (cat.).

Diagnosis. Frons only slightly divergent (D.I. 1.77) and broad (F.I. 5.9). Callus black, squared, and touching the eyes margins. Scutum and scutellum black. Notopleuron paler than adjacent scutum. Postpedicel shortest than style, nearly as high as long. Dorsolateral stripes reaching tergite 5.

Material examined. MEXICO, *Jalisco* (f#, m# FSCA).

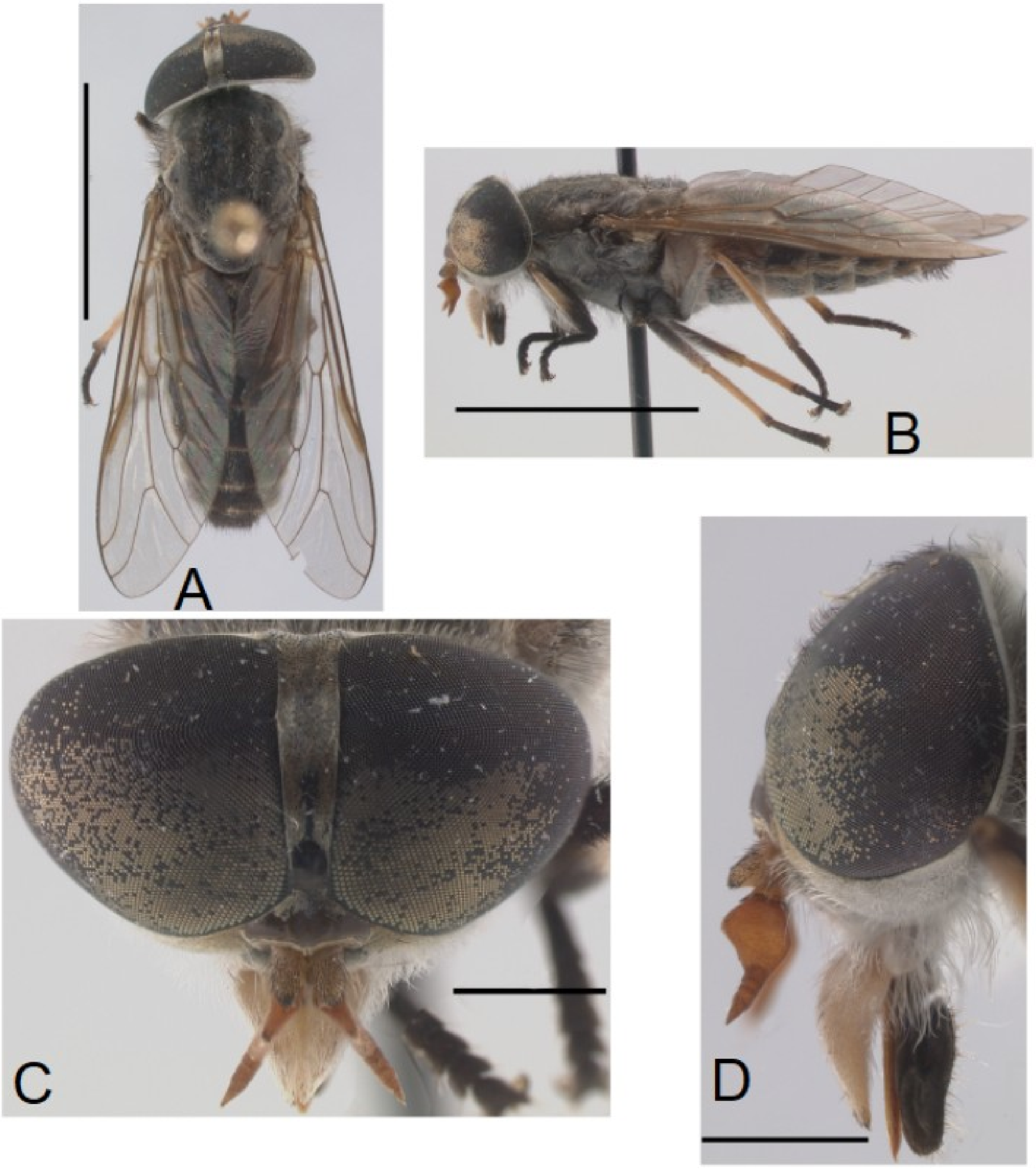


Figure 19. *Tabanus rhizonshine.* Female. A. Dorsal habitus. B. Lateral habitus. C. Head, anterior view. D. Head, lateral view. Scale bars. A, B. 5 mm. C, D. 1 mm. Photos obtained by courtesy of FSCA.

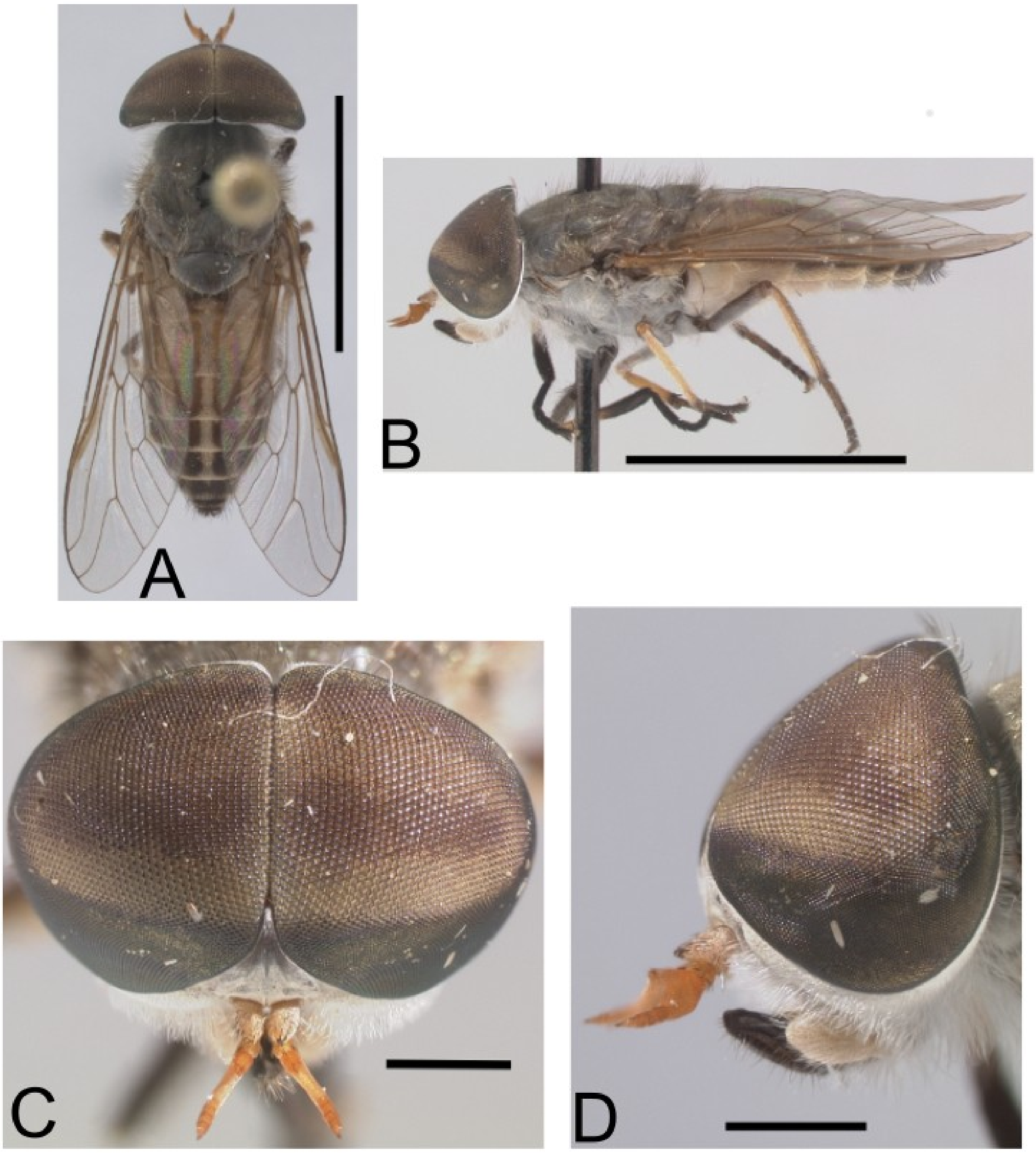


Figure 20. *Tabanus rhizonshine.* Male. A. Dorsal habitus. B. Lateral habitus. C. Head, anterior view. D. Head, lateral view. Scale bars. A, B. 5 mm. C, D. 1 mm. Photos obtained by courtesy of FSCA.

Tabanus schadei **Fairchild**

(Figures 21A–D, 36)

Tabanus schadei Fairchild, 1976: 294, fig. 12; Coscarón, 1979: 277, figs. 7L-V (taxonomy); Fairchild & Burger, 1994: 149 (cat.); Henriques, 1997: 88 (INPA spp.); Coscarón & Papavero, 2009: 142 (cat.); Krolow & Henriques, 2017: 4 (Mato Grosso do Sul spp.).

Diagnosis. Frons broad (F.I. less than 5) and nearly parallel. All coxae and femora yellow. Notopleuron with integument paler than adjacent scutum. Dorsolateral stripes a series of disconnected patches. Subcallus brown, conspicuously inflated at lateral view.

Comments. This species is easily recognized by the rather broad frons (Fig. 21C). The female genitalia was described by Coscarón (1979).

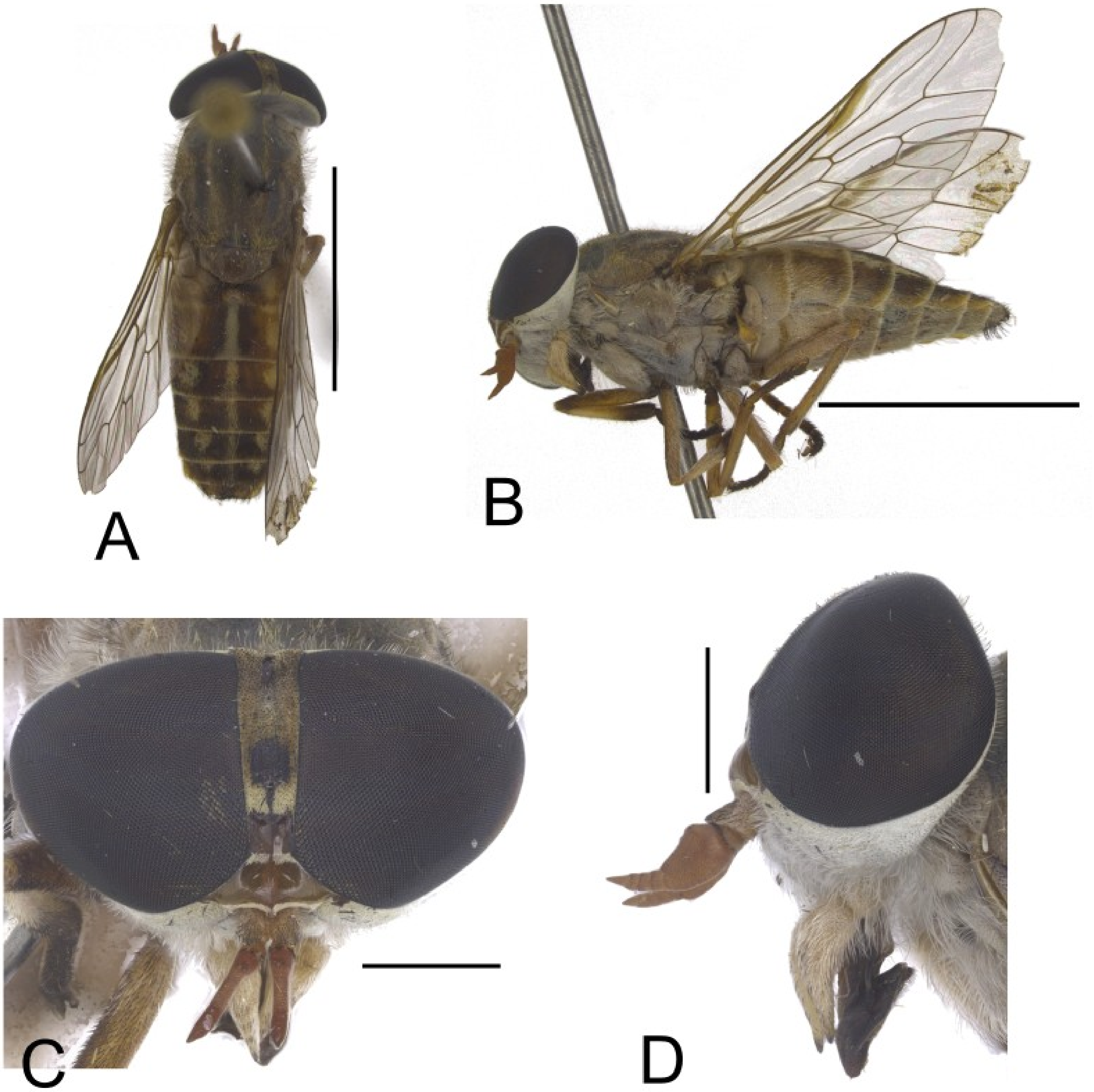


Figure 21. *Tabanus schadei.* Female. A. Dorsal habitus. B. Lateral habitus. C. Head, anterior view. D. Head, lateral view. Scale bars. A, B. 5 mm. C, D. 1 mm

Material examined. Holotype f#, PARAGUAY, *Cerro Pelado*, Sept-1937, F. Schade coll. (USNM). PARAGUAY, *San Pedro*, Carumbé (3 f#, m# INPA), BRASIL, *Mato Grosso do Sul*, Maracaju (12 f # MZUSP).

Tabanus sextriangulus **Gorayeb and Rafael**

(Figures 22A–D, 23A–D 32)

Tabanus sextriangulus Gorayeb & Rafael, 1984: 49, figs. 2, 3B, 4; Wilkerson & Fairchild, 1985: 52 (Peru spp.); Henriques & Gorayeb, 1993: 19 (MPEG spp.); Fairchild & Burger, 1994: 149 (cat.); Henriques, 1997: 88 (INPA spp.); Henriques & Rafael, 1999: 218 (distr.); Oliveira *et al*., 2007: 792, 794 (ecology); Coscarón & Papavero, 2009: 142 (cat.); Wolff & Miranda-Esquivel, 2016: 286 (cat.).

Tabanus platycerus Fairchild, of Cárdenas & Vieira, 2005: 155 (misident.), 2009: 528 and appendix 4: 19 (misident.); of Henriques, 2016: 182 (misident.).

Diagnosis. Frons strongly divergent (D.I. > 2.0). Notopleuron integument paler than adjacent scutum, this and scutellum black. All coxae and femora dark brown to black. Middorsal abdominal stripe a series of connected triangles through tergite 5, sometimes with faint indications at 6. Dorsolateral a series of disconnected triangles visible through tergite 6.

Comments. This species can be differentiated from *T. trivittatus* and *T. callosus,* sympatric species, by the notopleuron with integument paler than adjacent scutum. We found that the coxae integument of *T. sextriangulus* ranges from yellowish brown to black in the females examined. This variation is not accounted for in the species description of Gorayeb & Rafael (1984). However, this variation, does not difficult species determination, since the fore coxa is always darker than the remaining coxae and the femora is always darker than tibiae.

Material examined. Holotype f#, BRAZIL, *Amazonas*, Cidade Universitária, no cavalo [in horse], 19-VIII-1978, J.A. Rafael (MPEG); paratypes: *Rondônia*, Guajará Mirim; *Pará,* Oriximiná; *Amazonas,* Tabatinga, Rio Urucu (29 f# INPA); PERU, *Madre de Dios*; COLOMBIA, *Amazonas,* Leticia; BRASIL, *Amazonas,* Aripuanã; *Mato Grosso*; *Pará*, Serra Norte, Altamira; *Acre,* Porto Acre (24 f# MPEG); BRASIL, *Amazonas*, Manaus; Itacoatiara, *Pará*, Óbidos (20 f#, m# INPA).

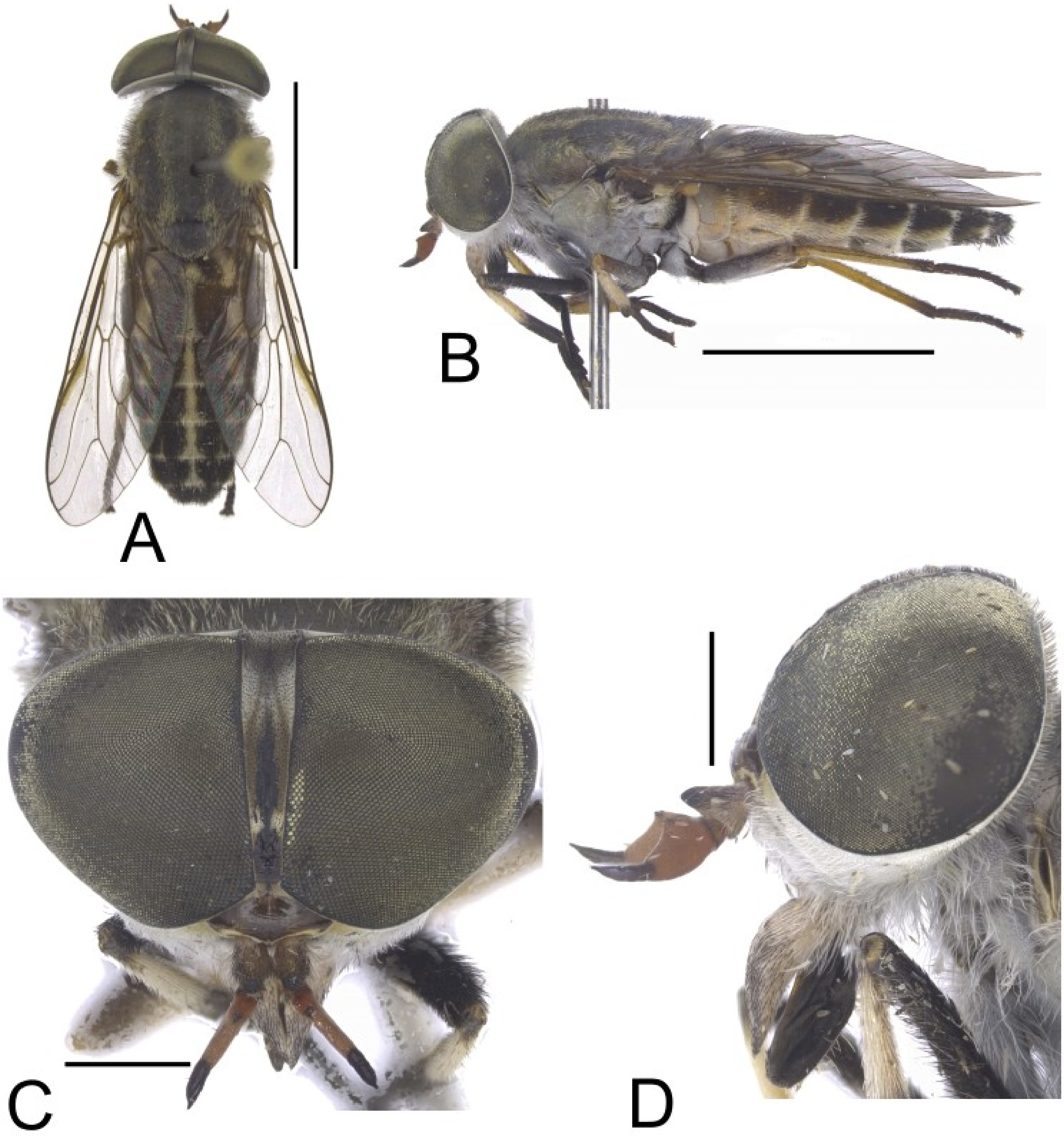


Figure 22. *Tabanus sextriangulus.* Female. A. Dorsal habitus. B. Lateral habitus. C. Head, anterior view. D. Head, lateral view. Scale bars. A, B. 5 mm. C, D. 1 mm.

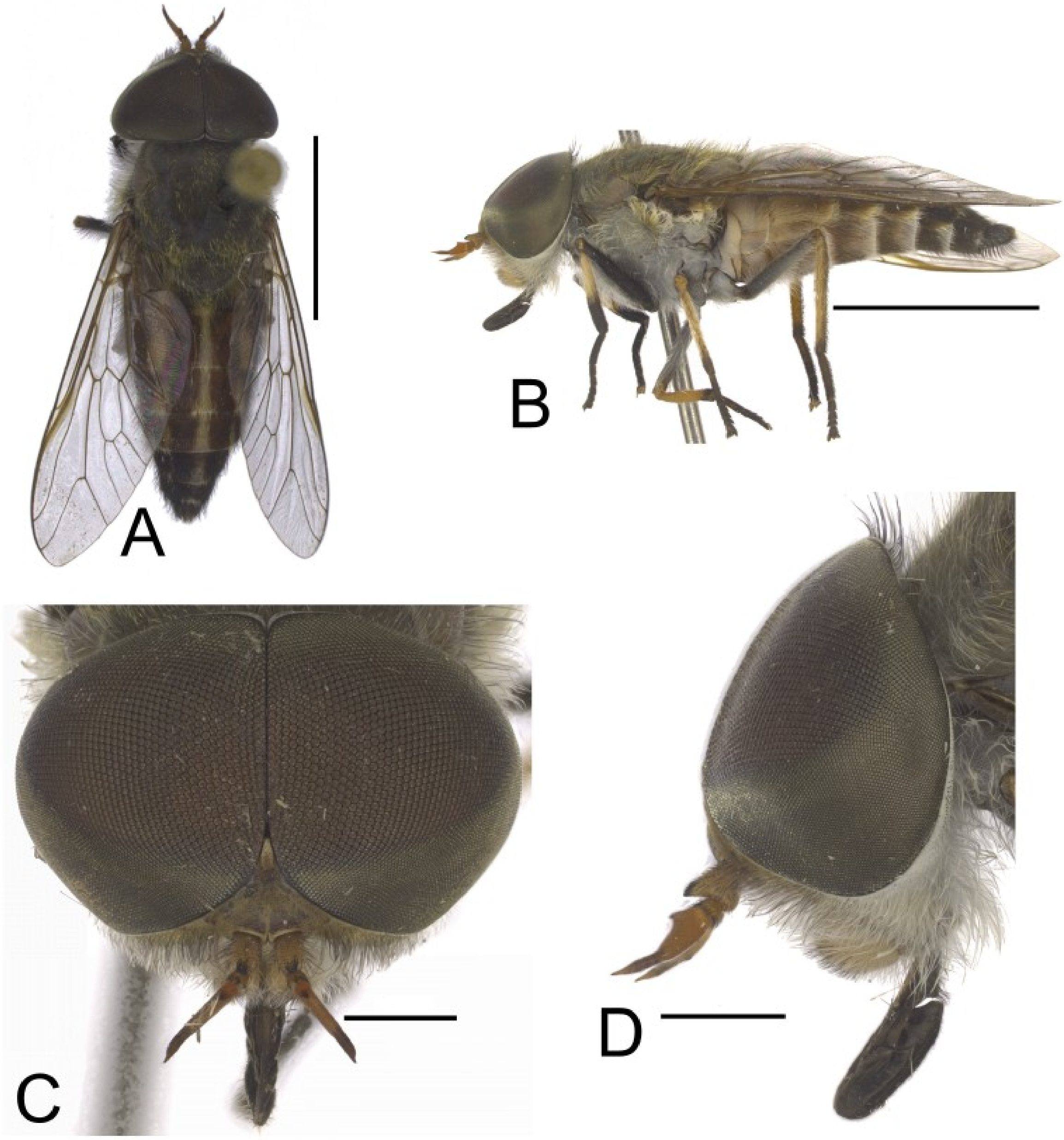


Figure 23. *Tabanus sextriangulus.* Male. A. Dorsal habitus. B. Lateral habitus. C. Head, anterior view. D. Head, lateral view. Scale bars. A, B. 5 mm. C, D. 1 mm.

***Tabanus tristichus* Fairchild**

(Figures 24A–E, 35)

Tabanus tristichus Fairchild, 1976: 256, fig. 13; Henriques & Gorayeb, 1993: 19 (MPEG spp.); Fairchild & Burger, 1994: 151 (cat.); Henriques, 1997: 88 (INPA spp.); Coscarón & Papavero, 2009: 145 (cat.); Krolow *et al*., 2017: 106 (French Guiana spp.).

Diagnosis. Frons not markedly divergent (D.I. 1.7). All coxae and femora yellow. Middorsal and dorsolateral abdominal stripes broad, even and contiguous through tergite 6

Comments. See *restrepoensis*.

Material examined. Paratype f#, labels as fig. 18E (FSCA). BRAZIL, *Pará*, Bragança, Ajuruteua (4 f# INPA).

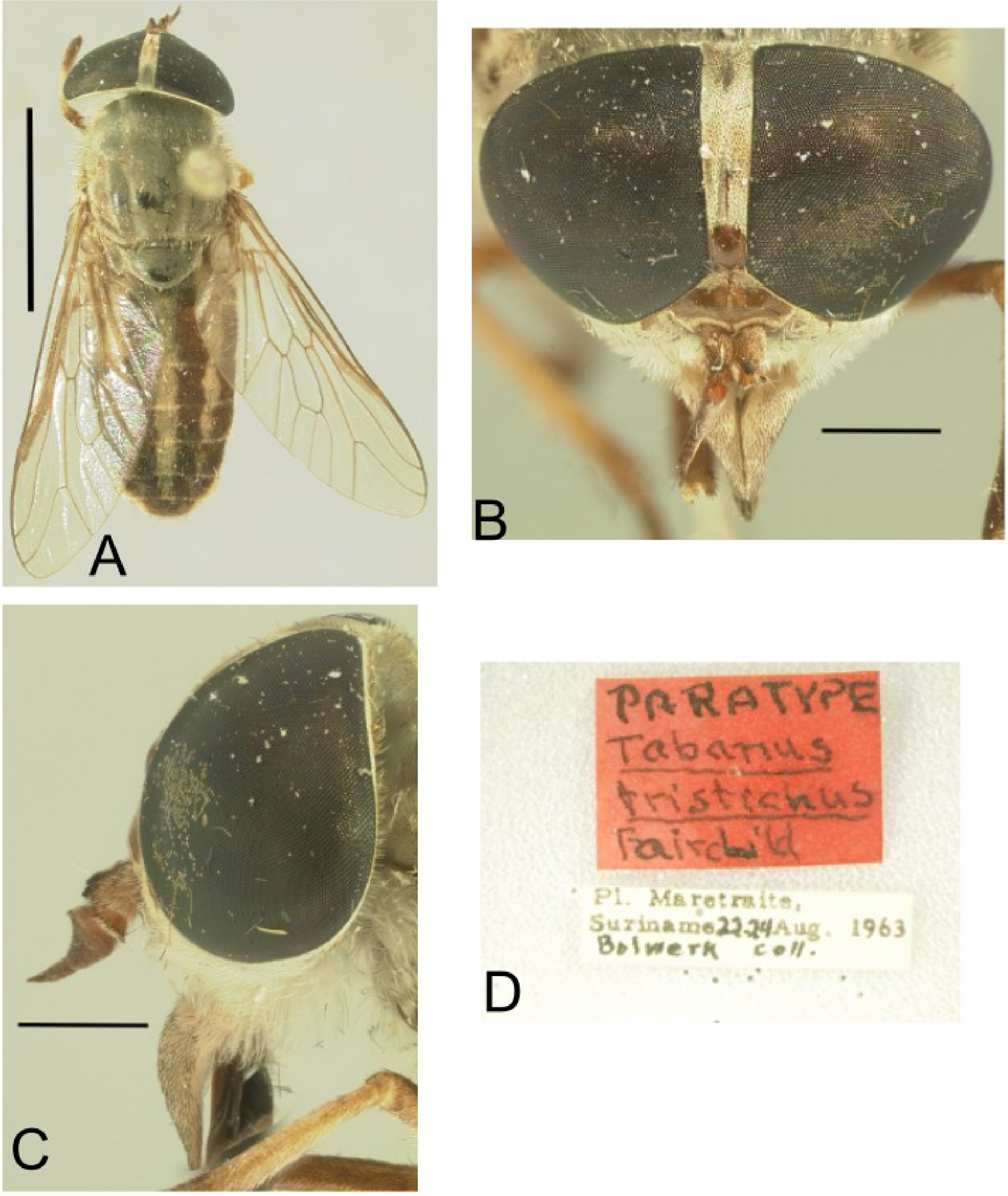


Figure 24. *Tabanus tristichus.* Paratype female. A. Dorsal habitus. B. Head, anterior view. C. Head, lateral view. D. Labels. Scale bars. A. 5 mm. B, C. 1 mm. Photos obtained by courtesy of FSCA.

***Tabanus trivittatus* Fabricius**

(Figures 25A–D, 26A–D 36)

Tabanus trivittatus Fabricius, 1805: 104; Wiedemann, 1821: 85 (taxonomy), 1828: 172 (taxonomy); Walker, 1854: 199 (BMNH spp.); Schiner, 1868: 86 (taxonomy); Hunter, 1901: 144 (cat.); Kertész, 1908: 288 (cat.); Hine, 1920: 190 (taxonomy); Kröber, 1934: 293 (cat.); Philip, 1954: 13 (Fabricius' TP); Barretto, 1957: 87 (Guyana spp.); Fairchild & Aitken, 1960: 8 (Guyana record); Fairchild, 1966: 24, fig. 3 (Fabricius spp.); Fairchild, 1970: 840 (French Guiana spp.), 1971: 103 (cat.), 1976: 258, fig. 14 (rev.); Moucha, 1976: 148 (cat.); Wilkerson & Fairchild, 1985: 52 (Peru spp.); Rafael *et al.*, 1991: 365 (Roraima spp.); Henriques & Gorayeb, 1993: 19 (MPEG spp.); Gorayeb, 1993: 249 (seasonality); Fairchild & Burger, 1994: 151 (cat.); Henriques, 1997: 88 (INPA spp.); Henriques & Rafael, 1999: 219 (distr.); Gorayeb, 2000: 33 (ecology); Gorayeb & Ribeiro, 2001: 79 (mark and recapture); Henriques, 2004: 148-149 (habitat); Luz-Alves *et al.*, 2007: 13 (bacteria on Tabanidae); Oliveira *et al.*, 2007: 792 (ecology); Coscarón & Papavero, 2009: 145 (cat.); Wolff & Miranda-Esquivel, 2016: 287 (cat., in part); Henriques, 2016: 184 (AMNH spp.); Krolow *et al.*, 2017: 107 (French Guiana spp.).

Tabanus fumatipennis Kröber, 1933: 341, 1934: 293 (cat.); Bequaert & Renjifo-Salcedo, 1946: 78 (Colombia spp., in part).

Tabanus brunniventris Kröber, 1933: 343 (as *callosus* var.; preocc. Schuurmans Stekhoven, 1926), 1934: 292 (cat.); Fairchild, 1967: 365 (Kröber spp.), 1975: 264 (Kröber spp.).

Tabanus bruniventris Barretto, 1957: 86 (misspell.).

Diagnosis. Postpedicel very long, usually twice as long as style, angle of dorsal tooth close to its base. Notopleuron concolorous with adjacent scutum. All coxae and femora black. Middorsal abdominal stripe slender, even, and contiguous through tergite 6. Dorsolateral disconnected, visible through tergite 5. Frons not markedly divergent (D.I. 1.7).

Comments. See under *T. callosus.*

Material examined. BRAZIL, *Rondônia*, Nova Mamoré, Parque Estadual do Guajará-Mirim, Rio Formoso; *Roraima*, Serra Pacaraima; *Amazonas*, Toototobi; Manaus, R. Ducke; São Gabriel da Cachoeira, BR 307; *Pará*, Rio Trombetas, Cachoeira da Fumaça; *Pará*, C.

Araguaia; FRENCH GUIANA, *Cayenne;* BOLIVIA, *Cochabamba,* Vila Tunari (60 f# INPA)*;* VENEZUELA, *Amazonas*; GUIANA, *Kayeteur* (11 f# AMNH).

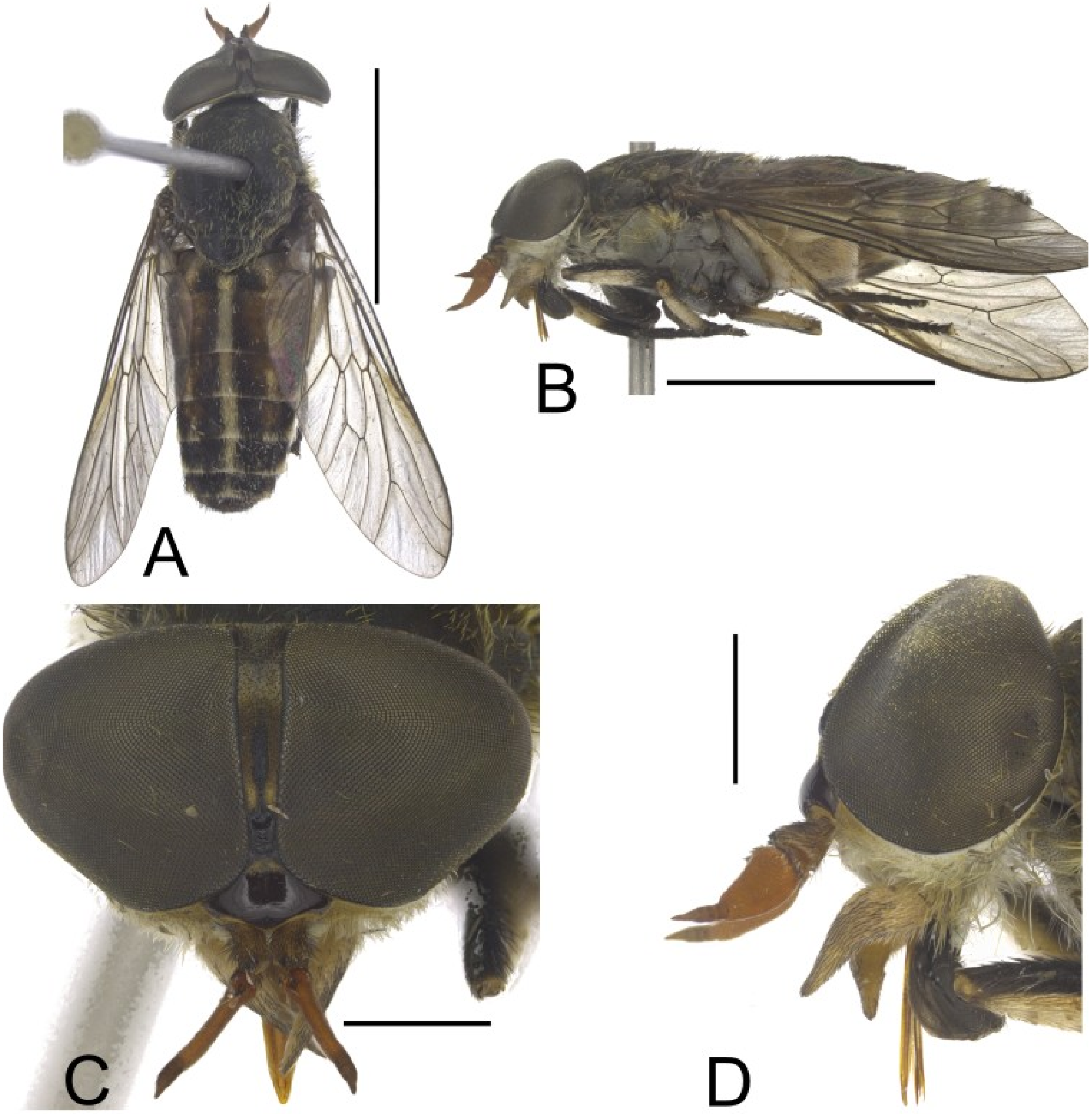


Figure 25. *Tabanus trivittatus.* Female. A. Dorsal habitus. B. Lateral habitus. C. Head, anterior view. D. Head, lateral view. Scale bars. A, B. 5 mm. C, D. 1 mm.

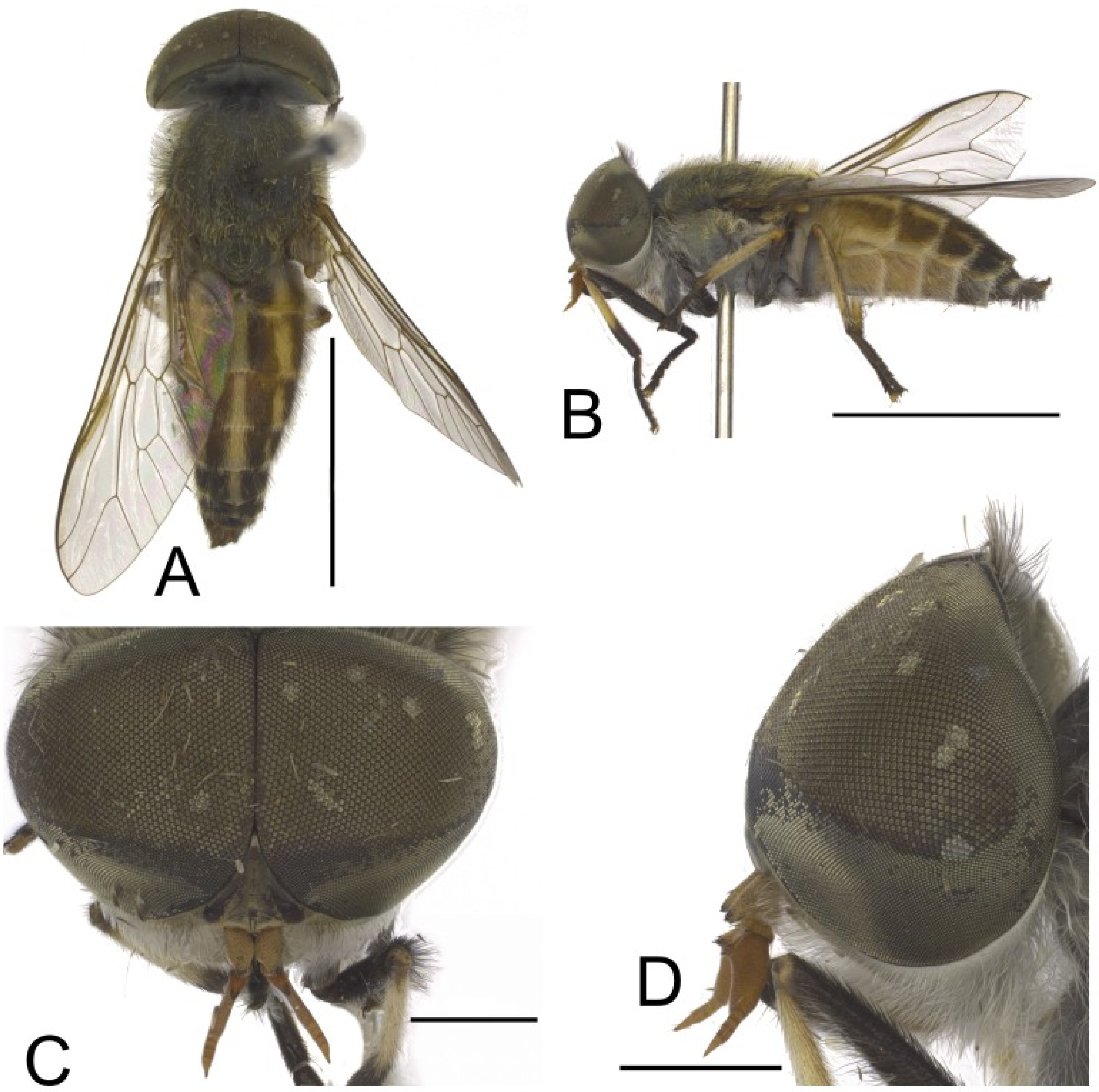


Figure 26. *Tabanus trivittatus.* Male. A. Dorsal habitus. B. Lateral habitus. C. Head, anterior view. D. Head, lateral view. Scale bars. A, B. 5 mm. C, D. 1 mm.

Tabanus unistriatus **Hine**

(Figures 27A–E, 28A–D 34)

Tabanus unistriatus Hine, 1906: 28, 1925: 28 (taxonomy); Kröber, 1933: 365 (taxonomy), 1934: 294 (cat.); Fairchild, 1942b: 162, pl. l, fig. 2 (taxonomy); Woke, 1947: 369 (Nicaragua spp.); Fairchild, 1947: 575 (Panama spp.); Fairchild, 1961: 31 (Costa Rica spp.); Lee *et al*., 1969: 455 (Colombia spp.); Fairchild, 1971: 104 (cat.); Hogue & Fairchild, 1974: 26 (Costa Rica spp.); Fairchild, 1976: 260, fig. 15 (rev.); Moucha, 1976: 149 (cat.); Wilkerson, 1979: 391 (Colombia spp.); Fairchild, 1986: 128 (Panama spp.); Henriques & Gorayeb, 1993: 19 (MPEG spp.); Fairchild & Burger, 1994: 152 (cat.); Coscarón & Papavero, 2009: 145 (cat.); Cárdenas *et al*., 2009: 528 and appendix 4: 21 (Ecuador spp., in part); Wolff & Miranda-Esquivel, 2016: 287 (cat., in part); Henriques, 2016: 184 (AMNH spp.).

Diagnosis. Antenna orange, the style black. Wings lightly to strongly infuscated. Costal cell yellow. Abdominal median stripe a series of connected triangles through tergite 6, slightly broader at tergites 1-4, tapered in the remainder, dorsolaterals absent or very weak.

Comments. According to Fairchild (1976) this species is very similar to *T. argentivittatus,* differing from the latter just by its smaller size and occurring only west of Andes and by the morphology of the male: eyes nearly as long as wide, antennal style black, pruinescent subcallus. (Figs. 6C and 27C).

The species distribution ranges from Guatemala to Ecuador west of Andes to Ecuador west of Andes. The Guiana record from Barretto (1957) remains to be confirmed. Wolff and Miranda-Esquivel (2016) record this species to Caquetá, Colombia based on an unpublished report, however, no illustrations or discussion about the species are provided in this work and the identity of the specimens need to be confirmed.

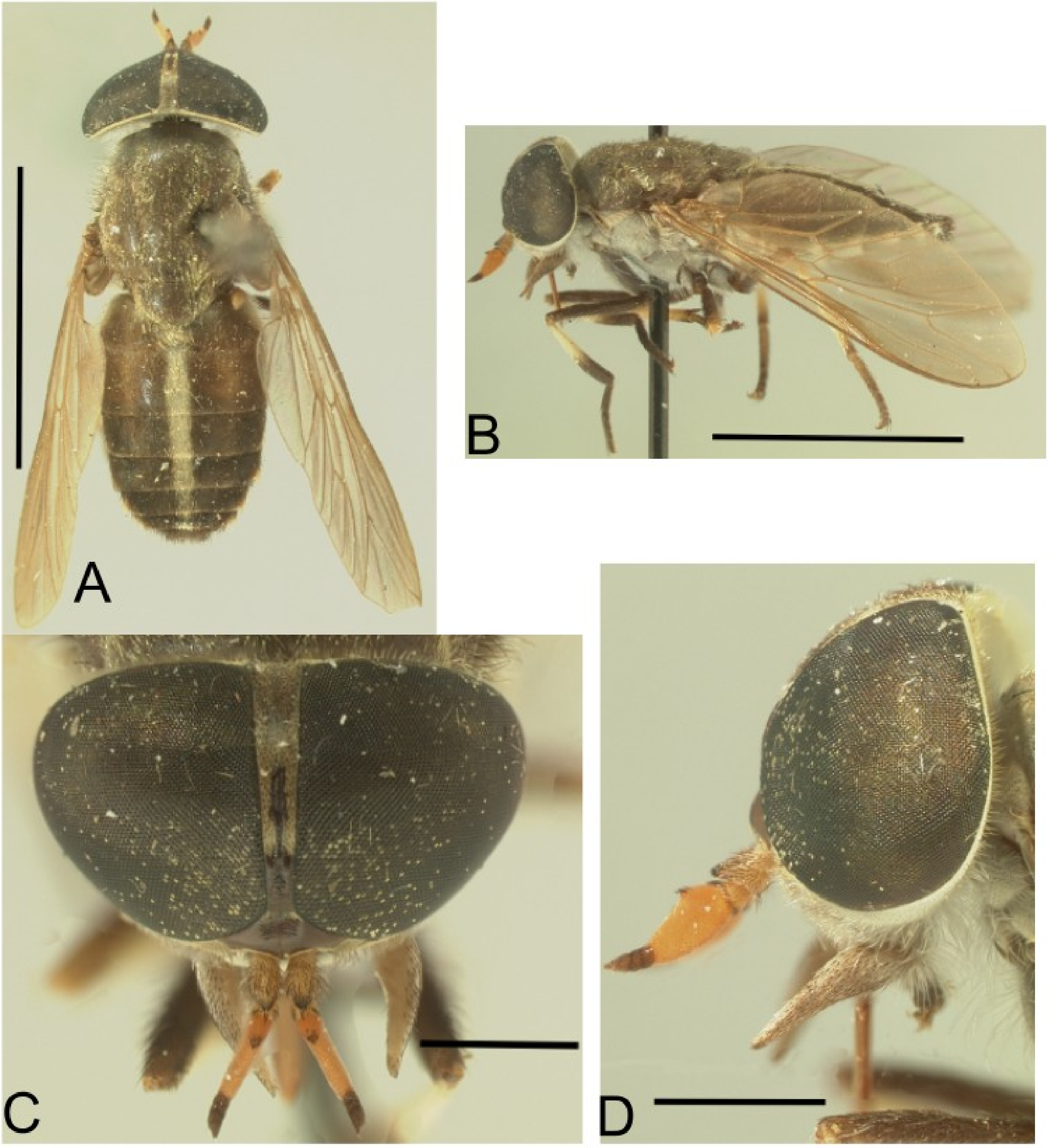


Figure 27. *Tabanus unistriatus.* Female. A. Dorsal habitus. B. Lateral habitus. C. Head, anterior view. D. Head, lateral view. Scale bars. A, B. 5 mm. C, D. 1 mm. Photos obtained by courtesy of FSCA.

Material examined. PANAMA, *Almirante,* VIII-21-44 (f#, FSCA); *Bocas del Toro*, Rio Changena, 2400 ft (m# FSCA). ECUADOR, *Esmeraldas*, Kumanii Lodge (f# INPA).

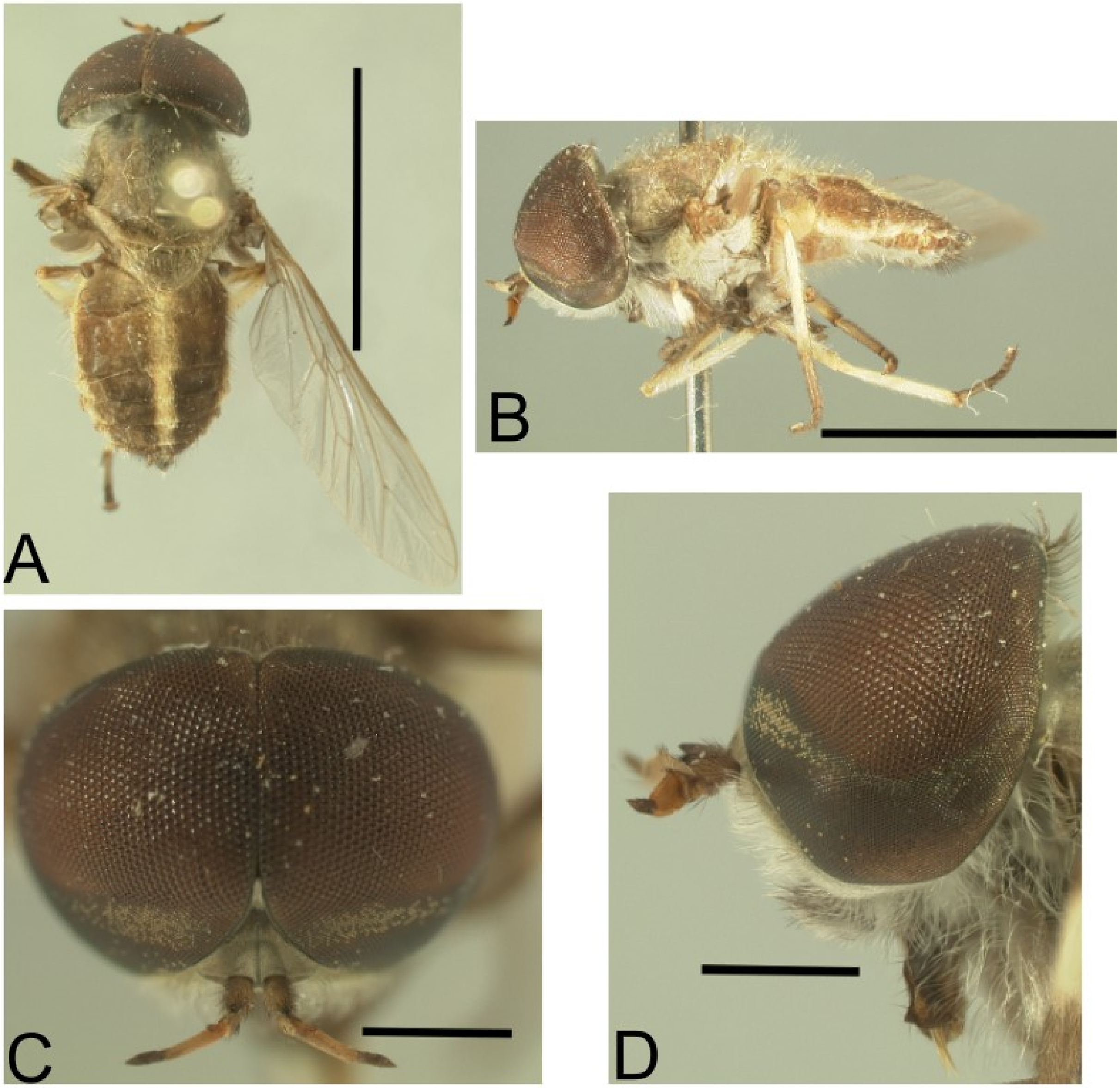


Figure 28. *Tabanus unistriatus.* Male. A. Dorsal habitus. B. Lateral habitus. C. Head, anterior view. D. Head, lateral view. Scale bars. A, B. 5 mm. C, D. 1 mm. Photos obtained by courtesy of FSCA.

Comments on the female genitalia.

Genital characters are a useful source of information for the taxonomy and phylogeny of Diptera (*e.g.* Sinclair *et al*. 1994; Carmo & Santos 2011; Fachin & Amorim 2015). The taxonomy of Tabanidae, at the genus level, is almost entirely based on females, with most taxonomic work dependent on external characters (*e.g.* Fairchild 1976; Fairchild 1984). Few researchers have used female terminalia characters of Tabanidae to identify species, and when those are used, they are scarce and limited to the sternite 8 (Ovazza *et al*. 1956; Mackerras 1971; Zeegers & Muller 2014).

In the present work we macerated the female genitalia of most species in the *T. trivitattus* species-group. We were unable to retrieve any useful characters for species delimitation in the complex. There are considerable similarities between different species (Figs. 35, 36) as well as intraspecific variation (Fig. 35). Despite such results, the genitalia of species related to *T. trivittatus* present similar format and share some traits, as a convex elevation at the anterior portion of the plate, and the lateral lobes positioned closer to the base of the structure. A detailed study of the female terminalia in *Tabanus* may confirm these characters as apomorphic to the group.

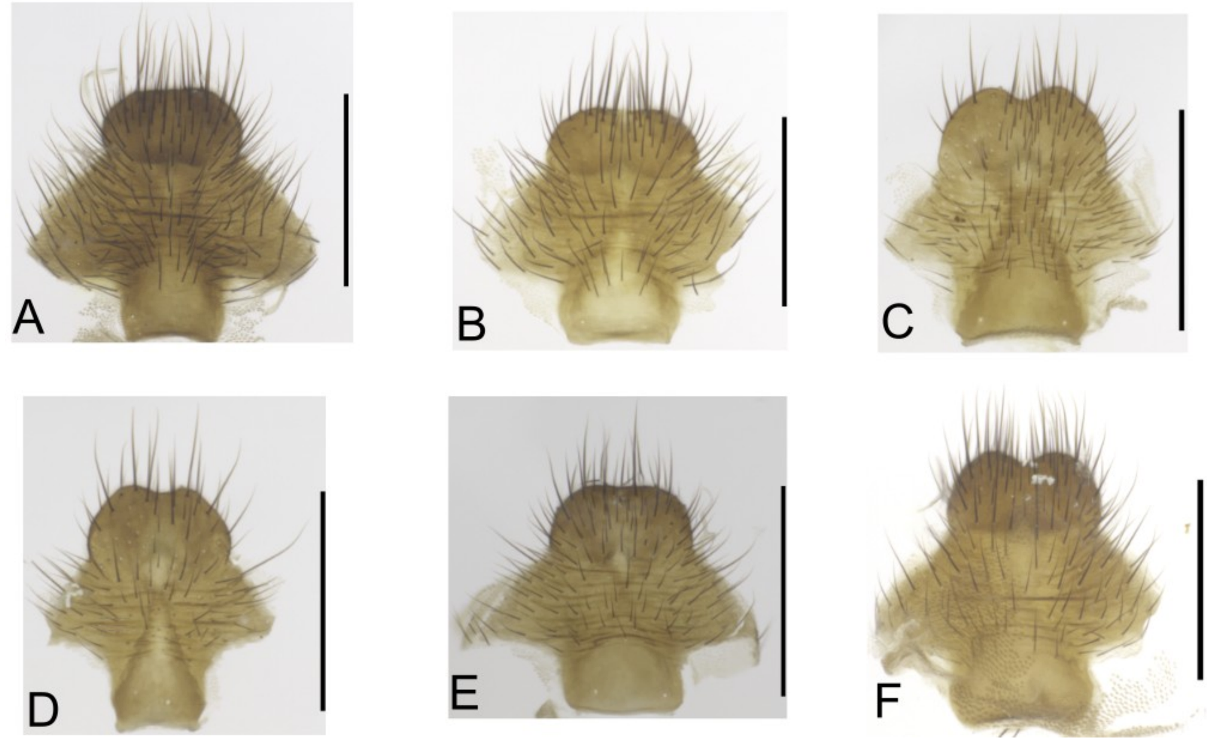


Figure 29. *V*ariation of the sternite 8 in the females of *Tabanus trivittatus* and *T. callosus.* A – C. *T. trivittatus.* D – F. *T. callosus*. Scale bars. 0.5 mm.

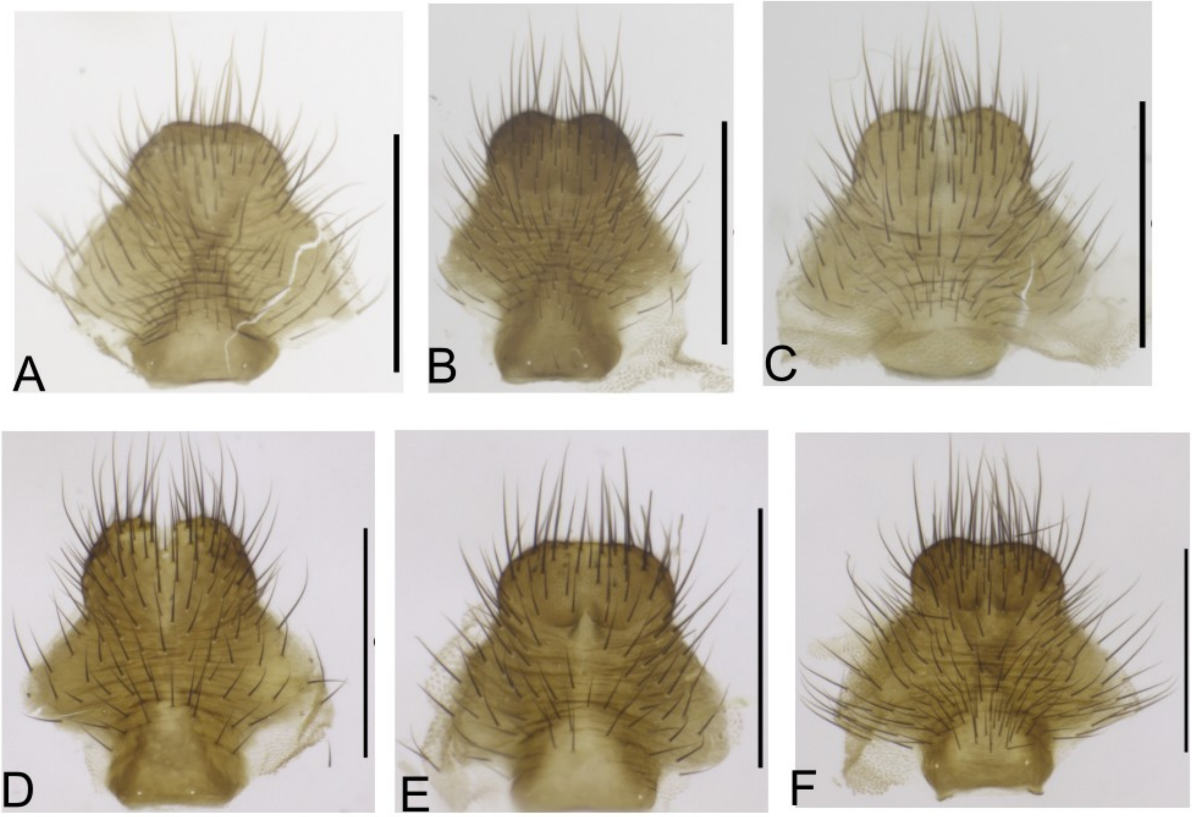


Figure 30. Sternite 8 of the females of the *Tabanus trivittatus* species-group. A. *T. palpalis.* B. *T. restrepoensis*. C. *T. sextriangulus.* D. *T. dorsorufus* sp. n E. *T. macrocerus* sp. n. F. *T. mackerrasi* sp. n. Scale bars. 0.5 mm.

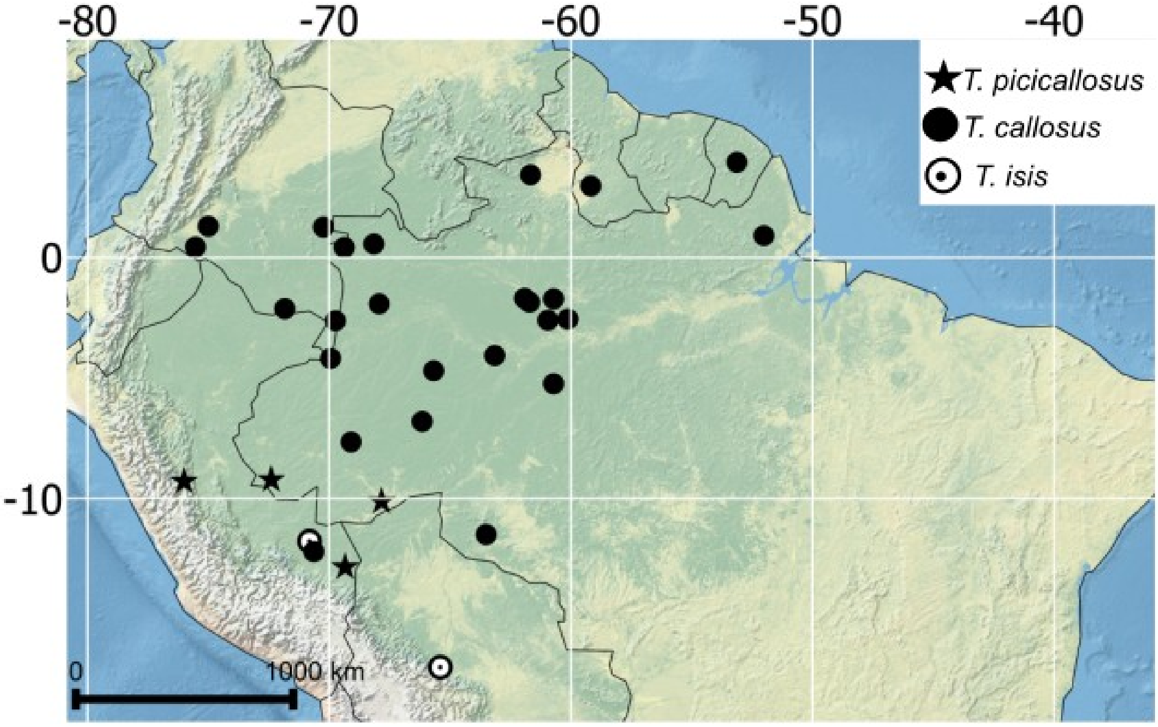


Figure 31. Distribution of *Tabanus trivittatus* species-group. *T. callosus, T. isis and T. picicallosus.*

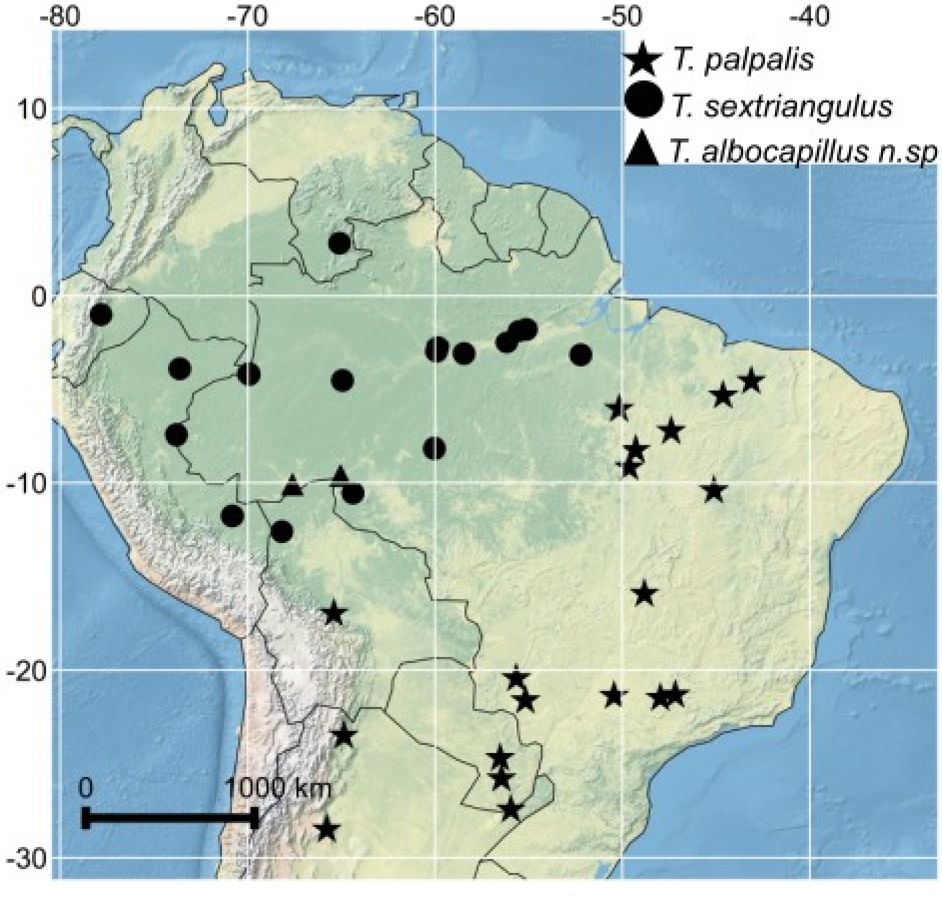


Figure 32. *D*istribution of *Tabanus trivittatus* species-group. *T. albocapillus* sp. n., *T. palpalis* and *T. sextriangulus.*

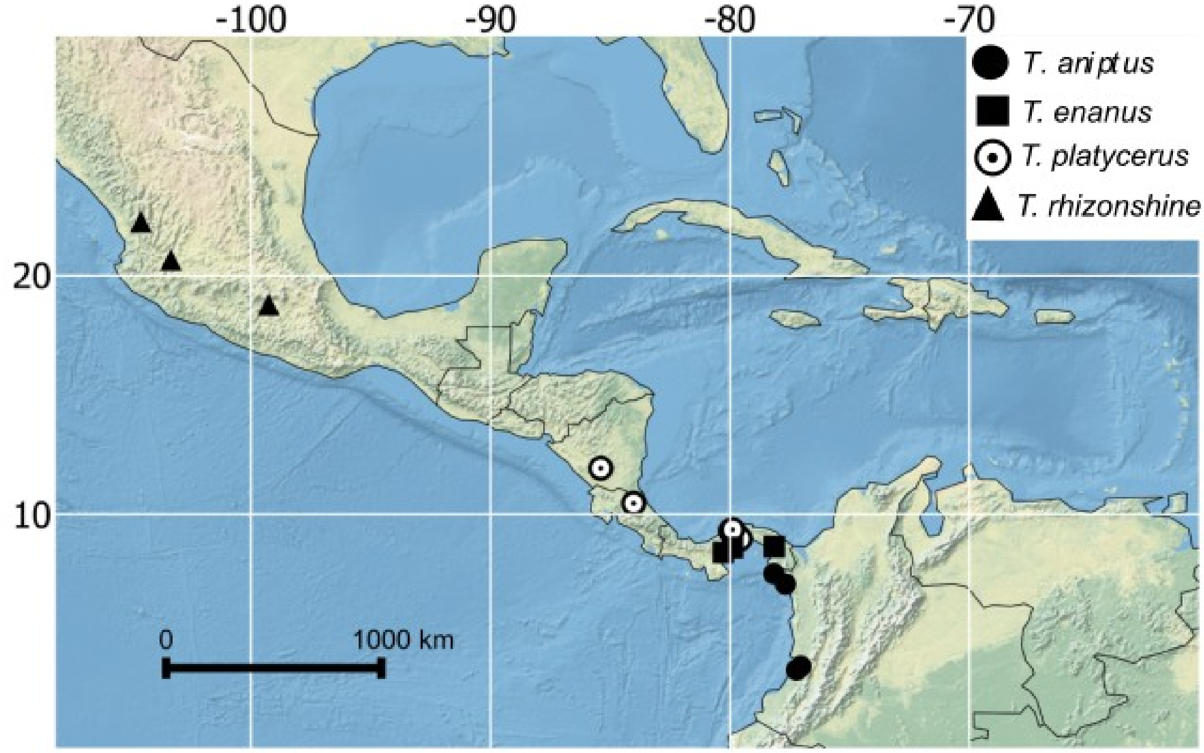


Figure 33. *Distribution of Tabanus trivittatus* species-group. *T. aniptus, T. enanus, T. platycerus* and *T. rhizonshine.*

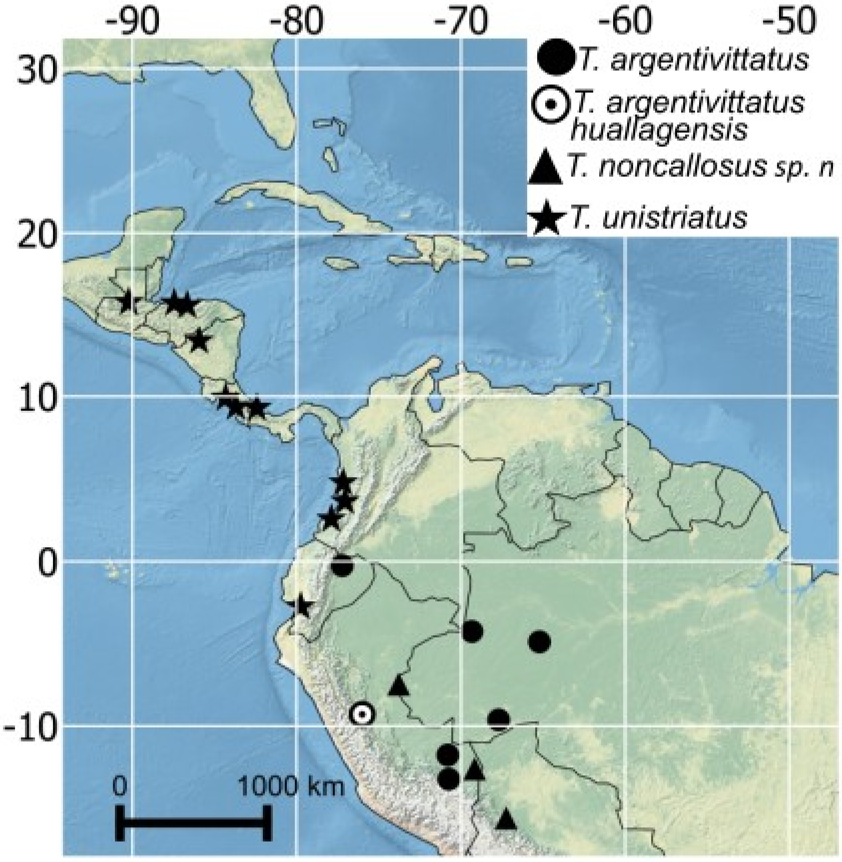


Figure 34. Distribution of *Tabanus* trivittatus species-group. *T. argentivittatus, T. argentivittatus huallagensis* , *T. noncallosus sp. n.* and *T. unistriatus.*

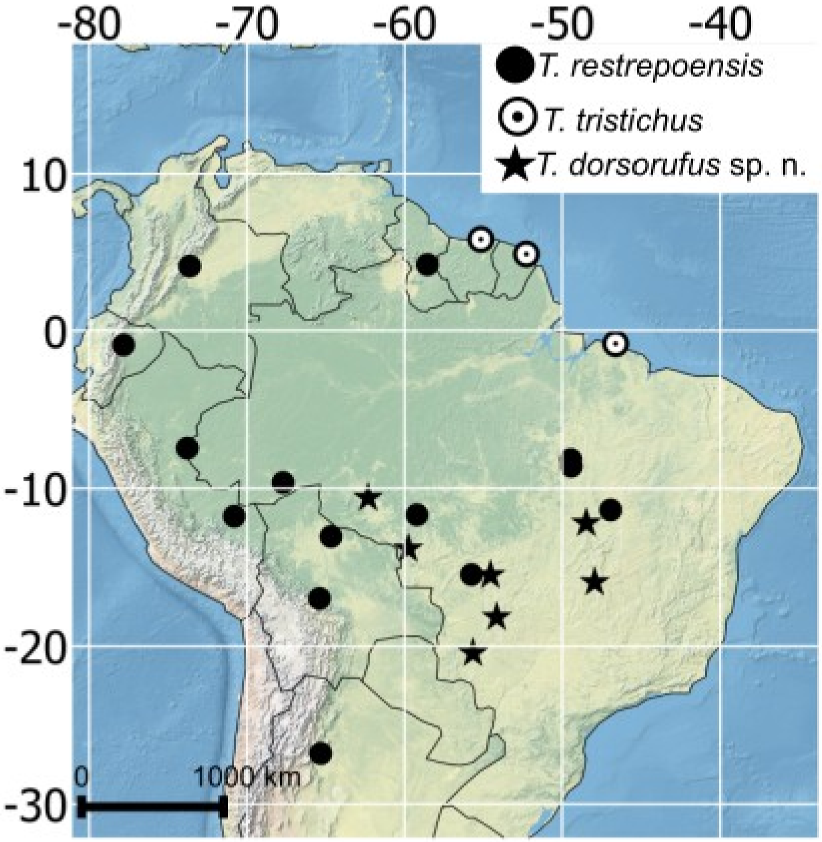


Figure 35. Distribution of *Tabanus trivittatus* species-group. *T. dorsorufus* sp. n., *T. restrepoensis* and *T. tristichus.*

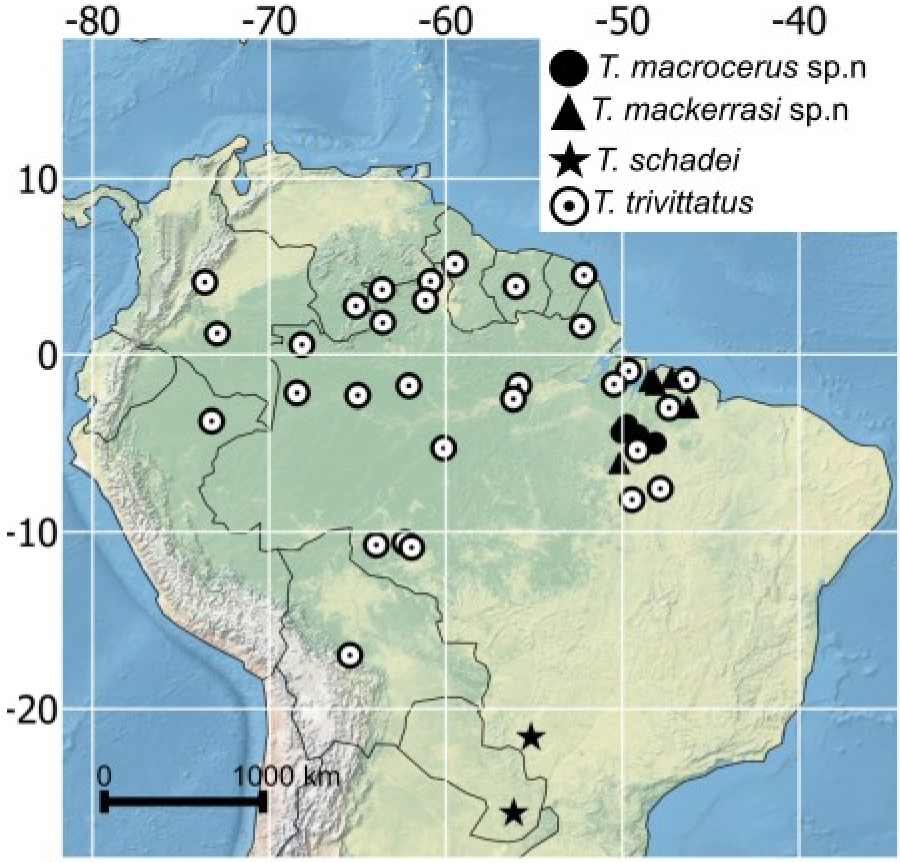


Figure 36. Distribution of *Tabanus trivittatus* species-group. *T. mackerrasi* sp. n., *T. macrocerus* sp. n. and *T. trivittatus.*

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Síntese

Os dois capítulos que compõem esse trabalho tratam da evolução e taxonomia de parte das espécies incluídas no gênero *Tabanus* na região Neotropical. Os resultados aqui obtidos aumentam nosso conhecimento sobre a história dos tabanídeos ao fornecer evidências para uma origem múltipla de *Tabanus* e a necessidade da divisão do grupo em diversos gêneros. Nesse trabalho, quatro novos gêneros são propostos - *Cephalogongylus* **gen.n**., *Chelotabanus* **stat. rev**., *Rhinoderus* **gen. n** e *Tapirotabanus* **gen.n.** São todos táxons endêmicos à região Neotropical, e ao menos *Chelotabanus* têm distribuição majoritariamente amazônica, com somente *Chelotabanus fuscus* ocorrendo na floresta atlântica. A taxonomia de *Cephalogongylus* é revisada no capítulo dois e cinco novas espécies são descritas.

Adicionalmente, foi obtida uma hipótese de tempos de divergência para as espécies da tribo Tabanini incluídas nessa análise, de forma que as evidências moleculares obtidas apontam para a origem da tribo no começo do Eoceno, e a diversificação dos gêneros novos descritos durante o Mioceno, diversificação, possivelmente associada aos eventos de orogenia na América do Sul, provocados pelo soerguimento dos Andes e as mudanças que ocorreram na região que compreende a bacia Amazônica.

Esta é a primeira tentativa de resolver a complicada evolução de Tabanus e espécies de Tabanini associadas usando métodos filogenéticos modernos com uma amostra abrangente. Apesar de variações, especialmente nos nós basais, no que diz respeito às relações internas entre conjuntos de dados morfológicos e filogenômicos, a maioria dos grupos foi obtida em ambas as análises, e os clados morfológicos tiveram estabilidade com vários clados sendo recuperados independentemente dos critérios de otimalidade empregados. Nesse contexto, a iluminação recíproca entre as topologias obtidas por dados morfológicos e moleculares, são indício da robustez dos táxons novos aqui propostos A afilia de Tabanus, corroborada em nossa análise, e a evidência de que o verdadeiro gênero é provavelmente Holártico em sua distribuição, abrem novas linhas interessantes para as futuras pesquisas filogenéticas e taxonômicas. A análise com o gênero deve continuar sendo realizada nos próximos anos, focando espécies de outras regiões zoogeográficas e até ampliando a amostragem Neotropical. A crescente facilidade em obter dados filogenômicos certamente proporcionará um grande avanço em nossa capacidade de entender a evolução de Tabanini e outros grupos complexos, entretanto, os resultados aqui apresentados mostram que, apesar de altamente variáveis, os caracteres morfológicos possuem sinal filogenético e o uso de tais caracteres em conjunto.

com as técnicas moleculares modernas é provavelmente a maneira mais robusta de desvendar verdadeiramente a história dos organismos em suas três dimensões, forma, tempo e espaço.

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Apêndices

Appendix 1: Character Matrix. P = Polymorphism

	1 2 3 4 5
	1234567890123456789012345678901234567890123456789012345678901234
Catachlorops amazonicus	1010112000101031011000000-000-00000010000--0-000011000
Catachlorops rufescens	2010112000100031011000100-000-00100000000--0-000011000
Atylotus_thoracicus	-011011---10100000100--010100-00110000000--0-000??????
Agkistrocerus megerlei	00101000011100301110001111100-110000010100-0-000??????
Phorcotabanus cinereus	20100101011000011000011011100-001000110100--1000?1100?
Poeciloderas quadricunctatus	211010011-1000111110000011110-210000110110-11100111000
Hybomitra astur	00201001001000000010010112100-00010001000--0-000011100
Hybomitra montana	002010011-1000001010010012100-00010011000--0-000111100
Hybomitra nigricornis	00201000001100001020011012101000010010101-111000111100
Glaucops fratelus	002001011-1000000010011013101-10110010-00--11000??????
Ancala fasciata	00100111001000000001000010-110-00110001100--0-000111100
Tabanus atratus	30100131000100110110010011110-11000011100--0-000110000
Tabanus antarcticus	11100120001010011010010112111110012011001-00-011011010
Tabanus vestitus	11100120001010011010000111101000010010101-010011011010
Tabanus acer	101001310011000110200001??110-001000001100-0-100111100
Tabanus amapaensis	101001200010100111210001??1010000000001101-00-101011010
Tabanus claripennis	311001311-00001110200100??1010000000111110-1-010111000
Tabanus duckei	111001200010102110200001??110-00000011100--0-000011000
Tabanus fuscofasciatus	211001010011000110210001??111000100011110--0-110111010
Tabanus humboldti	101001200110102111200001??1?0-00110001000--0-000111001
Tabanus bigoti	1010012000101021111000010-110-10000001000--0-000011010
Tabanus hirtitibia	1010012001101031111000010-110-000000111100-0-000??????
Tabanus thiemeanus	1010012001101031111000010-111100000011100--0-000011010
Tabanus fortis	1010012001101021111000010-110-000[01]0001100--0-000011000
Tabanus aaptus	1010012000101011111000010-101010000001100--0-000011000
Tabanus indecisus	1010012100101011101100000-110-00001011000--0-000011000
Tabanus nebulosus	1010012000101011112100000-110-00001011010100-000011000
Tabanus ornativentris	1011012000101011112100000-110-10001001000100-000011000

Tabanus importunus	10110120001010111120000000-110-00001011000--0-000P1100P	P=0/1
Tabanus lutzi	10100120011010111110000000-110-00001001100--0-000??????	
Tabanus glaucus	10110120001010111111100010-110-10001011011000-000011000	
Tabanus kwatta	21200131001000011120000011100-00000001111211100011000	
Tabanus lineola	21200131PP10000111100000012100-10100011011121110??????	P=0/1;0/2
Tabanus occidentalis	21200131001010011010000012100-100000110111211100011000	
Tabanus triangulum	21200131001010011110000011100-100000110111211100011000	
Tabanus vittiger	21200131001010011110000011100-10000011111121110??????	
Tabanus wilkersoni	012001311-10110110100000111010001000110111211100011000	
Tabanus wokei	01200131001010011020000011100-000000110111211100111000	
Tabanus amazonensis	10100120001010211110000010-100-10001001001-010100111000	
Tabanus discus	10000120011010211110000010-100-10001001100--0-000111000	
Tabanus nematocallus	10100120011010211110000010-100-P0001001101-010100111000	P=1/2
Tabanus pellucidus	10100120011010211110000010-100-1-001001101-010100111000	
Tabanus angustifrons	10100120011010111110000010-110-10001001101-010100011000	
Tabanus xenorhynchus	1000012001101001001110000-110-00000101001-30-000??????	
Tabanus sannio	2000012100101001001110000-110-00100101001-30-000111000	
Tabanus piceiventris	201001200?10101?111P00?00-110-00000001000--0-000011000	P=0/1
Tabanus argentivittatus	21200120002100011010010012100-00100010001-20-110010011	
Tabanus callosus	21200121002100011010010012100-00100010001-211110010011	
Tabanus enanus	21200121002101011020000012100-00100010001-211100??????	
Tabanus isis	21200121002101011020000012100-00100010001-211100??????	
Tabanus palpalis	21200121002100011020010012100-00100010101-211100010011	
Tabanus picicallosus	21200121002100001010000012100-00100010101-211100??????	
Tabanus platycerus	21200121002100011010010012100-00100010-01-211100??????	
Tabanus restrepoensis	21200121**P**02100011010010012100-00100010001-211100011010	P=0/1
Tabanus schadei	01200121002100011020010012100-00100010001-211100010011	
Tabanus tristichus	212001210021000110-0000012100-00100000101-211100011011	
Tabanus trivittatus	212001210021000110**P**00100**P**2100-00100010101-211110010011	p=1/2;0/1
Tabanus sextriangulus	21200121002100011010000012100-00100010001-211100010011	
Tabanus unistriatus	21100121002100011010010012100-00100010101-20-100011011	
Tabanus bovinus	20100121001000110110000011110-11010011111010-000??????	
Tabanus sudeticus	20100121001000110110000011110-11000011111010-000111100	
Tabanus spodopterus	2010012100101001102000000-110-11000001111010-000011100	
Tabanus sarbazensis	2010012000111000112000000-110-11000011111010-000??????	
Tabanus quatuornotatus	012000011-1100010010001012000-00100010101-11-011111100	
Tabanus nemoralis	012000211-0100010020001012210-001**P**0010101-111010??????	P=0/1
Tabanus glaucopis	212001201-1100010010001013200-010110000110111010011100	
Tabanus cordiger	312001201-100001002000100-100-01000011101-111110111100	
Tabanus bromius	21200120001101110020000010100-00110011001-111110011100	
Tabanus maculicornis	2120012100111001002000001?100-00110011101-00-010011100	
Tabanus tergestinus	201001211-101001102000011?100-00110011011010-000011100	
Tabanus iyoensis	212001210001000110100000??100-00110010100--0-010011100	
Tabanus humilis	212001210001001110000000??100-00100010000--0-010??????	
Tabanus triceps	2020012000101011002001010-110-10100001111120-100011100	
Tabanus striatus	2020012000100011002001010-110-00100011011120-100-01001	
Tabanus partitus	2020012000100010102000010-100-00001011011120-100-01001	
Tabanus marmorosus	1010012000100011011000010-100-11000001101-30-01-??????	
Tabanus sufis	312001310-100000002000-013201100100011001-011011-01100	

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Tabanus bakeri                10100121001000010020000110100-01010011001-10-00-010001
Tabanus ruficrus              2010012100101011112000010-110-00000001100--0-000011100
Tabanus parvicallosus         2110012100101010102000010-110-00100011010--0-010111000
Tabanus ceylonicus            20200121000110100010000112100-00100010000--0-00-111000
Tabanus exoticus              1110012000100011111000001??1111101000111011111101-011100
Tabanus albocirculus          1010012000101001101001011211111P0102011101100-011011010 P=0/1/2
Tabanus defilippii            1??001200110-021101100010-1?0-10002101001-00-000??????
Tabanus oculus                2?1001210010-00110100001111111120-12111101100-011011010
Tabanus polyphemus            2010012000101011111000010-1?0-00112101101100-000??????
Tabanus_pseudoculus           2??001200010-01110100001111?11---12111101100-001??????
Tabanus_unipunctatus          2??001200010-010101000010-1?0-0--12101001100-000??????
```

Matriz de caracteres contínuos

	55	56
Catachlorops amazonicus	1.4	5.3
Catachlorops rufescens	1.7	4.6
Atylotus thoracicus	1.2	3.3
Agkistrocerus megerlei	1.1	3
Phorcotabanus cinereus	1.4	2.2
Poeciloderas quadricunctatus	1.1	3.9
Hybomitra astur	1.1	2.9
Hybomitra montana	1.4	3.5
Hybomitra nigricornis	1.3	2.9
Glaucops fratelus	1.2	2.7
Ancala fasciata	0.7	3.1
Tabanus atratus	1	2.4
Tabanus antarcticus	2	9.4
Tabanus vestitus	1.6	7.4
Tabanus acer	1.5	4.5
Tabanus amapaensis	?	?
Tabanus claripennis	1.8	3.5
Tabanus duckei	1.5	6.8
Tabanus fuscofasciatus	1	3.7
Tabanus humboldti	2.2	11.4

Tabanus bigoti	1.3	6.5
Tabanus hirtitibia	1.2	6.5
Tabanus thiemeanus	1	5.4
Tabanus fortis	1.8	7.7
Tabanus aaptus	1.4	5.9
*Tabanus indecisu*s	1.3	5.2
Tabanus nebulosus	1.3	6.1
Tabanus ornativentris	1.6	5.3
Tabanus importunus	1.5	5.7
Tabanus lutzi	1.3	5.3
Tabanus glaucus	1	4.8
Tabanus kwatta	1.5	4.4
Tabanus lineola	2.1	6.7
Tabanus occidentalis	1.4	11.1
Tabanus triangulum	1.3	3.8
Tabanus vittiger	1.5	2.7
Tabanus wilkersoni	1.5	3.8
Tabanus wokei	1.4	3.2
Tabanus amazonensis	2.1	5.3
Tabanus discus	2.3	11.1
Tabanus nematocallus	2.0	9.1
Tabanus pellucidus	2.6	11.6
Tabanus angustifrons	2.2	10.9
Tabanus xenorhynchus	1.1	7.4
Tabanus sannio	1.3	4.9
Tabanus piceiventris	?	?
Tabanus argentivittatus	1.7	7.2
Tabanus callosus	1.5	7.6
Tabanus enanus	2	7.7
Tabanus isis	2.6	8.6
Tabanus palpalis	2	6.2
Tabanus picicallosus	1.8	5.8

Tabanus platycerus	1.8	8
Tabanus restrepoensis	2.4	7.9
Tabanus schadei	1.9	5
Tabanus tristichus	1.8	6.3
Tabanus trivittatus	1.7	6.6
Tabanus sextriangulus	2.2	9.2
Tabanus unistriatus	2.8	9.1
Tabanus bovinus	1.3	4.5
Tabanus sudeticus	1.2	3.9
Tabanus spodopterus	1.4	4.6
Tabanus sarbazensis	1.5	5
Tabanus quatuornotatus	1.3	3.1
Tabanus nemoralis	?	?
Tabanus glaucopis	1.7	4.7
Tabanus cordiger	1.8	3.6
Tabanus bromius	1.6	4.5
Tabanus maculicornis	1.8	4.6
Tabanus tergestinus	1.5	5.5
Tabanus iyoensis	1.7	5.8
Tabanus humilis	1.8	6
Tabanus triceps	1.5	5.5
Tabanus striatus	1.4	5.6
Tabanus partitus	1.4	5.4
Tabanus marmorosus	1.9	7.8
Tabanus sufis	2.1	2.8
Tabanus bakeri	2	9
Tabanus ruficrus	1.3	6.4
Tabanus parvicallosus	1.4	5.6
Tabanus ceylonicus	?	?
Tabanus exoticus	1.6	7.9
Tabanus albocirculus	1.9	9.9
Tabanus defilippii	?	?

Tabanus oculus	?	?
Tabanus polyphemus	1.6	5.6
Tabanus pseudoculus	?	?
Tabanus unipunctatus	?	?