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**TAXONOMIA E ANÁLISE FILOGENÉTICA DE *Dilophus* Meigen, 1803
(DIPTERA, BIBIONIDAE, BIBIONINAE)**

SÃO CARLOS – SP

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(DIPTERA, BIBIONIDAE, BIBIONINAE)**

Dissertação apresentada ao Programa de Pós-Graduação em Ecologia e Recursos Naturais da Universidade Federal de São Carlos, como parte dos requisitos para obtenção do título de Mestre em Ecologia e Recursos Naturais.

Área de concentração: Ecologia e Recursos Naturais.

Orientadora: Prof^a Dr^a Livia Maria Fusari

Coorientadora: Dr^a Rafaela Lopes Falaschi

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Dedico este trabalho a todos que
anseiam por conhecer a biodiversidade
da Terra.

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כל הדברים היפים באמת

מתגלים בזמנם

(Todas as coisas belas de verdade

São reveladas em seu tempo)

Daniela Spector

Resumo

A família Bibionidae possui aproximadamente 700 espécies viventes e mais de 345 fósseis. Conhecidas como “march flies” e “lovebugs”, suas larvas se alimentam de matéria orgânica ou de tecido vegetal vivo, enquanto os adultos podem ser importantes polinizadores. O gênero *Dilophus* Meigen é um dos mais diversos dentro da família, com cerca de 200 espécies descritas, sendo 80 delas na região Neotropical, onde o Chile possui a maior diversidade. Este estudo propôs preencher lacunas sobre a taxonomia e a filogenia de *Dilophus*, apresentando redescrições de quatro espécies, descrições de duas novas espécies e uma chave de identificação para as espécies neotropicais, além de explorar suas relações filogenéticas utilizando uma amostragem ampla do táxon e de outros bibionídeos.

Palavras-chave: Bibionomorpha; Biodiversidade; Cladística; Região Neotropical.

Abstract

The Bibionidae family has approximately 700 extant species and more than 345 fossils. Known as “march flies” and “lovebugs”, their larvae feed on organic matter or living plant tissue, while adults can be important pollinators. The genus *Dilophus* Meigen is one of the most diverse within the family, with approximately 200 described species, 80 of which are found in the Neotropics, where Chile has the greatest diversity. This study aimed to fill gaps in the taxonomy and phylogeny of *Dilophus*, presenting redescriptions of four species, descriptions of two new species and an identification key for the Neotropical species, in addition to exploring their phylogenetic relationships using a broad sample of the taxon and other bibionids.

Key Words: Bibionomorpha; Biodiversity; Cladistics; Neotropical Region.

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INTRODUÇÃO GERAL

Diptera é uma das quatro ordens megadiversas de insetos, contanto com cerca de 160 mil espécies viventes, distribuídas em cerca de 160 famílias ao redor do mundo (Pape *et al.* 2011, Carvalho *et al.* 2024). Na região Neotropical, mais de 31 mil espécies são conhecidas e distribuídas em 119 famílias (Carvalho *et al.* 2024). A ordem pode ser dividida em cinco grandes grupos, Bibionomorpha, Brachycera, Culicomorpha, Psychodomorpha e Tipulomorpha, além de incluir também famílias que não pertencem a esses grupos, como Deuterophlebiidae, Nymphomyiidae, Perissommatidae e Ptychopteridae (Wiegmann & Yeates 2017). Bibionomorpha é grupo irmão de Brachycera, formando o clado Neodiptera, que por sua vez é grupo irmão de Perissommatidae (Ševčík *et al.* 2016, Wiegmann & Yeates 2017).

Bibionomorpha *sensu stricto* compreende Bibionoidea e Sciaroidea. Já Bibionomorpha *sensu lato* inclui também Anisopodoidea e Scatopsoidea (Ševčík *et al.* 2016). Embora alguns autores classifiquem Scatopsoidea como parte de Psychodomorpha (Wood & Borkent 1989, Amorim 1994), estudos moleculares suportam a monofilia tanto de Bibionomorpha *sensu stricto*, quanto de Bibionomorpha *sensu lato* (Bertone *et al.* 2008, Wiegmann *et al.* 2011, Ševčík *et al.* 2016). Alguns trabalhos incluem Axymyiidae em Bibionomorpha (Oosterbroek & Courtney 1995, Wiegmann *et al.* 2011), já outros não recuperam a enigmática família como parte de Bibionomorpha (Fitzgerald 2004b, Ševčík *et al.* 2016).

Bibionoidea - *sensu* Ševčík *et al.* 2016 -compreende duas famílias viventes, Bibionidae e Pachyneuridae. A família fóssil †Protopleciidae por vezes é associada aos Bibionidae (Rohdendorf 1946, Lin *et al.* 2015). No entanto, outros autores a associam com os Sciaroidea (Hippa & Vilkkamaa 2005, Blagoderov & Grimaldi 2004). O posicionamento de †Protopleciidae e a monofilia da família e dos gêneros incluídos nela demanda estudos filogenéticos (portanto, podendo ou não fazer parte de Bibionoidea). Já Pachyneuridae é associada por alguns autores com as famílias fósseis †Elliidae e †Procramptonomyiidae com base em filogenias (Krzemiński & Krzemińska 1994, Coram & Jarzembowski 1999).

Bibionidae é uma família que foi descrita por John Fleming em 1821 (Fitzgerald 2004b). Entretanto, diversos táxons que eram incluídos no grupo antes do final da década de 1930 foram excluídos e atualmente são tratados como famílias separadas

(Axymyiidae, Canthyloscelidae, Pachyneuridae e Scatopsidae) (Fitzgerald 2004b).

Bibionidae possui distribuição mundial (exceto nas regiões polares) e compreende cerca de 700 espécies viventes em oito gêneros (Pinto & Amorim 2000, Fitzgerald 2004b, Fitzgerald *et al.* 2020). Além disso, mais de 345 espécies fósseis foram descritas, sendo assim a família de Diptera mais bem representada em relação à riqueza de espécies no registro fóssil (Pinto & Amorim 2000, Fitzgerald 2004b, Skartveit 2009). A família é particularmente especiosa na Região Neotropical, contando com 192 espécies viventes descritas em seis gêneros, cerca de 27% da diversidade mundial, sendo assim a região biogeográfica com mais espécies conhecidas (Fitzgerald 1997, 2004b, 2021a, b).

Os Bibionidae são popularmente conhecidos em inglês como *march flies*, “moscas/mosquitos de março”, devido à emergência de algumas espécies na primavera no Hemisfério Norte, e *lovebugs*, “insetos/bichos do amor”, devido ao hábito de voarem em cópula, em especial os membros do gênero *Plecia* Wiedemann (Fitzgerald 2004b). As larvas, em geral, vivem no solo e se alimentam de matéria orgânica em decomposição, mas também podem ser encontradas em madeira apodrecida e esterco (Fitzgerald 2009). Porém, algumas larvas se alimentam de tecido vegetal vivo, podendo ser consideradas pragas agrícolas (Fitzgerald 2009). A maior parte do ciclo de vida ocorre no solo, e a vida adulta é curta, de três a sete dias (Fitzgerald 2009). Algumas espécies de Bibionidae são sazonais, podendo eclodir uma (univoltino) ou duas (bivoltino) vezes por ano, ou até uma vez a cada dois anos (semivoltino) (Pinto & Amorim 2000, Fitzgerald 2004b). Porém, vale destacar que aparentemente algumas espécies com ciclo univoltino possuem duas populações com distintos períodos de eclosão, podendo erroneamente serem confundidas com espécies de ciclo bivoltino (Pinto & Amorim 2000). Além disso, algumas espécies podem ser encontradas durante todo o ano e possuem picos de frequência em determinados períodos, como *Plecia nearctica* Hardy (Pinto & Amorim 2000). Os adultos são frequentemente avistados em flores, onde poderiam se alimentar de néctar, pólen, melada ou outros líquidos vegetais (Fitzgerald 2009, Skartveit 2017). Devido ao hábito alimentar, alguns Bibionidae são considerados importantes polinizadores de plantas das famílias Orchidaceae e Iridaceae (Fitzgerald 2009, Skartveit 2017), e outros são aparentemente importantes polinizadores de árvores frutíferas, tais como a macieira e a pereira (Fitzgerald 2004b). No entanto, aparentemente alguns adultos de *Plecia* sp. não se alimentam (Pinto & Amorim 2000, Skartveit 2017).

A biologia dos Bibionidae neotropicais é pouco conhecida (Fitzgerald 2009). Apenas três espécies possuem estágios imaturos conhecidos e descritos: *Plecia* cf. *collaris* (Fabricius), *P. nearctica* Hardy, e *P. plagiata* (Wiedemann) (Kuitert 1975, Pinto & Amorim 1996). Quanto ao comportamento reprodutivo, apenas em *Dilophus sayi* (Hardy), *Plecia* cf. *collaris* (Fabricius) e *P. nearctica* Hardy foram observados (Thornhill 1976, Matthews & Matthews 1978, Pinto & Amorim 1996). E foi registrado o comportamento de polinização de *D. espeletiae* Sturm em plantas da subtribo Espeletiinae (Asteraceae, Asteroideae, Millerieae) (Sturm 1990).

Até o momento, Bibionidae compreende seis subfamílias, sendo quatro delas com representantes viventes e fósseis: Bibioninae, Hesperininae (*Hesperinus* Walker), Penthetriinae (*Penthetria* Meigen) e Pleciinae (*Plecia* Wiedemann), e duas que incluem apenas táxons fósseis: †Cretobibioninae (†*Cretobibio* Skartveit & Ansoerge) e †Burmahesperininae (†*Burmahesperinus* Ševčík, Skartveit, Krzemiński & Skibińska) (Fitzgerald 2004b, Skartveit & Ansoerge 2020, Ševčík *et al.* 2021). Há também gêneros fósseis cuja classificação em subfamílias é incerta. †*Cascoplecia* Poinar inicialmente foi classificado em uma família própria, †Cascopleciidae, e depois foi transferido para Bibionidae (Poinar 2010, Pape *et al.* 2011). †*Cretpenthetria* Li, Zhang & Xiao e †*Protopenthetria* Li, Skibińska, Krzemiński, Wang, Xiao & Zhang foram classificados em Pleciinae, porém em um sensu amplo e parafilético da subfamília que inclui *Penthetria* (Li *et al.* 2021). Também foi sugerido que †*Cascoplecia* seja parte Pleciinae (sensu Li *et al.* 2021), porém, nenhuma análise filogenética que incluísse algum dos três gêneros fósseis foi realizada (Pape *et al.* 2011, Li *et al.* 2021). Além disso, há gêneros fósseis que podem ou não fazer parte de Bibionidae, pois o posicionamento e a classificação dos mesmos é incerta por diferentes motivos. †*Clothonopsis* Hong & Wang e †*Fushunoplecia* Hong possuem descrições insuficientes e os respectivos materiais não estavam disponíveis para estudo quando Fitzgerald (2004b) realizou uma extensa revisão dos gêneros de Bibionidae. O material tipo de †*Lichnoplecia* Ren, Lu, Guo & Ji também necessita ser revisado para que sua identidade taxonômica seja esclarecida (Lukashevich *et al.* 2021). Por fim, †*Dinobibio* Baranov, Schädel & Haug, descrito a partir de uma larva fossilizada, pode ser tanto um grupo externo próximo de Bibionidae, quanto um grupo interno, requerendo assim análise de outros espécimes para entender melhor seu posicionamento (Baranov *et al.* 2019).

Bibioninae, a única subfamília que não é monotípica, é composta por duas

tribos: Bibionini e Dilophini (Pinto & Amorim 2000). Bibionini inclui os gêneros *Bibio* Geoffroy, *Bibiodes* Coquillett, *Bibionellus* Edwards e *Enicoscolus* Hardy; as relações filogenéticas entre os gêneros da tribo precisam ser melhor exploradas, assim como a monofilia de *Bibio* (Skartveit & Willassen 1996, Pinto & Amorim 2000, Fitzgerald 2004b). Já Dilophini inclui o gênero *Dilophus* Meigen e possivelmente o gênero fóssil †*Protodilophus* Skartveit (Pinto & Amorim 2000, Skartveit 2023).

As filogenias baseadas em dados morfológicos (Skartveit & Willassen 1996, Pinto & Amorim 2000, Fitzgerald 2004b) reconstróem as seguintes relações filogenéticas para Bibionidae: *Hesperinus* + (*Penthetria* + (*Plecia* + (Bibionini + *Dilophus*))). Parte dos autores (Krivosheina 1997, Skartveit 2009, Papp 2010) classificam *Hesperinus* em uma família separada, Hesperinidae. Em ambas classificações Bibionidae é um grupo monofilético, com ou sem o gênero, mudando apenas a delimitação do táxon. Uma nova hipótese filogenética foi proposta com base em dados moleculares por Ševčík *et al.* (2016): Bibioninae + (*Plecia* + (*Hesperinus* + *Penthetria*)), na qual apenas os gêneros *Bibio* e *Dilophus* foram amostrados para Bibioninae. Nessa nova hipótese *Hesperinus* deveria ser obrigatoriamente parte de Bibionidae para manter a monofilia da família. Entretanto, essa topologia requer caracteres morfológicos que a suportem e que expliquem se as sinapomorfias de Bibionidae (exceto *Hesperinus*) foram derivadas independentemente várias vezes ou se derivaram apenas uma vez e secundariamente foram perdidas em *Hesperinus*, ou seja, mais estudos são necessários para esclarecer essa nova hipótese (Ševčík *et al.* 2016). Skartveit & Ansoerge (2020) incorporaram *Penthetria* em Hesperininae com base nas evidências moleculares de Ševčík *et al.* (2016) e supostas similaridades morfológicas, porém tais similaridades não foram bem exploradas no trabalho e nenhuma sinapomorfia que suporte o clado (*Hesperinus* + *Penthetria*) foi apresentada (Skartveit & Ansoerge 2020). Um único gênero fóssil de Bibionidae, †*Cretobibio*, teve suas relações filogenéticas exploradas, sendo classificado como grupo irmão de Bibioninae (Skartveit & Ansoerge 2020). Por fim, as relações filogenéticas de Bibionidae com base em dados morfológicos pode ser sumarizada como: Hesperininae + (Penthetriinae + (Pleciinae + (†*Cretobibioninae* + Bibioninae))) (Skartveit & Willassen 1996, Pinto & Amorim 2000, Fitzgerald 2004b, Skartveit & Ansoerge 2020).

O fóssil mais antigo conhecido e inequivocamente pertencente à Bibionidae é †*Cretobibio montsecensis* Skartveit & Ansoerge do Barremiano (cerca de 130 MA) da Espanha (Skartveit & Ansoerge 2020). Já o Bibioninae mais antigo conhecido é

†*Protodilophus semispinosus* Skartveit do Cenomaniano (cerca de 99 MA) de Myanmar (Skartveit 2023). O fóssil mais antigo de um gênero vivente de Bibionidae é †*Bibiodes* sp. do Turoniano (cerca de 93 MA) de Botswana (Skartveit 2009). Quase todos os gêneros viventes da família possuem fósseis conhecidos, com exceção de *Bibionellus* e *Enicoscolus* (Fitzgerald 2004b, Skartveit 2009).

O gênero *Dilophus* foi descrito por Meigen em 1803 e possui distribuição mundial, exceto nas regiões polares (Pinto & Amorim 2000, Fitzgerald 2004b). O gênero é um dos mais diversos de Bibionidae, juntamente com *Bibio* (cerca de 190 espécies viventes) e *Plecia* (cerca de 260 espécies viventes), contando com cerca de 200 espécies viventes descritas (Fitzgerald 2004b, 2009, 2021a, Skartveit 2017). A fauna Neotropical conta com 79 espécies viventes, representando assim cerca de 40% das espécies descritas (Fitzgerald 2004b, Skartveit & Freidberg 2023). Entretanto, o número de espécies neotropicais possivelmente é subestimado, pois autores (Hardy 1966, Fitzgerald 2009) apontam que a fauna do gênero na região ainda é pouco conhecida. A última espécie Neotropical vivente descrita para o gênero é *Dilophus espeletiae* Sturm, 1990, há mais de 30 anos (Sturm 1990). Em relação à distribuição geográfica e diversidade, *Dilophus* possui mais espécies no Hemisfério Sul (cerca de 120 espécies, aproximadamente 60% da diversidade atual do gênero, distribuídas nas regiões Australasiana, Neotropical e no Sul da África) do que no Hemisfério Norte (Skartveit & Willassen 1996, Skartveit 2017). Em se tratando da região Neotropical, o Chile possui o maior número de espécies descritas (32), 40% da diversidade da região, sendo que 26 delas foram registradas apenas para o país (Fitzgerald *et al.* 2020). Entretanto, esse número pode mudar devido a futuras revisões das espécies, pois algumas possuem descrições insuficientes para identificá-las e o material tipo encontra-se perdido (Fitzgerald *et al.* 2020). Outro problema são as espécies descritas a partir de um dos sexos, o que pode inflar o número de espécies caso sejam descritas duas vezes, isso devido ao dimorfismo sexual acentuado entre machos e fêmeas que dificulta a associação entre os sexos (Fitzgerald *et al.* 2020).

Dilophus possui 12 espécies fósseis descritas, a maioria para Região Paleártica (9), uma Australasiana, uma Neártica e uma Neotropical (Fitzgerald & Greenwalt 2022; Nel *et al.* 2022). Todas as espécies são baseadas em indivíduos adultos, exceto por *D. campbelli* Harris, descrita a partir de uma larva fossilizada (Fitzgerald & Greenwalt 2022; Nel *et al.* 2022). Oito espécies foram encontradas preservadas em rochas sedimentares, como calcário e folhelho, e quatro foram encontradas em âmbar (Fitzgerald & Greenwalt

2022; Nel *et al.* 2022). Todos fósseis conhecidos são do Cenozoico e englobam as seguintes épocas: Eoceno (seis), Oligoceno (três) e Mioceno (três), sendo *D. campbelli* (Eoceno Inferior ao Médio, Nova Zelândia) e *D. idanos* Fitzgerald & Greenwalt (Eoceno Médio, 46.6 a 45.8 MA, Estados Unidos da América) os registros mais antigos para o gênero (Harris 1983, Fitzgerald & Greenwalt 2022).

A fauna Neotropical de *Dilophus* foi inventariada e/ou revisada por diversos trabalhos, como Reed (1888) (Chile), Hunter (1900) (América do Sul), Kertész (1902) (Mundial), Edwards (1930) (Chile), Stuardo (1946) (Chile), Hardy (1953) (Argentina e Chile), Hardy (1959) (Neotropical), Hardy (1966) (Neotropical), Maes 1990 (Nicarágua), Fitzgerald (2000) (México), Falaschi *et al.* (2016) (Colômbia), Fitzgerald *et al.* (2020) (Chile), Fitzgerald (2023) (Guatemala), e Falaschi & Schelesky-Prado (2024) e Oliveira *et al.* (2024) (Brasil, catálogo online e artigo, respectivamente). Em relação às chaves de identificação, as únicas disponíveis na literatura que contemplam espécies neotropicais são as de Edwards (1930) (espécies da Patagônia e sul do Chile) e de Hardy (1953), que contempla as mesmas espécies da chave anterior com o acréscimo de espécies da Argentina.

O conhecimento sobre os estágios imaturos do gênero é limitado, possuindo apenas quatro espécies viventes com larvas descritas, todas da Região Paleártica (Skartveit 2002). Já em relação ao conhecimento molecular, apenas duas espécies paleárticas possuem dados moleculares publicados, além de alguns espécimes não identificados a nível de espécie (NCBI).

Dilophus é um grupo monofilético (Skartveit & Willassen 1996, Pinto & Amorim 2000, Fitzgerald 2004b) e entre suas sinapomorfias destacam-se as fileiras de espinhos no dorso do tórax (ver Fitzgerald 2004b, p. 57, Figura 6.a) e nas tíbias anteriores (ver Fitzgerald 2004b, p. 77, Figura 8.d). As fêmeas de *Dilophus*, assim como as fêmeas de *Bibio* e possivelmente de outros gêneros de Bibioninae, usam as tíbias anteriores modificadas para cavar uma câmara no solo na qual depositam seus ovos (Fitzgerald 2004b). Entretanto, as estruturas presentes em Bibionini e *Dilophus* não são homólogas: nos Bibionini, o ápice das tíbias anteriores se estende dorsalmente e forma um espinho robusto (ver Fitzgerald 2004b, p. 77, Figura 8.a), já em *Dilophus* há a presença de uma ou duas fileiras medianas de espinhos e um anel apical de espinhos (ver Fitzgerald 2004b, p. 77, Figura 8.d), sendo esses derivados das cerdas tibiais (Pinto & Amorim 2000, Fitzgerald 2004b).

As relações filogenéticas entre as espécies do gênero não são claras e foram pouco exploradas na literatura: apenas dois trabalhos, Skartveit & Willassen (1996) e Fitzgerald (2004b), exploraram tais relações. Ambos trabalhos não tinham como objetivo desvendar especificamente a filogenia de *Dilophus*, mas de grupos mais inclusivos (Bibioninae e Bibionidae, respectivamente). Ambos tiveram uma baixa amostragem de espécies de *Dilophus* (14 e quatro espécies, respectivamente) e não abrangeram todas regiões biogeográficas em que o gênero ocorre (ambos trabalhos abrangeram quatro regiões). Além disso, fósseis do gênero não foram incluídos em nenhum dos trabalhos. Um outro estudo, Pinto & Amorim (2000), focado em elucidar a filogenia de Bibionidae, incluiu um número expressivo de espécies (39), sobretudo neotropicais, porém, os terminais da matriz foram gêneros e não espécies, assim, as relações filogenéticas entre as espécies de *Dilophus* não foram exploradas.

Poucos trabalhos propuseram grupos de espécies para o gênero. Haenni (1981, 1982) propôs o grupo *Dilophus febrilis*, compreendendo 26 espécies das regiões Paleártica (13) e Afrotropical (13) (Skartveit & Willassen 1996, Skartveit & Freidberg 2023). Skartveit & Willassen (1996) propuseram o grupo *Dilophus bispinosus*, composto por cinco espécies paleárticas. Fitzgerald (2004a) sugeriu que algumas espécies do Pacífico Sul formam um complexo, incluindo pelo menos dez espécies da região Australasiana/Oceânica.

Tendo em vista estes dois cenários, o primeiro relativo à demanda de estudos focados nas espécies neotropicais de *Dilophus*, e o segundo relativo à necessidade de estudos filogenéticos com ampla amostragem do gênero (tanto em relação ao número de espécies, quanto em relação às regiões biogeográficas), esse trabalho se propõe a preencher lacunas em ambos os cenários. Para tal, foram elaborados dois capítulos em formato de artigo. O primeiro capítulo consiste em um estudo taxonômico de algumas espécies neotropicais de *Dilophus*, compilando os dados da literatura para cada espécie e incluindo redescrições de espécies já conhecidas (algumas com descrições inéditas de terminálias masculinas e femininas), ampliação do conhecimento sobre a distribuição geográfica e sazonalidade através de novos registros e descrições de novas espécies. Notas sobre a biologia das espécies também foram feitas, incluindo visitaç o floral e alimenta o de produtos florais. Tamb m foi confeccionada a primeira chave de identifica o para todas as esp cies neotropicais identific veis do g nero. J  o segundo cap tulo foi dedicado a explorar as rela oes filogen ticas entre as esp cies do g nero

utilizando um expressivo número de espécies de todas as regiões biogeográficas, permitindo assim uma discussão sobre a validade dos grupos de espécies propostos na literatura, além de proposições de novos grupos. Espécies fósseis de *Dilophus* foram utilizadas pela primeira vez em um contexto filogenético e o posicionamento de †*Protodilophus* foi investigado.

REFERÊNCIAS

- Amorim, D. S. (1994) A new suprageneric classification of the Scatopsidae (Diptera: Psychodomorpha). *Iheringia, Série Zoologia* (77):107-112.
- Baranov, V.; Schädel, M.; Haug, J.T. (2019). Fly Palaeo-Evo-Devo: Immature Stages of Bibionomorphan dipterans in Baltic and BitterfeldAmber. *PeerJ* 2019, 7, e7843.

- Bertone, M. A.; Courtney, G. W. & Wiegmann, B. M. (2008) Phylogenetics and temporal diversification of the earliest true flies (Insecta: Diptera) based on multiple nuclear genes. *Systematic Entomology* 33(4):668-687.
- Blagoderov, V. & Grimaldi D. (2004) Fossil Sciaroidea (Diptera) in Cretaceous ambers, exclusive of Cecidomyiidae, Sciaridae, and Keroplatidae. *American Museum Novitates*, 3433, 1–76.
- Carvalho, C.J.B. de; Rafael, J.A.; Couri, M.S.; Riccardi, P.R.; Silva, V.C.; Oliveira, S.S.; Lamas, C.J.E. (2024) Cap. 36, Diptera Linnaeus, 1758, pp. 783-831. In: Rafael, J.A.; Melo, G.A.R.; Carvalho, C.J.B. de; Casari, S. & Constantino, R. (eds). *Insetos do Brasil: Diversidade e Taxonomia*. 2ª ed. Instituto Nacional de Pesquisas da Amazônia, Manaus. 880 pp. <https://doi.org/10.61818/56330464c36>
- Coram, R. & Jarzembowski, E.A. (1999). New Fossil Flies (Insecta: Diptera) from the Purbeck Limestone Group (Lower Cretaceous, Berriasian) of Dorset, UK, *Cret. Res.*, vol. 20, pp. 857–861.
- Edwards, F.W. (1930) Bibionidae. In: *Diptera of Patagonia and South Chile*. Part 2. Fascicle 3. British Museum (Natural History), London, pp. 77–88.
- Falaschi RL, Oliveira SS, Amorim DS (2016). Bibionidae. In: Wolff M, Nihei SS, de Carvalho CJB (Eds) *Catalogue of Diptera of Colombia*, *Zootaxa* 4122: 20–25. <https://doi.org/10.11646/zootaxa.4122.1.5>
- Falaschi RL, Schelesky-Prado DC (2024) Bibionidae. *Catálogo Taxonômico da Fauna do Brasil*. PNUD. Disponível em <<http://fauna.jbrj.gov.br/fauna/faunadobrasil/1843>> [Acesso em 27.X.2024].
- Fitzgerald, S.J. (1997). A Revision of *Biblio* (Diptera: Bibionidae) of Mexico and Central America. *Trans. Am. Ent. Soc.* 123(4): 225-287.
- Fitzgerald SJ (2000) Bibionidae. In: Llorente Bousquets JE, Gonzalez Soriano E, Papavero N (Eds) *Biodiversidad, Taxonomia y Biogeografía de Artropodos de Mexico*, vol. II, Universidad Nacional Autonoma de Mexico, D.F., Mexico, 627–634.
- Fitzgerald, S.J. (2004a) Bibionidae (Diptera) of New Caledonia. *Bishop Mus. Bull*, in *Entomol.* 12: 79-88.
- Fitzgerald, S.J. (2004b) Evolution and classification of Bibionidae (Diptera: Bibionomorpha). Ph.D. thesis, Oregon State University, Corvallis, Oregon, 385 pp.

Fitzgerald, S.J. (2009) Bibionidae. In: Brown, B.V., Borkent, A., Cumming, J.M., Wood, D.M., Woodley, N.E. & Zumbado, M.A. (Eds.), Manual of Central American Diptera: Vol. 1. NRC Research Press, Ottawa, Ontario, 714 pp.

Fitzgerald, S.J. (2021a) *Penthetria* Meigen (Diptera: Bibionidae): Revision of New World species and world catalog. *Zootaxa*, 4926 (4), 451–500. <https://doi.org/10.11646/zootaxa.4926.4.1>

Fitzgerald, S.J. (2021b) New species of Neotropical *Plecia* Wiedemann (Diptera: Bibionidae) and delineation of the *americana*-, *nigra*-, and *xyele*- species-groups. *Zootaxa*, 5005 (1): 021–040. <https://doi.org/10.11646/zootaxa.5005.1.2>

Fitzgerald SJ (2023) Capítulo 6: Bibionidae (Diptera) of Guatemala. In: Schuster JC, Yoshimoto J, Sierra JM (Eds) Biodiversidad de Guatemala, vol. 3, Universidad del Valle de Guatemala, Guatemala, 95–104 pp.

Fitzgerald, S. J., C. R. González & M. Elgueta. 2020. A catalog of the Bibionidae (Diptera: Bibionomorpha) of Chile. *Zootaxa* 4766(1): 48–60.

Fitzgerald, S.J. & Greenwalt, D.A. (2022) Family Bibionidae Fleming, 1821. In: Greenwalt, D.A., D. Des Souza Amorim, M. Hauser, P.H. Kerr, S.J. Fitzgerald, J.M. Cumming, N.L. Evenhuis & B.J. Sinclair, 2022. Diptera of the Middle Eocene Kishenehn Formation II. *Palaeontologica Electronica* 2 (2) (a22): 1-52.

Fleming, J. (1821) Insecta. In: Stewart, D., Playfair, J. & Brande, W.T. (Eds.), Supplement to the fourth, fifth and sixth editions of the Encyclopedia Britannica. A. Constable & Co., Edinburgh, 5 (Pt. 1), pp. 41–56. [(1815)–1824].

Haenni, J.P. (1981) North African *Dilophus* Meigen, with description of *D. maghrebensis* n. sp. (Diptera: Bibionidae) *Entomologica Scandinavica* 12:429-432.

Haenni, J.-P. (1982) Revision des espèces européennes du groupe de *Dilophus febrilis* (L.), avec description d'une espèce nouvelle (Diptera, Bibionidae). *Revue Suisse Zool.* 89(2): 337-354.

Hardy, D.E. (1953) The Argentine Bibionidae (Diptera). *Acta Zoológica Lilloana*, 12, 343–376.

Hardy, D.E. (1959) Catalogue of the Neotropical Bibionidae. *Acta Zoológica Lilloana*, 17, 437–476.

- Hardy, D.E. (1966) 18. Family Bibionidae. In: Papavero, N. (Ed.), A Catalogue of the Diptera of the Americas south of the United States. Departamento de Zoologia da Secretaria da Agricultura do Estado de São Paulo, São Paulo, pp. 1–20.
- Harris, A.C. (1983) An Eocene larval insect fossil (Diptera: Bibionidae) from North Otago, New Zealand. *Journal of the Royal Society of New Zealand*, 13:93-105.
- Hippa H, Vilkamaa P. (2005). The genus *Sciarotricha* gen. n. (Sciaridae) and the phylogeny of recent and fossil Sciaroidea (Diptera). *Insect Systematics, Evolution* 36:121–144. <https://www.doi.org/10.1163/187631205788838492>
- Hunter, W.D. (1900) Catalogue of the Diptera of South America. Part. I. Bibliography and Nematocera. *Transactions of the American Entomological Society*, 26, 260–298.
- Kertész, C. (1902) *Catalogus dipterorum Hucusque Descriptorum*. Vol. I. Lipsiae, Budapestini, 339 pp.
- Krivosheina, N.P. (1997) Chapter 2.4. Family Hesperinidae. In: Papp, L. & Darvas, B., *Contributions to a manual of Palaearctic Diptera (with special reference to flies of economic importance)*. Vol. 2. Nematocera and Lower Brachycera. Science Herald, Budapest, pp. 35–39.
- Krzemiński, W. & Krzemińska, E. (1994) *Procramptonomyia marianna*, a new species from the Upper Jurassic of Great Britain (Diptera, Anisopodomorpha, Procramptonomyiidae). *Acta Zoologica Cracoviensia* 32, 101–105.
- Kuitert, L.C. (1975) Sexual dimorphism in *Plecia nearctica* pupae (Diptera: Bibionidae). *Note. Florida Entomologist*, 58, 212.
- Li, L.-W., Skibinska, K., Krzeminski, W., Wang, B. & Xiao, C.-T. (2021) A new March fly *Protopenethria skartveiti* gen. nov. et sp. nov. (Diptera, Bibionidae, Plecinae) from mid-Cretaceous Burmese amber. *Cretaceous Research*, 127, 104924. <https://doi.org/10.1016/j.cretres.2021.104924>
- Lin X, Shih C, Ren D. (2015) Revision of the genus *Epimesoplecia* Zhang, 2007 (Diptera, Nematocera, Protopleciidae) with five new species. *Zookeys*. 2015 Mar 30;(492):123-43. doi: 10.3897/zookeys.492.6852
- Lukashevich, E.D., Amorim, D.S. & Ribeiro, G.C. (2021) A Gondwanan record of the extinct genus *Cretobibio* (Diptera: Bibionidae). *Palaeoentomology*, 4, 468–474. <https://doi.org/10.11646/palaeoentomology.4.5.13>.

- Maes, J. M. (1990) Catalogo de los Diptera de Nicaragua. 8. Bibionidae (Nematocera). *Revista Nicaraguense de Entomologia* 14B: 23–26.
- Matthews, R. W. & J. R. Matthews (1978) *Insect Behavior*. -New York, John Wiley & Sons.
- Meigen, J.G. (1803) Versuch einer neuen Gattungs Eintheilung der europäischen zweiflügeligen Insekten. *Magazin für Insektenkunde*, 2, 264.
- National Center for Biotechnology Information (NCBI) [Internet]. Bethesda (MD): National Library of Medicine (US), National Center for Biotechnology Information; [1988]. Disponível em: <<https://www.ncbi.nlm.nih.gov/>> [Acesso em 27.X.2024].
- Nel, A., Legal, S. & Coster, P. (2022) A new species of the March fly genus *Dilophus* Meigen, 1803 (Diptera: Bibionidae) from the Oligocene of Provence (France), *Palaeoentomology* 5 (4), pp. 347-353 : 348-349.
- Oliveira SS, Afiune GPS, Schelesky-Prado DC, Maia VC, Amorim DS, Falaschi RL (2024) Taxonomic Catalog of the Brazilian Fauna: Bibionomorpha (Diptera) diversity and distribution. *Zoologia* 41: e23103. <https://doi.org/10.1590/S1984-4689.v41.e23103>
- Oosterbroek, P. & Courtney, G. (1995) Phylogeny of the nematocerous families of Diptera (Insecta). *Zoological Journal of the Linnean Society*, 115, 267–311. <http://dx.doi.org/10.1111/j.1096-3642.1995.tb02462.x>
- Pape, T., Blagoderov, V., Mostovski, M. B. (2011) Order DIPTERA Linnaeus, 1758, in: Zhang, Z-Q. (Ed.), *Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness*. *Zootaxa* 3148 (1), 222–229. <https://doi.org/10.11646/zootaxa.3148.1.42>
- Papp, L. (2010) A study on *Hesperinus* Walker with description of a new species (Diptera: Hesperinidae). *Acta Zoologica Academiae Scientiarum Hungaricae* 56(4): 347–370.
- Pinto, L.G. & Amorim, D.S. (1996) Description of immature stages of two Neotropical species of *Plecia*, with a discussion about the evolution of immature characters in Bibionidae (Insecta, Diptera, Bibionidae). *Mitteilungen aus dem Museum für Naturkunde in Berlin* 72(2): 311–326. <https://doi.org/10.1002/mmnz.19960720215>

Pinto, L.G. & Amorim, D.S. (2000) Bibionidae (Diptera: Bibionomorpha). Morfologia e análise filogenética. Holos, Ribeirão Preto, 98 pp.

Poinar, G. (2010) *Cascoplecia insolitis* (Diptera: Cascopleciidae), a new family, genus, and species of flower-visiting, unicorn fly (Bibionomorpha) in Early Cretaceous Burmese amber. *Cretaceous Research*, 31(1):71-76. <https://doi.org/10.1016/j.cretres.2009.09.007>

Reed, E.C. (1888) Catálogo de los insectos dípteros de Chile. *Anales de la Universidad de Chile*, 73, 271–316.

Rohdendorf BB (1946) The evolution of the Wing and the Phylogeny of Oligoneura (Diptera, Nematocera). *Trudy Paleontologicheskogo Institution Akademii Nauk SSSR Moscow, Leningrad*, 1–108. [In Russian, with English summary]

Ševčík, J., Kaspřák, D., Mantič, M., Fitzgerald, S., Ševčíková, T., Tóthová, A., & Jaschhof, M. (2016) Molecular phylogeny of the megadiverse insect infraorder Bibionomorpha sensu lato (Diptera). *PeerJ*, e2563. <https://doi.org/10.7717/peerj.2563>

Ševčík J, Skartveit J, Krzemiński W, Skibińska K. (2021) A Peculiar New Genus of Bibionomorpha (Diptera) with Brachycera-Like Modification of Antennae from Mid-Cretaceous Amber of Myanmar. *Insects*. 12(4):364. <https://doi.org/10.3390/insects12040364>

Skartveit, J. (2002) The larvae of European Bibioninae (Diptera, Bibionidae). *J. Nat. list.* 36: 449-485.

Skartveit, J. (2009) Fossil Hesperinidae and Bibionidae (Diptera: Bibionoidea) from Baltic amber. *Studia dipterologica*, 15, 3–42.

Skartveit, J. (2017) Bibionidae. In: Kirk-Spriggs, A.H. & Sinclair, B.J.(Eds.), *Manual of Afrotropical Diptera*. Vol. 2. Suricata 5. South African National Biodiversity Institute, Pretoria, pp. 497–504.

Skartveit J. (2023) When the past meets the present: the oldest known Bibioninae, and the youngest known Cretobibioninae (Diptera, Bibionidae) from mid-Cretaceous Myanmar amber. *Zootaxa*. 5258(5):548-556. <https://doi.org/10.11646/zootaxa.5258.5.4>.

Skartveit, J. & Ansoerge, J. (2020) A new genus and subfamily of fossil Bibionidae (Diptera) from the Lower Cretaceous, with new classification of the Bibionidae. *Palaeoentomology*, 3 (2), 163–172.

Skartveit J, Freidberg A. (2023) Revision of the genus *Dilophus* Meigen, 1803 (Diptera, Bibionidae) from the Afrotropical Ecozone. *Zootaxa*. Oct 27;5360(3):301-354. doi: <https://doi.org/10.11646/zootaxa.5360.3.1>

Skartveit, J. & Willassen, E. (1996) Phylogenetic relationships in Bibioninae (Diptera, Bibionidae). In Skartveit, J. Studies on the systematics and life histories of Bibioninae (Diptera, Bibionidae). Ph.D. dissertation. University of Bergen, Bergen, Norway.

Stuardo, C. (1946) Catálogo de los dípteros de Chile. Ministerio de Agricultura, Impresiones Universitaria, Santiago, 250 pp.

Sturm, H. (1990) Eine neue *Dilophus*-Art (Insecta, Diptera, Bibionidae) aus den Hochanden Kolumbiens. *Annalen des Naturhistorischen Museums in Wien. Serie B.* 91: 197-204.

Thornhill, R. (1976) Biology and reproductive behavior of *Dilophus sayi* (Diptera: Bibionidae). *Florida Entomologist* 59: 1–4.

Wiegmann, B.M. & Yeates, D.K. (2017) Phylogeny of Diptera. In: Kirk-Spriggs, A.H. & Sinclair, B.J. (Eds.), *Manual of Afrotropical Diptera*. Vol. 1. Introductory chapters and keys to Diptera families. *Suricata* 4. South African National Biodiversity Institute, Pretoria, pp. 69–87. [ISBN 978-1-928224-11-2]

Wiegmann, B. M.; Trautwein, M. D.; Winkler, I. S.; Barr, N. B.; Kim, J. W.; Lambkin, C.; Bertone, M. A.; Cassel, B. K.; Bayless, K. M.; Heimberg, A. M.; Wheeler, B. M.; Peterson, K. J.; Pape, T.; Sinclair, B. J.; Skevington, J. H.; Blagoderov, V.; Caravas, J.; Kutty, S. N.; Schmidt- Ott , U.; Kampmeiern, G. E.; Thompson, C.; Grimaldi, D. A.; Beckenbach, A.T.; Courtney, G. W.; Friedrich, M.; Meier, R. & Yeates, D. K. (2011) Episodic radiations in the fly tree of life. *Proceedings of the National Academy of Sciences of the United States of America* 108(14):5690-5695.

Wood, M. & Borkent, A. (1989) Phylogeny and classification of the Nematocera. In: McAlpine, J. F.; Peterson, B. V.; Shewell, G. E.; Teskey, H. J.; Vockeroth, J. R. & Wood, D. M. eds. *Manual of Nearctic Diptera*. Ottawa, Research Branch, Agriculture Canada, p. 1333-1370.

CAPÍTULO 1: Taxonomic Review of Neotropical *Dilophus* Meigen, 1803 (Diptera: Bibionidae)

Abstract

This study presents a comprehensive taxonomic review of the genus *Dilophus* Meigen, 1803, focusing on the Neotropical species. Through detailed morphological examination, we provide redescriptions of four described species: *Dilophus bicoloripes* Edwards, 1938 (with new records for four Brazilian states), *Dilophus flavicornis* Edwards, 1938, *Dilophus pectoralis* Wiedemann, 1828 (new records for two provinces and for the federal district of Argentina and one Brazilian state) and *Dilophus trisulcatus* Macquart, 1838

(new records for three Brazilian states), and describe two new species from Brazil, enhancing our understanding of the biodiversity within this genus. The genus has new records for five states in Brazil.

Key Words: Bibionomorpha, Neotropical Region, New species, Taxonomy.

Introduction

Bibionidae comprises about 700 extant species distributed in eight genera (Pinto & Amorim 2000, Fitzgerald 2004). The family is especially diverse in the Neotropical region, with 192 described species in six genera (Fitzgerald 1997, 2004, 2021a,b). *Dilophus* Meigen, 1803 is one of the largest genera in the family, with about 200 extant species distributed worldwide, in addition to 12 fossil species (Fitzgerald 2009, Skartveit 2017, Fitzgerald & Greenwalt 2022, Nel *et al.* 2022). In the Neotropical region, 79 extant species are known, representing about 40% of the described species, in addition to one fossil species (Pinto & Amorim 2000, Fitzgerald 2004, Fitzgerald & Greenwalt 2022). Most Neotropical species are from Chile (32), representing 40% of the region's diversity, and 26 of which were recorded only for the country (Fitzgerald *et al.* 2020). However, this number may be inaccurate, as some species have insufficient descriptions to identify them and the type material is presumably lost and some species were described from one sex, which can inflate the number of species if they are described twice, due to sexual dimorphism that makes association between sexes difficult (Fitzgerald *et al.* 2020).

The Neotropical fauna of *Dilophus* has been inventoried or reviewed by several works, such as Reed (1888), Hunter (1900), Kertész (1902), Edwards (1930), Stuardo (1946), Hardy (1953), Hardy (1959), Hardy (1966), Maes (1990), Fitzgerald (2000), Falaschi *et al.* (2016), Fitzgerald *et al.* (2020), and Fitzgerald (2023). However, only two identification keys that include Neotropical species are available in the literature: Edwards (1930) (species from Patagonia and Southern Chile) and Hardy (1953), which includes the same species as the previous key with the addition of some species from Argentina. There are no immature stages of the genus described for the Neotropical region, nor are there species with molecular data published, only Palearctic immatures and molecular data of Palearctic species are known (NCBI, Skartveit 2002).

The diversity of Neotropical *Dilophus* remains insufficiently explored, leading to the presence of numerous undescribed species (Hardy 1966, Fitzgerald 2009, Fitzgerald *et al.* 2020). The latest Neotropical species described, *Dilophus matilei* Waller, Nel & Menier, was found in Miocene Dominican amber and described in 2000. The latest extant species described for the region was *Dilophus espeletiae* Sturm, described from Colombia in 1990, almost 35 years ago. Throughout the 1970s and 1980s, no Neotropical *Dilophus* species were described, and the earliest descriptions, predating *D. espeletiae*, trace back to Hardy (1961). Thus, since 1962, only one fossil and one extant species of *Dilophus* have been described within the Neotropical region. Furthermore, the most recent catalog focused on the region, Hardy (1966), was published almost 60 years ago.

It is evident the lack of knowledge concerning the Neotropical fauna of *Dilophus*. Then, in this context, the first key that covers the entire Neotropical region is provided, four species are redescribed, including a compilation of the works that included each species, an overview of the geographic and seasonal distribution. Some redescriptions included the first description of the terminalia of male, female, or both. The material examined made it possible to expand the geographic and seasonal distribution of some species. Furthermore, two new species were found and described.

Material and methods

The studied specimens were obtained from the institution listed below, and are detailed in the section “Results”.

MZUSP – Museu de Zoologia da Universidade de São Paulo, São Paulo, São Paulo, Brazil.

CEDU - UNILA – Coleção Entomológica Danúncia Urban, Foz do Iguaçu, Paraná, Brazil. (high resolution photographs)

NHMUK – Natural History Museum, London, United Kingdom. (high resolution photographs)

ZUFG – Coleção Zoológica da Universidade Federal de Goiás, Goiânia, Goiás, Brazil.

The adult male and female terminalia were dissected for each studied species. The terminalia were dehydrated in 80% alcohol for 10 min and subsequently were placed in a solution of KOH on a hot plate at a temperature of 40°C for 90–120 minutes, followed by neutralization in 10% acetic acid and preservation in glycerin or slide-mounted with Canada Balsam. Photographs were taken with an MC170 HD camera (Leica, Wetzlar, Germany) coupled to an M205 C stereomicroscope (Leica) using the LAS 4.8.0 software (Leica Application Suite). The material prepared on permanent slides was photographed using an epifluorescence microscope (BX41, Olympus, Tokyo, Japan) with a digital camera (CCD DP71, Olympus) using DP controller software (Olympus). The vectorized illustrations were prepared using the Adobe Illustrator CC software.

The adult specimens were identified by comparing the morphological characters with those described in the literature. The material from CEDU - UNI and NHMUK was only observed through high resolution photographs that allowed the identification or redescription of the specimens. The species redescribed here were chosen because we have access to the specimens and they lack the description of male terminalia, female terminalia or both. Records from iNaturalist, a citizen science social network, are reported here. Species records from iNaturalist are used only when it is possible to undoubtedly identify the specimens, i.e., species with conspicuous features that separates them from similar species, and photos that clearly present these features. The adult morphological terminology mainly follows Fitzgerald (2004) and Skartveit (2017), but also included new terms, as “upper set” and “lower set”. A summary of the terminology used in this study and in selected Bibionidae studies is provided in Table 1.

In the literature, “comb” and “row” are used to refer to the groups of spines present on the mesonotum of *Dilophus*. Here, the term “thoracic comb” is used to refer to the transverse rows of spines present on the mesonotum, that may include posteriorly displaced spines and additional longitudinal rows of spines. The two combs are called anterior and posterior comb due to their positions. Then, the term “row” is used to refer only to the transverse rows, that could be divided or undivided. In the male of *Dilophus inconnexus*, the posterior row is absent, but the posterior comb is present, composed of two longitudinal rows of spines.

The spines on the fore tibiae of *Dilophus* can be categorized into two types: the medial spines, located before the apices in a dorsal position, and the apical spines, that form the apical circlet of spines. The medial spines usually can be arranged in two ways: single transverse set or two transverse sets of spines. The set can be straight or oblique, it can present spines distally displaced or even a row of longitudinal spines. Here, when two sets are present, the more basal one is called “upper set”, and the more apical one is called “lower set”. Some species of *Dilophus* have modified setae on their mid tibiae, called spine-like setae. These spine-like setae are thicker than the typical setae, but thinner than the spines of the fore tibiae.

The coordinates of both previous (from literature) and new records (from the material examined and iNaturalist observations) of the species were used to create the distribution maps. Records lacking precise coordinates or with very vague locality information, such as only a country or state designation, were either excluded (when more accurate records from the same locality were available) or represented with a question mark (when no more precise record was available for the locality). In cases where the locality was not highly imprecise but lacked coordinates, estimates were made based on label data. The updated distributions for the species are presented, and the new records for countries and states are underlined.

Abbreviations.

Adults (both sexes, except for terminology specific to male terminalia). A₁ first branch of anal vein; an lb anal lobe; bM₃₊₄ basal portion of third branch of media; bRs basal portion of Radial sector; C costal vein; c costal cell; cerc cercus; CuA anterior branch of cubital vein; CuP posterior branch of cubital vein; cx coxa; goncx gonocoxite; gonst gonostylus; h humeral crossvein; M₁ first branch of media; M₂ second branch of media; M₍₃₊₄₎ third branch of media; m₄ fourth medial cell; m-cu medial-cubital crossvein; m-m medial crossvein; pv pseudovein; R₁ anterior branch of radial vein; R₂₊₃ second branch of radius; R₄₊₅ third branch of radius; r-m radial-medial crossvein; Rs radial sector; Sc subcostal vein; st sternite; syngoncx synsternogonocoxite; tg tergite.

Table 1. Comparison between terminologies used in literature and in this study.

Terminology used in this study	Edwards (1938)	Hardy (1945)	Fitzgerald (2004)	Skartveit (2017)	Skartveit & Freidberg (2023)
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thoracic comb	comb	thoracic comb	row of spines, mesonotal comb	transverse row of spines	row	spine comb or row
anterior comb	anterior comb	anterior (thoracic) comb, prothoracic comb	mesonotal comb	-	-	pronotal spine row, prothoracic spine comb
posterior comb	posterior comb	-	mesonotal comb	-	-	mesonotal spine row, mesothoracic comb
medial spines (single set or two sets)	-	median set (when is a single set)	medial spines, set(s) of preapical dorsal spines	mesal spines	-	mesal spines
upper set	-	top set	-	-	-	-
lower set	-	middle set, middle comb	-	-	-	-
apical circling of spines	apical spines, apical row	apical or third set	apical circling of spines	apical circling of spines	apical circling of spines	apical circling of spines
spine-like setae	bristly spines, spiny bristles	-	spine-like setae	-	-	spinose setae, spine-like setae
R ₁	R ₁	R ₁₊₂	R ₁	R ₁	-	R ₁
R ₂₊₃	R ₄	R ₃₊₄	R ₄	R ₂₊₃	-	-
R ₄₊₅	R _s (when R ₂₊₃ is absent)	R ₅	R ₅	R ₄₊₅	-	R ₄₊₅
bM ₍₃₊₄₎	m-cu	-	bM ₍₃₊₄₎	bm-m	-	-
m-m	m-cu	-	m-m	bm-m	-	M-CuA
M ₍₃₊₄₎	Cu1	M ₃₊₄	M ₍₃₊₄₎	M ₄	-	CuA ₁
m-cu	basal portion of Cu1	m-cu	m-cu	-	-	basal portion of CuA ₁
CuA	Cu2	Cu1	CuA	CuA	-	CuA ₂
pseudovein	-	-	pseudovein	-	-	-
CuP	-	A ₁	CuP	CuP	-	CuP
A ₁	-	-	A ₁	A ₁	-	A ₁
epandrium	tergite	ninth tergum	epandrium, tergite nine	epandrium	-	epandrium
hypandrium	sternite	ninth sternum	hypandrium, sternite nine	hypandrium, sternite 9	-	sternite
synsternogonocoxite	-	-	synsternogonocoxite	-	-	gonocoxosternite
gonostylus	styles	clasper(s) harpago(nes) stylus	gonostylus	gonostylus	-	gonostylus

Results

Key to the species of Neotropical *Dilophus**

*Only the recognizable species and known sexes were included, i.e., species with insufficient descriptions for identification and diagnosis were not included in the key, as well as the unknown sexes of some species, which will appear only once in the key instead of twice. This key includes the two new species described here.

1. Holoptic eyes (Fig. 1.B); Males..... 2
 - Dichoptic eyes (Fig. 10.D); Females..... 45
2. (1) Fore tibia with a single set of medial spines..... 3
 - Fore tibia with two sets of medial spines (upper and lower set)..... 12
3. (2) Set with all spines forming a single row..... 6
 - Set with one spine placed more apically than the others..... 4
4. (3) Wing membrane with brownish fumose basally and sub-hyaline apically.....
 - *D. golbachii* (Hardy)
 - Wing membrane entirely hyaline..... 5
5. (4) Anterior veins brown; Southern Chile..... *D. arenarius* Edwards
 - Anterior veins yellow; Central America..... *D. ornatus* (Hardy)
6. (3) Dorsum orange, except for the brown to black anterior portion, which sometimes extends the entire length of the mesonotum.....
 - *D. pectoralis* Wiedemann
 - Dorsum entirely brownish or black..... 7
7. (6) Tibiae yellow..... *D. serenus* (Hardy)
 - Tibiae brown or black..... 8
8. (7) Dorsum setae whitish; hind femora and tibiae with long whitish setae.....
 - *D. piliferus* Edwards
 - Dorsum setae black..... 9
9. (8) Mesonotum surface wrinkled; hind tibiae clavate..... *D. villosus* Edwards
 - Mesonotum surface not wrinkled; hind tibiae not clavate..... 10
10. (9) Epandrium narrow, about three to four times wider than long; Mexico and USA *D. sayi* (Hardy)
 - Epandrium less than three times wider than long; South America..... 11
11. (10) Gonostyli with a cluster of long setae basally; epandrium distinctly clefted; Argentina and Brasil..... *D. trisulcatus* Macquart
 - Gonostyli without a cluster of long setae basally; epandrium only slightly clefted; Colombia..... *D. espeletiae* Sturm
12. (2) Upper set with one or two spines..... 13
 - Upper set with three to four spines..... *D. anomalus* (Hardy)
13. (12) Upper set with one spine, Southern Brazil..... 14
 - Upper set with two spines..... 18
14. (13) Dorsum yellowish..... 15
 - Dorsum black..... 16
15. (14) Anterior comb with 12-14 spines; legs mainly yellow.....
 - *D. dichrous* Edwards
 - Anterior comb with ten spines; legs mainly black..... *D. plaumanni* Edwards
16. (14) Wing membrane milky..... *D. edwardsi* (Hardy)
 - Wing membrane yellowish or light brownish fumose..... 17
17. (16) Hind tarsi yellow..... *D. flavitarsis* Edwards
 - Hind tarsi dark brown to black..... *D. segregatus* (Hardy)

18. (13) Lower set with two or three spines..... 19
 - Lower set with four to seven spines..... 38
19. (18) Lower set with two spines..... 20
 - Lower set with three spines..... 31
20. (19) M₁ vein basally interrupted..... *D. quadridens* (Hardy)
 - M₁ vein complete..... 21
21. (20) Dorsum setae white to yellow..... 22
 - Dorsum setae brown to black..... 26
22. (21) Halteres knobs yellow..... 23
 - Halteres knobs brown to black..... 24
23. (22) Hind femora bicolored, basally yellow-brownish, apically brown; anterior comb slightly divided..... *D. bicoloripes* Edwards
 - Hind femora brown to black; anterior comb undivided.... *D. flavihalter* Edwards
24. (22) Mesonotum with conspicuous shagreen-like texture; legs mainly yellow....
 *D. flavicornis* Edwards
 - Mesonotum without shagreen-like texture; legs mainly light brownish or brown
 25
25. (24) Hind tibiae distinctly clavate; hind legs covered with yellow setae;
 Argentina..... *D. microcerus* Edwards
 - Hind tibiae not distinctly clavate; hind legs covered with brown setae; Brazil
 *D. megacanthus* Edwards
26. (21) Rostrum very elongated, equal to the length of the eyes; legs entirely black
 *D. elephas* Edwards
 Rostrum not so elongated, less than half the length of the eyes; at least some
 parts of the legs brown, yellow or reddish..... 27
27. (26) Hind femora and tibiae brownish, sometimes tibiae lighter than femora,
 slightly yellowish..... *D. macrorhinus* Macquart
 - Hind femora dark brown to black, much darker than the yellow hind tibiae..... 28
28. (27) Hind tarsi swollen; Peru..... *D. peruensis* (Hardy)
 - Hind tarsi not swollen; Argentina and Chile..... 29
29. (28) M₁₊₂ stem short, shorter than m-m vein..... *D. gracilipes* Edwards
 - M₁₊₂ stem longer than m-m vein..... 30
30. (29) Wing membrane smoky..... *D. tetracanthus* Edwards
 - Wing membrane hyaline or nearly so..... *D. luteus* Edwards
31. (19) Mesonotum mainly reddish or yellow..... 32
 - Mesonotum entirely black..... 33
32. (31) Dorsum setae pale yellowish; Argentina and Chile..... *D. dorsalis* (Philippi)
 - Dorsum setae black; Caribbean..... *D. quinquespinae* (Hardy)
33. (31) Dorsum setae and halteres knobs yellow..... *D. flavistigma* Edwards
 - Dorsum setae and halteres knobs brown to black..... 34
34. (33) M₁ vein basally interrupted..... *D. interruptus* Edwards
 - M₁ vein joined with M stem..... 35
35. (34) Mid and hind tibiae brownish-yellow..... *D. gracilipes* Edwards
 - Legs all black..... 36
36. (35) Wing membrane brownish fumose, basal half yellowish, distal half slightly
 darker; Peru..... *D. nubilipennis* Edwards
 - Wing membrane hyaline to milky white; Argentina..... 37

37. (36) Fore tibial apical spur elongated, two times longer than the spines.....
..... *D. calcaratus* Edwards
- Fore tibial apical spur not longer than the spines..... *D. patagonicus* Edwards
38. (18) Lower set with four to five spines; transverse row of posterior comb present
..... 39
- Lower set with six spines; transverse row of posterior comb absent.....
..... *D. inconnexus* (Hardy)
39. (38) Mesonotum mainly reddish or yellow..... 40
- Mesonotum mainly brown to black..... 41
40. (39) Mesonotum entirely yellow; Costa Rica..... *D. minimus* (Hardy)
- Mesonotum with anterior brown area; Colombia..... *D. pictus* Schiner
41. (39) Legs mainly brown; gonostylus basally with a cluster of long setae.....
..... *D. sp. nov. A*
- Legs with at least some parts yellow..... 42
42. (41) Wing membrane hyaline..... *D. rhynchops* Coquillett
- Wing membrane fumose yellowish brown to brownish..... 43
43. (42) Hind basitarsi swollen; coxae brown..... *D. globosus* (Hardy)
- Fore coxae yellow..... 44
44. (43) Rostrum short, much shorter than the length of the eyes; Brazil.....
..... *D. sp. nov. B*
- Rostrum long, longer than the length of the eyes; Nicaragua.....
..... *D. fumosus* Coquillett
45. (1) Fore tibia with a single set of medial spines..... 46
- Fore tibia with two sets of medial spines (upper and lower set)..... 58
46. (45) Wing membrane brown to black fumose..... 47
- Wing membrane hyaline or nearly so, faintly fumose or slightly milky..... 51
47. (46) Dorsum orange or reddish with dark area medially..... 48
- Dorsum entirely dark brown to black..... 49
48. (47) Pile of abdomen yellowish; Colombia..... *D. balfouri* Edwards
- Pile of abdomen brown; Argentina, Brazil and Uruguay.....
..... *D. pectoralis* Wiedemann
49. (47) Smaller specimens (less than 4 mm); Mexico and USA..... *D. sayi* (Hardy)
- Larger specimens (more than 5.5 mm); South America..... 50
50. (49) Posterior comb with 16 spines; Northern South America.... *D. tapir* Schiner
- Posterior comb with more than 20 spines; Argentina and Brazil.....
..... *D. trisulcatus* Macquart
51. (46) Dorsum setae black..... *D. espeletiae* Sturm
- Dorsum setae white to yellow..... 52
52. (51) Dorsum entirely yellow or orange..... 53
- Dorsum dark brown to black or at least with black stripes..... 56
53. (52) Legs mainly yellow..... 54
- Legs partially yellow or orange and partially brown..... 55
54. (53) Set of spines like the spread fingers of a hand..... *D. distinguendus* Edwards
- Set of spines not as above..... *D. luteus* Edwards
55. (53) Fore coxae brown; Argentina..... *D. serenus* (Hardy)
- Fore coxae yellow; Central America..... *D. ornatus* (Hardy)
56. (52) Legs brownish yellow to dark brown; Peru..... *D. piliferus* Edwards

- Legs mainly yellow..... 57
- 57. (56) Tarsi apically dark brown..... *D. tetracanthus* Edwards
- Tarsi concolorous to the rest of the legs or nearly so.....
..... *D. hyalipennis* (Blanchard)
- 58. (45) Upper set with one or two spines..... 59
- Upper set with three spines..... *D. anomalus* (Hardy)
- 59. (58) Upper set with one spine..... 60
- Upper set with two spines..... 66
- 60. (59) Dorsum black..... 61
- Dorsum mainly yellow or red to dark red..... 62
- 61. (60) Hind tarsi yellowish..... *D. flavitarsis* Edwards
- Hind tarsi dark brown to black..... *D. segregatus* (Hardy)
- 62. (60) Dorsum with black anterior area..... *D. giganteus* Macquart, 1846
- Dorsu without black anterior area..... 63
- 63. (62) Legs entirely yellow..... *D. dichrous* Edwards
- Legs brown and yellowish or red..... 64
- 64. (63) Fore coxae brown to black; Venezuela..... *D. inconnexus* (Hardy)
- Fore coxae pale to yellow; Brazil..... 65
- 65. (64) Antennal scape black..... *D. plaumanni* Edwards
- Antennal scape yellow..... *D. brazilensis* (Hardy)
- 66. (59) Lower set with two spines..... 67
- Lower set with three to seven spines..... 74
- 67. (66) Dorsum setae black..... *D. elephas* Edwards
- Dorsum setae pale to yellow..... 68
- 68. (67) M₁ vein basally interrupted..... *D. quadridens* (Hardy)
- M₁ vein complete..... 69
- 69. (68) Dorsum orange or reddish..... 70
- Dorsum brownish to black, sometimes with yellow parts..... 71
- 70. (69) Hind femora bicolored, basally yellow-brownish, apically brown.....
..... *D. bicoloripes* Edwards
- Hind femora yellowish to reddish brown..... *D. macrorhinus* Macquart
- 71. (69) Halteres knobs yellow..... *D. flavihalter* Edwards
- Halteres knobs brown to black..... 72
- 72. (71) Mesonotum with conspicuous shagreen-like texture.....
..... *D. flavicornis* Edwards
- Mesonotum without shagreen-like texture..... 73
- 73. (72) Hind tarsi with black setae..... *D. megacanthus* Edwards
- Hind tarsi with yellow setae..... *D. gracilipes* Edwards
- 74. (66) Lower set with three spines..... 75
- Lower set with four to seven spines..... 82
- 75. (74) Anterior comb medially divided..... 76
- Anterior comb undivided..... 77
- 76. (75) Anterior comb with 14 to 20 spines; Chile..... *D. castanipes* (Bigot)
- Anterior comb with six to eight spines; Caribbean..... *D. quinquespinae* (Hardy)
- 77. (75) Femora and tibiae black..... 78
- At least one of the leg segments reddish or yellow..... 79
- 78. (77) Crossvein r-m almost three times longer than bRs.... *D. calcaratus* Edwards

- Crossvein r-m less than two times longer than bRs..... *D. patagonicus* Edwards
- 79. (77) Femora and tibiae yellow..... *D. gracilipes* Edwards
- Tibiae black..... 80
- 80. (79) Femora reddish; wing membrane black fumose..... *D. dorsalis* (Philippi)
- Femora yellow; wing membrane slightly smoky..... 81
- 81. (80) Dorsum yellow with black stripes..... *D. antarcticus* (Walker)
- Dorsum entirely black..... *D. flavifemur* Edwards
- 82. (74) Dorsum yellow or red with anterior brown area..... 83
- Dorsum entirely reddish or yellowish brown or brown, without an anterior dark area..... 85
- 83. (82) Dorsum mainly red; lower set with six to seven spines; Venezuela.....
..... *D. lucifer* Schiner
- Dorsum mainly yellow; lower set with four to five spines..... 84
- 84. (83) Abdomen brownish black; Panama..... *D. variceps* (Hardy)
- Abdomen light brownish yellow; Brazil..... *D. sp. nov. B*
- 85. (82) Rostrum elongated, longer than the length of the eyes.. *D. globosus* (Hardy)
- Rostrum short, shorter than the length of the eyes..... 86
- 86. (85) Ocellar tubercle strongly developed; Venezuela.... *D. fulvimacula* (Walker)
- Ocellar tubercle only slightly developed; Brazil..... *D. sp. nov. A*

Taxonomy

Bibionidae Fleming, 1821

Bibioninae Newman, 1834

Dilophini Pinto & Amorim, 2000

Genus *Dilophus* Meigen

Philia Meigen, 1800: 20. Type species: *Tipula febrilis* Linnaeus (designated by Coquillett, 1910: 588). Suppressed by ICZN, 1963: 339.

Dilophus Meigen, 1803: 264. Type species: *Tipula febrilis* Linnaeus (designated by Latreille, 1810: 442).

Acanthocnemis Blanchard, 1852: 355. No type designation.

Cnemidoctenia Enderlein, 1934: 181. Type species: *Dilophus crassicus* Lundström (original designation) (Synonymized by Hardy 1953: 358).

Dactylodiscia Enderlein, 1934: 181. Type species: *Dilophus hiemalis* Becker (original designation) (Synonymized by Hardy 1953: 358).

Tridicroctena Enderlein, 1934: 181. Type species: *Dilophus africanus* Becker (original designation) (Synonymized by Hardy 1953: 358).

Triploctenia Enderlein, 1934: 181. Type species: *Dilophus tenuis* Meigen (original designation) (Synonymized by Hardy 1953: 358).

Reference: Fitzgerald, 2004: 302.

***Dilophus bicoloripes* Edwards, 1938**

Dilophus bicoloripes Edwards, 1938: 324. Type locality: Brazil, [Santa Catarina, Seara] Nova Teutônia. References: Hardy 1953: 361 (redesc.), 1959: 460 (cat.), 1966: 8 (cat.); Sturm 1990: 202 (com.); Falaschi & Schelesky-Prado, 2024 (cat.).

Material examined. Type material. 3 males, Brasilien [Brazil], [Santa Catarina, Seara], Nova Teutonia, 27°11'B. 52°23'L. [B.=*breite*, latitude in german, here means S (South); L.=*längengrad*, longitude in german, here means W (West)], Fritz Plaumann, 29.VII.1936 [syntypes] (photos of pinned specimens) [NHMUK]; 1 female, Brasilien [Brazil], [Santa Catarina, Seara], Nova Teutonia, 27°11'B. 52°23'L., Fritz Plaumann, 29.VII.1934 [syntype] (photos of pinned specimen) [NHMUK]; 1 male, Brasilien [Brazil], [Santa Catarina, Seara], Nova Teutonia, 27°11'B. 52°23'L., Fritz Plaumann, 6.VIII.1934 [syntype] (photos of pinned specimen) [NHMUK].

Additional material. 10 males, 12 females, Minas Geraes [Minas Gerais], Borda da Mata, vii.56, P. Pereira (some Pa. Pereira) (specimens pinned) [MZUSP]; 1 male, 8 females, BRAZIL, Paraná, Colombo, Bairro Santa Rita, 25°22'45.91"S 49°07'56.73"W, Malaise - 913m, viii.2012, Savaris, M. col. (in 80% ethanol) [MZUSP]; 3 females, BRAZIL, Paraná, Colombo, Bairro Santa Rita, 25°22'45.91"S 49°07'56.73"W, Malaise - 913m, ix.2014, Lampert, S. & Savaris, M. col. (in 80% ethanol) [MZUSP]; 1 female, (1) Foz do Iguaçu, PR [Paraná], BR [Brazil], -25.6120, -54.4819, F. Zanella 1/IX/2024 (2) *Dilophus bicoloripes* Edwards, 1938., Bibionidae, Det. Daniel Schelesky-Prado, 2024 (specimen pinned) [CEDU]; 71 males, 80 females, BRAZIL, Paraná, Ponta Grossa, Distrito de Itaiacoca, 25°07'19"S 49°56'24"W, Malaise B, 21.ix-05.x.2016, Almeida, M.C.; Tozetto, L.; Santos, M.H. cols. (in 80% ethanol) [MZUSP]; 1 male, BRAZIL, Paraná, Ponta Grossa, Distrito de Itaiacoca, 25°07'19"S 49°56'24"W, Malaise B, 13-31.vii.2017, Almeida, M.C.; Araujo, E.; Santos, M.H. cols (in 80% ethanol) [MZUSP]; 1 male, BRAZIL, Paraná, Ponta Grossa, Distrito de Itaiacoca, 25°07'19"S 49°56'24"W, Malaise B, 26.ix-29.x.2018, Almeida, M.C.; Araujo, E.; Santos, M.H. cols (in 80% ethanol) [MZUSP]; 16 males, 10 females, BRAZIL, Paraná, Ponta Grossa, Distrito de Itaiacoca, 25°07'05.4"S 49°56'27.7"W, Malaise A, 27.iv-12.v.2017, Almeida, M.C.; Araujo, E.; Tozetto, L.; Santos, M.H.. cols. (in 80% ethanol) [MZUSP]; 12 males, 6 females, BRAZIL, Paraná, Ponta Grossa, Distrito de Itaiacoca, 25°07'05.4"S 49°56'27.7"W, Malaise A, 12-25.viii.2017, Almeida, M.C.; Araujo, E.; Santos, M.H. cols (in 80% ethanol) [MZUSP]; 26 males, 1 female, Brasilien, Nova Teutonia, 27°11' B. 52°23' L., 300 . 500 m, viii.1970, Fritz Plaumann (specimens pinned) [MZUSP]; 3 females, Brasilien, Nova Teutonia, 27°11' B. 52°23' L., 300 . 500 m, ix.1970, Fritz Plaumann (specimens pinned) [MZUSP]; 15 males, 1 female, Brasilien, Nova Teutonia, 27°11' B. 52°23' L., 300 . 500 m, vii.1971, Fritz Plaumann (specimens pinned) [MZUSP]; 1 female, Brasilien, Nova Teutonia, 27°11' B. 52°23' L., 300 . 500 m, ix.1971, Fritz Plaumann (specimen pinned) [MZUSP]; 1 male, BRASIL: SP, Piracaia, Bairro dos Cubas, Sítio Cedro Velho, 17.viii.1997, C.R.F. Brandão col. (specimen pinned) [MZUSP]; 1 male, Argentina, Buenos Aires, Ezeiza, -34.83457, -58.5806, Sep 29, 2022, Andrés Vidal [137027022-iNaturalist]; 1 male, 1 female, Argentina, Misiones, San Ignacio, -27.27935, -55.57827, Aug 5, 2022, "aacocucci" [133015258-iNaturalist]; 1

female, Argentina, Misiones, Guaraní, -26.98162, -54.50393, Aug 4, 2023, Iván Eroles [203429792-iNaturalist]; 1 female, Argentina, Misiones, Guaraní, -27.24717, -54.03961, Aug 19, 2023, “Federico” [180609538-iNaturalist]; 1 female, Argentina, Misiones, Guaraní, -26.98162, -54.50393, Aug 4, 2023, Iván Eroles [203429792-iNaturalist]; 1 female, Argentina, Misiones, Cainguás, -27.00057, -54.63362, Aug 27, 2018, Roberto Guller [39996252-iNaturalist]; 1 female, Argentina, Misiones, Iguazú, -25.68235, -54.45993, Aug 15, 2017, Eamon C. Corbett [17149154-iNaturalist]; 1 female, Argentina, Misiones, Iguazú, Puerto Iguazú, -25.60315, -54.55454, Aug 5, 2023, Gustavo Fernando Durán [179205057-iNaturalist]; 1 female, Argentina, Misiones, Iguazú, Puerto Iguazú, -25.60519, -54.55959, Aug 6, 2023, Gustavo Fernando Durán [177776779-iNaturalist]; 1 male, Argentina, Misiones, Oberá, -27.46072, -55.15973, Aug 18, 2021, Lucas Rubio [94751683-iNaturalist]; 1 female, Argentina, Misiones, Posadas, -27.38159, -55.89124, Aug 11, 2023, Maria Victoria Boaglio [177898065-iNaturalist]; 1 female, Argentina, Misiones, San Ignacio, -27.28933, -55.5917, Aug 8, 2022, “aacocucci” [134103655-iNaturalist]; 1 male, Argentina, Misiones, San Ignacio, -27.28934, -55.59171, Aug 8, 2022, “aacocucci” [134103653-iNaturalist]; 1 male, Argentina, Misiones, General Manuel Belgrano, -25.85743, -53.9762, Aug 8, 2022, Evaristo Santos Ortega [130165076-iNaturalist]; 1 male, 1 female (mating), Brazil, Paraná, Foz do Iguaçu, -25.64795, -54.45715, Sep 3, 2021, Bhrenno Trad [93581948-iNaturalist]; 1 female, Brazil, Paraná, Foz do Iguaçu, -25.61854, -54.4745, Aug 13, 2022, Bhrenno Trad [130749086-iNaturalist]; 1 female, Brazil, Paraná, Foz do Iguaçu, -25.55111, -54.59066, Aug 26, 2024, “Dido” [238170270-iNaturalist]; 1 female, Brazil, Paraná, Pato Branco, Centro, -26.22833, -52.67139, Aug 23, 2022, Joao Ortolan [135672639-iNaturalist]; 1 male, Brazil, Rio Grande do Sul, Barra do Quaraí, Ilha Brasileira, -30.18243, -57.63052, Sep 9, 2023, Fernando Sessegolo [182876825-iNaturalist]; 1 female, Brazil, Rio Grande do Sul, Barra do Quaraí, Ilha Brasileira, -30.18243, -57.63052, Sep 9, 2023, Fernando Sessegolo [182876830-iNaturalist]; 1 male, Brazil, Rio Grande do Sul, Cruz Alta, Meu Jardim Vila São Francisco, -28.65053, -53.5937, Sep 23, 2020, Fernando Sessegolo [60568661-iNaturalist]; 1 female, Brazil, Rio Grande do Sul, Cruz Alta, Meu Jardim Vila São Francisco, -28.65053, -53.5937, Sep 25, 2020, Fernando Sessegolo [60857366-iNaturalist]; 1 female, Brazil, Rio Grande do Sul, Cruz Alta, Meu Jardim Vila São Francisco, -28.65053, -53.5937, Sep 27, 2020, Fernando Sessegolo [61038340-iNaturalist]; 1 male, Brazil, Rio Grande do Sul, Porto Alegre, Jardim Botânico, -30.05175, -51.17683, Sep 29, 2023, “kgigs” [188724404-iNaturalist]; 1 male, Brazil, Rio Grande do Sul, Porto Alegre, Jardim Botânico, -30.05175, -51.17683, Sep 29, 2023, “kgigs” [188724398-iNaturalist]; 1 female, Brazil, Rio Grande do Sul, Porto Alegre, Jardim Botânico, -30.05175, -51.17683, Sep 29, 2023, “kgigs” [188724301-iNaturalist]; 1 male, 1 female (mating), Brazil, Rio Grande do Sul, Santa Maria, -29.66176, -53.91462, Sep 10, 2023, Frank Thomas Sautter [182720003-iNaturalist]; 1 male, 1 female (mating), Brazil, Rio Grande do Sul, Sarandi, -27.94097, -52.92173, Aug 21, 2022, Carolina Signori [131778731-iNaturalist]; 1 female, Brazil, Rio Grande do Sul, Esmeralda, 95380-000, -28.05963, -51.18657, Sep 7, 2022, Edson Luis Fabro Gasperin [134090177-iNaturalist].

Diagnosis. Rostrum elongated; hind femora conspicuously bicolored, basally yellow-brownish, apically brown; gonostyli apex remarkable with a strong protuberance in the outer surface and is acutely pointed in the inner surface.

Redescription. Male (Fig. 1A–B). **Head.** Black. Compound eye holoptic, divided into a large, brownish red dorsal region with short black ommatrichia; ventral region smaller, darker. Ocellar tubercle developed, with setose posteriorly. Head ventrally covered with relatively long dark setae, a few of them extend to the base of the rostrum (both ventrally and dorsally). Antennae black except for the pedicel basally pale; with 11 flagellomeres. Rostrum elongated, about as long as the length of the eyes. Mouthparts dark brown; more than two times longer than the eyes when extended. Maxillary palps 5-segmented; first (basal) segment minute, second segment slightly slender, third and fourth segments slightly swollen, fifth (apical) segment short, less than two times longer than wide; 2-5 segments with setae. Labium with short setae. **Thorax.** Mainly shining black, except for the yellowish humeral ridges and parascutellum. Pleura dark brown with reddish tinge. Anterior comb with 10 strong spines, slightly divided in the middle; posterior comb with 12–14 smaller spines, one or two on each side displaced backwards. Dorsum with long yellowish white setae. Scutellum with long yellowish setae. Pleura with few white setae. **Legs.** Some parts are bright yellow-brownish, such as the fore trochanters, fore and mid femora, and, basally, the hind femora; the rest of legs brownish to black. Fore tibiae with two sets of medial spines, each with two blunt spines (2:2) (two aberrant specimens with a single spine on the upper set); apical circlet of spines with seven spines (“about eight” according to Hardy 1953); the apical spur darker, thicker and longer than the spines. Mid tibiae with medial and apical spine-like setae. Hind femora strongly clavate, hind tibiae clavate and hind basitarsi slender. **Wing.** Membrane milky hyaline, very slightly fumose on costal margin may be present, microtrichia present. Stigma brown. Anterior veins brown to yellowish, darker than the membrane; posterior veins pale, concolorous with the membrane. The C vein with short setae. Wing margin with short brownish setae fringe, except for the ending of anal lobe and alular margin, that are long and pale. Crossvein r-m about two to three times longer than bRs. Halteres yellow. **Abdomen.** Black, covered with pale setae. **Terminalia** (Fig. 2A–B). Gonostylus apically wide and becoming thinner towards the base, the remarkable apex is composed of a strong protuberance in the outer surface and is acutely pointed in the inner surface. Setae are present throughout the longitudinal length of gonostylus, specially before the apex and next to the acute apex of the inner surface. **Female** (Fig. 1C–D). **Head.** Black. Ocellar tubercle only slightly developed. Head with few, sparse short setae. Antennae black, except for the pale pedicel; with 11 flagellomeres. Rostrum elongated, about two times longer than the eyes; the posterior portion of the head slightly shorter than the eyes. Mouthparts more than four times longer than the eyes when extended. **Thorax.** Mainly shining yellow-brownish to orange, except for the brownish pleura. Some specimens with the thorax conspicuously darker, brown orange. Anterior comb with 9–11 strong spines, medially divided or nearly undivided; posterior comb with 12–15 smaller spines, some displaced backwards. **Legs.** Coloration as in male, except for the yellow fore and mid coxae. Arrangement of fore tibial spines as in male (but more strongly developed). Mid tibiae with medial and apical spine-like setae. Hind femora strongly clavate, hind tibiae clavate and hind basitarsi slender. **Wing.** Membrane light yellowish-brown fumose, microtrichia present. Stigma light brown to pale. Anterior veins brownish yellow, slightly darker than the membrane; posterior veins pale, concolorous with the membrane. Venation and other aspects virtually as in male. **Abdomen.** Brownish, apically lighter, with pale setae, especially apically. **Terminalia** (Fig. 2C–D). Tergite 9 with a cleft (about two thirds of the segment) on posterior margin (thinner medially, more produced laterally, anterior margin

apparently straight; laterally with long setae. Tergite 9 over five times wider than long. Cerci covered with setae; apically rounded; over two times longer than wide. Sternite 8 cleft about one third of the segment, lobes with rounded apex, with long setae. Sternite 10 broad and rounded.

Distribution. Argentina (Buenos Aires, Misiones), Brazil (Minas Gerais, Paraná, Rio Grande do Sul, Santa Catarina, São Paulo).

Comments. The geographic distribution was expanded to four more states of Brazil and one province of Argentina (Fig. 3). Two iNaturalist records are from Ilha Brasileira, an island that has been claimed by both Brazil and Uruguay. Since the island is administered by the Brazilian government, here the record is considered for Brazil, Rio Grande do Sul, Barra do Quaraí, and not Uruguay. However, the presence of this species in the north of Uruguay is likely. In the literature, the species was recorded for the months of July, August, and September. Here, the records are expanded to the months of April/May and possible October. Since the label includes both April and May (27.iv–12.v.2017), it is not possible to know the exact month of the record. For the same reason, the record for October is uncertain, because the label includes September and October (21.ix–05.x.2016). Both male and female terminalia are described for the first time. This species is easily recognized by its color pattern and arrangement of the fore tibial medial spines. According to Edwards (1938), *Dilophus rhynchops* Coquillett, 1904, from Nicaragua, has a similar color pattern, but a distinct arrangement of fore tibial medial spines (2:4 rather than 2:2). Some insights on the flower-visiting behavior and pollination are possible. According to Fernando C. V. Zanella, the specimen collected by him was found visiting *Pisonia* sp. (Caryophyllales, Nyctaginaceae) in Foz do Iguaçu, Paraná, Brazil (Fernando Zanella pers. comm.). Furthermore, in some iNaturalist observations specimens were found visiting and feeding on flowers of *Terminalia* sp. (Myrtales, Combretaceae), with their bodies covered in pollen, from Porto Alegre, Rio Grande do Sul, Brazil; visiting and feeding on flowers of *Mikania* sp. (Asterales, Asteraceae), with their bodies covered in pollen, from Cruz Alta, Rio Grande do Sul, Brazil; visiting *Cyrtocymura scorpioides* (Asterales, Asteraceae), from Ilha Brasileira, Barra do Quaraí, Rio Grande do Sul, Brazil; visiting and feeding on flowers of an unknown Angiospermae, body covered in pollen, from Cainguás, Misiones, Argentina.



Figure 1. *Dilophus bicoloripes*, habitus. **A.** male, lateral view. **B.** male, dorsal view. **C.** female, lateral view. **D.** female, dorsal view.

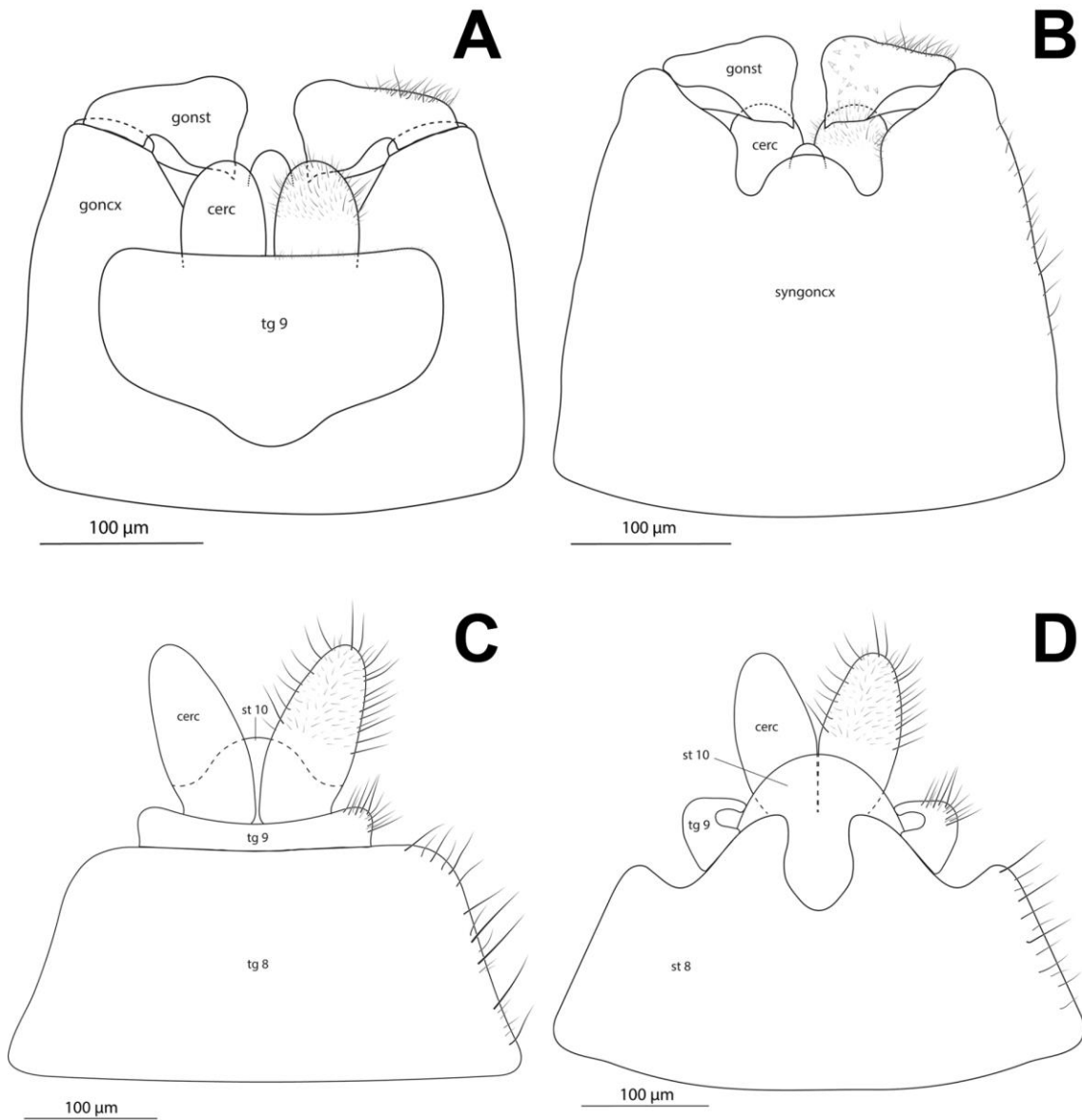


Figure 2. *Dilophus bicoloripes*, terminalia. **A.** male, dorsal view. **B.** male, ventral view. **C.** female, dorsal view. **D.** female, ventral view.

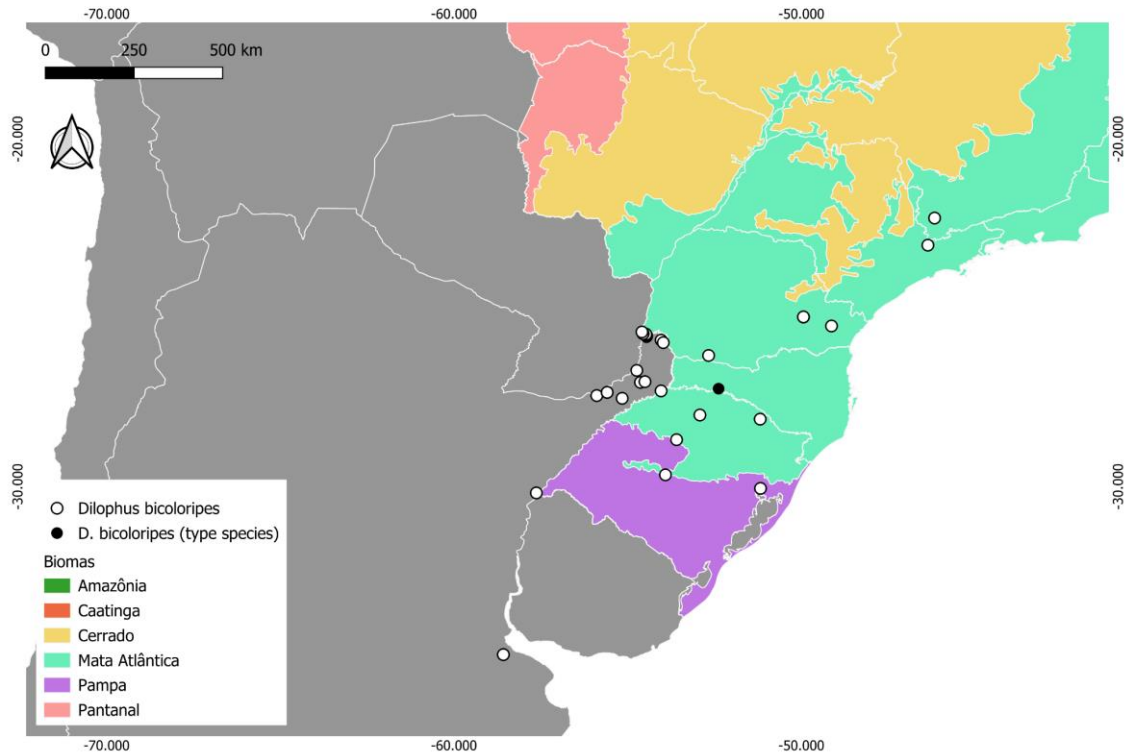


Figure 3. *Dilophus bicoloripes*, distribution map.

Dilophus flavicornis Edwards, 1938

Dilophus flavicornis Edwards, 1938: 325. Type locality: Brazil, [Santa Catarina, Seara], Nova Teutônia. References: Hardy, 1959: 463 (cat.), 1966: 8 (cat.); Falaschi & Schelesky-Prado, 2024 (cat.).

Material examined. Type material. 2 males, Brasilien [Brazil], [Santa Catarina, Seara], Nova Teutonia, 27°11' B. 52°23' L. [B.=breite, latitude in german, here means S (South); L.=längengrad, longitude in german, here means W (West)], Fritz Plaumann, 24.V. 1938 [syntypes] (photos of pinned specimens) [NHMUK]; 1 female, Brasilien [Brazil], [Santa Catarina, Seara], Nova Teutonia, 27°11' B. 52°23' L., Fritz Plaumann, 10.V. 1937 [syntype] (photos of pinned specimen) [NHMUK].

Additional material. 1 male, Brasilien [Brazil], [Santa Catarina, Seara], Nova Teutonia, 27°11' B. 52°23' L., 300 . 500 m, xii.1971, Fritz Plaumann (pinned) [MZUSP]; 1 male, Brasilien [Brazil], [Santa Catarina, Seara], Nova Teutonia, 27°11' B. 52°23' L., 300 . 500 m, xi.1967, Fritz Plaumann (pinned) [MZUSP].

Diagnosis. Mesonotum with conspicuous shagreen-like texture; fore tibiae with two closely spaced sets of medial spines, each with two spines; cell m4 wide, with m-cu longer than the distal part of M₃₊₄.

Redescription. Male (Fig. 4A–B). **Head.** Mainly black. Compound eye holoptic, divided into a large, brownish red dorsal region, apparently bare; ventral region smaller, darker. Three ocelli on a developed tubercle; without long setose posterior to ocellar tubercle

(only few shorter setae). Head ventrally with a few short setae. Antennae brownish yellow except for the lightest scape, pedicel and basal part of the first flagellomere; with apparently 9 flagellomeres. Rostrum shortened, much shorter than the length of the compound eyes. Mouthparts dark brown. Maxillary palps at least 4-segmented (hard to see in dry specimens); apical segment long, more than two times longer than wide; visible segments with setae. Labium hard to see. **Thorax.** Black. Anterior comb with 10–12 spines, row convex and almost forming a semicircle; posterior comb with 6–8 smaller spines in a straight row. Mesonotum with conspicuous shagreen-like texture. Dorsum with long yellowish white setae. Scutellum with long yellowish setae. **Legs.** Mainly yellow, except for the brownish tarsi and posterior coxae. Fore tibiae with two closely spaced sets of medial spines, each with two spines, spines on upper set closely spaced, spines on lower set well-separated; apical circlet of spines with seven spines; the apical spur slightly darker, thicker and slightly longer than the spines. Mid tibiae without spine-like setae. Hind tibiae slightly clavate and hind basitarsus slender. **Wing.** Membrane hyaline to milky, microtrichia present. Stigma brown. Anterior veins brown to yellowish, much lighter basally; posterior veins pale, concolorous with the membrane. C vein with short setae; reaching about half away the distance between R_{4+5} and M_1 . Humeral vein absent. Crossvein r-m about two times longer than bRs. Cell m4 wide, with m-cu longer than the distal part of M_{3+4} . Halteres with black knob and yellow stem. **Abdomen.** Light dark brown to black; covered with dark setae. **Terminalia** (Fig. 5A–B). Epandrium slightly clefted, covered with setae; setae of the lateral sides elongated. Synsternogonocoxite posterior margin W-shaped, with a deep narrow median cleft. Gonostylus apex slightly enlarged, apically pointed, covered with short setae, with some elongated setae present. Cerci rounded, apex conspicuously covered with setae, few of them elongated. **Female. Head.** Black. Ocellar tubercle developed. Head with few, sparse short setae. Antennae light brown, apical flagellomeres darker; with eight or nine flagellomeres. Rostrum shortened, much shorter than the length of the compound eyes; the posterior portion of the head subequal to the eyes length. **Thorax.** Dark brown to black, except for the lighter sides of mesonotum. Mesonotum, as in male, with conspicuous shagreen-like texture. Dorsum with long yellowish white setae. Scutellum apparently bare. **Legs.** Light brown to brown, fore tarsi notably darker. Arrangement of fore tibial spines apparently as in male. Hind femora and tibiae clavate, hind basitarsi slender. Hind tibia a little sinuous (according to Edwards, “possibly an individual anomaly”). **Wing.** Membrane light brown fumose, microtrichia present. Stigma dark brown. Anterior veins brown, basally yellowish; posterior veins light brown, slightly darker than the membrane. Venation and other aspects virtually as in male. **Abdomen.** Brownish, apparently covered with setae. **Terminalia.** Cerci brown, covered with setae.

Distribution. Brazil (Santa Catarina).

Comments. In the original description, Edwards (1938: 325) says that the fore tibiae have “four rather small sharp spines in a group just before middle of dorsal surface”, which could mean that a single set of four spines is present. However, based on photos of the types and the material at hand, two closely spaced sets of medial spines are present, each with two spines. Edwards also states that the female abdomen is shining black and the cerci black, but in the type’s photos both structures look brown, probably due to the effect of time (they were probably darker when fresh or recently collected). In the literature, the species was recorded only for May. Here, the records are expanded to the months of

November and December. The male terminalia is described for the first time. This species is easily recognized by its shagreen-like texture on the mesonotum and the wide m4 cell. Some other species have a similar arrangement of the fore tibial medial spines, with the spines on the upper set closely spaced and the spines on lower set well-separated, such as *Dilophus megacanthus* Edwards, 1938 and *Dilophus tetracanthus* Edwards, 1930. However, they are easily separated from *D. flavicornis* by lacking of the mentioned thoracic and wing venation features, and also *D. megacanthus* and *D. tetracanthus* have several spine-like setae on their mid tibiae, while *D. flavicornis* has no spine-like setae on mid tibiae.

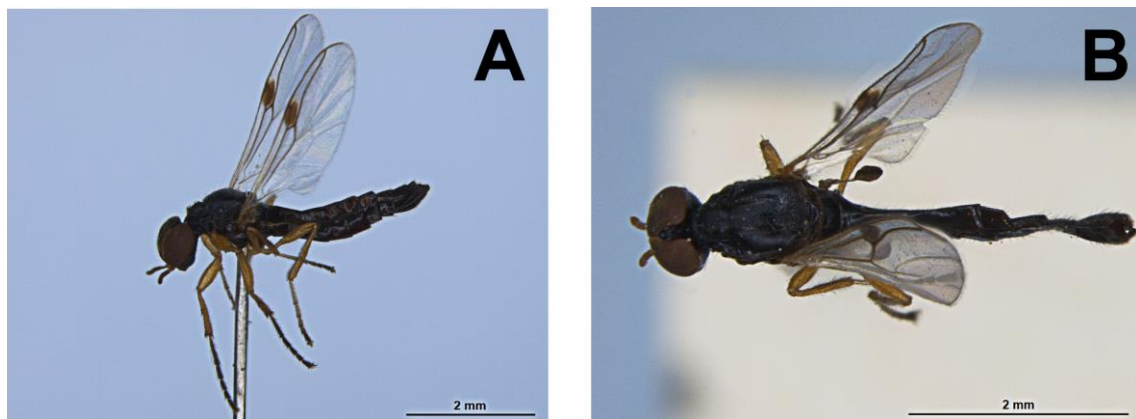


Figure 4. *Dilophus flavicornis*, male, habitus. **A.** lateral view. **B.** dorsal view.

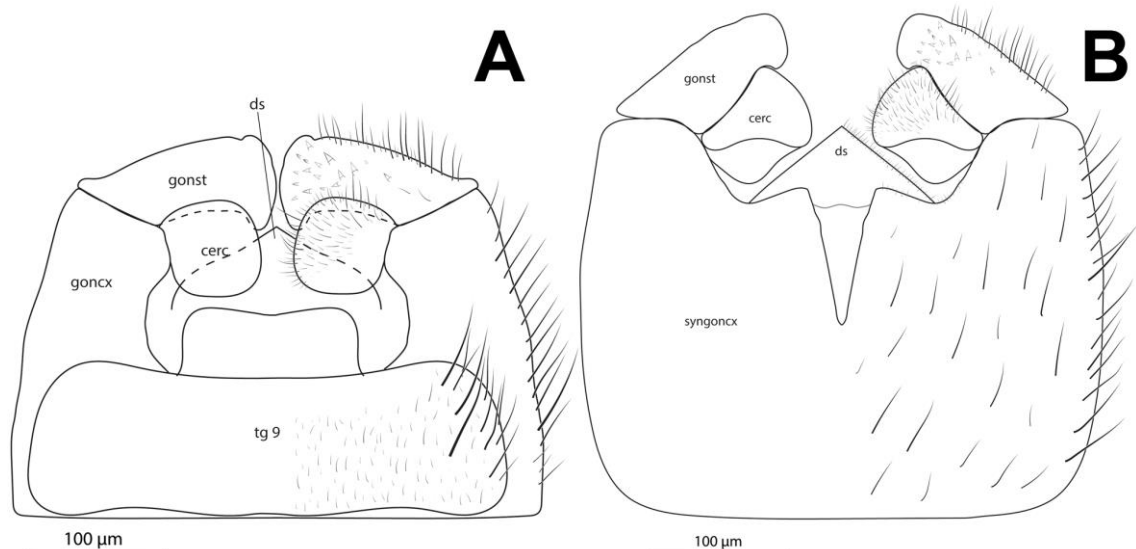


Figure 5. *Dilophus flavicornis*, male terminalia. **A.** dorsal view. **B.** ventral view.

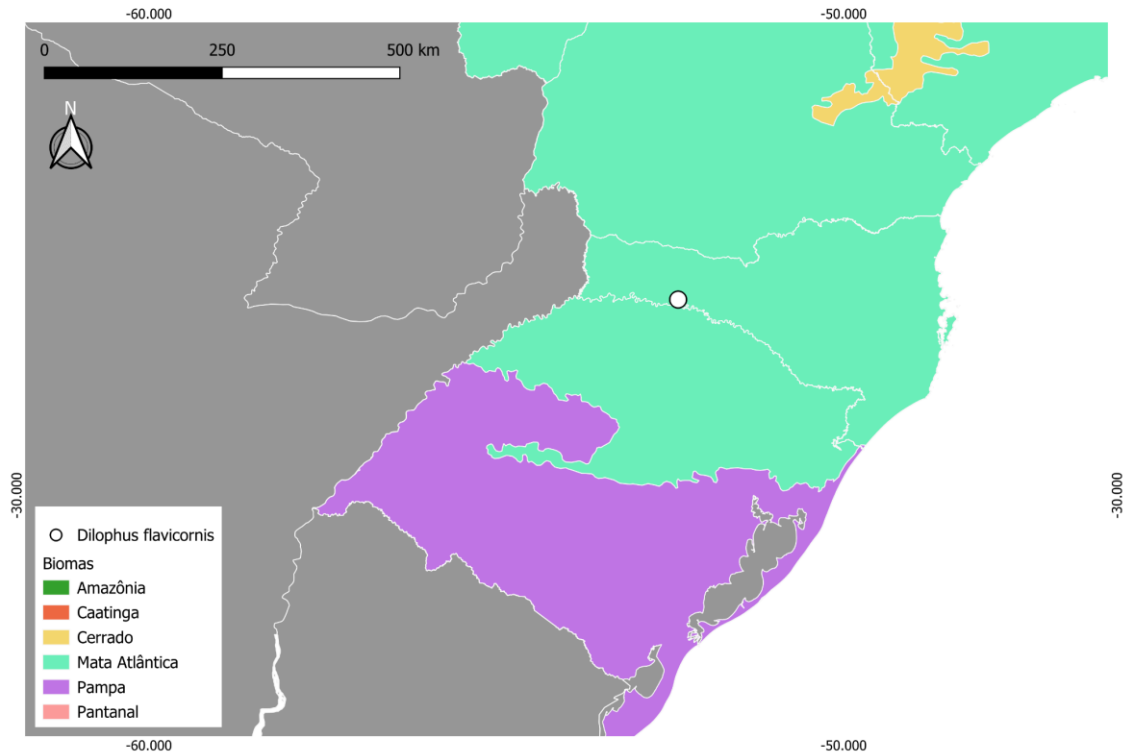


Figure 6. *Dilophus flavicornis*, distribution map.

Dilophus pectoralis Wiedemann, 1828

Dilophus pectoralis Wiedemann, 1828: 76. Type locality: Uruguay, [Montevideo] Montevideo. References: Lynch Arribálzaga, 1881: 119 (cat.); Hunter, 1900: 294 (cat.); Kertész, 1902: 153 (cat.); Brèthes, 1908: 280 (cat.); Hardy, 1953: 368 (redesc.), 1959: 469 (cat.), 1966: 10 (cat.), 1967: 179 (com.); Sturm, 1990: 202 (com.); Falaschi & Schelesky-Prado, 2024 (cat.).

Material examined. 3 males, 2 females, Cienaguila [correct spelling is Cieneguilla], 3500m. [Santa Catalina] Jujuy, Argentina, II.1970, L. E. Peña col. (specimens pinned, one male and one female with terminalias in microvials) [MZUSP]; 1 male, R^{ep}-[República] ARGENTINA, Prov. [Provincia] Buenos Aires, 18.xi.1905, C. Bruch (specimen pinned) [MZUSP]; 3 females, Pelotas - RS. [Brazil], 20.10.1963 [20.x.1963], C. M. Biezanko col. (specimens pinned) [MZUSP]; 2 females, Pelotas – RS. [Brazil], 23.10.1963 [23.x.1963], C. M. Biezanko col. (specimens pinned) [MZUSP]; 1 male, 1 female (mating), Argentina, Ciudad de Buenos Aires, Lago Lugano, -34.68113, -58.44516, Mar 5, 2022, “RAP” [107980312-iNaturalist]; 1 male, 1 female (mating), Argentina, Ciudad de Buenos Aires, Lago Lugano, -34.68113, -58.44516, Oct 31, 2021, “RAP” [100346817-iNaturalist]; 1 male, Argentina, Ciudad de Buenos Aires, Lago Lugano, -34.68113, -58.44516, Nov 2, 2020, “RAP” [65597702-iNaturalist]; 1 male, Argentina, Ciudad de Buenos Aires, Lago Lugano, -34.68113, -58.44516, Nov 12, 2020, “RAP” [64790441-iNaturalist]; 1 male, Argentina, Ciudad de Buenos Aires, Monte Castro, -34.61699, -58.50533, Oct 24, 2020, Braulio Menendez [150947914-iNaturalist]; 1 male, Argentina, Ciudad de Buenos Aires, C1417, -34.61758, -58.5171, Nov 6, 2021,

Laura Veronica Bianchi [100452208-iNaturalist]; 1 male, Argentina, Ciudad de Buenos Aires, Reserva Ecológica Costanera Sur, -34.6027, -58.35969, Oct 27, 2021, Javier Chiavone [99697298-iNaturalist]; 1 male, Argentina, Ciudad de Buenos Aires, -34.58153, -58.44435, Oct 25, 2021, Leonel Roget [99397293-iNaturalist]; 1 male, Argentina, Buenos Aires, San Isidro, Ruta Provincial 195 16001-16099, -34.46884, -58.50844, Oct 20, 2023, Lucila Trussi [188309697-iNaturalist]; 1 male, Argentina, Buenos Aires, Quilmes, -34.71666, -58.25924, Nov 14, 2022, “ngizmo” [142065005-iNaturalist]; 1 male, Argentina, Buenos Aires, La Plata, -34.90553, -57.93268, Nov 6, 2022, Martín Arregui [141330774-iNaturalist]; 1 male, Argentina, Buenos Aires, La Matanza, Ramos Mejía, -34.65005, -58.57255, Oct 16, 2022, “Federico” [139035304-iNaturalist]; 1 male, Argentina, Buenos Aires, Mar Chiquita, -37.74445, -57.42227, Nov 3, 2018, Luciano Peralta [106510894-iNaturalist]; 1 male, Argentina, Buenos Aires, Pilar, -34.39878, -58.91041, Nov 5, 2021, “Federico” [100356333-iNaturalist]; 1 male, Argentina, Buenos Aires, Vicente López, Unnamed Road, -34.52744, -58.4596, Oct 25, 2021, Sebastián Fornés [99401639-iNaturalist]; 1 male, Argentina, Buenos Aires, Mar Chiquita, -37.74147, -57.42677, Apr 3, 2021, Roberto Guller [73540595-iNaturalist]; 1 male, Argentina, Buenos Aires, Lobería, -38.41563, -58.73038, Apr 3, 2021, Ricardo Ernesto Doumecq Milieu [72821413-iNaturalist]; 1 male, Argentina, Buenos Aires, Florencio Varela/Quilmes, -34.73456, -58.27511, March 2021, Gabriel Albelda [70885400-iNaturalist]; 1 male, Argentina, Buenos Aires, General Villegas, -35.04223, -63.00986, Oct 29, 2020, Verónica André [63799512-iNaturalist]; 4 males, 2 females [approximately], Argentina, Buenos Aires, Chascomús, -35.62618, -57.98866, Nov 11, 2010, Eric Lopresti [52660666-iNaturalist]; 1 male, Argentina, Buenos Aires, Chascomús, -35.53905, -58.14337, Nov 12, 2016, Gerónimo Martín Alonso [5730555-iNaturalist]; 1 male, 1 female (mating), Argentina, Córdoba, Oncativo, -31.91343, -63.68206, Mar 9, 2022, Gonzalo Trucco [108272414-iNaturalist]; 1 male, 1 female (mating), Argentina, Córdoba, Marcos Juárez, -32.68325, -62.08858, October 2021, José Luis Barberán [98599171-iNaturalist]; 1 male, Argentina, Córdoba, General San Martín, Villa Nueva, -32.43563, -63.24809, Oct 9, 2021, “Federico” [97710856-iNaturalist]; 1 male, Argentina, Córdoba, Marcos Juárez, -32.65073, -62.18606, October 2020, José Luis Barberán [63820877-iNaturalist]; 1 male, Argentina, Córdoba, Marcos Juárez, -32.75348, -62.04845, October 2019, José Luis Barberán [35134160-iNaturalist]; 1 male, 1 female (mating), Argentina, Córdoba, Marcos Juárez, -32.78556, -62.11359, January 2018, José Luis Barberán [9349900-iNaturalist]; 1 female, Argentina, Río Negro, San Antonio, San Antonio Oeste, -40.72897, -64.94407, Nov 4, 2022, “diapontiamc” [141086065-iNaturalist]; 1 male, Argentina, Santa Fe, La Capital, Santa Fe de la Vera Cruz, -31.63668, -60.67365, Mar 6, 2021, Eduardo Luis Beltrocco [239553931-iNaturalist]; 1 male, Argentina, Santa Fe, La Capital, Santa Fe de la Vera Cruz, -31.63668, -60.67365, Mar 6, 2021, Eduardo Luis Beltrocco [239553919-iNaturalist]; 1 male, Argentina, Santa Fe, San Jerónimo, Coronda, S2240, -31.97903, -60.91617, Oct 28, 2022, Antonela Boggian [140924647-iNaturalist]; 1 male, 1 female (mating), Argentina, Santa Fe, San Jerónimo, Coronda, -31.97777, -60.91575, Oct 31, 2022, Romina Flury [140723190-iNaturalist]; 1 male, Argentina, Santa Fe, La Capital, Santo Tomé, Uruguay 3075, S3016CYL, -31.68024, -60.77975, Oct 18, 2022, Antonela Boggian [140186444-iNaturalist]; 1 male, Argentina, Santa Fe, San Jerónimo, Coronda, -31.97863, -60.91597, Oct 27, 2022, Laura Gallione [140185940-iNaturalist]; 1 male, Argentina, La Pampa, Utracán, General Acha, -37.36879, -64.59987, Apr 29, 2022, Daniel Oscar Molina

[113607167-iNaturalist]; 1 male, Argentina, La Pampa, Utracán, General Acha, -37.36879, -64.59987, Apr 30, 2022, Daniel Oscar Molina [114721336-iNaturalist]; 1 male, Argentina, La Pampa, Utracán, General Acha, -37.36879, -64.59987, Apr 30, 2022, Daniel Oscar Molina [115241958-iNaturalist]; 1 male, 1 female (mating), Brazil, Rio Grande do Sul, Esmeralda, R. P D V Bôas, 297, 95380-000, -28.05357, -51.19633, Mar 9, 2019, Edson Luis Fabro Gasperin [24190684-iNaturalist]; 2 males, Brazil, Rio Grande do Sul, Esmeralda, São Sebastião, 95380-000, -27.91942, -51.34277, Oct 22, 2023, Edson Luis Fabro Gasperin [188832963-iNaturalist]; 1 male, 1 female (mating), Brazil, Rio Grande do Sul, Esmeralda, 95380-000, -28.05472, -51.19528, Jul 23, 2019, Edson Luis Fabro Gasperin [29386778-iNaturalist].

Diagnosis. Dorsum orange, with anterior dark area in males; fore tibiae with a single set with four to eight spines; gonostyli shortened.

Redescription. Male (Fig. 7A-B). **Head.** Black. Compound eye holoptic, divided into a large, brownish red dorsal region with long brown ommatrichia; ventral region smaller, darker. Ocellar tubercle developed, with setose posteriorly. Head ventrally covered with relatively long brown setae, extending to the rostrum (both ventrally and dorsally). Antennae brown to black except for the pale pedicel; with nine flagellomeres. Rostrum short, much shorter than the length of the eyes. Mouthparts dark brown; longer than the eyes when extended. Maxillary palps at least 4-segmented (hard to see in dry specimens); apical segment short, less than two times longer than wide; visible segments with setae. Labium with relatively elongated setae. **Thorax.** Dorsum mainly shining orange, except for the anterior brown to black area on the mesonotum, sometimes extending the full length of mesonotum. Scutellum and pleura dark brown to black. Anterior comb with 16 strong spines, divided in the middle; posterior comb with smaller spines. Dorsum with long yellowish to brown setae. Scutellum with long brown setae. **Legs.** Brown to black (see comments). Fore tibiae with a single set with four to six spines in a oblique row; apical circlet of spines with seven spines; the apical spur darker, thicker and slightly longer than the spines. Mid tibiae with medial spine-like setae. Hind femora clavate, hind tibiae slightly clavate and hind basitarsi slender. **Wing.** Membrane milky hyaline to brown fumose, microtrichia present. Stigma brown, darker than membrane. Anterior veins light to dark brown, always darker than the membrane; posterior veins pale, concolorous with the membrane, to brownish, almost concolorous with the membrane. C vein with short setae. Wing margin with short brownish setae fringe, except for the ending of anal lobe and alular margin, that are long and pale. Crossvein r-m about four times longer than bRs. Halteres brown. **Abdomen.** Dark brown, covered with long brown setae. **Terminalia** (Fig. 8A-B). Epandrium slightly clefted; setae on the lateral sides elongated. Synsternogonocoxite posterior margin W-shaped. Gonostylus shortened, apically pointed and with a longitudinal notch, covered with setae. Cerci elongated, with long setae. **Female** (Figs. Fig. 7C-D). **Head.** Black. Ocellar tubercle developed. Head with short to elongated setae. Antennae black; with ten flagellomeres. Rostrum short, subequal to the eyes length; the posterior portion of the head subequal to the eyes. **Thorax.** Mainly shining orange, except for the dark brown to black scutellum. Some specimens with an anterior brown to black area on the mesonotum, as in male, and with the pleura brown. Anterior comb with 18 strong spines, medially divided; posterior comb with about 22 smaller spines, some displaced backwards. **Legs.** Coloration as in male (see comments). Arrangement of fore tibial spines as in male, but with four to eight spines. Mid tibiae with

medial spine-like setae. Hind femora clavate, hind tibiae clavate and hind basitarsi slender. **Wing.** Membrane light to dark brown fumose, microtrichia present. Stigma brown. Anterior veins brown, darker than the membrane; posterior veins brownish, slightly darker than the membrane. Venation and other aspects virtually as in male. **Abdomen.** Brownish, with short brown setae. **Terminalia** (Fig 8C-D). Tergite 9 with a shallow cleft on posterior margin; laterally with long setae. Tergite 9 about ten times wider than long. Cerci covered with setae, some of them elongated on the apex; with distinct shape dorsally (apex becoming abruptly thinner and curved); comma shaped laterally. Cerci about two times longer than wide.

Distribution. Argentina (Autonomous City of Buenos Aires, Buenos Aires, Córdoba, Jujuy, La Pampa, Mendoza, Río Negro, Santa Fe, Tucumán), Brazil (Rio Grande do Sul), Uruguay (Montevideo).

Comments. The geographic distribution was expanded to two provinces and for the federal district of Argentina and one state of Brazil (Fig. 9), being the first records with precise localities for the country (see discussion below). Hardy (1967) reported the only records of *D. pectoralis* from Brazil, and they are labeled as “Brasilia, coll., WINTHEM”. As Uruguay was part of Brazil until the first half of the 19th century, these records for the country are somewhat uncertain. However, as there are records from Montevideo in Winthem’s collection (Alexssandro Camargo pers. comm.), it can be assumed that the material reported as “Brasilia” is actually from Brazil, and not Uruguay, since the collector could reference the specific city as he did with the material from Montevideo. In the literature, the species was recorded for the months of January, February, March, September, October, November, and December. Here, the records are expanded to the months of April and July. Both male and female terminalia are described for the first time. Some authors (Lynch Arribáizaga 1881, Hunter 1900, Hardy 1953) suggested that *Dilophus similis* Rondani, 1868 is a junior synonym of *D. pectoralis*. However, according to Hardy (1953), *D. similis* is not recognizable from the original description, and is not considered a synonym of *D. pectoralis* in Hardy’s (1966) catalog. Two species, *Dilophus serenus* (Hardy, 1953) and *Dilophus golbachii* (Hardy, 1953), both known from Argentina, share some similarities with *D. pectoralis*, such as the presence of a single set of medial spines on fore tibiae, male thorax colored with brown to black and orange (except for *D. serenus*), and female dorsum orange (*D. golbachii* female unknown). They could be separated from *D. pectoralis* by the orange dorsum of male with a darker area anteriorly (the dorsum is black with a reddish spot on each side in *D. golbachii* and black in *D. serenus*), the black female tibiae (they are orange in *D. serenus*), and by genital characters, such as the short gonostylus (relatively elongated in the other species). Furthermore, in an iNaturalist observation a specimen was found visiting and feeding on flowers of *Conium maculatum* (Apiales, Apiaceae) from Ciudad de Buenos Aires, Argentina.

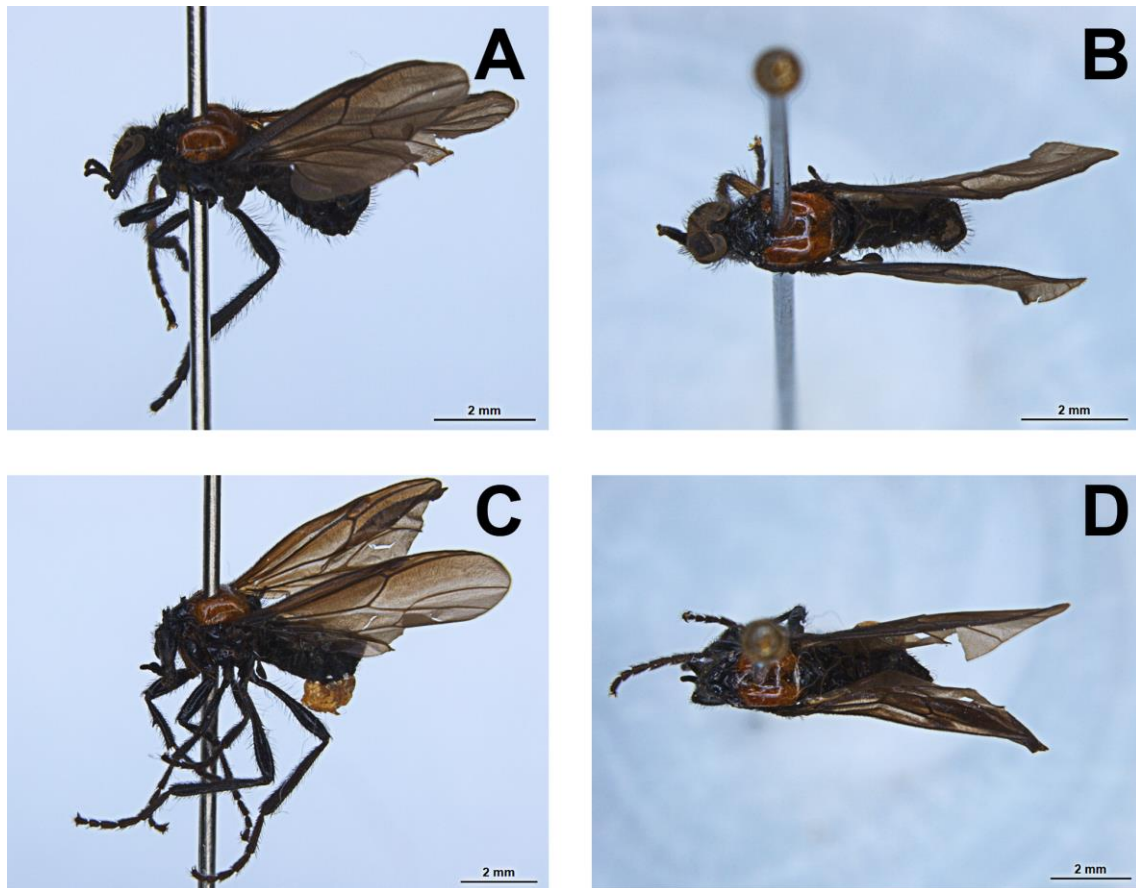


Figure 7. *Dilophus pectoralis*, habitus. **A.** male, lateral view. **B.** male, dorsal view. **C.** female, lateral view. **D.** female, dorsal view.

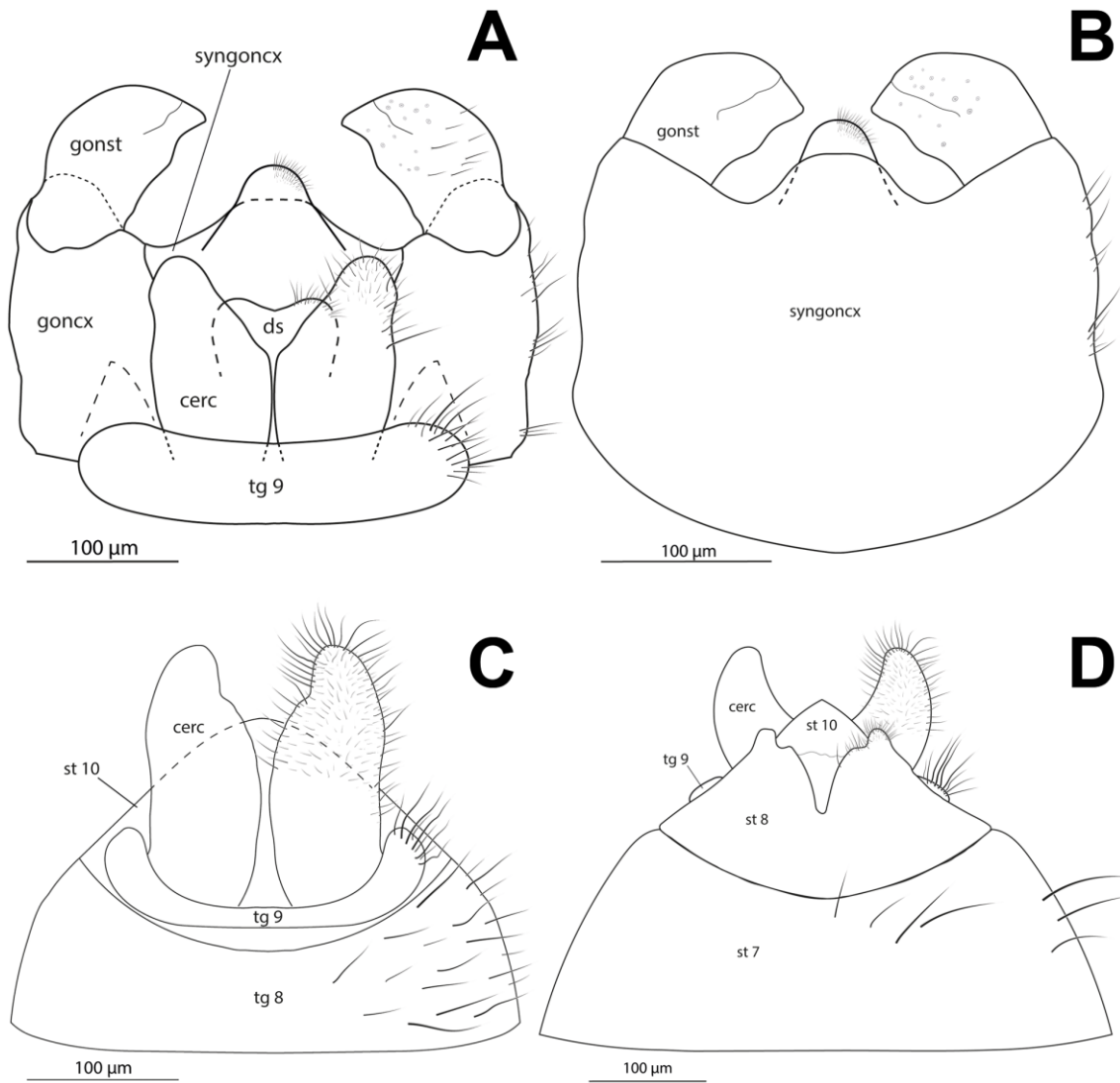


Figure 8. *Dilophus pectoralis*, terminalia. **A.** male, dorsal view. **B.** male, ventral view. **C.** female, dorsal view. **D.** female, ventral view.

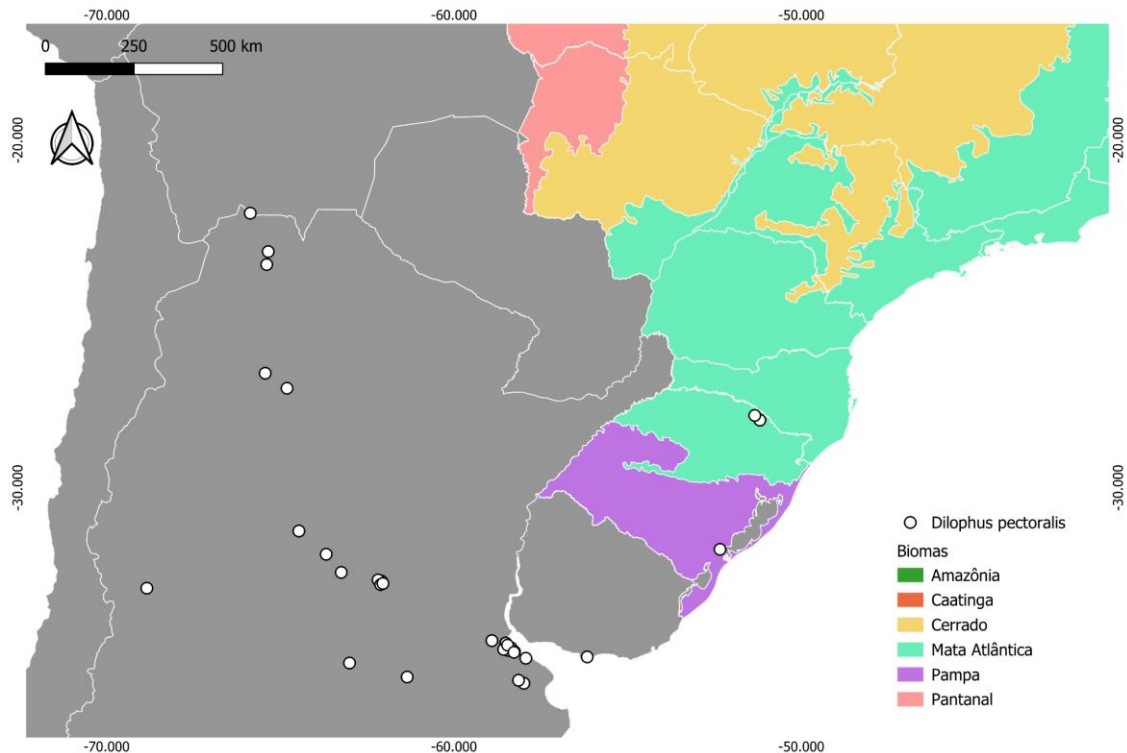


Figure 9. *Dilophus pectoralis*, distribution map.

***Dilophus trisulcatus* Macquart, 1838**

Dilophus trisulcatus Macquart, 1838: 92. Type locality: “Brazil”. References: Wulp, 1881: 146 (com.), Hunter, 1900: 295 (cat.), Kertész, 1902: 154 (cat.), Edwards, 1938: 323 (com.), Hardy, 1953: 373 (redesc.), 1959: 473 (cat.), 1966: 11 (cat.); Falaschi & Schelesky-Prado, 2024 (cat.).

Material examined. 1 male, 1 female, Brasilien, Nova Teutonia, 27°11' B. 52°23' L. [B.=breite, latitude in german, here means S (South); L.=längengrad, longitude in german, here means W (West)], 300 . 500 m, ix.1965, Fritz Plaumann (pinned) [MZUSP]; 2 females, Brasilien, Nova Teutonia, 27°11' B. 52°23' L., 300 . 500 m, x.1968, Fritz Plaumann (pinned) [MZUSP]; 7 males, 3 females, Brasilien, Nova Teutonia, 27°11' B. 52°23' L., 300 . 500 m, x.1971, Fritz Plaumann (pinned) [MZUSP]; 1 female, Brasilien, Nova Teutonia, 27°11' B. 52°23' L., 300 . 500 m, ii.1972, Fritz Plaumann (pinned) [MZUSP]; 1 female, Barueri, São Paulo, Brasil, 25.ii.66, K. Lenko col. (pinned) [MZUSP]; 1 female, BARUERI, S. Paulo, BRASIL, 22.i.1967, K. Lenko leg. (pinned) [MZUSP]; 2 females, BR-S.P.: R. Paraná, PORTO CABRAL, 20-31.iii.1944, Trav. Fo. & Carrera & E. Dente (pinned) [MZUSP]; 1 male, 1 female, Brasil, SP, São Carlos, UFSCar, DHb, -21.983571, -47.878520, 30.iii.2023 (in 80% ethanol, with terminalias in microvial) [MZUSP]; 2 males, ANHEMBÍ-S.P. [Brazil, São Paulo, Anhembi] 4-7.out.956 [4-7.x.1956], Fazenda Barreiro Rico, J.C.Magalhaes + D.S.Dias, M. Kuhlmann + L.Trav.F. (specimens spinned) [MZUSP]; 1 male, (1) Brasil: MS: Bodoquena, Fazenda Califórnia, S20°41'55.9'' W056°52'49.4'', Malaise 6, 06.x.2011, Lamas eq. col., SISBIOTA- CNPQ/FAPESP (2) 21.ix-06.x.2011 [accurate date] (specimen pinned)

[MZUSP]; 1 male, Brasil: MS: Bodoquena, Faz. Califórnia, S20°41'55.9'' W56°52'99.4'' [correct: W56°52'49.4''], Malaise 06, 21.ix-06.x.2011, Lamas, Nihei & eq. col., SISBIOTA- CNPQ/FAPESP (specimen pinned) [MZUSP]; 1 male, BRASIL, MS, Serra da Bodoquena, Fazenda Califórnia, S20°42'06.4'' W056°52'41.2'', Luz [light], 31.iii.2012, Lamas, Nihei eq. col., SISBIOTA- CNPQ/FAPESP (specimen pinned) [MZUSP]; 1 female, Brasil: MS: Bodoquena, Fazenda Califórnia – Topo, S20°41'55.9'' W56°52'49.4'', Malaise 06, 06.viii-06.ix.2012, Lamas, Nihei & eq. cols., SISBIOTA- CNPQ/FAPESP (specimen pinned) [MZUSP]; 1 female, Brasil: MS: Bodoquena, Fazenda Califórnia – Topo, S20°41'55.9'' W56°52'49.4'', Malaise 06, 06-21.ix.2012, Lamas, Nihei & eq. cols., SISBIOTA- CNPQ/FAPESP (specimen pinned) [MZUSP]; 1 female, Brasil: MS: Bodoquena, Fazenda Califórnia – Ciliar, S20°41'49.9'' W56°52'54'', Malaise 04, 06-21.x.2012, Lamas, Nihei & eq. cols., SISBIOTA- CNPQ/FAPESP (specimen pinned) [MZUSP]; 1 female, Brasil: MS: Bodoquena, Fazenda Califórnia – Ciliar, S20°41'49.9'' W56°52'54'', Malaise 04, 21.iii-06.iv.2012, Lamas, Nihei & eq. cols., SISBIOTA- CNPQ/FAPESP (specimen pinned) [MZUSP]; 1 female, Brasil: MS: Bodoquena, Fazenda Califórnia – Ciliar, S20°41'49.9'' W56°52'54'', Malaise 04, 21.vi-06.vii.2012, Lamas, Nihei & eq. cols., SISBIOTA- CNPQ/FAPESP (specimen pinned) [MZUSP]; 1 female, Brasil: MS: Bodoquena, Fazenda Califórnia – Transição, S20°41'53.5'' W56°52'55.7'', Malaise 05, 21.ii-06.iii.2012, Lamas, Nihei & eq. cols., SISBIOTA- CNPQ/FAPESP (specimen pinned) [MZUSP]; 1 female, Brasil: MS: Bodoquena, Fazenda Califórnia – Transição, S20°41'53.5'' W56°52'55.7'', Malaise 05, 21.vi-06.vii.2012, Lamas, Nihei & eq. cols., SISBIOTA- CNPQ/FAPESP (specimen pinned) [MZUSP]; 1 female, BRASIL, RS, Gramado, 29°23'21.5''S 50°52'59.4''W, 10.I.2024, D. C. Schelesky-Prado [MZUSP].

Diagnosis. Mesonotum with three longitudinal furrows; male gonostylus with long setae basally.

Redescription. Male (Fig. 10A–B). **Head.** Dark brown to Black. Compound eye holoptic, divided into a large, brownish red dorsal region with short black ommatrichia; ventral region smaller, darker. Three ocelli on a developed tubercle; scarce setose posterior to ocellar tubercle. Head ventrally covered with relatively long dark setae, a few of them extend to the rostrum (both ventrally and dorsally). Antennae dark brown except for the pale pedicel; with 9 flagellomeres. Rostrum not elongated, shorter than the length of the compound eyes. Mouthparts dark brown; as long as the length of the compound eyes when extended. Maxillary palps at least 4-segmented; apical segment short, less than two times longer than wide; visible segments with setae. Labium with relatively elongated setae. **Thorax.** Mainly black, except for the brown-reddish humeral ridges. Anterior comb with 14 spines; posterior comb with about 26–28 smaller spines, three or four on each side much displaced backwards. Mesonotum with three distinct longitudinal furrows, a median one and two lateral. Dorsum with some long black setae. Scutellum with long black setae. **Legs.** Dark brown, femora reddish brown. Fore tibiae with a single set with four to five spines in an oblique row; the apical spur darker, and slightly thicker and longer than the spines. Mid tibiae with strong spine-like setae. Hind femora clavate; hind tibia and tarsi slender. **Wing.** Membrane light brownish basally and hyaline apically, microtrichia present. Stigma dark brown. Anterior veins dark brown, much darker than the membrane; posterior veins pale, concolorous or slightly darker than the membrane. C vein with short setae, reaching slightly over one third the distance between R₄₊₅ and M₁.

Humeral vein absent. Sc apically incomplete. R1 apically incomplete. Crossvein r-m about three times longer than bRs. CuP ends well before the margin. Halteres brown. **Abdomen.** Dark brown to black, covered with dark setae. **Terminalia** (Fig. 11A–B). Epandrium longer than wide, slightly clefted on posterior margin, setae on the lateral sides elongated. Synsternogonocoxite with a deep narrow median cleft. Gonostylus basally wide and becoming thinner towards the apex; apex pointed; basally with long setae, sometimes being longer than gonostylus length, rest of surface with sparse, short setae. Cerci with elongated setae. **Female** (Fig. 10B–C). **Head.** Dark brown to Black. Ocellar tubercle developed. Antennae black; with ten flagellomeres. Rostrum short, subequal to the eyes length; the posterior portion of the head subequal to the eyes. **Thorax.** Dark brown to black. Median furrow on the mesonotum distinct. **Legs.** Dark brown. Fore tibiae with a single set with five to six spines in a transverse row; Hind femora clavate, hind tibiae clavate and hind basitarsi slender. **Wing.** Membrane dark brown fumose, microtrichia present. Stigma brown. Anterior veins brown, darker than the membrane; posterior veins brownish, slightly darker than the membrane. Venation and other aspects virtually as in male. **Abdomen.** Brownish, with short brown setae. **Terminalia** (Fig. 11C–D). Tergite 9 with a deep cleft (about two thirds of the segment) on posterior margin, anterior margin straight; laterally with long setae. Tergite 9 about two and a half times wider than long. Cerci covered with setae; with distinct shape dorsally (apex becoming abruptly thinner and curved); comma shaped laterally. Cerci about two times longer than wide. Sternite 8 cleft deep, lobes with a broad apex, bilobed, with long setae. Sternite 10 square shaped.

Distribution. Argentina (Córdoba, Misiones, Salta, Tucumán), Brazil (Mato Grosso do Sul, Rio Grande do Sul, Santa Catarina, São Paulo).

Comments. The geographic distribution was expanded to three more states of Brazil (Fig. 12). The records for Mato Grosso do Sul were possible due to material from SISBIOTA-BRASIL, a research program of the Brazilian government that aimed to document plants and animals in understudied or endangered areas and biomes in the country (Lamas *et al.* 2023). In the literature, the species was recorded for the months of January, February, March, May, September, October, November, and December. The literature records of September and October are uncertain, because the labels include both months (Sept.–Oct. 1929) or October and November (Oct.–Nov. 1948). Here, the records are expanded to the months of June/July, possible April and August. Since the label includes both June and July (21.vi–06.vii.2012), it is not possible to know the exact month of the record. For the same reason, the records for April and August are uncertain, because the labels include March and April (21.iii-06.iv.2012) and August and September (06.viii–06.ix.2012). Additionally, specific records for the months of September and October are provided. The female terminalia is described for the first time. According to Hardy (1953), this species is related with *Dilophus melanarius* Wulp, 1881, known from Mexico and Central America, however, he did not examine *D. melanarius* specimens, which makes the comparison between the species difficult.

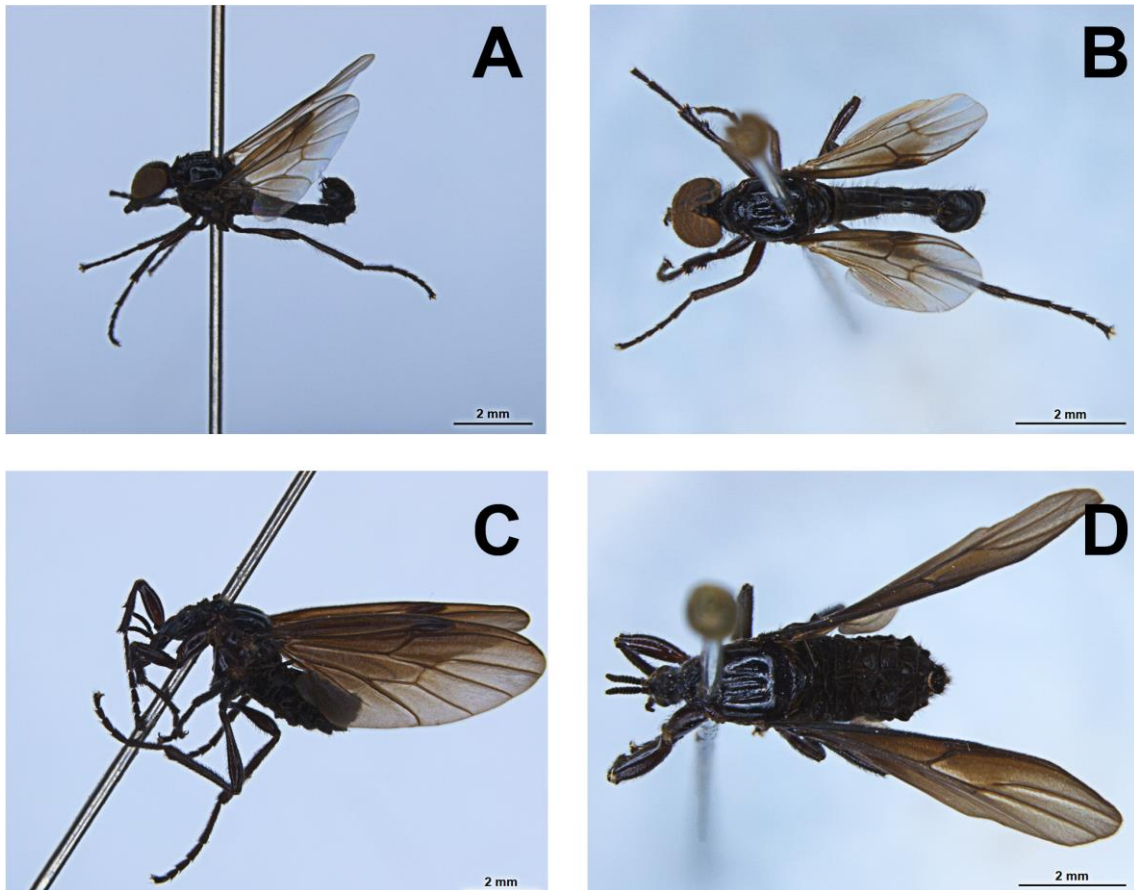


Figure 10. *Dilophus trisulcatus*, habitus. **A.** male, lateral view. **B.** male, dorsal view. **C.** female, lateral view. **D.** female, dorsal view.

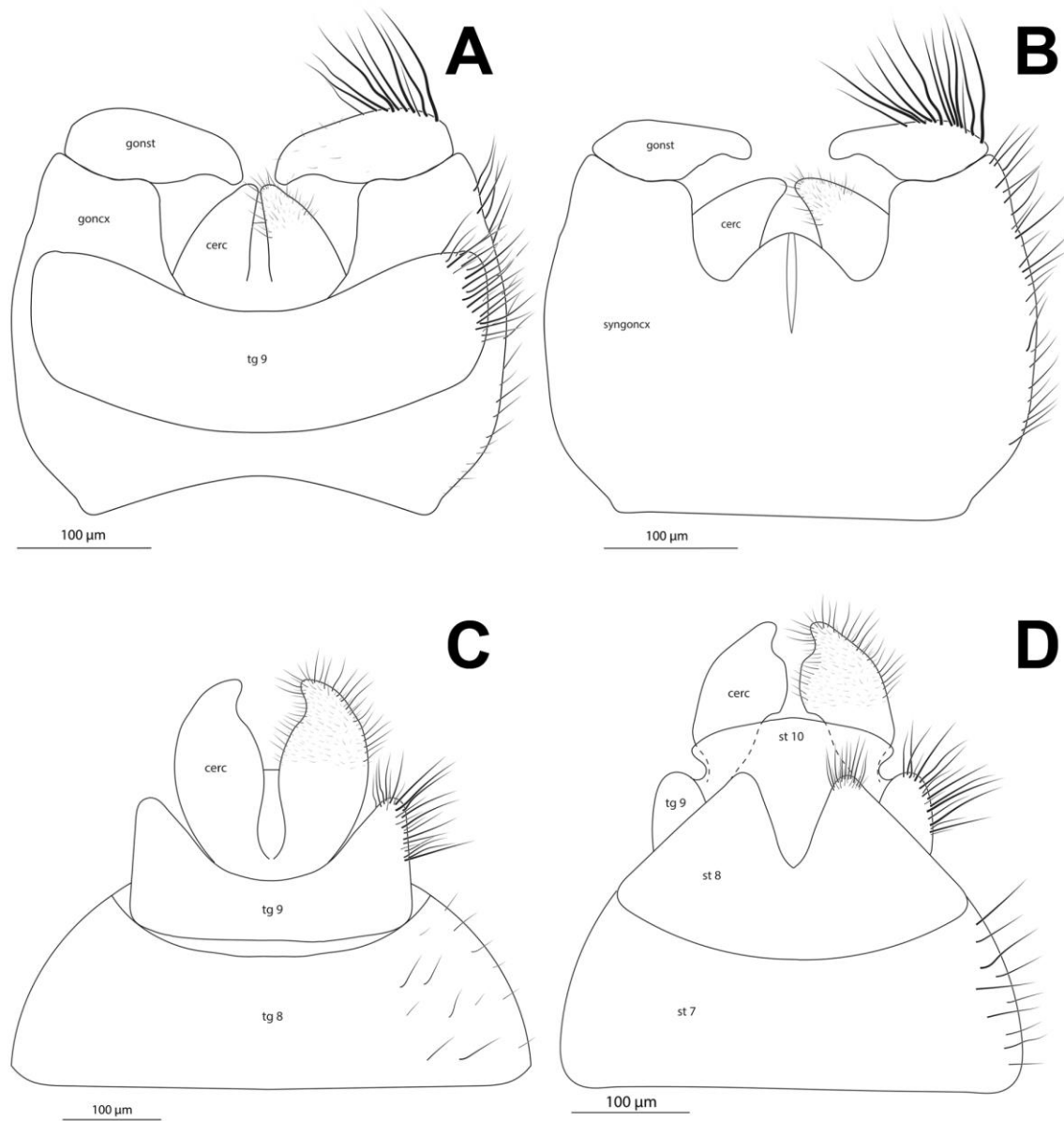


Figure 11. *Dilophus trisulcatus*, terminalia. **A.** male, dorsal view. **B.** male, ventral view. **C.** female, dorsal view. **D.** female, ventral view.

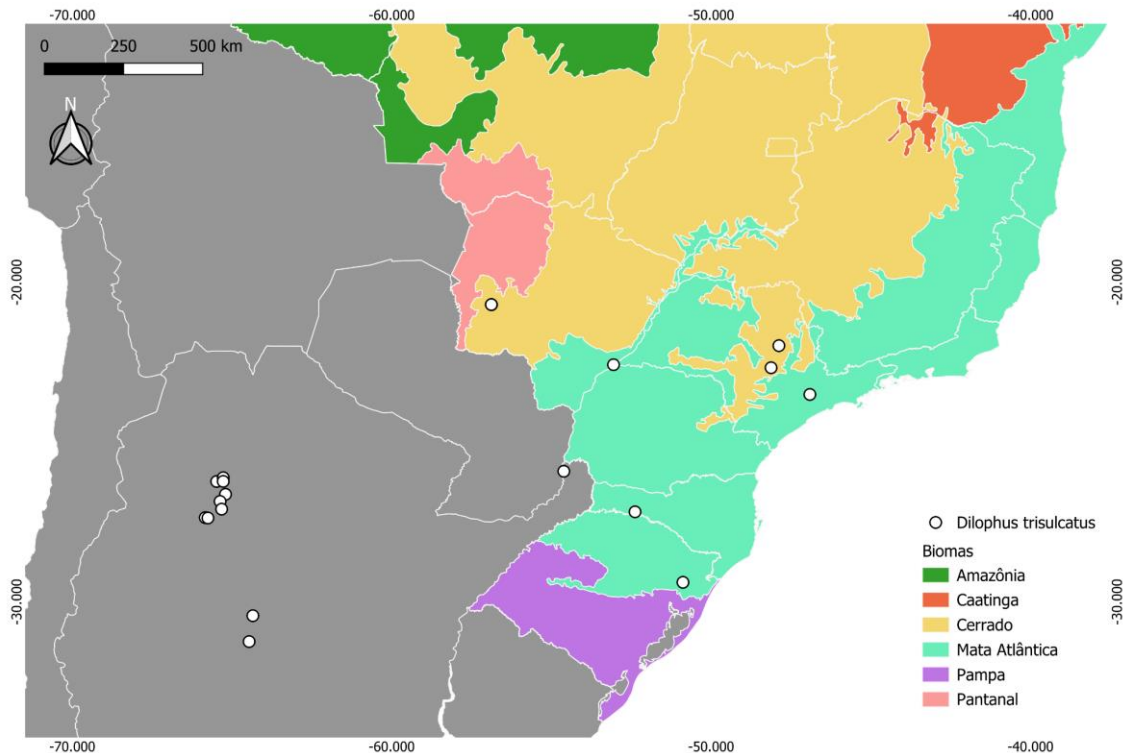


Figure 12. *Dilophus trisulcatus*, distribution map.

Dilophus sp. nov. A

Type material. Holotype. Male, BRAZIL, Paraná, Ponta Grossa, Distrito de Itaiacoca, 25°07'05.4"S 49°56'27.7"W, Malaise B, 23.viii-27.ix.2019, Almeida, M.C.; Araujo, E.; Santos, M.H. cols (in 80% ethanol with terminalia in microvial) [MZUSP]. **Paratypes.** Three males and three females, same data as holotype (one female in 80% ethanol with terminalia in microvial, other specimens in 80% ethanol) [MZUSP]. One female, same data as holotype, except 25.viii–24.ix.2020 (in 80% ethanol) [MZUSP].

Additional material examined. One female, BRAZIL, Paraná, Carambeí, Alto Carambeí, 24°55'30.0"S 50°4'51.6"W, Malaise, 24.ii.2021–25.iii.2021, Amaral, E. M. (in 80% ethanol) [MZUSP].

Diagnosis. Male lower set oblique, female set almost straight; male gonostylus broad basally, but gradually narrowing towards the curved apex.

Description. Male (Fig. 13A-B). **Head** (Figs. X–X). Mainly dark brown to black. Compound eye holoptic, divided into a large, brownish red dorsal region with minute sparse ommatrichia; ventral region smaller, darker. Ocellar tubercle slightly developed, with setose posteriorly. Head ventrally covered with long dark setae that extend to the rostrum. Antennae dark brown except for the yellowish brown scape, pedicel and, basally, first flagellomere; with 10 or 11 flagellomeres. Rostrum short, much shorter than the length of the eyes. Mouthparts yellow to brown. Maxillary palps 5-segmented; first (basal) segment minute, second segment slightly slender, third and fourth segments slightly swollen, fifth (apical) segment about two times longer than wide; first two

segments yellow, remaining segments darker; 2-5 segments with setae. Labium yellow with relatively long setae. **Thorax.** Dark brown to black. Anterior comb with about 14 strong spines, medially divided; posterior comb with about 15 smaller spines. Dorsum with brown setae. Scutellum with long brown setae. **Legs.** Brown to dark brown. Fore tibiae with two sets of medial spines, upper set with two spines, lower set with four to five spines (four apparently the typical number for males) in an oblique row with the spines more or less grouped (one specimen with a spine between the upper set and the other four of the lower set); apical circlet of spines with nine spines; the apical spur thicker, but not longer than the spines. Mid tibiae with medial spine-like setae. Hind femora and tibiae clavate, hind basitarsi slender. **Wing.** Membrane with brownish fumose, microtrichia present. Stigma darker than membrane. Anterior veins brown, darker than the membrane; posterior veins lighter, but slightly darker than the membrane. C vein with short setae. Crossvein r-m over four times longer than bRs. Halteres brown. **Abdomen.** Brown, covered with long brown setae. **Terminalia** (Fig. 14A-B). Epandrium about one and a half times wider than long, with long setae laterally; posterior margin straight. Synsternogonocoxite posterior margin W-shaped. Gonostylus broad basally, but gradually narrowing towards the curved apex; basally and medially with long setae. Cerci dark, covered with setae. **Female** (Fig. 13C-D). **Head.** Dark brown. Ocellar tubercle only slightly developed. Antennae brownish, with 10 flagellomeres. Rostrum shorter than the length of the eyes; the posterior portion of the head slightly shorter than the eyes. **Thorax.** Brown. Anterior comb with 10 strong spines, medially divided; posterior comb with about 18 smaller spines. **Legs.** Coloration as in male. Arrangement of fore tibial spines different: upper set with two spines, lower set with four to five spines (five apparently the typical number for females) arranged in a transverse row. Mid tibiae with medial and apical spine-like setae. Hind femora clavate, hind tibiae slightly clavate and hind basitarsi slender. **Wing.** Membrane brown fumose, microtrichia present. Stigma darker than the membrane. Anterior veins brown, slightly darker than the membrane; posterior veins slightly lighter, but darker than the membrane. Venation and other aspects virtually as in male. **Abdomen.** Brownish, with brownish setae. **Terminalia** (Fig. 14C-D). Tergite 9 with a relatively deep cleft (more than half of the segment) on posterior margin, anterior margin apparently straight; laterally with long setae. Tergite 9 more than six times wider than long. Cerci covered with setae; apically pointed; about two times longer than wide; comma shaped laterally. Sternite 8 cleft deep, lobes with irregular shaped apex, with long setae. Sternite 10 somewhat square shaped.

Distribution. Brazil (Paraná).

Comments. The species was recorded for the months of February–March, May–June and August–September. Since each label includes two months (24.ii.2021–25.iii.2021, 23.v.2017–12.vii.2017 and 25.viii–24.ix.2020), it is not possible to know the exact month of each record. This species resembles *D. fulvimacula* (Walker) from Venezuela, but is distinguished by the slightly developed ocellar tubercle of female (strongly developed in *D. fulvimacula*).

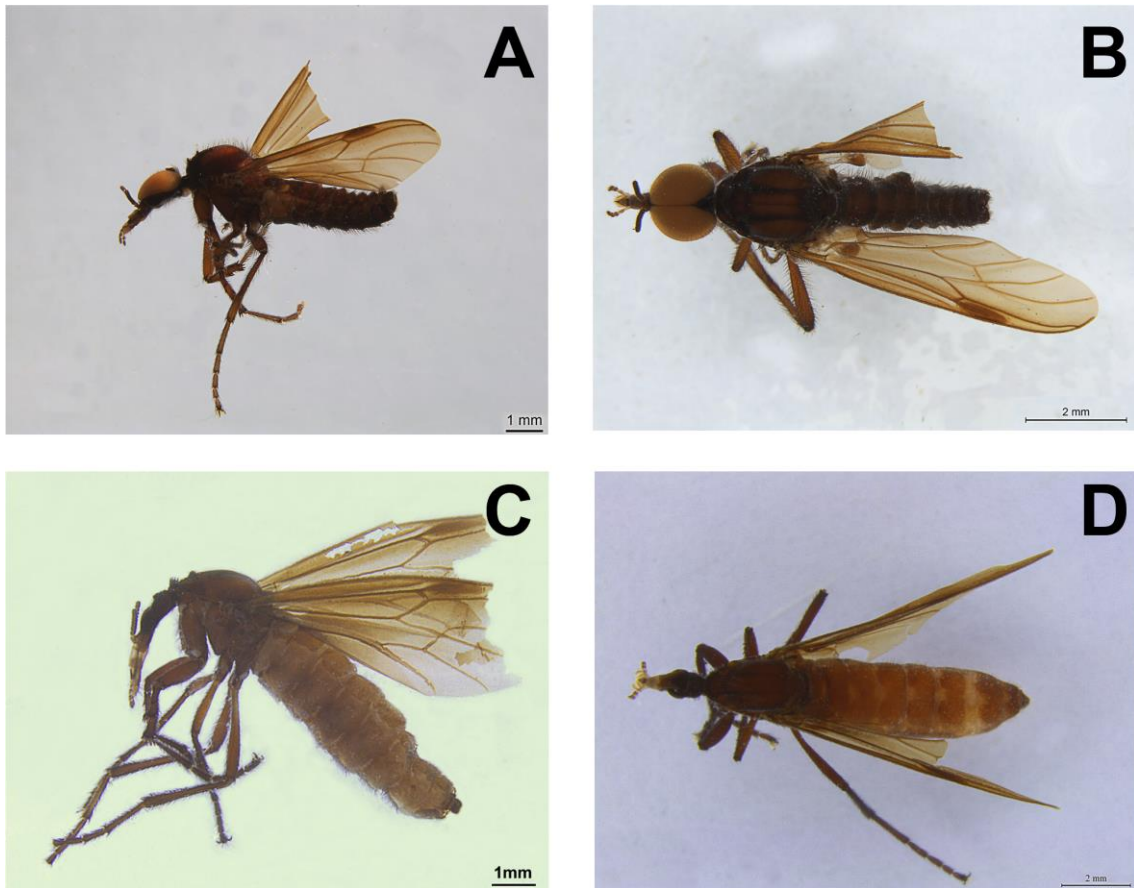


Figure 13. *Dilophus* sp. nov. **A.** habitus. **A.** male, lateral view. **B.** male, dorsal view. **C.** female, lateral view. **D.** female, dorsal view.

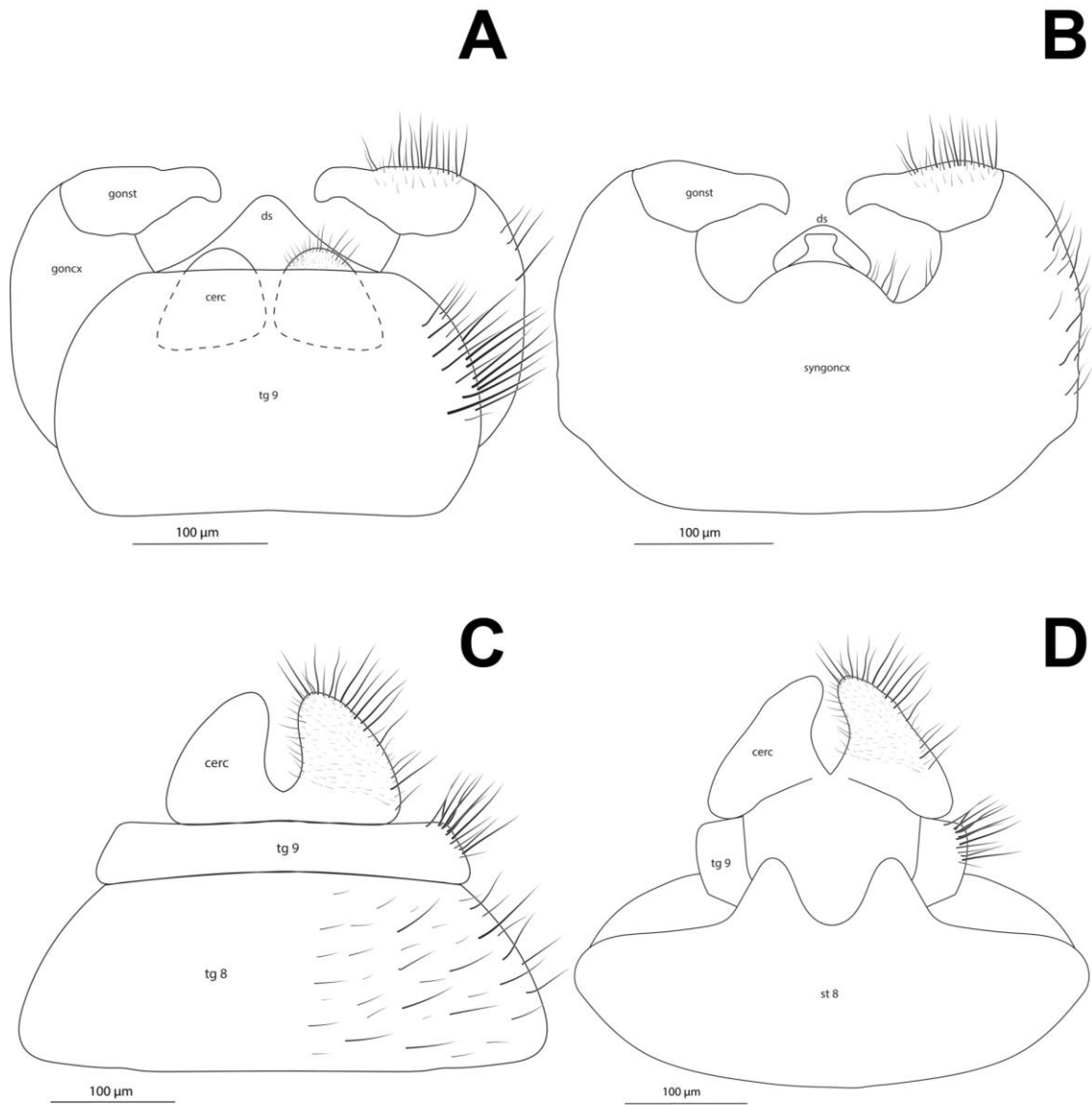


Figure 14. *Dilophus* sp. nov. **A**, terminalia. **A**. male, dorsal view. **B**. male, ventral view. **C**. female, dorsal view. **D**. female, ventral view.

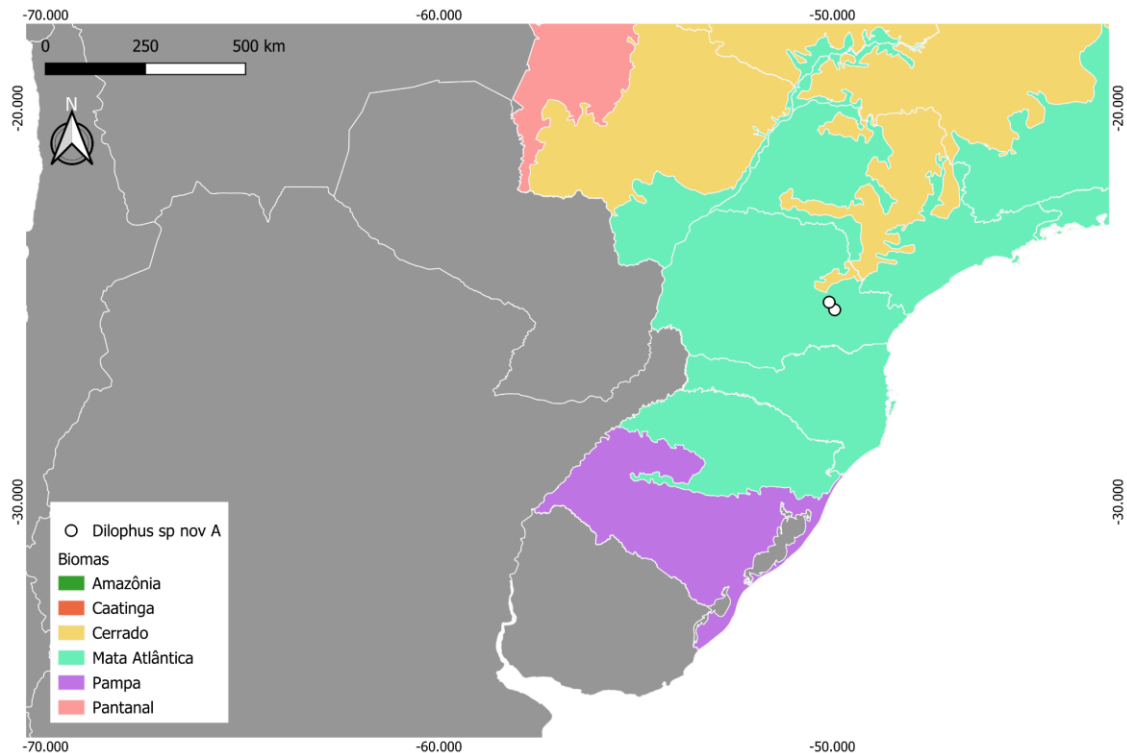


Figure 15. *Dilophus sp. nov. A*, distribution map.

Dilophus sp. nov. B

Type material. Holotype. Male, BRAZIL, GO, Mineiros, Parque Nacional de Emas, Malaise - Parcela 7 Mata, -17.907, -52.98416666666667, 23.v.2017–12.vii.2017, Cols. Oliveira & Lopes (in 80% ethanol with terminalia in microvial) [MZUSP]. **Paratypes.** 1 male, 4 females, same data as holotype (one female in 80% ethanol with terminalia in microvial, other specimens in 80% ethanol) [MZUSP]; 1 female, BRAZIL, GO, Mineiros, Parque Nacional de Emas, Malaise–Parcela 2 Mata, -17.9022253779, -52.9964093068, 23.v.2016–30.vii.2016, Cols. Oliveira, Lopes & Fava (in 80% ethanol) [ZUFG].

Diagnosis. Male dorsum dark brown to black, female dorsum yellow with two brown stripes; male gonostylus almost subequally wide through the length, except for the wider blunt apex.

Description. Male (Fig. 16A–B). **Head.** Dark brown to black, except for the yellowish antennae and mouthparts. Compound eye holoptic, divided into a large, brownish red dorsal region with very short and sparse black ommatrichia; ventral region smaller, darker. Ocellar tubercle developed, with few short setose posteriorly. Head ventrally with few setae. Antennae yellowish, last flagellomeres slightly darker; with nine or 10 flagellomeres. Rostrum short, much shorter than the length of the eyes. Mouthparts yellowish. Maxillary palps 5-segmented; first (basal) segment minute, second segment slightly slender, third and fourth segments slightly swollen, fifth (apical) segment short, less than two times longer than wide; 2–5 segments with setae. Labium with relatively long setae. **Thorax.** Mainly dark brown to black, except for the yellowish humeral ridges

and lighter scutellum. Anterior comb with 10 strong spines, undivided; posterior comb with about 14 smaller spines. Dorsum with long brown setae. Scutellum with medium sized brown setae. **Legs.** Mainly yellow-brownish, fore tibiae and all tarsi apically darker. Fore tibiae with two sets of medial spines, upper set with two spines, lower set with four to five spines (four apparently the typical number): two dorsolateral externally, two dorsolateral internally more apically, and a single spine after the upper set and before the other four of the lower set may be present; apical circlet of spines with apparently eight spines; the apical spur darker and thicker, but not longer than the spines. Mid tibiae with apical spine-like setae. Hind femora clavate, hind tibiae and hind basitarsi slender. **Wing.** Membrane with slightly brownish fumose, microtrichia present. Stigma slightly darker than membrane. Anterior veins brown, darker than the membrane; posterior veins lighter, but slightly darker than the membrane. C vein with short setae. Wing margin with short pile setae fringe, except for the ending of anal lobe and alular margin, that are long. Crossvein r-m about three and a half times longer than bRs. Halteres brown. **Abdomen.** Brown, covered with brownish setae. **Terminalia** (Fig. 17A–B). Epandrium more than two times wider than long, with long setae on posterior margin; with a cleft. Synsternogonocoxite posterior margin W-shaped. Gonostylus almost subequally wide through the length, except for the wider blunt apex; basally with long setae. Cerci large, covered with setae. **Female** (Fig. 16C–D). **Head.** Dark brown, except for the yellowish antennae. Ocellar tubercle only slightly developed. Antennae yellow, with apparently nine flagellomeres. Rostrum shorter than the length of the eyes; the posterior portion of the head slightly longer than the eyes. **Thorax.** Mainly yellow, except for the two brown stripes extending from the anterior comb to approximately halfway down the dorsum, and the brown stripe on the pleura. Anterior comb with 10–11 strong spines, medially divided; posterior comb with 10–11 smaller spines, one displaced backwards. **Legs.** Coloration as in male. Arrangement of fore tibial spines different: upper set with two spines, lower set with four to five spines (four apparently the typical number) arranged in parallel two subgroups of two to three spines each. Mid tibiae with medial and apical spine-like setae. Hind femora clavate, hind tibiae and hind basitarsi slender. **Wing.** Membrane brown fumose, microtrichia present. Stigma light brown, almost concolorous with the membrane. Anterior veins brown, slightly darker than the membrane; posterior veins slightly lighter, but darker than the membrane. Venation and other aspects virtually as in male. **Abdomen.** Light brownish yellow, with brownish setae. **Terminalia** (Fig. 17C–D). Tergite 9 with a relatively deep cleft (half of the segment) on posterior margin, anterior margin apparently straight; laterally with long setae. Tergite 9 about three times wider than long. Cerci covered with setae; apically pointed; about two times longer than wide; comma shaped laterally. Sternite 8 cleft short, lobes with irregular shaped apex, with long setae. Sternite 10 broad and triangular.

Distribution. Brazil (Goiás).

Comments. The species was recorded for the months of May–June–July. Since the labels cover the period between the three months (23.v.2017–12.vii.2017 and 23.v.2016–30.vii.2016), it is not possible to know the exact month(s) of the records. This species resembles *D. fumosus* Coquillett (only male known) from Nicaragua and *D. variceps* (Hardy) (only female known) from Panama, but is distinguished by the short rostrum, much shorter than the length of the eyes (longer than the eyes in *D. fumosus*) and by the light brownish yellow abdomen of female (brownish black in *D. variceps*).



Figure 16. *Dilophus sp. nov.* **B.** habitus. **A.** male, lateral view. **B.** male, dorsal view. **C.** female, lateral view. **D.** female, dorsal view.

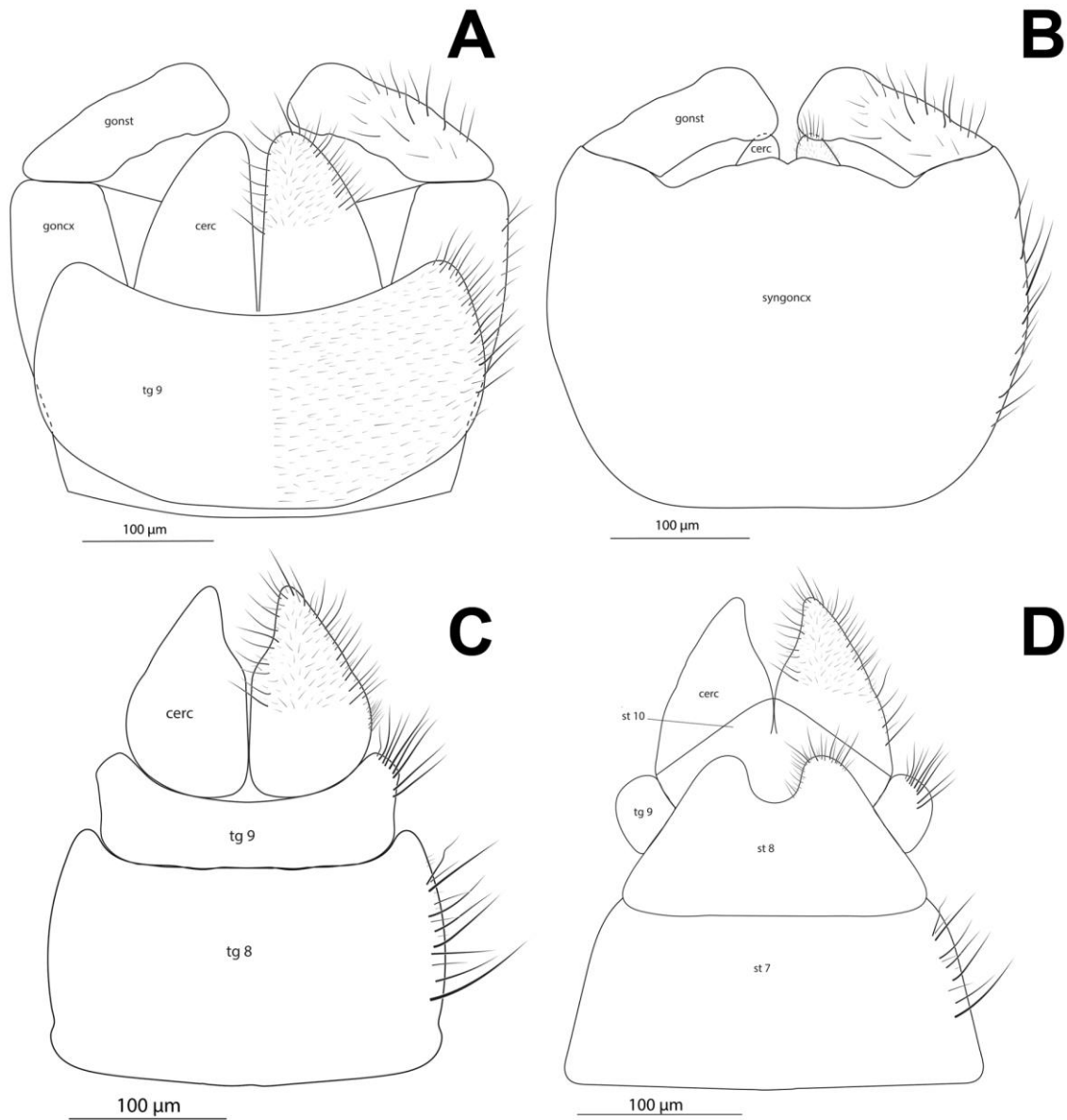


Figure 17. *Dilophus sp. nov.* **B**, terminalia. **A**. male, dorsal view. **B**. male, ventral view. **C**. female, dorsal view. **D**. female, ventral view.

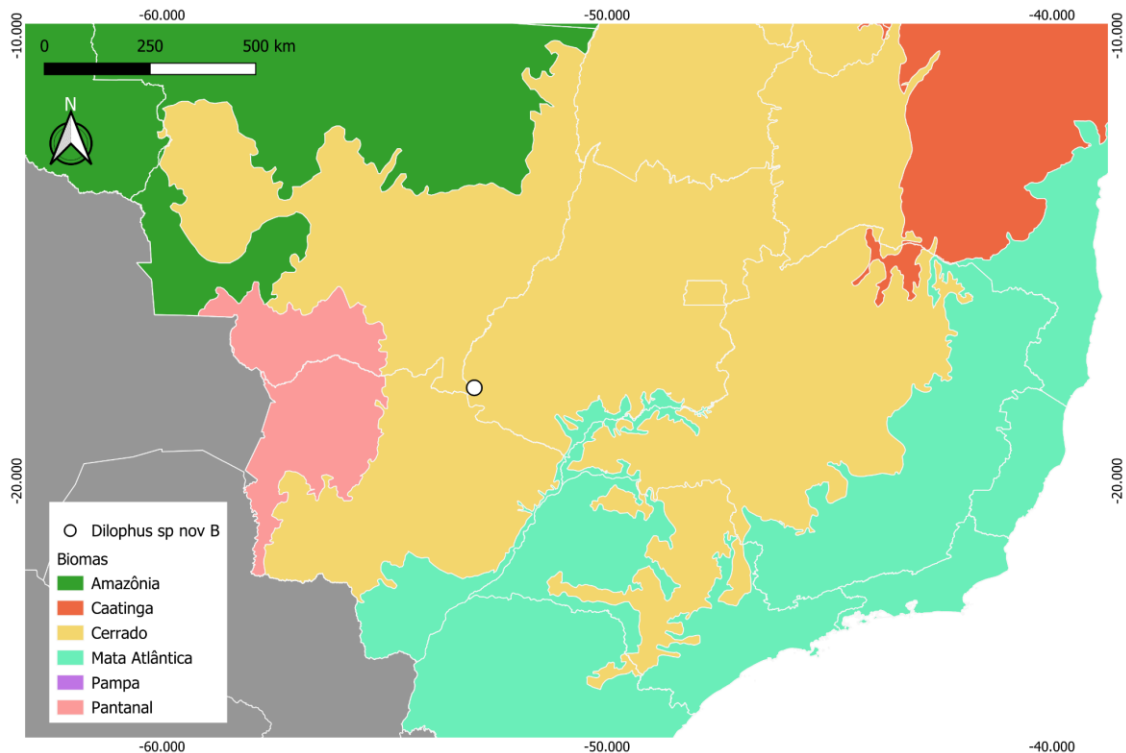


Figure 18. *Dilophus sp. nov. B*, distribution map.

Discussion

Despite Hardy (1953) redescribed some species presented here (*Dilophus bicoloripes*, *D. pectoralis*, and *D. trisulcatus*), the terminalias were not described or illustrated (except for the male of *D. trisulcatus*). This is possibly due to the fact that these are species that are easily recognized without dissection (using features of the thorax, legs, etc.). For females, in general, the terminalias are not described in the literature, since some of them are difficult to identify without association with the male. Here, four species are redescribed, three of them with the male terminalia described for the first time (*D. bicoloripes*, *D. pectoralis*, and *D. flavicornis*), and three of them with the female terminalia described for the first time (*D. bicoloripes*, *D. pectoralis*, and *D. trisulcatus*). Furthermore, two new species were described, including both male and female terminalias described and illustrated.

The female terminalias described here demonstrate the potential of using females for identification of Neotropical *Dilophus* species. Differences in the proportions of the terminalia parts, in the shape of cerci, tergite 9, sternite 10, and the lobes and cleft of sternite 8 were observed. This indicates that, at least for some species, it is possible to identify from females without the need for association with males. Furthermore, characters of female terminalia can be used in phylogenetic studies, representing valuable data for the understanding of *Dilophus* evolution. Likewise, the male terminalias described here help to characterize each species and can be used in phylogenies.

The geographic distribution was expanded for three species (*D. bicoloripes*, *D. pectoralis*, and *D. trisulcatus*), and the seasonality was expanded for all four species. In the Brazilian context, only three states had records for *Dilophus* (Rio de Janeiro, Santa Catarina, and São Paulo), and all of them are located in the Atlantic Forest (Falaschi & Schelesky-Prado 2024). Here, new records for five states are reported (Goiás, Mato Grosso do Sul, Minas Gerais, Paraná, and Rio Grande do Sul), representing also new records for the Cerrado and Pampas biomes. Some species occur in more than one biome, like *D. bicoloripes*, *D. pectoralis*, and *D. trisulcatus*, since other are recorded from only one biome, such as *D. flavicornis*, *D. sp. nov. A*, and *D. sp. nov. B*, which may represent species with the distribution restricted to the specific biome or simply they were not recorded for another biome yet.

Information on the biology of Bibionidae, especially the Neotropical fauna, are scarce. Here, insights on the flower-visiting and feeding behavior are reported for *Dilophus bicoloripes* and *D. pectoralis*.

References

- Bréthes, J. (1908) Catálogo de los Dípteros de las Repúblicas del Plata. Anales del Museo Nacional de Buenos Aires, Serie III, 9, 277–306
- Edwards, F.W. (1930) Bibionidae. In: Diptera of Patagonia and South Chile. Part 2. Fascicle 3. British Museum (Natural History), London, pp. 77–88.
- Edwards, F.W. (1938) Bibionidae (Diptera) collected by Mr. F. Plaumann in Brazil. The Annals and Magazine of Natural History, 11 (2), 321–330.
- Falaschi RL, Schelesky-Prado DC (2024) Bibionidae. Catálogo Taxonômico da Fauna do Brasil. PNUD. Available in <http://fauna.jbrj.gov.br/fauna/faunadobrasil/1843> [Access in 27.X.2024].
- Falaschi RL, Oliveira SS, Amorim DS (2016). Bibionidae. In: Wolff M, Nihei SS, de Carvalho CJB (Eds) Catalogue of Diptera of Colombia, Zootaxa 4122: 20–25. <https://doi.org/10.11646/zootaxa.4122.1.5>
- Fitzgerald, S.J. (1997). A Revision of *Biblio* (Diptera: Bibionidae) of Mexico and Central America. Trans. Am. Ent. Soc. 123(4): 225-287.
- Fitzgerald SJ (2000) Bibionidae. In: Llorente Bousquets JE, Gonzalez Soriano E, Papavero N (Eds) Biodiversidad, Taxonomía y Biogeografía de Artropodos de Mexico, vol. II, Universidad Nacional Autónoma de Mexico, D.F., Mexico, 627–634.

- Fitzgerald, S.J. (2004) Evolution and classification of Bibionidae (Diptera: Bibionomorpha). Ph.D. thesis, Oregon State University, Corvallis, Oregon, 385 pp.
- Fitzgerald, S.J. (2009) Bibionidae. In: Brown, B.V., Borkent, A., Cumming, J.M., Wood, D.M., Woodley, N.E. & Zumbado, M.A. (Eds.), Manual of Central American Diptera: Vol. 1. NRC Research Press, Ottawa, Ontario, 714 pp.
- Fitzgerald, S.J. (2021a) *Penthetria* Meigen (Diptera: Bibionidae): Revision of New World species and world catalog. *Zootaxa*, 4926 (4), 451–500. <https://doi.org/10.11646/zootaxa.4926.4.1>
- Fitzgerald, S.J. (2021b) New species of Neotropical *Plecia* Wiedemann (Diptera: Bibionidae) and delineation of the *americana*-, *nigra*-, and *xyele*- species-groups. *Zootaxa*, 5005 (1): 021–040. <https://doi.org/10.11646/zootaxa.5005.1.2>
- Fitzgerald SJ (2023) Capítulo 6: Bibionidae (Diptera) of Guatemala. In: Schuster JC, Yoshimoto J, Sierra JM (Eds) Biodiversidad de Guatemala, vol. 3, Universidad del Valle de Guatemala, Guatemala, 95–104 pp.
- Fitzgerald, S. J., C. R. González & M. Elgueta. 2020. A catalog of the Bibionidae (Diptera: Bibionomorpha) of Chile. *Zootaxa* 4766(1): 48–60.
- Fitzgerald, S.J. & Greenwalt, D.A. (2022) Family Bibionidae Fleming, 1821. In: Greenwalt, D.A., D. Des Souza Amorim, M. Hauser, P.H. Kerr, S.J. Fitzgerald, J.M. Cumming, N.L. Evenhuis & B.J. Sinclair, 2022. Diptera of the Middle Eocene Kishenehn Formation II. *Palaeontologica Electronica* 2 (2) (a22): 1-52.
- Fleming, J. (1821) Insecta. In: Stewart, D., Playfair, J. & Brande, W.T. (Eds.), Supplement to the fourth, fifth and sixth editions of the Encyclopedia Britannica. A. Constable & Co., Edinburgh, 5 (Pt. 1), pp. 41–56. [(1815)–1824].
- Hardy, D.E. (1945) Revision of Nearctic Bibionidae, including Neotropical *Plecia* and *Penthetria* (Diptera). The University of Kansas Science Bulletin, 30, 367–547.
- Hardy, D.E. (1953) The Argentine Bibionidae (Diptera). *Acta Zoológica Lilloana*, 12, 343–376.
- Hardy, D.E. (1959) Catalogue of the Neotropical Bibionidae. *Acta Zoológica Lilloana*, 17, 437–476.
- Hardy, D.E. 1961. Notes and descriptions of exotic Bibionidae. *Proceedings of the Entomological Society of Washington* 63(2): 81-99.

Hardy, D.E. (1966) 18. Family Bibionidae. In: Papavero, N. (Ed.), A Catalogue of the Diptera of the Americas south of the United States. Departamento de Zoologia da Secretaria da Agricultura do Estado de São Paulo, São Paulo, pp. 1–20.

Hardy, D.E. 1967. The types of Bibionidae (Diptera) in the Naturhistorisches Museum, Wien. *Annalen des Naturhistorisches Museum in Wien*, 70: 169-181.

Hunter, W.D. (1900) Catalogue of the Diptera of South America. Part. I. Bibliography and Nematocera. *Transactions of the American Entomological Society*, 26, 260–298.

iNaturalist community. Observations of *Dilophus bicoloripes* and *Dilophus pectoralis*, observed until 26 August 2024, exported from <https://www.inaturalist.org> on 27 October 2024.

Kertész, C. (1902) *Catalogus dipterorum Hucusque Descriptorum*. Vol. I. Lipsiae, Budapestini, 339 pp.

Lamas, C.J.E., Fachin, D.A., Falaschi, R.L., Alcantara, D.M.C., Ale-Rocha, R., Amorim, D.S., Araújo, M.X., Ascendino, S., Baldassio, L., Bellodi, C.F., Bravo, F., Calhau, J., Capellari, R.S., Carmo-Neto, A.M., Cegolin, B.M., Couri, M.S., Carvalho, C.J.B., Dios, R.V.P., Falcon, A.V.G., Fusari, L.M., Garcia, C.A., Gil-Azevedo, L.H., Gomes, M.M., Gracioli, G., Gudín, F.M., Henriques, A.L., Krolow, T.K., Mendes, L.L., Limeira-de-Oliveira, F., Maia, V.C., Marinoni, L., Mello, R.L., Mello-Patiu, C.A., Morales, M.N., Oliveira, S.S., Patiú, C., Proença, B., Pujol-Luz, C.V.A., Pujol-Luz, J.R., Rafael, J.A., Riccardi, P.R., Rodrigues, J.P.V., Roque, F.O., Sallum, M.A.M., Santis, M.D., Santos, C.M.D., Santos, J.R., Savaris, M., Shimabukuro, P.H.F., Silva, V.C., Schelesky-Prado, D.C., Silva-Neto, A.M., Camargo, A., Sousa, V.R., Urso-Guimarães, M.V., Wiedenbrug, S., Yamaguchi, C. & Nihei, S.S. (2023) The SISBIOTA-Diptera Brazilian Network: A longterm survey of Diptera from unexplored Brazilian Western Arc of Amazon, Cerrado. *Revista Brasileira de Entomologia*, 67 (4), e20230051. <https://doi.org/10.1590/1806-9665-RBENT-2023-0051>

Macquart, J. 1838. Diptères exotiques, nouveaux ou peu connus 1(1):84-89.

Maes, J. M. 1990. Catalogo de los Diptera de Nicaragua. 8. Bibionidae (Nematocera). *Revista Nicaraguense de Entomologia* 14B: 23–26.

Meigen, J.G. (1803) Versuch einer neuen Gattungs Eintheilung der europäischen zweiflügeligen Insekten. *Magazin für Insektenkunde*, 2, 264.

National Center for Biotechnology Information (NCBI) [Internet]. Bethesda (MD): National Library of Medicine (US), National Center for Biotechnology Information; [1988]. Available from: <https://www.ncbi.nlm.nih.gov/> [Access in 27.X.2024].

Nel, A., Legal, S. & Coster, P. (2022) A new species of the March fly genus *Dilophus* Meigen, 1803 (Diptera: Bibionidae) from the Oligocene of Provence (France), *Palaeoentomology* 5 (4), pp. 347-353 : 348-349.

Pinto, L.G. & Amorim, D.S. (2000) Bibionidae (Diptera: Bibionomorpha). *Morfologia e análise filogenética*. Holos, Ribeirão Preto, 98 pp.

Reed, E.C. (1888) Catálogo de los insectos dípteros de Chile. *Anales de la Universidad de Chile*, 73, 271–316.

Rondani, C. 1868. Diptera aliqae in America meridionali lecta a Prof. S. Strobel annis 1866 et 1867. *Annuario della Soc. dei Nat. Modena*: 39-40.

Skartveit, J. (2002) The larvae of European Bibioninae (Diptera, Bibionidae). *J. Nat. list.* 36: 449-485.

Skartveit, J. (2017) Bibionidae. In: Kirk-Spriggs, A.H. & Sinclair, B.J.(Eds.), *Manual of Afrotropical Diptera*. Vol. 2. Suricata 5. South African National Biodiversity Institute, Pretoria, pp. 497–504.

Skartveit J, Freidberg A. (2023) Revision of the genus *Dilophus* Meigen, 1803 (Diptera, Bibionidae) from the Afrotropical Ecozone. *Zootaxa*. Oct 27;5360(3):301-354. doi: <https://doi.org/10.11646/zootaxa.5360.3.1>

Stuardo, C. (1946) Catálogo de los dípteros de Chile. Ministerio de Agricultura, Impresiones Universitaria, Santiago, 250 pp.

Sturm, H. (1990) Eine neue *Dilophus*-Art (Insecta, Diptera, Bibionidae) aus den Hochanden Kolumbiens. *Annalen des Naturhistorischen Museums in Wien. Serie B.* 91: 197-204.

Waller, A., Nel, A., and Menier, J.-J. (2000) Le premier *Dilophus* fossile de l'ambre dominicain (Diptera, Bibionidae). *Revue Francaise d' Entomologie (Nouvelle Serie)*, 22:149-153.

Wiedemann, C.R.W. (1828) *Aussereuropäische zweifügelige Insekten*. Vol. 1. In der Schulzischen Buchhandlung, Hamm, 608 pp. [pp. 72–81].

Wulp, F.M. van der (1881) Amerikaansche Diptera. Tijdschrift voor Entomologie, 24, 141–168.

CAPÍTULO 2 - Phylogeny of *Dilophus* Meigen, 1803 (Diptera: Bibionidae)

Abstract

Dilophus Meigen is one of the larger genera of Bibionidae, comprising more than 200 described species. The genus is considered monophyletic by many authors, but the phylogenetic relationships among its species need to be better understood. Additionally, fossils of *Dilophus* have never been included in a phylogeny. Here, a data matrix consisting of 91 morphological features of 129 terminal taxa was carried out to investigate the aforementioned problem. The recently described fossil genus †*Protodilophus* was placed as part of *Dilophus*. The two species groups proposed in the literature, “*Dilophus febrilis*-group” and “*D. bispinosus*-group” were not recovered. Some clades within *Dilophus* were recovered with varying degrees of support, but further studies with more terminals and characters are necessary to elucidate the genus’ relationships.

Key Words: Bibionomorpha, Cladistics, Fossil, Taxonomy.

Introduction

Bibionidae (Diptera: Bibionomorpha) is a family with a worldwide distribution (except for polar areas) and comprises about 700 extant species in eight genera (Pinto & Amorim 2000; Fitzgerald 2004b; Fitzgerald *et al.* 2020). Moreover, more than 345 fossil species have been described (including exclusively fossil genera), making it best-represented dipteran family in terms of species richness in the fossil record (Pinto & Amorim 2000; Fitzgerald 2004b; Skartveit 2009). Bibionidae comprises six subfamilies, of which five are monotypic: †Burmahesperinae (†*Burmahesperinus* Ševčík, Skartveit, Krzemiński & Skibińska), †Cretobibioninae (†*Cretobibio* Skartveit & Ansorge), Hesperinae (*Hesperinus* Walker), Penthetriinae (*Penthetria* Meigen), and Pleciinae (*Plecia* Wiedemann), and Bibioninae, which includes two tribes, Bibionini and Dilophini (Pinto & Amorim 2000; Fitzgerald 2004b; Skartveit & Ansorge 2020; Ševčík *et al.* 2021). Dilophini has been a monotypic tribe, including only *Dilophus* Meigen, until the recently described fossil genus †*Protodilophus* Skartveit was assigned to the tribe (Skartveit 2023). Furthermore, there are fossil genera whose classification is problematic due to the lack of phylogeny that includes them: †*Cascoplecia* Poinar, †*Cretpenthetria* Li, Zhang & Xiao, and †*Protopenthetria* Li, Skibińska, Krzemiński, Wang, Xiao & Zhang, all suggested to be part of Pleciinae, but in a broad and paraphyletic concept of the subfamily that includes *Penthetria* (Li *et al.* 2021). Indeed, the only fossil genus included in a phylogeny was †*Cretobibio* (Skartveit & Ansorge 2020). The phylogeny of Bibionidae based on morphological characters is as follows: *Hesperinus* + (*Penthetria* + (*Plecia* + Bibioninae)) (Pinto & Amorim 2000; Fitzgerald 2004b). However, a novel hypothesis based on molecular evidence suggested the following phylogeny: ((*Hesperinus* + *Penthetria*) + *Plecia*) + Bibioninae (Ševčík *et al.* 2016). Due to these conflicting hypotheses, further studies are needed to clarify the relationships between the genera of

Bibionidae. Additionally, †*Cretobibio* was recovered as the sister group of Bibioninae (Skartveit & Ansoerge 2020).

Dilophus is one of the largest genera of Bibionidae, alongside with *Bibio* Geoffroy (comprising about 190 extant species) and *Plecia* (with about 260 extant species), totaling around 200 extant species (Fitzgerald 2004b, 2009, 2021; Skartveit 2017). The genus has a worldwide distribution (excluding polar areas) and is particularly diverse in the Neotropical Region, where it accounts for approximately 80 extant species, representing roughly 40% of the described species (Pinto & Amorim 2000; Fitzgerald 2004b; Skartveit & Freidberg 2023). Moreover, *Dilophus* exhibits greater species richness in the Southern Hemisphere (approximately 120 species), constituting roughly 60% of the current diversity of the genus. These species are distributed across the Australasian, Neotropical, and Southern African (Afrotropical) regions, compared to the Northern Hemisphere, including the Nearctic and Palearctic regions (Skartveit & Willassen 1996; Skartveit 2017).

The fossil fauna of *Dilophus* comprises 12 described species, most of them from the Palearctic Region (nine), with one each from the Australasian, Nearctic, and Neotropical regions, respectively (Fitzgerald & Greenwalt 2022; Nel *et al.* 2022). All species are described based on adult specimens, except for *D. campbelli* Harris, which was described from a fossilized larva (Fitzgerald & Greenwalt 2022; Nel *et al.* 2022). Eight species were found preserved in sedimentary rocks such as limestone and shale, while four were found in amber (Fitzgerald & Greenwalt 2022; Nel *et al.* 2022). All known fossils are from the Cenozoic Era and span the following epochs: Eocene (six), Oligocene (three), and Miocene (three), with *D. campbelli* (from the Lower to Middle Eocene, from New Zealand) and *D. idanos* Fitzgerald & Greenwalt (Middle Eocene, 46.6 to 45.8 million years ago, from United States of America) representing the oldest records for the genus (Harris 1983; Fitzgerald & Greenwalt 2022).

Interestingly, †*Protodilophus* is considerably older than the known *Dilophus* fossils, dating back to the Mesozoic era: Late Cretaceous, specifically the Cenomanian period (approximately 99 million years ago, from Myanmar), representing the oldest known record of Bibioninae (Skartveit 2023). The number of extant and fossil described species of *Dilophus* by biogeographical region is summarized below (Table 1).

Table 1. Number of extant and fossil *Dilophus* species by biogeographic region.

Region	Nearctic	Palearctic	Neotropical	Afrotropical	Oriental	Australasian-Oceanian	Total
Extant	19	39	81*	15	14	38	206
Fossil	1	9	1	0	0	1	12
Total	20	48	82	15	14	39	218

*Including two unpublished new species of Neotropical *Dilophus*.

Dilophus is strongly supported as monophyletic (Skartveit & Willassen 1996; Pinto & Amorim 2000; Fitzgerald 2004b), with notable synapomorphies such as the

transverse thoracic combs of spines (see Fitzgerald 2004b, p. 57, Figure 6a) and the presence of medial and apical spines on fore tibiae (see Fitzgerald 2004b, p. 77, Figure 8d). However, the phylogenetic relationships between *Dilophus* species remains unclear and have received limited attention in the literature. Only two studies, by Skartveit & Willassen (1996) and Fitzgerald (2004b), have explored these relationships.

Skartveit & Willassen (1996) aimed to elucidate the phylogenetic relationships within Bibioninae, analyzing 14 *Dilophus* terminals, mostly from the Palearctic region, with limited representation from other regions. This study sampled approximately 7% of the known living species diversity (206) of the genus and did not include fossil taxa. Fitzgerald (2004b) focused on the phylogeny of Bibionidae, including four *Dilophus* species but with even less representation of biogeographic regions and species diversity. Only about 2% of known living species diversity was sampled in this study, and fossil taxa were also not included.

A study by Pinto & Amorim (2000), aiming to understand the phylogenetic relationships between the genera of Bibionidae, included a larger sample of *Dilophus* species (39), particularly from the Neotropical region. However, the terminal taxa in the matrix represented bibionid genera rather than species, thus not exploring the relationships between *Dilophus* species.

Few studies have proposed species groups within *Dilophus*. Haenni (1981, 1982) suggested the *Dilophus febrilis*-group, comprising 26 species from the Palearctic (13) and Afrotropical (13) regions (Skartveit & Willassen 1996; Haenni & Báez 2001; Haenni & Bosák 2007; Haenni 2009; Skartveit 2009; Skartveit & Freidberg 2023). Skartveit & Willassen (1996) proposed the “*Dilophus bispinosus*-group”, consisting of five Palearctic species. Fitzgerald (2004a) suggested that some South Pacific species form a complex of species, presumably including at least ten species from the Australasian/Oceanic region. The species included in each proposed group are listed below (Table 2).

Table 2. List of species included in each proposed group.

Group	Species
<i>Dilophus febrilis</i> -group (Palearctic)	<i>D. febrilis</i> (Linnaeus) <i>D. antipedalis</i> Wiedemann <i>D. beckeri</i> (Hardy) <i>D. borealis</i> Skartveit <i>D. femoratus</i> Meigen <i>D. humeralis</i> Zetterstedt <i>D. maderae</i> Wollaston <i>D. maghrebensis</i> Haenni <i>D. martinovskyi</i> Haenni & Bosák <i>D. neglectus</i> Haenni <i>D. oceanus</i> Haenni & Báez † <i>D. palaeofebrilis</i> Skartveit <i>D. sardous</i> Haenni
<i>Dilophus febrilis</i> -group (Afrotropical)	<i>D. atrimas</i> Edwards <i>D. baleensis</i> Skartveit & Freidberg

	<i>D. bicolor</i> Wiedemann <i>D. buxtoni</i> (Hardy) <i>D. capensis</i> Edwards <i>D. disagrus</i> (Speiser) <i>D. erythraeus</i> Bezzi <i>D. lucidus</i> (Hardy) <i>D. malagasicus</i> Skartveit & Freidberg <i>D. obsoletus</i> (Hardy) <i>D. paucidens</i> Hardy <i>D. riftensis</i> Skartveit & Freidberg <i>D. suberythraeus</i> Edwards
“ <i>Dilophus bispinosus</i> -group”	<i>D. bispinosus</i> Lundström <i>D. clavicornus</i> Skartveit & Kaplan <i>D. hiemalis</i> Becker <i>D. lingens</i> Loew <i>D. tridentatus</i> Walker
“South Pacific group”	<i>D. tuthilli</i> (Hardy) <i>D. arboreus</i> Fitzgerald <i>D. exiguus*</i> (Hardy) <i>D. gracilis</i> Hardy <i>D. collessi</i> Hardy <i>D. discretus</i> Hardy <i>D. modicus</i> Hardy <i>D. parvus</i> Hardy <i>D. pictipes</i> Skuse <i>D. sexspinosus</i> Hardy

* May represent a complex of species (Hardy 1968a,b).

Some limitations regarding knowledge of *Dilophus* may have hampered the phylogenetic analyzes of the genus or even taxonomic revisions and species identification, such as: only a few species with immatures stages described (Skartveit 2002), species described based on one of the sexes due the sexual dimorphism (Fitzgerald *et al.* 2020), and only two species with published molecular data (and some unidentified *Dilophus*) (NCBI). Besides, a relatively small number of fossils are known when compared to other genera, such as *Bibio* and *Plecia* (Pinto & Amorim 2000; Fitzgerald & Greenwalt 2022).

Here, a phylogenetic analysis of *Dilophus* is conducted based on morphological characters from 129 terminal taxa, with 120 belonging to *Dilophus*. This study represents the first phylogeny to include a wide sampling of species from all biogeographic regions, except Antarctica, where there is no records of *Dilophus* exist. Additionally, this is the first phylogeny to incorporate fossil species of the genus. Besides, the phylogenetic positioning of †*Protodilophus* is explored.

Material and methods

Examined material. The specimens utilized in this study are housed in the collections of MZUSP (Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil), NHMUK (Natural History Museum, London, United Kingdom), and MNHN (Muséum national

d'Histoire naturelle, Paris, France). Specimens from MZUSP were examined in person, while those from the NHMUK and MNHN were examined using photographs. Additionally, some specimens photographs from iNaturalist, a citizen science social network, were analyzed when confident species-level identifications and observation of key structures were possible.

Phylogenetic analysis. Data from the literature were also incorporated to compile the list of characters and states used in the matrix. Morphological terminology mainly followed Fitzgerald (2004b) and Skartveit (2017), but also included new terms, herein highlighted.

The phylogenetic analysis was conducted using a morphological data matrix based on male and female adults of both extant and fossil species. The matrix (see Appendix 1) comprises a total of 129 terminal taxa (see Appendix 2), including nine outgroups. The outgroups encompass species from various genera, including *Pachyneura fasciata* Zetterstedt (Pachyneuridae), used to root the tree, along with bibionid species from *Bibio*, *Bibiodes* Coquillett, *Bibionellus* Edwards, *Hesperinus*, *Penthetria*, *Plecia*, and †*Protodilophus*.

Within the matrix, a total of 120 *Dilophus* species were included, representing approximately 55% of described species in the genus. These *Dilophus* species were selected from all biogeographic regions where the genus occurs: 12 species from the Nearctic (60%), 23 from the Palearctic (about 48%), 33 from the Neotropical (about 40%), 15 from the Afrotropical (100%), eight from the Oriental (about 57%), and 36 from the Australasian-Oceanian region (about 92%).

Some of the characters utilized in this analysis were proposed in previous phylogenetic studies by Blaschke-Berthold (1994), Skartveit & Willassen (1996), Pinto & Amorim (2000), Fitzgerald (2004b), and Skartveit & Ansoerge (2020). Additionally, novel characters were proposed for the first time in this study.

The character matrix was constructed using the Mesquite software version 2.75 (Maddison & Maddison 2011). States with no information and inapplicable data were coded respectively as “?” and “-”. Multistate characters were coded from 0 to 9, with state 10 represented as “A”. Polymorphisms were coded as states enclosed in brackets ([]).

The data matrix was evaluated under the maximum parsimony criterion using the TNT software (Goloboff & Catalano 2016). All characters were treated as ordered under the implied weighting (Goloboff 1993). The topologies in TNT were obtained using New Search Technology with all new technologies selected, following Souza (2024). The following parameters were used for the analysis: Max. trees 50,000; Random seed=0; init. addsequest=10; Find min. length=50. The final tree was obtained using WinClada software version 1.89 (Nixon 2002) and edited in Adobe Illustrator CC.

Results

The matrix (see Appendix 1) consists of a total of 91 discrete characters, comprising 64 binary and 27 multistate characters. These characters are distributed across various anatomical structures, including 13 from the head, 18 from the thorax, 19 from

the legs, 21 from the wings, one from the abdomen, 12 from male terminalia, and seven from female terminalia. Notably, 43 of these characters are presented for the first time in a phylogenetic context for *Dilophus*.

Each character is described below, along with relevant discussions when applicable.

1. Male compound eye development

- (0) dichoptic
- (1) holoptic

According to several studies, such as Hennig (1973), Blaschke-Berthold (1994) (character 20), Skartveit & Willassen (1996) (character 111: state 1), Pinto & Amorim (2000) (13:1), and Fitzgerald (2004b) (1:1), the holoptic development of male compound eyes is a synapomorphy of Bibionidae excluding *Hesperinus*. Here this character supports the aforementioned clade.

2. Male compound eye division

- (0) undivided
- (1) divided

According to Pinto & Amorim (2000) (15:1) and Fitzgerald (2004b) (3:1), the divided compound eyes of male support Bibionidae excluding *Hesperinus*. Here this character supports the aforementioned clade.

3. Female compound eye division

- (0) undivided
- (1) divided

Fitzgerald (2004b) treated the division of males and females eyes as independent conditions, since some species have males with divided eyes and females with undivided eyes. According to Fitzgerald (2004b) (5:1), the divided compound eyes of females support *Dilophus*. Here this character does not support *Dilophus*.

4. Male flagellum

- (0) with 15 flagellomeres
- (1) with 14 flagellomeres
- (2) with 13 flagellomeres
- (3) with 12 flagellomeres
- (4) with 11 flagellomeres
- (5) with 10 flagellomeres
- (6) with 9 flagellomeres
- (7) with 8 flagellomeres
- (8) with 7 flagellomeres
- (9) with 6 flagellomeres
- (10) with 5 flagellomeres

In the literature, the states and respective synapomorphies of this character differ slightly. According to Skartveit & Willassen (1996) (21:2), the presence of seven flagellomeres (sex not discriminated) supports the clade *Bibio* + *Bibiodes* + *Bibionellus* (all Bibionini). According to Pinto & Amorim (2000) (5:1), the presence of ten flagellomeres (both sexes) support Bibionidae, and nine flagellomeres of male (6:1) supports both *Plecia* and Bibionini (homoplasy). According to Fitzgerald (2004b) (10:5), ten flagellomeres of male (10:5) support Bibionidae, eight flagellomeres (10:7) support (*Plecia* + Bibioninae) and 11 flagellomeres (10:4) support *Dilophus*. Here this character does not support these clades and is rather problematic and homoplastic.

5. Female flagellum

- (0) with 15 flagellomeres
- (1) with 14 flagellomeres
- (2) with 13 flagellomeres
- (3) with 12 flagellomeres
- (4) with 11 flagellomeres
- (5) with 10 flagellomeres
- (6) with 9 flagellomeres
- (7) with 8 flagellomeres
- (8) with 7 flagellomeres
- (9) with 6 flagellomeres
- (10) with 5 flagellomeres

According to Pinto & Amorim (2000) (7:1), the presence of nine flagellomeres supports Bibionini. Here this character does not support this clade.

6. Sclerotized rostrum of female

- (0) shorter than the eye length
- (1) equal to the eye length or nearly so
- (2) longer than the eye length

According to (Skartveit & Willassen (1996) (46:1) rostrum prolonged supports (*Dilophus tridentatus* + *D. hiemalis*). Here some clades within *Dilophus* are supported by this character (see discussion below).

7. Female rostrum (antennae)

- (0) well produced beyond the bases of antennae
- (1) slightly or not produced beyond the bases of antennae

8. Posterior portion of female head

- (0) shorter than the eye length
- (1) equal to the eye length or nearly so
- (2) longer than the eye length

9. Female ocellar tubercle

- (0) undeveloped
- (1) developed

10. Mouthparts

- (0) not telescopically extensible
- (1) telescopically extensible

According to Skartveit & Willassen (1996) (10:1), the telescopically extensible mouthparts support *Dilophus*. Here this character does not support *Dilophus*.

11. Maxillary palp

- (0) 5-segmented
- (1) 4-segmented

According to Skartveit & Willassen (1996) (40:0), 4-segmented palp supports (*Dilophus bispinosus* + *D. tridentatus* + *D. lingens* + *D. hiemalis*) and 5-segmented (40:1) supports (*Dilophus borealis* + *D. femoratus* + *D. beckeri* + *D. febrilis* + *D. antipedalis*) (but the latter without a good support). Here this character does not support these clades.

12. Third segment of palpus

- (0) slender
- (1) swollen

According to Skartveit & Willassen (1996) (1:1) swollen third segment supports Bibioninae (but in Fitzgerald, 2004b this condition is reported for all Bibionidae), and slender condition (1:0) supports (*Dilophus tridentatus* + *D. lingens* + *D. hiemalis*). Here this character does not support these clades.

13. Apical segment of palpus

- (0) elongated
- (1) shorted

14. Dorsum of thorax with modified setae

- (0) absent
- (1) present

According to several studies, such as Skartveit & Willassen (1996) (11:1), Pinto & Amorim (2000) (30:1), Fitzgerald (2004b) (22:1), and Skartveit & Ansoerge (2020) (13:1), the presence of spine combs supports *Dilophus*. Here the presence of spines supports *Dilophus* (including †*Protodilophus*), but only spine-like setae are present in †*Protodilophus*.

15. Modified setae of dorsum (development)

- (0) spine-like setae
- (1) spines

16. Anterior comb, transverse row division

- (0) undivided
- (1) medially divided
- (2) divided into three parts

17. Anterior comb with

- (0) all spines in the transverse row
- (1) some spines displaced posteriorly to the row

18. Anterior comb of male (number)

- (0) 6 spines
- (1) 7 spines
- (2) 8 spines
- (3) 9 spines
- (4) 10 spines
- (5) 11 spines
- (6) 12 spines
- (7) 13 spines
- (8) 14 spines
- (9) 15 spines
- (A) 16 spines
- (B) 17 spines
- (C) 18 spines
- (D) 19 spines
- (E) 20 spines

19. Anterior comb of female (number)

- (0) 6 spines
- (1) 7 spines
- (2) 8 spines
- (3) 9 spines
- (4) 10 spines
- (5) 11 spines
- (6) 12 spines
- (7) 13 spines
- (8) 14 spines
- (9) 15 spines
- (A) 16 spines
- (B) 17 spines
- (C) 18 spines

- (D) 19 spines
- (E) 20 spines

20. Posterior comb, transverse row division

- (0) undivided
- (1) medially divided
- (2) divided into three parts

21. Posterior comb with

- (0) all spines in the transverse row
- (1) some spines displaced posteriorly to the row
- (2) one longitudinal row of spines on each side of the transverse row

22. Posterior transverse row of male

- (0) present
- (1) absent

23. Posterior comb of male (number)

- (0) 6 spines
- (1) 7 spines
- (2) 8 spines
- (3) 9 spines
- (4) 10 spines
- (5) 11 spines
- (6) 12 spines
- (7) 13 spines
- (8) 14 spines
- (9) 15 spines
- (A) 16 spines
- (B) 17 spines
- (C) 18 spines
- (D) 19 spines
- (E) 20 spines

24. Posterior comb of female (number)

- (0) 6 spines
- (1) 7 spines
- (2) 8 spines
- (3) 9 spines
- (4) 10 spines
- (5) 11 spines
- (6) 12 spines
- (7) 13 spines
- (8) 14 spines
- (9) 15 spines
- (A) 16 spines
- (B) 17 spines

- (C) 18 spines
- (D) 19 spines
- (E) 20 spines

25. Dorsum (ground color)

- (0) similar in both sexes
- (1) male darker

26. Mesonotum of male with anterior dark spot

- (0) absent
- (1) present

27. Mesonotum of female with anterior dark spot

- (0) absent
- (1) present

28. Mesonotum setae

- (0) brown to black
- (1) white to yellow

29. Male scutellum marginal setae

- (0) absent
- (1) present

30. Male scutellum marginal setae (length)

- (0) short
- (1) long

31. Area posterior to prothoracic spiracles with microtrichia

- (0) absent
- (1) present

According to Skartveit & Willassen (1996) (26:1), the area posterior to prothoracic spiracles with microtrichia supports (*Dilophus bispinosus* + *Dilophus tridentatus* + *D. lingens* + *D. hiemalis*). Here this character does not support this clade.

32. Fore tibiae with modified setae

- (0) absent
- (1) present

According to Pinto & Amorim (2000) (57:1), the presence of medial and apical spines on the fore tibiae is a synapomorphy of *Dilophus*. Fitzgerald (2004b) considered the medial spines (40:1) and the apical circlet of spines (37:1) as distinct characters, but both supporting *Dilophus*. For Skartveit & Ansorge (2020) (12:1), the medial spines support *Dilophus*. Here the fully developed medial and apical spines support *Dilophus* (including †*Protodilophus*), but only spine-like setae are present in †*Protodilophus*.

33. Modified setae of fore tibiae (development)

- (0) spine-like setae
- (1) spines

34. Fore tibial medial spines

- (0) with two sets of spines
- (1) with one set of spines

According to Skartveit & Willassen (1996), the presence of two sets of medial spines (39:1) supports the “*D. bispinosus*-group” and one set (39:0) of spines supports the *D. febrilis*-group. However, it is argued that the polarity of this character is problematic, as it is not present in the outgroup. Here this character does not support these clades.

35. Single set of medial spines

- (0) with 2 spines
- (1) with 3 spines
- (2) with 4 spines
- (3) with 5 spines
- (4) with 6 spines
- (5) with 7 spines
- (6) with 8 spines

36. Single set of medial spines with

- (0) all spines grouped on a row
- (1) one spine placed more apically than the others
- (2) an additional longitudinal row of spines

This character was used by Skartveit & Willassen (1996) (86), but the only terminal with the displaced spine was *D. febrilis*.

37. Upper set of spines

- (0) with 1 spine
- (1) with 2 spines
- (2) with 3 spines
- (3) with 4 spines

38. Lower set of spines

- (0) with 1 spine
- (1) with 2 spines
- (2) with 3 spines
- (3) with 4 spines
- (4) with 5 spines
- (5) with 6 spines

(6) with 7 spines

(7) with 8 spines

39. Apical circlet of spines

(0) with 6 spines

(1) with 7 spines

(2) with 8 spines

(3) with 9 spines

(4) with 10 spines

(5) with 11 spines

(6) with 12 spines

This character was used by Skartveit & Willassen (1996) (80) and had only three states: (0) six spines, (1) eight spines, and (2) ten spines.

40. Apical spur

(0) same length as the spines or nearly so

(1) longer than the spines

41. Fore tibia with apical strong spine

(0) absent

(1) present

According to several studies, such as Pinto & Amorim (2000) (58:1), Fitzgerald (2004b) (36:1), and Skartveit & Ansoerge (2020) (11:1), the presence of a strong apical spine is a synapomorphy of Bibionini. However, here this character was recovered as a synapomorphy of Bibioninae and was lost in Dilophini.

42. Fore femur

(0) not swollen

(1) swollen

According to several studies, such as Skartveit & Willassen (1996) (8:1), Pinto & Amorim (2000) (56:1), Fitzgerald (2004b) (33:1), and Skartveit & Ansoerge (2020) (10:1), the presence of a swollen fore femur is synapomorphic to Bibioninae. Here this character does not support Bibioninae, despite being present only in this taxon.

43. Male mid tibia with medial spine-like setae

(0) absent

(1) present

According to Skartveit & Willassen (1996) (17:1), the presence of a row of spine-like setae on mid tibia (sex not discriminated) support *Dilophus*. Here this character does not support *Dilophus*, but a clade within the genus (Figure 1.B).

44. Female mid tibia with medial spine-like setae

- (0) absent
- (1) present

45. Male mid tibia with an apical circlet of spine-like setae

- (0) absent
- (1) present

According to Skartveit & Willassen (1996) (43:1), the presence of an apical circlet of spinelike setae on mid tibia (sex not discriminated) support (*D. tridentatus* + *D. lingens* + *D. hiemalis*). Here this character does not support this clade.

46. Female mid tibia with an apical circlet of spine-like setae

- (0) absent
- (1) present

47. Male hind femur

- (1) not clavate
- (2) clavate

According to Fitzgerald (2004b) (41:1) supports Bibionidae excluding *Hesperinus*. Here this character supports the aforementioned clade. This character was also used by Skartveit & Willassen (1996) (83).

48. Male hind tibia

- (1) not clavate
- (2) clavate

According to Skartveit & Willassen (1996) (42:1), the club-shaped hind tibia of male supports (*D. tridentatus* + *D. lingens* + *D. hiemalis*). Here this character does not support this clade. However, according to Pinto & Amorim (2000) (52:1) and Fitzgerald (2004b) (42:1), the clavate hind tibia supports Bibionidae excluding *Hesperinus*. Here this character supports this clade.

49. Male hind basitarsus

- (0) slender
- (1) robust
- (2) swollen

According to Skartveit & Willassen (1996) (87:1) suggest that the greatly swollen male hind basitarsus could be synapomorphic to (*D. hiemalis* + *D. lingens*). According to Fitzgerald (2004b) (46:1), the robust condition supports Bibionidae excluding *Hesperinus* and the slender condition supports *Dilophus*. Here this character does not support both clades.

50. Spurs on hind tibia with microtrichia

- (1) absent
- (2) present

According to Skartveit & Willassen (1996) (25:1), spurs on hind tibia with microtrichia supports (*Dilophus bispinosus* + *Dilophus tridentatus* + *D. lingens* + *D. hiemalis*). Here this character does not support this clade.

51. Costa

- (0) extends considerably beyond the apex of R₄₊₅
- (1) ends at or just slightly beyond the apex of R₄₊₅

According to several studies, such as Skartveit & Willassen (1996) (30:1), Pinto & Amorim (2000) (35:1), and Skartveit & Ansoerge (2020) (14:1), the costa ending at or very near to the apex of R₄₊₅ supports Bibionini, but the state 0 is found in *Bibionellus* (possible reversion). Here this character does not support Bibionini.

52. Humeral vein

- (0) present
- (1) absent

53. Costal cell

- (0) concolorous with the rest of membrane
- (1) darker than the rest of membrane

According to Skartveit & Willassen (1996) (50:1), the costal cell darker than the rest of membrane support (*D. beckeri* + *D. febrilis* + *D. cf. antipedalis*). Here this character does not support this clade.

54. Sc vein

- (0) complete
- (1) apically incomplete

According to Pinto & Amorim (2000) (37:1), an apically incomplete Sc supports *Bibiodes* + *Enicoscolus*). According to Fitzgerald (2004b) (50), this condition is present in most Bibioninae, except some *Dilophus*. Here this character supports Bibioninae.

55. R₁

- (0) complete
- (1) apically incomplete

56. R₁ with setae

- (0) absent
- (1) present

57. Rs sector

- (0) furcated
- (1) not furcated

According to several studies, such as Skartveit & Willassen (1996) (7:1), Pinto & Amorim (2000) (39:1), Fitzgerald (2004b) (53:0), and Skartveit & Ansoerge (2020) (8:2), the absence of R_{2+3} , *i.e.*, Rs sector not furcated, supports Bibioninae. Additionally, Skartveit & Ansoerge (2020) (8:1) considered †*Cretobibio* with the condition R_{2+3} present, but weakened. Here this character supports Bibioninae.

58. Vein M1

- (0) joined with M stem
- (1) basally interrupted

59. Vein M2

- (0) joined with M stem
- (1) greatly interrupted basally

60. Crossvein r-m (length)

- (0) shorter than bRs
- (1) subequal to bRs
- (2) longer than bRs

According to Skartveit & Willassen (1996) (14:1), the crossvein r-m much longer than basal Rs supports *Dilophus*. According to Pinto & Amorim (2000) (40:3), r-m longer than twice the base of Rs supports *Dilophus*. Here this character does not support *Dilophus*, despite being present mainly in this taxon.

61. Crossvein r-m (position)

- (0) perpendicular or nearly perpendicular
- (1) oblique

According to Fitzgerald (2004b) (56:1), the r-m basal to its origin in Rs supports Bibioninae. According to Skartveit & Ansoerge (2020) (7:1), the oblique r-m supports (†*Cretobibio* + Bibioninae).

62. Vein $bM_{(3+4)}$

- (0) present
- (1) absent

Some authors (Pinto & Amorim 2000; Skartveit & Ansoerge 2020) treat the veins $bM_{(3+4)}$ and m-m as if they were the same vein. Here we treat them as different veins. According to Fitzgerald (2004b) (60:2), the loss of $bM_{(3+4)}$ supports Bibioninae.

63. Vein m-m

- (0) absent
- (1) present

According to Pinto & Amorim (2000) (42:1), a distal “m-cu” supports Bibioninae. Here this vein is interpreted as m-m and is always distal to bM_{3+4} (but when one is present, the other one is not).

64. Vein m-m, insertion

- (0) inserted between the base of r-m (or obliterated r-m) and the base of M1
- (1) joined with the base of M1
- (2) inserted after the base of M1

The insertion of this vein is quite variable; therefore, the character was modified to cover such states.

65. Cell m4; shape

- (0) elongated
- (1) trapezoid

66. Vein CuP

- (0) reaching the wing margin or nearly so
- (1) ending well before the margin

According to Pinto & Amorim (2000) (48:1), the CuP ending well before the wing margin supports Bibioninae. For Fitzgerald (2004b) (62:0), the CuP not reaching the wing margin supports Bibioninae. Here this character does not support Bibioninae, despite being present only in this taxon.

67. Vein A1

- (0) present
- (1) absent

According to Pinto & Amorim (2000) (49:1), the absence of the vein A1 supports Bibionini. Here this character does not support Bibionini.

68. Anal lobe, shape

- (0) obtuse angled
- (1) acute angled

According to Skartveit & Willassen (1996) (13:1), the acute angled anal lobe supports *Dilophus*. Here this character does not support *Dilophus*.

69. Wing posterior veins of male

- (0) concolorous with anterior veins or nearly so
- (1) much lighter than anterior veins

This character was used by Skartveit & Willassen (1996) (76). Here the state 0 supports some clades within *Dilophus*.

70. Wing membrane color

(0) similar in both sexes

(1) female darker

According to Skartveit & Willassen (1996) (52:1), the wing membrane darker in females support (*D. febrilis* + *D. cf. antipedalis*). Here this character does not support this clade.

71. Halter knob

(0) brown to black

(1) yellow

72. Male abdominal spiracles VIII

(0) in front of epandrium

(1) in emarginations of anterior margin of epandrium

According to Skartveit & Willassen (1996) (15:1), the male abdominal spiracles VIII in emarginations of the anterior margin of epandrium supports *Dilophus*. Here this character does not support this clade.

73. Posterior margin of epandrium

(0) straight or slightly concave

(1) U-shaped cleft

(2) V-shaped cleft

(3) convex

According to Skartveit & Willassen (1996) (51:0), the straight posterior margin of epandrium supports (*D. beckeri* + *D. febrilis* + *D. cf. antipedalis*). According to Fitzgerald (2004b) (79:0), this condition supports *Dilophus*. Here a slightly modified version of this character is presented. Here this character does not support both clades.

74. Epandrium (proportion)

(0) wider than long

(1) longer than wide

(2) subquadrate

This character was used by Fitzgerald (2004b) (86). Here this character supports some clades within *Dilophus*.

75. Epandrium setae

(0) over most of its surface

(1) only near hind margin

According to Skartveit & Willassen (1996) (48:1), the presence of setae only near the hind margin of epandrium supports both (*D. hiemalis* + *D. tridentatus*) and (*D. humeralis* + *D. borealis* + *D. femoratus* + *D. beckeri* + *D. febrilis* + *D. cf. antipedalis*). Here this character does not support both clades.

76. Epandrium with long setae laterally

- (0) absent
- (1) present

77. Posterior margin of hypandrium/synsternogonocoxite; shape

- (0) straight or slightly concave
- (1) U-shaped cleft
- (2) V-shaped cleft
- (3) W-shaped cleft
- (4) convex

78. Deep narrow median cleft on hypandrium/synsternogonocoxite

- (0) absent
- (1) present

79. Hypandrium/synsternogonocoxite

- (0) undivided medially
- (1) medially divided

80. Gonostylus

- (0) simple
- (1) with small notch
- (2) bilobed or with large notch
- (3) trilobed

According to Pinto & Amorim (2000) (77:1), the bilobed gonostylus support *Bibiodes*. However, this condition is found in other taxa, including *Dilophus*. Here this character supports some clades within *Dilophus*.

81. Gonostylus apex

- (0) pointed
- (1) rounded
- (2) truncated

82. Gonostylus; shape

- (0) basally wide and becoming thinner towards the apex
- (1) subequally wide through the length
- (2) apex wide and becoming thinner towards the base, or just medially constricted
- (3) medially enlarged, wider than base and apex

According to Skartveit & Willassen (1996) (47:1), the expanded apically gonostylus supports (*D. hiemalis* + *D. tridentatus*). Here this character does not support this clade, but supports other clades within *Dilophus*.

83. Gonostylus; proportions

- (0) longer than wide
- (1) subquadrate

84. Gonostylus with cluster of long setae basally

- (0) absent
- (1) present

This character was used by Skartveit & Willassen (1996) (92).

85. Tergite 9 (proportion)

- (0) two times wider than long or shorter
- (1) more than two and less than three times wider than long
- (2) three to four times wider than long
- (3) more than four times wider than long

86. Posterior margin of Tergite 9

- (0) straight or nearly so
- (1) with a cleft

According to Skartveit & Willassen (1996) (5:1), the clefted tergite 9 of female supports Bibioninae

Here this character does not support this clade. This character was used by Pinto & Amorim (2000) (65).

87. Long lateral lobes of Tergite 9

- (0) absent
- (1) present

This character was used by Pinto & Amorim (2000) (66).

88. Tergite 9 laterally with long setae

- (0) absent
- (1) present

89. Female cerci

- (0) two-segmented
- (1) one-segmented

According to several studies, such as Blaschke-Berthold (1994) (8), Pinto & Amorim (2000) (72:1), and Fitzgerald (2004b) (137:1), the one-segmented cerci supports (*Plecia* + Bibioninae). Skartveit & Ansoerge (2020) (9:1) proposed that the same condition supports (*Plecia* + †*Cretobibio* + Bibioninae).

90. Female cerci (proportion)

- (0) two times wider than long or shorter
- (1) more than two and less than three times wider than long
- (2) three times wider than long or longer

91. Apex of female cerci

- (0) slender
- (1) rounded
- (2) pointed

According to Skartveit & Willassen (1996) (41:1), pointed cerci of female support (*D. bispinosus* + *D. tridentatus* + *D. lingens* + *D. hiemalis*) Here this character does not support this clade.

Discussion

The analysis resulted in three trees from which the strict consensus tree was obtained (Figure 1A-G). Some more inclusive clades described in the literature were recovered, and the relationships between the clades were as follows: *Hesperinus* + (*Penthetria* + (*Plecia* + (*Bibionini* + *Dilophini*))).

The monophyly of the Dilophini was well supported (14:1, 32:1, 56:1). However, *Dilophus* was not recovered as monophyletic, unless †*Protodilophus* is included in the genus. Then, the tribe becomes monotypic again. Both *D. febrilis*-group and “*D. bispinosus*-group” were not recovered in this analysis. Some more or less supported clades were recovered within *Dilophus* and will be discussed below, focusing on the ones with exclusive synapomorphies.

The clade containing *D. disagrus* and the subclade containing *D. flavicornis* (Fig. 1B) is supported by the single set of medial spines with four spines (35:1), although many terminals have more than one set of medial spines on fore tibiae. The clade containing the subclades that include *D. erythraeus* and *D. sardous* (Figs. 1C-D) is supported by male mid tibia with an apical circlet of spinose setae (45:1). The clade containing *D. trispinosus*, the subclade containing *D. arizonaensis* and “clade D” (Fig. 1D) is supported by spurs on hind tibia with microtrichia (50:1) and tergite 9 of female laterally with long setae (88:1). The clade *D. palaeofebrilis* + *D. segregatus* (Fig. 1E) is supported by the upper set of spines with a single spine (37:0). The clade *D. inconnexus* + *D. quinquespinae* (Fig. 1E) is supported by the absence of the posterior transverse row of male (22:1). The clade *D. spinipes* + (*D. obesulus* + *D. serotinus*) is supported by the apical circlet of spines with 10 spines (39:4). The “clade E” (Fig. 1F) is supported by the absence of microtrichia on the area posterior to prothoracic spiracles (31:0). Lastly, the clade *D. succineus* + *D. transvestis* (Fig. 1G) is supported by the female flagellum with 12 flagellomeres (5:3).

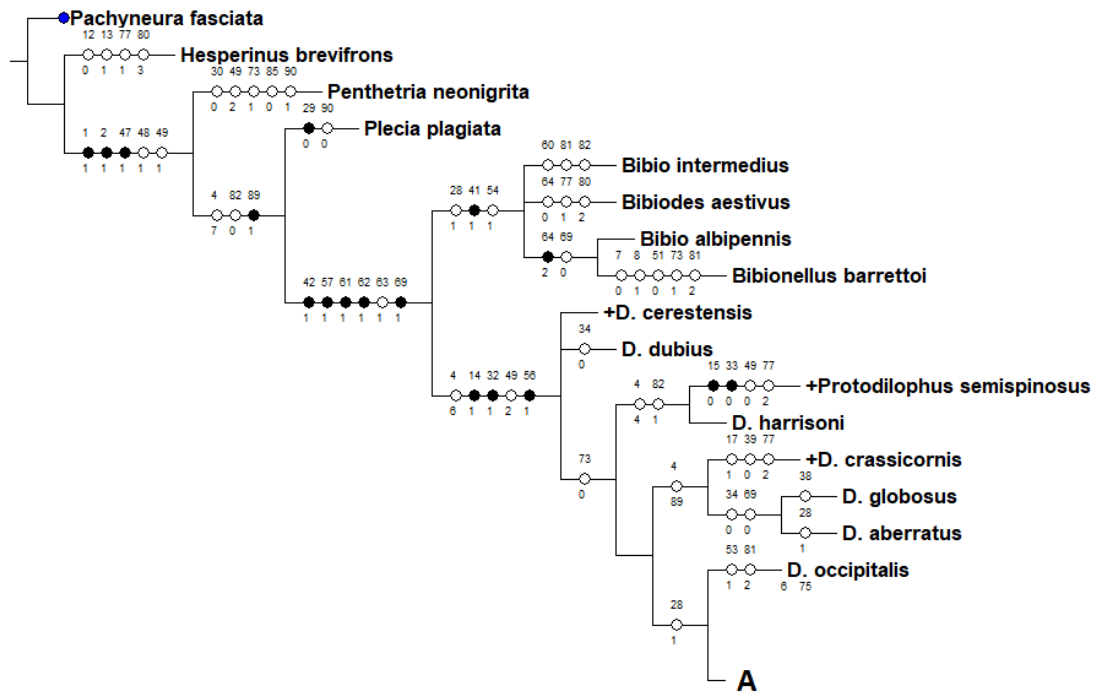


Figure 1. A. Distribution of characters in the strict consensus phylogenetic tree.

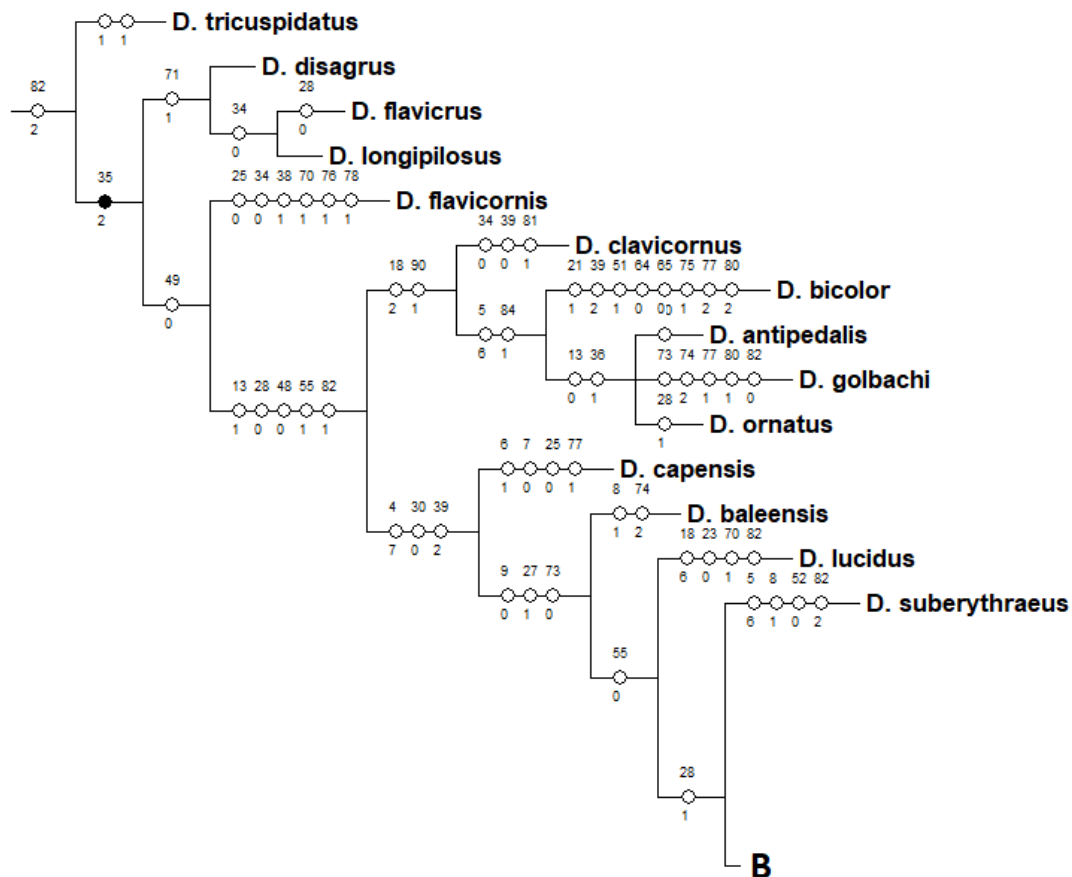


Figure 1. B. "Clade A" (continuation of the tree).

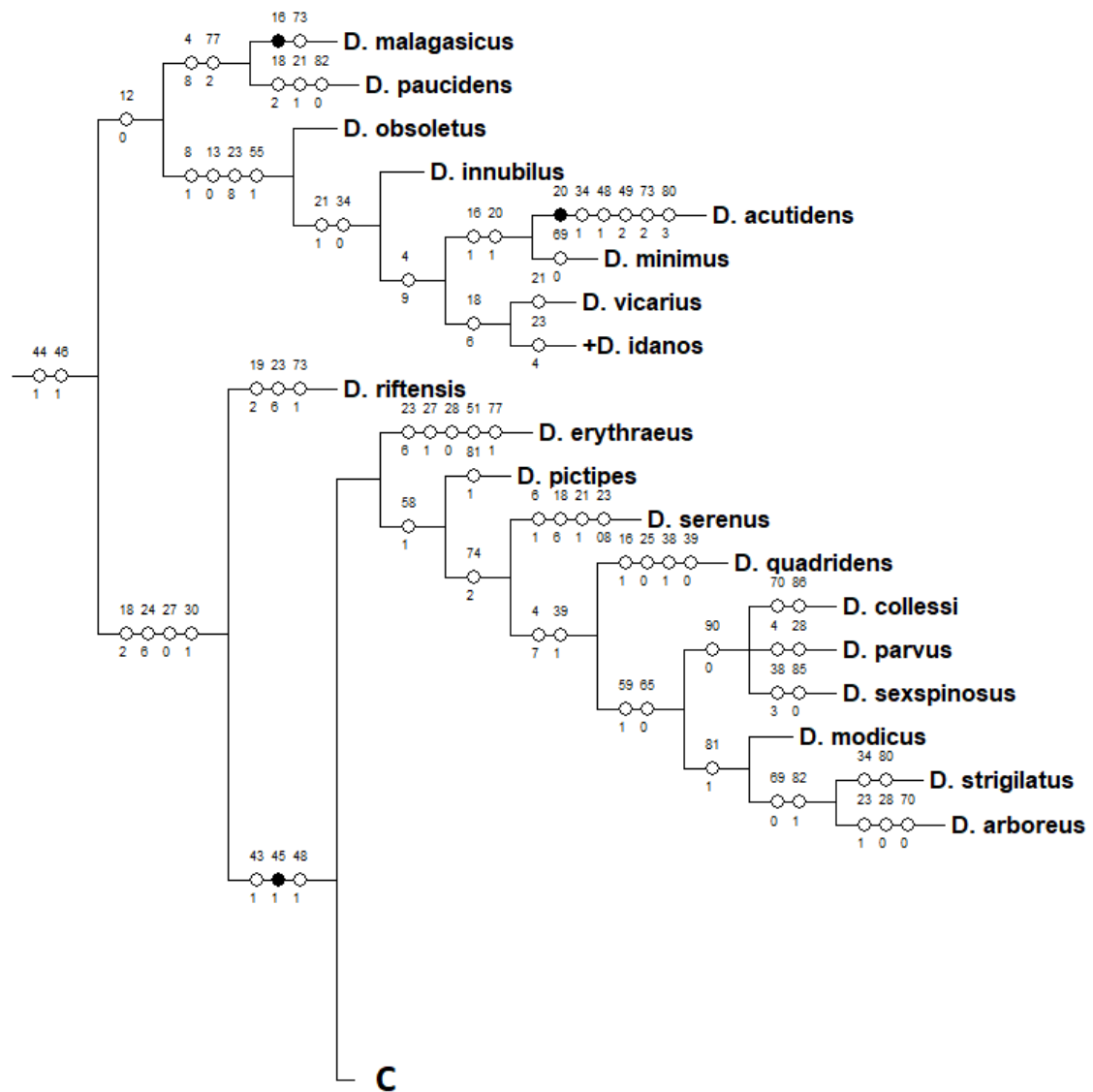


Figure 1. C. "Clade B" (continuation of the tree).

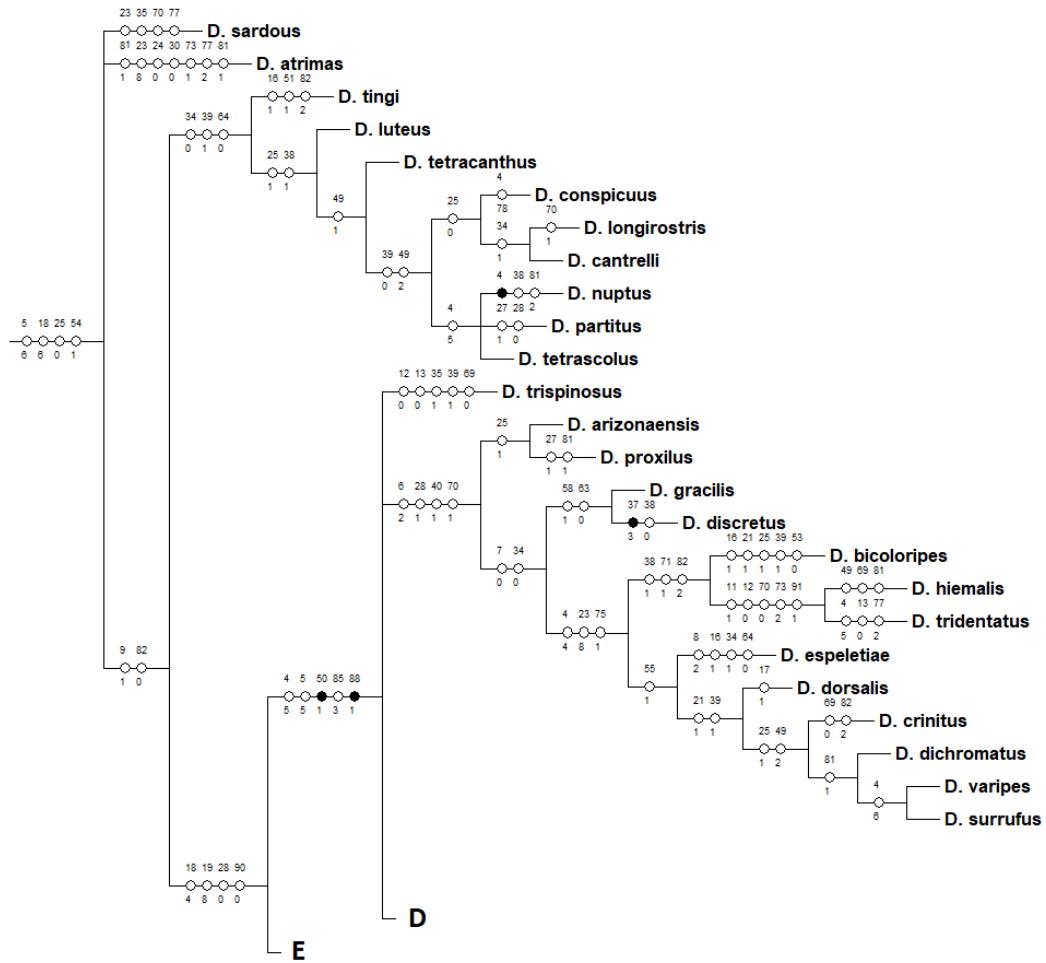


Figure 1. D. “Clade C” (continuation of the tree).

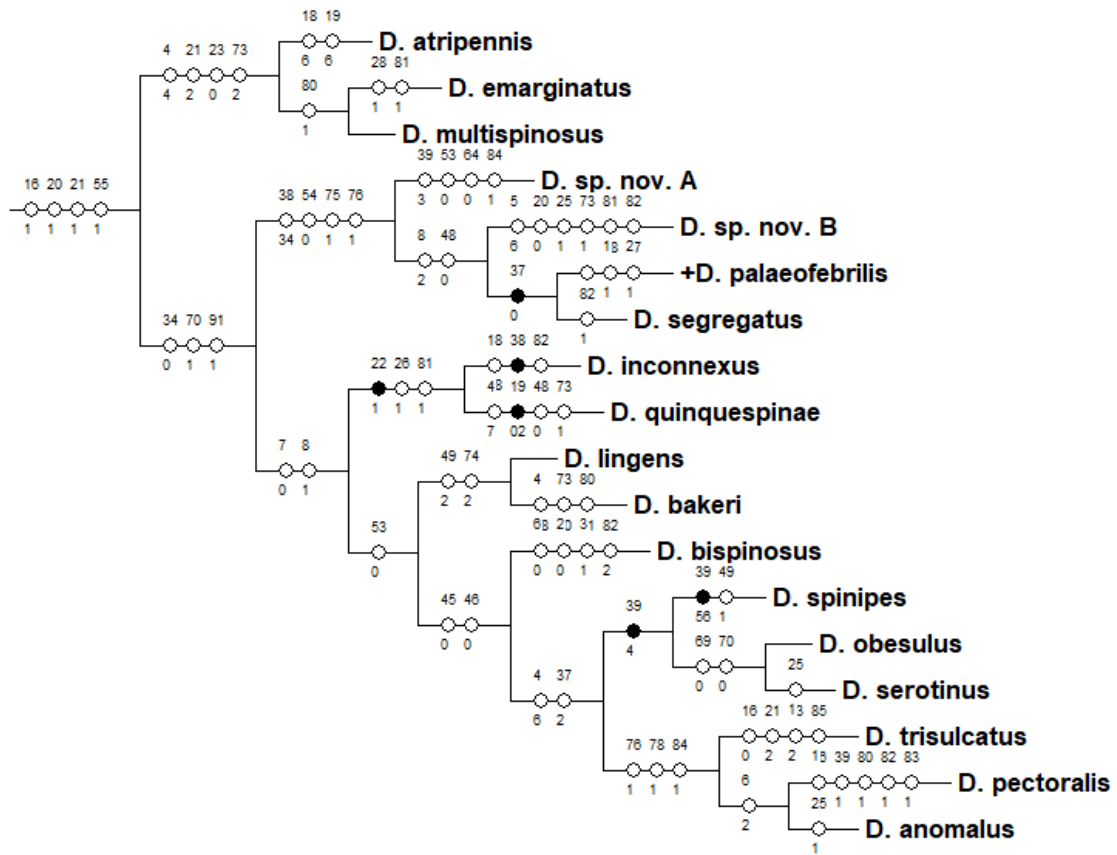


Figure 1. E. "Clade D" (continuation of the tree).

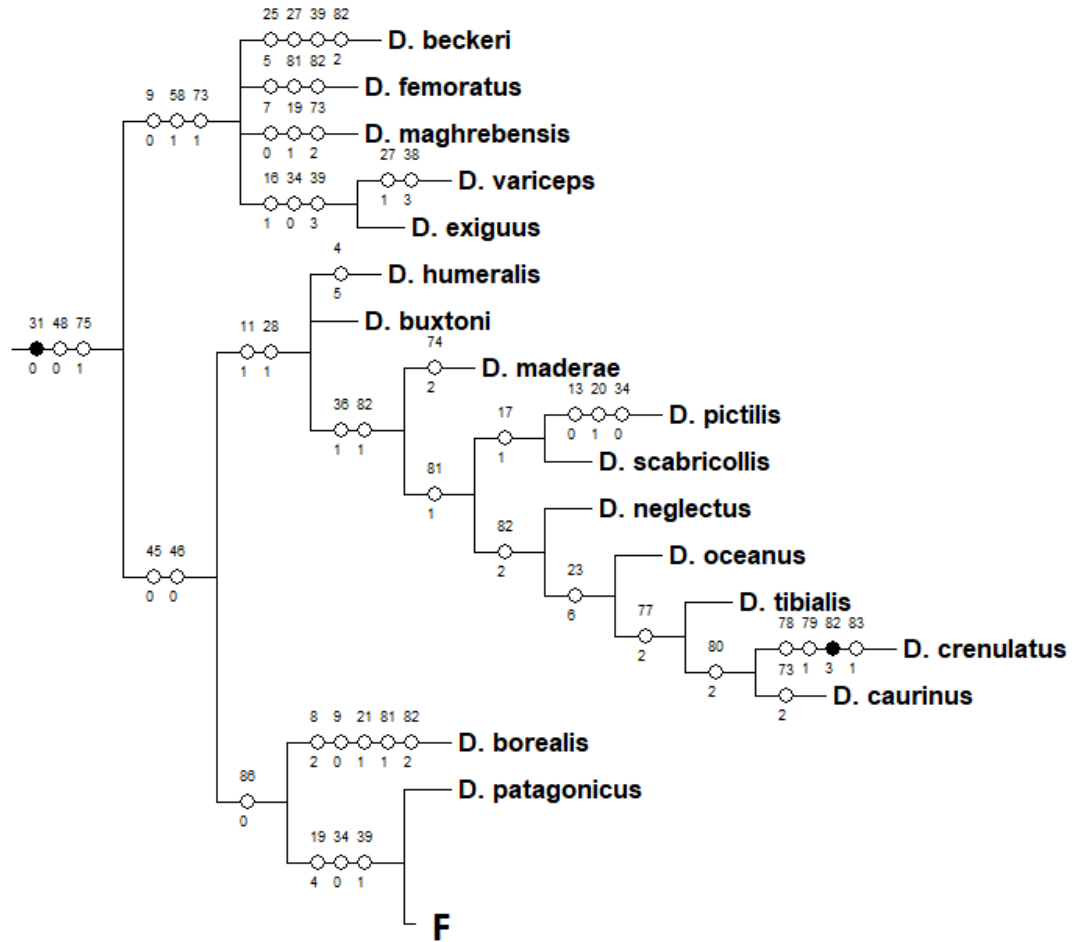


Figure 1. F. "Clade E" (continuation of the tree).

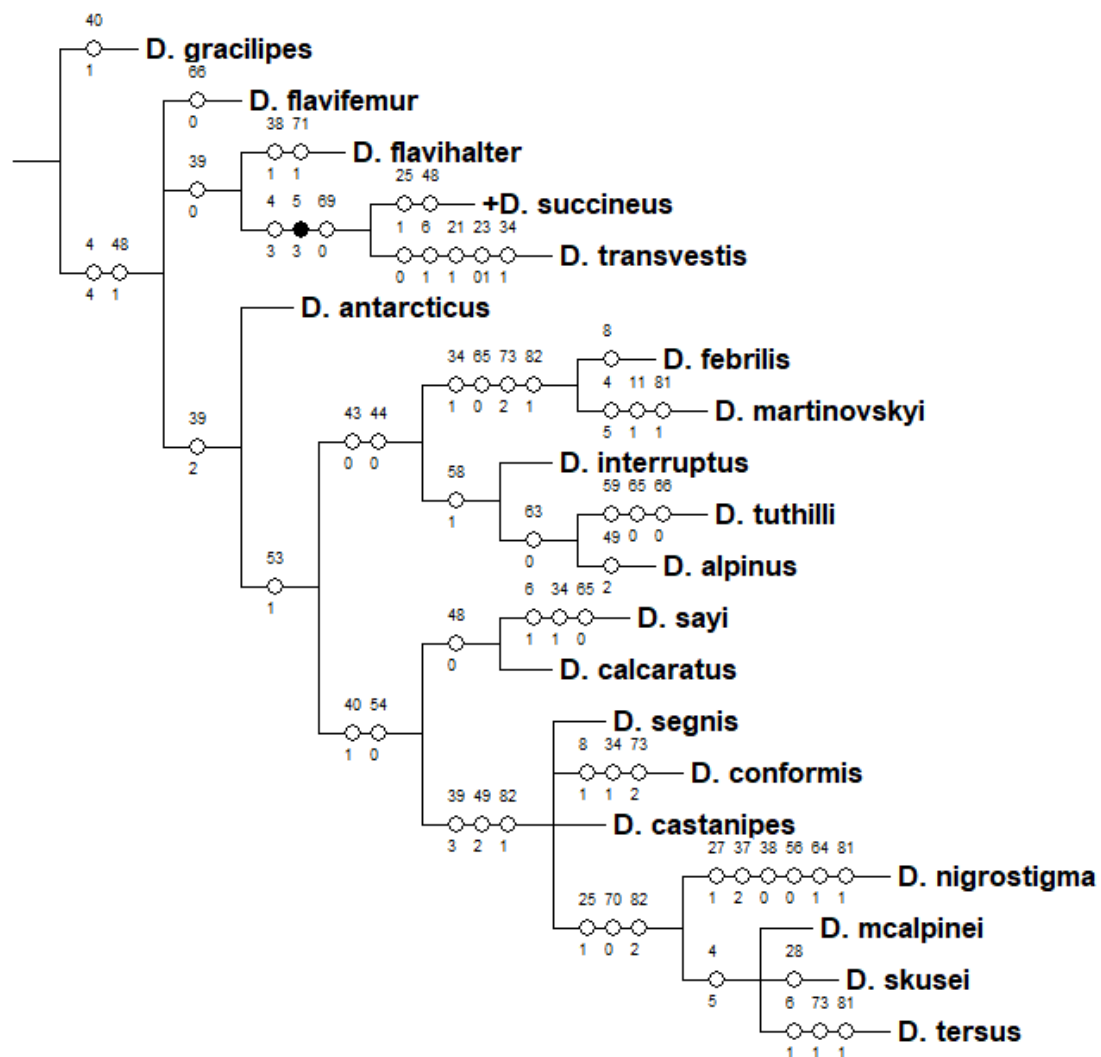


Figure 1. G. “Clade E” (continuation of the tree).

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References

Amorim, D. S. & L. G. Pinto. 2004. First known male of *Enicoscolus* (Diptera: Bibionidae), with a redescription of *E. brachycephalus*. *Zootaxa* 665: 1–8.

- Báez, M. 1984, Dipteros de Canarias. XII: Bibionidae. *Vieraea* 13 (1983):103-112.
- Blaschke-Berthold, U. 1994. Anatomie und Phylogenie der Bibionomorpha (Insecta: Diptera). *Bonner zoologische Monographien* 34. Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn. 206 pp.
- Duda, O. 1930. Bibionidae. In: *Die Fliegen der palaearktischen Region*. Vol. 2 (1), Fasc. 4. Edit. E. Lindner. Schweizerbart, Stuttgart. pp. 1-75.
- Edwards, F.W. (1938) Bibionidae (Diptera) collected by Mr. F. Plaumann in Brazil. *The Annals and Magazine of Natural History*, 11 (2), 321–330.
- Falaschi, RL, SS Oliveira & CJE Lamas, 2018. Catalogue of Bibionidae (Diptera: Bibionomorpha) types housed in the collection of the Museu de Zoologia da Universidade de São Paulo, Brazil. *Papéis Avulsos de Zoologia*, 58: e20185827. DOI: <https://doi.org/10.11606/1807-0205/2018.58.27>
- Fitzgerald, S.J. (1997). A Revision of *Biblio* (Diptera: Bibionidae) of Mexico and Central America. *Trans. Am. Ent. Soc.* 123(4): 225-287.
- Fitzgerald, S.J. (2004a) Bibionidae (Diptera) of New Caledonia. *Bishop Mus. Bull*, in *Entomol.* 12: 79-88.
- Fitzgerald, S.J. (2004b) Evolution and classification of Bibionidae (Diptera: Bibionomorpha). Ph.D. thesis, Oregon State University, Corvallis, Oregon, 385 pp.
- Fitzgerald, S.J. (2009) Bibionidae. In: Brown, B.V., Borkent, A., Cumming, J.M., Wood, D.M., Woodley, N.E. & Zumbado, M.A. (Eds.), *Manual of Central American Diptera*: Vol. 1. NRC Research Press, Ottawa, Ontario, 714 pp.
- Fitzgerald, S.J. (2021) *Penthetria* Meigen (Diptera: Bibionidae): Revision of New World species and world catalog. *Zootaxa*, 4926 (4), 451–500.
<https://doi.org/10.11646/zootaxa.4926.4.1>
- Fitzgerald SJ (2023) Capítulo 6: Bibionidae (Diptera) of Guatemala. In: Schuster JC, Yoshimoto J, Sierra JM (Eds) *Biodiversidad de Guatemala*, vol. 3, Universidad del Valle de Guatemala, Guatemala, 95–104 pp.
- Fitzgerald, S. J., C. R. González & M. Elgueta. 2020. A catalog of the Bibionidae (Diptera: Bibionomorpha) of Chile. *Zootaxa* 4766(1): 48–60.
- Fitzgerald, S.J. & Greenwalt, D.A. 2022. Family Bibionidae Fleming, 1821. In: Greenwalt, D.A., D. Des Souza Amorim, M. Hauser, P.H. Kerr, S.J. Fitzgerald, J.M. Cumming, N.L. Evenhuis & B.J. Sinclair, 2022. *Diptera of the Middle Eocene Kishenehn Formation II*. *Palaeontologica Electronica* 2 (2) (a22): 1-52.
- Goloboff, P.A. (1993) Estimating character weights during tree search. *Cladistics*, 9, 83–91. <http://dx.doi.org/10.1006/clad.1993.1003>
- Goloboff PA, Catalano SA. TNT version 1.5, including a full implementation of phylogenetic morphometrics. *Cladistics*. 2016 Jun;32(3):221-238. doi: 10.1111/cla.12160. Epub 2016 Apr 25. PMID: 34727670.
- Haenni, J.P. 1981. North African *Dilophus* Meigen, with description of *D. maghrebensis* n. sp. (Diptera: Bibionidae) *Entomologica Scandinavica* 12:429-432.

- Haenni, J.-P. 1982. Revision des espèces européennes du groupe de *Dilophus febrilis* (L.), avec description d'une espèce nouvelle (Diptera, Bibionidae). *Revue Suisse Zool.* 89(2): 337-354.
- Haenni, J.-P. 2009. The Bibionidae (Diptera) of Sardinia, with description of two new species. In P. Cerretti, F. Mason, A. Minelli, G. Nardi and D. Whitmore (Eds), *Research on the Terrestrial Arthropods of Sardinia (Italy)*. *Zootaxa* 2318: 427–439.
- Haenni, J.-P. & Báez, M. (2001) The Madeiran species of *Dilophus* Meigen (Diptera, Bibionidae). *Mitteilungen der Schweizerischen Entomologischen Gesellschaft*, 74(1–2), 85–90.
- Haenni, J.-P. and Bosák, J. 2007. An unusual new species of *Dilophus* (Diptera, Bibionidae) from Afghanistan. *Mitteilungen-Schweizerische Entomologische Gesellschaft*, 80(3/4):185.
- Hardy, D.E. (1942) Studies in New World *Philia* (Bibionidae) Part I. *Journal of the Kansas Entomological Society*, 15 (4), 127–134.
- Hardy, D.E. (1945) Revision of Nearctic Bibionidae, including Neotropical *Plecia* and *Penthetria* (Diptera). *The University of Kansas Science Bulletin*, 30, 367–547.
- Hardy, D.E. 1953a. The Argentine Bibionidae (Diptera). *Acta Zoológica Lilloana*, 12, 343–376.
- Hardy, D.E. 1953b. The Bibionidae of New Zealand (Diptera). *Pac. Sci.* 7(4): 513-521.
- Hardy, D.E. 1961a. Notes and descriptions of exotic Bibionidae. *Proceedings of the Entomological Society of Washington* 63(2): 81-99.
- Hardy 1961b. The Bibionidae of California. *Bulletin of the California Insect Survey* 6(7): 179-195.
- Hardy 1981. Bibionidae, p. 217-222. In: McAlpine, J.F., B., V. Peterson, G.E. Shewell, H.J. Teskey, JR. Vockeroth & D.M. Wood (coords.), *Manual of Nearctic Diptera*. Volume 1. Canada Department of Agriculture Research Branch Monograph 27.
- Harris, A.C. 1983. An Eocene larval insect fossil (Diptera: Bibionidae) from North Otago, New Zealand. *Journal of the Royal Society of New Zealand*, 13:93-105.
- Hennig, W. 1973. Diptera. in: Helmcke, J.-G., D. Stack and H. Wermuth (eds.): *Handbuch der Zoologie*, 4(2) 2/31, 337 pp. de Gruyter, Berlin and New York.
- iNaturalist community. Observations from <https://www.inaturalist.org> on May 2024.
- Iwata, K. & Nagatomi, A. (1981) Female terminalia of *Axymyia* and *Hesperinus* (Diptera, Axymyiidae and Bibionidae). *Kontyu*, 49 (4), 558–562.
- Krivosheina, NP, 1999. Fam. Hesperinidae. In: Lehr, PA (Ed.). *Opredelitel' nasekomykh Dal'nego Vostoka Rossii* [Keys to the insects of the Russian Far East], Diptera and Siphonaptera, 6: 130-134.
- Li, L.-W., Skibinska, K., Krzeminski, W., Wang, B. & Xiao, C.-T. (2021) A new March fly *Protopenhetria skartveiti* gen. nov. et sp. nov. (Diptera, Bibionidae, Plecinae) from mid-Cretaceous Burmese amber. *Cretaceous Research*, 127, 104924. <https://doi.org/10.1016/j.cretres.2021.104924>
- Maddison, W. P. and D.R. Maddison. 2011. Mesquite: a modular system for evolutionary analysis. Version 2.75 <http://mesquiteproject.org>

Melander, A. L. (1912). The dipterous genus *Bibiodes*. Bulletin of the American Museum of Natural History. 31: 337–341. R

National Center for Biotechnology Information (NCBI)[Internet]. Bethesda (MD): National Library of Medicine (US), National Center for Biotechnology Information; [1988]. Available from: <https://www.ncbi.nlm.nih.gov/> [Access in 27.X.2024].

Nel, A., Legal, S. & Coster, P., 2022, A new species of the March fly genus *Dilophus* Meigen, 1803 (Diptera: Bibionidae) from the Oligocene of Provence (France), *Palaeoentomology* 5 (4), pp. 347-353 : 348-349.

NIXON, K. C. (2002) WinClada, versão Asado 1.89. Publicado pelo autor, Ithaca, New York. Disponível em: <<http://www.cladistics.com/Downloads.html>>.

Paramonov NM, Salmela J. Pachyneuridae (Diptera): new data on the geographic range and designation of the lectotype of *Pachyneura fasciata* Zetterstedt, 1838. *Zootaxa*. 2016 Jun 2;4117(4):513-28. doi: 10.11646/zootaxa.4117.4.4. PMID: 27395190.

Pinto, L.G. and D.S. Amorim. 1997. Taxonomy and phylogeny of the Neotropical genus *Bibionellus* (Diptera: Bibionidae). *Iheringia, Sér. Zool., Porto Alegre* 83: 65-84.

Pinto, L.G. & Amorim, D.S. (2000) Bibionidae (Diptera: Bibionomorpha). *Morfologia e análise filogenética*. Holos, Ribeirão Preto, 98 pp.

Ševčík, J., Kaspřák, D., Mantič, M., Fitzgerald, S., Ševčíková, T., Tóthová, A., & Jaschhof, M. (2016) Molecular phylogeny of the megadiverse insect infraorder Bibionomorpha sensu lato (Diptera). *PeerJ*, e2563. <https://doi.org/10.7717/peerj.2563>

Ševčík, J., Skartveit, J., Krzeminski, W. & Skibinska, K. (2021) A peculiar new genus of Bibionomorpha (Diptera) with Brachycera-like modification of antennae from mid-Cretaceous amber of Myanmar. *Insects*, 12, 364 (11 pp.)

<https://doi.org/10.3390/insects12040364>

Skartveit, J. 1993. Description of *Dilophus borealis* sp. n. (Dipt.: Bibionidae) from Scandinavia. *Dipterological Research* 4: 3-11.

Skartveit, J., 2009. Fossil Hesperinidae and Bibionidae (Diptera: Bibionoidea) from Baltic amber. *Studia dipterologica*, 15, 3–42.

Skartveit, J. (2017) Bibionidae. In: Kirk-Spriggs, A.H. & Sinclair, B.J.(Eds.), *Manual of Afrotropical Diptera*. Vol. 2. Suricata 5. South African National Biodiversity Institute, Pretoria, pp. 497–504.

Skartveit J. 2023. When the past meets the present: the oldest known Bibioninae, and the youngest known Cretobibioninae (Diptera, Bibionidae) from mid-Cretaceous Myanmar amber. *Zootaxa*;5258(5):548-556. doi: 10.11646/zootaxa.5258.5.4

Skartveit, J. & Ansoerge, J. (2020) A new genus and subfamily of fossil Bibionidae (Diptera) from the Lower Cretaceous, with new classification of the Bibionidae. *Palaeoentomology*, 3 (2), 163–172.

Skartveit J. & Freidberg A. (2023) Revision of the genus *Dilophus* Meigen, 1803 (Diptera, Bibionidae) from the Afrotropical Ecozone. *Zootaxa*. 2023 Oct 27;5360(3):301-354. doi: 10.11646/zootaxa.5360.3.1

Skartveit, J. and F. Kaplan. 1996. The Bibionidae (Diptera) of Israel. *Israel J. of Ent.* 30: 71-90.

Skartveit, J. & Willassen, E. (1996) Phylogenetic relationships in Bibioninae (Diptera, Bibionidae). In Skartveit, J. Studies on the systematics and life histories of Bibioninae (Diptera, Bibionidae). Ph.D. dissertation. University of Bergen, Bergen, Norway.

Sturm, H. (1990) Eine neue Dilophus-Art (Insecta, Diptera, Bibionidae) aus den Hochanden Kolumbiens. Annalen des Naturhistorischen Museums in Wien, 91, 197–204.

Swofford, D.L. & Olsen, G. (1990) Phylogeny reconstruction. In: Hillis, D.M. & Moritz, C. (Eds.), Molecular Systematics. Sinauer, Sunderland, MA, pp. 411–501.

Appendix 1. Data matrix.

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										0	1	2	3	4	5		7				0
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2	0	0	0	5	5	-	-	0	?	0	0	0	1	0	0	-	-	-	-	-	-
3	1	1	0	5	5	0	1	?	?	0	0	1	0	0	-	-	-	-	-	-	-
4	1	1	0	7	6	0	1	0	1	0	0	1	0	0	-	-	-	-	-	-	-
5	1	1	0	8	8	0	1	0	1	0	0	?	?	0	-	-	-	-	-	-	-
6	1	1	?	7& 8	?	0	1	?	?	0	0	1	0	0	-	-	-	-	-	-	-
7	1	1	0	7	?	?	?	?	?	0	0	1	0	0	-	-	-	-	-	-	-
8	1	1	0	9	?	0	0	1	1	0	0	1	1	0	-	-	-	-	-	-	-
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10	1	1	1	4	?	0	1	1	1	1	0	1	0	1	1	?	?	?	?	?	?
11	?	?	?	?	?	0	1	1	1	?	?	?	0	1	1	?	?	?	?	?	?
12	1	1	?	6	?	?	?	?	?	1	0	1	?	1	1	0	0	?	?	?	0
13	1	1	?	6& 7	6	0	1	2	0	1	0	1	0	1	1	0	0	4	8	8	0
14	1	1	?	6	5	0	1	0	0	1	0	1	?	1	1	0	?	?	?	?	0
15	?	?	?	5	6	0	1	0	1	1	1	?	?	1	1	?	?	?	?	?	?
16	?	?	?	6	?	?	?	?	?	?	?	?	?	1	1	0	0	4	?	?	?
17	?	?	?	6	6	0	0	0	0	?	?	?	?	1	1	?	?	2	1	?	?
18	1	?	?	5	4	0	1	0	?	?	1	?	0	1	1	?	?	?	?	?	?
19	?	?	?	?	7	0	1	0	1	1	1	1	1	1	1	?	?	4	6	?	?
20	?	?	?	6	?	?	?	?	?	?	?	?	?	1	1	0	0	2& 5	?	?	?
21	1	1	?	3	?	?	?	?	?	?	?	1	0	1	1	?	?	4& 5	?	?	?
22	1	1	?	6	6	0	1	0	0	?	?	?	?	1	1	?	?	6	6	?	?
23	1	1	?	6	6	0	1	1	0	?	?	?	?	1	1	1	0	0	6	6	0
24	1	1	?	6& 7	7& 8	0	1	1	0	?	?	?	?	1	1	1	0	0	4	8	0
25	1	1	?	6	6	0	1	0	1	?	?	?	?	1	1	1	0	0	2	6&7&8	0
26	?	?	?	?	6	0	1	0	1	?	?	?	?	1	1	1	0	0	?	8	0
27	1	1	?	7	7	1	0	0	1	?	?	?	?	1	1	0	0	4	4	?	0
28	?	?	?	?	7	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	?
29	1	1	?	8	7	0	1	0	0	?	?	?	?	1	1	1	0	0	2	3&4&5& 6	0
30	1	1	?	7	7	0	1	0	?	?	?	?	?	1	1	0	0	6	8	?	0
31	1	1	?	8	7	0	1	0	?	?	?	?	?	1	1	1	2	0	4	6	0
32	1	1	?	6& 7	6& 7	0	1	1	?	?	?	0	0	1	1	0	0	4& 6	?	?	0
33	1	1	?	8	?	?	?	?	?	?	?	0	1	1	1	0	0	2	?	?	0
34	1	1	?	7	7	0	1	0	?	?	?	?	?	1	1	0	0	2	2	?	0
35	1	1	?	7	6	0	1	1	0	1	?	1	1	1	1	0	0	4	4	?	0
36	1	1	?	5	?	?	?	?	?	1	1	1	?	1	1	?	?	?	?	?	?
37	1	1	?	6	7	0	1	0	1	1	0	1	1	1	1	0	0	2	2	?	0
38	1	1	?	4	?	?	?	?	?	1	1	0	1	1	1	0	0	?	?	?	0
39	1	1	?	5	?	1	0	?	?	1	1	0	1	1	1	?	?	?	?	?	?
40	1	1	?	5	?	2	0	0	1	1	1	0	0	1	1	?	?	?	?	?	?
41	1	1	?	2& 3	?	0	1	0	1	?	?	?	?	1	1	0	0	6	6	?	0
42	1	1	?	9	?	?	?	?	?	?	?	?	?	0	1	1	0	0	6	?	0
43	?	?	?	6	?	?	?	?	?	?	?	?	?	1	?	1	1	?	?	?	?
44	1	1	?	8& 9	8	0	1	0	1	?	0	1	0	1	1	?	1	4	4	?	?
45	1	1	?	3	3	0	1	1	?	?	?	?	1	0	1	1	?	?	?	4	?
46	1	1	0	4	4	2	0	0	1	1	0	1	1	1	1	1	0	4	3&5	?	0

47	1	1	?	6	7	0	1	1	1	1	?	?	0	1	1	0	0	4&6	?	0	
48	1	1	?	6	5	2	0	1	1	1	?	1	1	1	1	0	A	C	?		
49	1	1	1	6	5	1	?	1	?	1	?	?	?	1	1	0	0	8	?	1	
50	1	1	?	4&5	5	0	1	0	1	1	0	?	?	1	1	1	0	?	?	1	
51	1	1	?	5	6	0	1	2	1	1	0	1	1	1	1	0&1	0	?	?	0	
52	?	1	?	7	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	
53	?	1	?	7	7	?	?	?	?	?	?	?	?	1	1	1	0	2&4	2&4	0	
54	?	1	?	8	?	1	?	0	?	?	?	?	?	1	1	0	0	6	?	0	
55	?	1	?	5	5	0	0	?	1	?	?	?	?	1	1	1	0	6&8	6&8	-	
56	1	1	?	5	5	?	1	2	?	1	?	?	?	1	1	1	0	4	?	1	
57	?	?	?	7	?	1	?	1	1	1	?	?	?	1	1	1	0	4	0&2	?	
58	1	?	?	?	?	2	0	2	?	1	?	1	1	1	1	1	0	?	4&6&8	0	
59	?	?	?	9	7	1	1	1	?	?	?	?	?	1	1	1	0	4	6	2	
60	?	1	?	6	?	?	?	?	?	?	?	?	?	1	1	1	0	4	?	1	
61	1	?	?	4	?	?	?	?	?	?	?	?	?	1	1	0	0	4	4	0	
62	?	1	?	6	?	1	?	1	?	?	?	?	?	1	1	0	?	?	?	0	
63	?	?	?	6	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	
64	?	?	?	6&7	?	?	?	?	?	?	?	?	?	1	1	0	0	4	?	0	
65	?	?	?	6	?	?	?	?	?	?	?	?	0	1	1	0	1	8	?	1	
66	?	?	?	6&7	?	?	?	?	?	?	?	?	?	1	1	1	0	0	4	?	0
67	?	?	?	?	6	1	1	2	?	?	?	?	1	1	1	0	1	?	?	0	
68	?	?	?	5	5	0	1	0	?	?	0	0	0	1	1	0	0	?	?	0	
69	?	1	?	?	5	2	?	?	?	?	?	?	?	1	1	1	0	6	?	?	
70	?	1	?	8&9	8&9	?	?	?	?	?	?	?	?	1	1	0	0	6	?	0	
71	?	1	?	8	6	0	1	?	?	1	0	1	0	1	1	0	0	6	?	0	
72	?	1	?	9	?	?	?	?	?	?	?	?	?	1	1	1	0	4	?	1	
73	?	?	?	?	6	0	?	0	?	?	?	?	?	1	1	1	0	?	6&8	?	
74	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	
75	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	
76	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	3&5	?	?	
77	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	4&5	?	?	
78	?	?	?	?	?	0	?	0	?	?	?	?	?	1	1	?	?	?	?	?	
79	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	0	0	1&2	2&4	0	
80	1	1	1	5	?	1	1	0	1	?	?	?	?	1	1	?	?	?	?	?	
81	1	?	1	6	?	?	?	?	?	1	1	1	?	1	1	?	?	?	?	?	
82	1	1	?	?	?	1	0	1	1	1	?	?	?	1	1	?	0	?	?	?	
83	?	?	?	?	?	0	?	?	?	?	?	?	?	1	1	0	0	?	?	?	
84	1	1	?	?	6	?	?	0	?	1	?	?	?	1	1	1	0	4&6	?	?	
85	1	?	?	9	?	?	?	?	?	?	?	?	?	1	1	0	0	6	?	0	
86	?	1	?	?	?	?	?	?	?	?	?	?	?	1	1	0	?	?	?	?	
87	1	1	1	4	4	?	?	0	1	?	?	?	?	1	1	?	?	?	?	?	
88	1	?	?	4	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	
89	1	?	?	4	?	0	1	?	?	?	?	?	?	1	1	?	?	?	?	?	
90	0	1	?	3	3	1	1	2	1	?	?	?	?	1	1	1	1	0	6	?	0
91	1	?	?	4	4	0	1	1	1	?	0	1	1	1	1	1	0	6	?	?	
92	1	1	?	4	4	2	0	0	1	1	?	?	?	1	1	1	0	6	?	?	
93	1	1	?	4	?	0	?	0	1	?	?	?	?	1	1	1	0	0&4	2&8	?	
94	?	1	?	?	6	2	0	0	?	1	?	1	1	1	1	?	?	?	?	?	
95	1	1	0	7&8	7&8	0	?	?	0	1	?	?	?	1	1	1	0	0	2	0&2	0
96	1	1	?	4	?	0	?	0	1	1	?	?	?	1	1	0	0	?	6	0	
97	1	1	?	6	?	?	?	?	?	?	?	?	?	1	1	1	0	?	?	0	
98	1	1	?	5	?	?	?	?	?	?	?	?	?	1	1	1	0	?	4	?	0
99	?	1	?	7	?	0	1	0	0	?	?	?	?	?	1	1	0	?	?	?	0
100	1	1	?	8	?	0	?	0	?	?	?	?	?	1	1	0	?	?	?	?	
101	1	1	?	8	?	?	?	?	?	?	?	?	?	1	1	0	?	?	?	?	
102	?	1	?	?	7	0	1	0	0	?	?	?	?	1	1	0	?	?	?	?	
103	?	1	?	7	?	0	1	0	?	?	?	?	?	1	1	0	?	?	?	?	

10	?	1	?	?	?	2	0	?	?	?	?	?	?	1	1	0	?	?	?	?	
4																					
10	1	?	?	4	4	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	
5																					
10	1	1	0	5	5	2	1	0	0	1	?	?	?	1	1	1	1	0	6	7&8	0
6																					
10	?	1	?	5	?	0	1	?	?	?	?	?	?	1	1	0	?	?	?	?	?
7																					
10	?	?	?	4	4	0	?	0	?	?	?	?	?	1	1	1	0	6	6		1
8																					
10	1	1	?	6	6	1	?	0	?	?	?	?	?	1	1	0	0	?	?	?	0
9																					
11	1	1	?	7&	?	0	1	?	?	?	?	?	?	1	1	1	0	?	?	?	?
0				8																	
11	?	1	?	6	?	0	1	?	?	?	?	?	?	1	1	0	?	?	?	?	?
1																					
11	?	1	?	?	?	0	?	?	?	?	?	?	?	1	1	0	?	?	?	?	?
2																					
11	?	1	?	?	?	0	1	?	?	?	?	?	?	1	1	0	?	?	?	?	?
3																					
11	?	?	?	5	?	0	?	0	?	?	?	?	?	1	1	0	0	6	?	?	?
4																					
11	?	1	?	?	?	?	0	?	?	?	?	?	?	1	1	0	?	?	?	?	?
5																					
11	?	1	?	6	?	?	?	?	?	?	?	?	?	1	1	0	?	?	?	?	?
6																					
11	1	1	?	5	4	1	0	0	1	1	0	1	1	1	1	0	?	?	?	?	?
7																					
11	1	1	?	5	?	0	?	0	?	1	?	1	1	1	1	0	?	?	?	?	0
8																					
11	?	?	?	?	?	0	?	?	1	?	?	?	?	1	1	0	?	?	?	?	?
9																					
12	1	1	?	?	4	0	1	?	1	1	?	?	?	1	1	0	0	?	8	?	?
0																					
12	?	?	?	?	4	0	1	0	1	1	?	?	?	1	1	1	?	?	8&E	?	?
1																					
12	1	1	?	4	4	2	?	0	?	1	?	?	?	1	1	0	1	4	?	?	?
2																					
12	?	?	?	?	4	0	1	0	1	?	?	?	?	1	1	0	?	?	?	?	?
3																					
12	1	1	?	4	4	0	1	0	1	1	?	?	?	1	1	0	?	4	?	?	?
4																					
12	1	1	?	6	5	0	1	0	1	1	?	?	?	1	1	0	?	4	4&6	?	?
5																					
12	1	1	?	?	?	?	?	?	?	1	?	?	?	1	1	0	?	?	?	?	?
6																					
12	1	1	?	?	?	0	1	0	1	1	?	?	?	1	1	0	0	?	?	?	0
7																					
12	1	1	?	6	6	0	1	0	1	1	?	?	?	1	1	0	?	4&	4&6	?	?
8																		6			
12	1	1	?	6	6	0	1	0	1	1	?	?	?	1	1	0	0	4	4		0
9																					

	21	2	23	24	25	26	27	28	2	3	3	3	3	3	3	3	3	37	38	39	40	
1	-	-	-	-	0	0	0	0	1	1	?	0	-	-	-	-	-	-	-	-	-	
2	-	-	-	-	0	0	?	?	?	?	?	0	-	-	-	-	-	-	-	-	-	
3	-	-	-	-	0	0	0	0	1	0	?	0	-	-	-	-	-	-	-	-	-	
4	-	-	-	-	0	0	0	0	0	?	?	0	-	-	-	-	-	-	-	-	-	
5	-	-	-	-	0	0	0	1	1	1	1	0	-	-	-	-	-	-	-	-	-	
6					0																	
					&																	
					1	0	0	1	1	1	?	0	-	-	-	-	-	-	-	-	-	
7	-	-	-	-	0	0	0	1	1	?	?	0	-	-	-	-	-	-	-	-	-	
8	-	-	-	-	0	0	0	1	1	?	?	0	-	-	-	-	-	-	-	-	-	
9	-	-	-	-	?	?	?	?	?	?	?	1	0	-	-	-	-	-	-	-	-	
1																						
0	?	?	?	?	0	0	0	?	1	0	0	1	1	1	2			1	-	-	2	?
1																						
1	?	?	?	?	?	?	?	?	?	?	?	1	1	1	2			?	-	-	?	?
1																						
2	0	0	?	?	1	?	1	0	?	?	0	1	1	1	0&1&2			0	-	-	1	?
1																						
3	1	0	4	8	0	0	0	0	?	?	0	1	1	1	2&3			0	-	-	2	?

1																					
4	?	0	?	?	0	?	?	?	?	?	0	1	1	1	2	0	-	-	2	?	
1																					
5	?	?	?	?	0	?	?	?	?	?	0	1	1	1	2&3	0	-	-	2	?	
1																					
6	?	?	C	?	?	0	?	1	?	?	?	1	1	1	2	1	-	-	2	?	
1																			0		
7																			&		
	?	?	4	6	0	0	0	?	?	?	?	1	1	1	2	?	-	-	2	?	
1																					
8	?	?	?	?	0	0	0	0	?	?	?	1	1	1	1&2	1	-	-	2	0	
1																					
9	?	?	C	7	0	0	0	?	?	?	0	1	1	1	2	1	-	-	2	?	
2			5&																		
0	?	?	6	?	?	0	?	1	?	?	?	1	1	1	2	1	-	-	2	?	
2																					
1	?	?	4	?	?	0	?	?	?	?	?	1	1	0	-	-	0	1	2	?	
2			A																		
2			&	6&7																	
	?	?	C	&8	0	0	0	1	?	?	?	1	1	1	1	0	-	-	?	?	
2																					
3	0	0	8	A	0	0	0	1	1	0	?	1	1	1	1&2	0	-	-	2	?	
2																					
4	0	0	4	4	1	0	1	0	1	0	?	1	1	1	1&2	0	-	-	2	?	
2			C																		
5	1	0	&E	C	1	0	0	0	?	?	?	1	1	1	2	0	-	-	2	?	
2																					
6	0	0	?	E	?	?	0	1	?	?	?	1	1	1	2	0	-	-	2	?	
2																					
7	0	0	4	6	0	0	0	0	1	0	?	1	1	1	2	0	-	-	2	?	
2																					
8	?	?	?	?	1	0	0	1	?	?	?	1	1	1	2	0	-	-	2	0	
2																					
9	0	0	6	5&6	1	0	1	0	?	?	?	1	1	1	2	0	-	-	2	?	
3																					
0	&		A																		
	1	0	&E	8	1	0	1	0	1	?	?	1	1	1	2	0	-	-	2	?	
3																					
1	0	0	4	8	1	0	1	1	1	0	?	1	1	1	2	0	-	-	2	?	
3			6&																		
2	0	0	8	?	1	0	1	?	1	0	?	1	1	1	1&2	0	-	-	2	?	
3																					
3	1	0	4	?	?	0	?	?	?	?	?	1	1	1	2	?	-	-	2	?	
3																					
4	0	0	6	6	?	0	0	1	1	1	?	1	1	1	2	0	-	-	2	?	
3																					
5	0	0	?	8	1	0	1	1	1	0	?	1	1	1	2	0	-	-	2	?	
3																					
6	?	?	?	?	?	?	?	?	?	?	?	1	1	1	0	-	-	1	1	2	?
3																					
7	0	0	4	4	1	0	?	?	1	1	?	1	1	0	-	-	2	0	0	?	
3																					
8	0	0	?	?	0	0	0	1	?	?	?	1	1	1	0	-	-	1	1	2	?
3																					
9	?	?	?	?	?	0	0	?	?	?	?	1	1	1	0	-	-	1	2	2	?
4																					
0	?	?	?	?	0	0	0	1	?	?	?	1	1	1	0	-	-	1	1	2	?
4																					
1	0	0	8	6	1	0	0	?	?	?	?	1	1	0	-	-	1	0	0	?	
4																					
2	0	0	8	?	?	0	?	1	?	?	?	1	1	0	-	-	1	1	2	?	
4																					
3	?	?	?	?	?	?	?	?	?	?	?	1	1	1	0&1	?	-	-	?	?	
4																					
4	?	?	?	2	0	?	?	0	?	?	?	1	1	1	1	0	-	-	0	?	
4																					
5	0	0	4	4	1	?	?	0	?	?	?	1	1	0	-	-	1	2	0	?	
4			6&																		
6	1	0	8	6&9	1	0	0	1	1	1	?	1	1	0	-	-	1	1	1	1	1
4			0&																		
7	0	0	2	?	0	0	0	1	1	1	?	1	1	0	-	-	1	1	1	0	0
4								0	0												
8								&	&											2&3&4	
	1	0	?	E	0	1	1	1	1	1	?	1	1	1	&5&6	0	-	-	1	1	1
4																					
9	2	0	E	?	0	0	0	0	?	?	?	1	1	1	2&3&4	0	-	-	?	?	?

5																	3		
0																	&	4	
	?	0	?	?	0	0	0	0	1	1	?	1	1	0	-	-	1	3	0
5	0							0									3		
1	&							&									&		
	1	0	?	?	1	0	1	0	1	0	?	1	1	0	-	-	1	4	0
5																			
2	?	?	?	?	?	0	?	0	?	?	?	1	1	1	2	1	-	-	0
5			2&																
3	0	0	4	2&4	0	0	0	1	?	?	?	1	1	0	-	-	1	1	0
5			8&																
4	1	0	A	?	1	0	0	1	1	1	?	1	1	1	2	0	-	-	2
5	1															0			2
5	&			C&												&			&
	2	1	0	E	0	1	0	0	1	1	?	1	1	0	-	-	1	5	?
5																		3	
6																		&	
	1	0	?	?	0	0	0	0	?	?	?	1	1	0	-	-	0	4	?
5																			
7	?	1	-	3&4	?	1	?	0	1	?	?	1	1	0	-	-	1	2	?
5				4&6															0
8	0	0	?	&8	0	0	0	0	1	1	?	1	1	1	2	0	-	-	2
5																			1
9	2	0	2	A	1	0	1	?	?	?	?	1	1	1	2&3	0	-	-	?
6																			?
0	1	0	4	?	?	0	?	0	?	?	?	1	1	0	-	-	1	1	?
6																			?
1	?	0	6	6	0	0	0	0	1	1	?	1	1	1	1	0	-	-	1
6					0														0
2					&														
	?	0	?	?	1	0	0	1	?	?	?	1	1	1	1	0	-	-	?
6																			?
3	?	?	?	?	1	0	1	0	?	?	?	1	1	1	1&2	0	-	-	1
6			6&																1
4	1	0	8	?	?	0	?	1	?	?	?	1	1	0	-	-	1	2	?
6																			?
5	0	0	2	?	?	0	?	1	?	?	?	1	1	0	-	-	1	2	?
6																			?
6	1	0	6	?	?	0	?	1	?	?	?	1	1	1	2	1	-	-	?
6	0																		0
7	&																		
	2	0	?	?	0	0	0	?	?	?	?	1	1	1	2&3&4	2	-	-	?
6																			0
8	0	0	?	?	0	0	?	0	1	?	?	1	1	1	1	0	-	-	?
6																			1
9																			?
	?	?	6	?	1	0	0	0	?	?	?	1	1	0	-	-	3	4	?
7																			2
0	?	0	6	?	1	0	0	0	?	?	?	1	1	0	-	-	1	3	?
7																			1
1	0	0	?	?	1	0	0	1	?	?	?	1	1	1	2	1	-	-	0
7																			
2	?	0	?	?	?	0	?	?	?	?	?	1	1	0	-	-	1	3	?
7																			2
3	?	?	?	?	?	?	1	?	?	?	?	1	1	0	-	-	1	3	?
7																			3
4	?	?	?	?	1	0	0	?	?	?	?	1	1	1	?	?	-	-	?
7																			?
5	?	?	?	?	0	0	0	1	?	?	?	1	1	1	?	?	-	-	?
7																			?
6	?	?	?	?	0	0	0	1	?	?	?	1	1	1	?	?	-	-	?
7																			?
7	?	?	?	?	0	0	0	1	?	?	?	1	1	1	?	?	-	-	?
7																			?
8	?	?	?	?	1	0	0	1	?	?	?	1	1	1	-	-	?	?	?
7																			?
9	?	0	4	?	1	0	0	1	?	?	?	1	1	1	2	0	-	-	?
8																			?
0	?	?	?	?	0	0	0	0	?	?	?	1	1	1	2	0	-	-	?
8																			?
1	?	?	?	?	1	0	?	1	?	?	?	1	1	1	?	0	-	-	4
8						0													5
2					&														&
	1	0	?	?	0	1	0	?	?	?	?	1	1	0	-	-	2	3	6

8					0															
3					&															
	?	?	?	?	1	0	0	1	?	?	?	1	1	1	?	-	-	-	?	?
8																				
4	?	?	?	?	0	0	0	1	?	?	?	1	1	0	-	-	1	2	1	?
8																				
5	1	0	4	?	?	0	?	?	?	?	?	1	1	0	-	-	1	1	2	?
8																	0			
6	?	?	?	?	1	0	0	1	1	1	?	1	1	0	-	-	1	2	?	?
8																				
7	?	0	?	?	1	0	1	0	1	0	?	1	1	0	-	-	2	0	3	1
8																				
8	?	?	?	?	1	0	0	0	1	1	?	1	1	0	-	-	1	2	?	1
8																				0
9	?	?	?	?	?	0	0	?	1	0	?	1	1	0	-	-	1	2	?	&
9																				1
0			A																	
	1	0	&																	
			C	?	0	0	?	1	1	0	?	1	1	1	2&3	0	-	-	?	?
9																				
1	?	?	?	?	0	0	?	?	?	?	?	1	1	1	2&3	0	-	-	?	?
9			8&																	
2	2	0	C	?	1	0	0	0	1	1	?	1	1	1	2	0	-	-	?	?
9																				2
3			A																	&
	2	0	&E	?	0	0	0	0	1	?	?	1	1	1	2&3&4	0	-	-	3	1
9					0															
4					&															
	?	?	?	?	1	0	0	1	?	?	?	1	1	1	2	?	-	-	?	0
9																				
5	0	0	1	2&3	?	0	0	0	?	?	?	1	1	0	-	-	1	2	1	?
9																				1
6																				&
	0	0	?	4	0	0	?	0	1	1	?	1	1	0	-	-	1	2	?	0
9					0															
7					&															
	0	0	?	?	1	?	0	?	1	1	?	1	1	0	-	-	1	2	3	0
9																				
8	?	0	4	?	?	0	?	?	?	?	?	1	1	0	-	-	1	2	?	?
9					0															
9					&															
	?	0	?	?	1	0	1	1	?	?	?	1	1	0	-	-	1	2	?	?
1					0															
0					&															
	?	?	?	?	1	0	?	0	?	?	?	1	1	0	-	-	1	2	?	?
1																				
0																				
1	?	?	?	?	1	0	?	1	?	?	?	1	1	0	-	-	1	2	?	?
1																				
0																				
2	?	?	?	?	?	?	0	?	?	?	?	1	1	0	-	-	1	3	?	?
1																				
0																				
3	?	?	?	?	1	0	?	1	?	?	?	1	1	0	-	-	1	2	?	?
1					0															
0					&															
4	?	?	?	?	1	0	0	1	?	?	?	1	1	0	-	-	3	0	?	?
1																				
0																				
5	?	?	?	?	?	0	1	?	?	?	?	1	1	0	-	-	?	?	?	?
1																				
0																				
6	0	0	?	9	1	0	1	1	?	?	?	1	1	1	1&2	?	-	?	2	1
1																				
0																				
7	?	?	?	?	1	0	1	0	1	?	?	1	1	0	-	-	1	1	?	?
1																				
0																				
8	2	0	0	0	0	0	0	0	1	0	?	1	1	1	2	0	-	-	?	0
1																				
0																				
9	?	0	?	?	0	0	0	1	?	?	?	1	1	1	2	0	-	-	?	?
1																				
1																				
0	?	?	?	?	0	0	?	1	1	?	?	1	1	0	-	-	1	0	0	0

1																					
1																					
1	?	?	?	?	0	?	?	0	?	?	?	1	1	0	-	-	1	2	?	?	
1																					
1																					
2	?	?	?	?	1	?	0	0	1	?	?	1	1	0	-	-	1	2	?	?	
1																					
1																					
3	?	?	?	?	1	?	?	1	?	?	?	1	1	0	-	-	1	2	?	?	
1																					
1																					
4	?	?	2	?	1	?	0	0	?	?	?	1	1	0	-	-	1	2	?	?	
1																					
1					0																
1					&																
5	?	?	?	?	1	0	0	1	?	?	?	1	1	0	-	-	1	2	?	?	
1																					
1																					
6	?	?	?	?	?	?	?	0	1	?	?	1	1	0	-	-	1	2	?	?	
1																					
1																					
7	?	?	?	?	1	0	0	0	1	?	?	1	1	0	-	-	1	2	?	?	
1																					
1																					
8	?	0	?	?	1	0	0	1	1	?	?	1	1	0	-	-	1	1	?	?	
1																					
1																					
9	?	?	?	?	?	?	0	?	?	?	?	1	1	0	-	-	1	2	2	?	
1																					
2																					
0	1	0	?	8	0	0	0	0	1	1	?	1	1	0	-	-	1	2	2	1	
1																					
1																					
2																					
1	0	0	?	?	?	?	?	?	?	?	?	1	1	0	-	-	1	2	3	1	
1																					
2																					
2	1	0	6&	8	?	0	?	?	1	?	?	?	1	1	0	-	-	1	2	1	1
1																					
2																					
3	?	?	?	?	?	?	0	0	?	?	?	1	1	0	-	-	1	2	1	0	
1																					
2																					
4	0	0	4	?	0	?	?	1	?	?	?	1	1	0	-	-	1	1	0	0	
1																					
2																					
5	?	?	4	4&6	?	0	?	0	1	1	?	1	1	0	-	-	1	2	1	1	
1																					
2																					
6	?	?	?	?	?	?	?	0	1	1	?	1	1	0	-	-	1	2	?	?	
1																					
2									0												
7	0	0	?	?	1	?	?	1	1	?	?	1	1	0	-	-	1	1	?	0	
1																					
2									0												
8	?	?	4&	6	4&6	1	?	?	1	1	1	?	1	1	0	-	-	1	1	1	0
1																					
2																					
9	0	0	4	4	0	?	?	0	1	1	?	1	1	0	-	-	1	2	1	0	

	4	4	4	4	4	4	4	4	48	49	5	5	5	5	5	55	5	5	5	5	6
1	0	0	0	0	0	0	0	0	0	0	?	1	0	0	0	0	?	0	0	0	0
2	0	0	?	?	?	?	0	0	0	0	?	0	0	0	0	0	?	0	0	0	0
3	0	0	?	?	?	?	1	1	2	?	?	0	0	1	0	0	?	0	0	0	0
4	0	0	0	0	0	0	1	1	1	?	?	0	0	1	0	0	0	0	0	0	0
5	1	1	1	1	0	0	1	1	1	0	1	0	0	0	1	0	?	1	0	0	0
6									0&	0&1&											
	1	1	?	?	?	?	?	1	2	?	1	?	1	?	0	?	?	1	0	0	1
7	1	1	?	?	?	?	1	1	1	?	1	0	?	1	0	?	?	1	0	0	-
8	1	1	?	?	?	?	1	1	1	?	?	0	0	0	1	0	0	1	0	0	?
9	0	1	?	?	?	?	?	?	0	?	?	0	0	?	0	0	?	1	?	?	1
10	0	1	0	0	0	0	1	?	0	0	0	1	1	1	0	?	?	1	0	0	2
11	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?
12	0	1	1	1	1	1	1	0	0	0	0	?	1	?	?	?	?	1	?	?	2
13	0	1	1	1	0	0	1	0	0	0	0	?	0	?	?	?	?	1	?	?	2

14	0	1	1	1	1	1	1	0	0	0	0	?	0	1	0&	?	1	1	0	2	
15	0	1	1	1	0	0	1	0	0	0	0	?	0	?	?	?	1	?	?	2	
16	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	
17	0	?	?	?	?	?	?	0	0	?	0	?	?	?	?	?	1	?	?	?	
18	0	1	?	?	?	?	1	1	0	?	0	?	1	?	0	?	1	?	?	2	
19	0	1	1	1	0	0	1	0	0	0	0	?	0	?	?	?	1	?	?	2	
20	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	
21	0	1	?	?	?	?	1	?	0	?	0	?	?	?	0	?	1	0	0	2	
22	0	1	?	?	?	?	1	1	0	?	0	?	0	1	0	?	1	0	0	2	
23	0	1	?	?	?	?	1	?	?	?	0	1	0	1	?	?	1	0	0	2	
24	0	1	0	0	0	0	1	0	0	?	0	1	0	1	1	?	1	0	0	2	
25	0	?	0	0	0	0	1	0	1	?	1	1	?	?	1	?	1	0	0	2	
26	0	1	?	?	?	?	?	?	?	?	0	1	?	1	0	?	1	0	0	2	
27	0	1	0	0	0	0	1	0	0	?	0	1	0	?	1	?	1	0	0	2	
28	0	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	1	?	?	?	
29	0	?	?	1	1	?	1	1	0	?	1	1	0	?	?	?	1	0	0	2	
30	0	1	0	0	0	0	1	0	0	?	0	1	0	?	0	?	1	0	0	2	
31	0	1	0	?	0	?	1	0	0	?	0	1	0	?	0	?	1	0	0	2	
32	0	1	0	1	0	1	1	0	0	?	0	1	0	?	1	?	1	0	0	2	
33	0	?	?	?	0	?	1	0	0	?	0	?	0	?	0	?	1	0	0	2	
34	0	1	0	1	0	1	1	0	?	?	0	1	0	0	0	?	1	0	0	2	
35	0	1	0	0	0	0	1	0	0	?	0	0	0	0	0	?	1	0	0	2	
36	0	1	1	1	0	0	1	0	0	1	0	?	0	?	?	?	1	?	?	2	
37	0	1	0	0	0	0	1	0	0	?	0	?	0	?	1	?	1	?	?	2	
38	0	1	1	1	1	1	1	1	2	1	0	?	1	?	0	?	1	0	0	2	
39	0	1	1	1	1	1	1	1	2	1	0	?	0	?	?	?	1	?	0	2	
40	0	1	1	1	1	1	1	1	0	1	0	?	1	?	?	?	1	?	?	2	
41	0	1	?	?	?	?	1	1	2	?	0	1	?	?	?	?	1	?	?	2	
42	0	?	?	?	?	?	1	0	0	?	0	1	0	?	?	?	1	0	0	2	
43	0	1	?	?	?	?	1	1	2	?	1	?	?	?	0	?	1	?	?	0	
44	0	1	?	?	?	?	1	1	2	?	0	?	?	0	0	?	1	?	?	2	
45	0	1	?	?	?	?	1	0	0	?	0	?	0	?	?	?	1	?	?	?	
46	0	1	1	1	1	1	1	1	0	?	0	1	0	?	0	?	1	0	0	2	
47	0	1	0	?	0	?	1	1	0	?	0	1	0	?	0	?	1	0	0	2	
48	0	1	1	1	0	0	1	1	0	?	0	1	0	1	1	?	1	0	0	2	
49	0	?	?	?	?	?	1	?	0	?	0	1	?	1	1	?	1	0	0	2	
50	0	1	1	1	?	1	1	1	0	?	0	1	0	0	1	?	1	0	0	2	
51	0	1	?	1	1	?	1	0	0	?	0	?	?	?	?	?	1	0	0	2	
52	0	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	1	0	0	?	
53	0	?	?	?	?	?	?	?	?	?	0	?	?	0	0	?	1	1	0	2	
54	0	?	?	?	?	?	?	?	0	?	0	?	?	?	?	?	1	1	0	?	
55	0	?	?	?	?	?	1	1	?	?	0	?	1	?	?	?	1	0	0	?	
56	0	1	?	?	?	?	1	0	0	?	0	?	1	0	?	?	1	?	0	2	
57	0	?	?	?	?	?	?	0	0	?	0	?	1	?	?	?	?	?	?	?	
58	0	?	?	1	?	1	?	?	?	?	0	1	?	1	1	1	1	0	0	2	
59	0	?	?	?	?	?	1	1	2	?	0	?	1	?	?	?	1	0	0	2	
60	0	?	?	?	?	?	1	1	2	?	0	?	?	?	?	?	1	?	?	?	
61	0	?	0	?	0	?	1	1	2	?	0	?	0	?	?	?	1	0	0	?	
62	0	?	?	?	?	?	?	?	2	?	?	?	?	?	?	?	1	1	0	0	?
63	0	?	?	?	?	?	?	1	2	?	0	?	?	?	1	1	1	?	?	?	
64	0	?	?	?	?	?	?	0	0	?	0	?	0	0	1	?	1	0	0	2	
65	0	?	?	?	?	?	?	?	?	?	?	?	0	?	0	?	1	?	?	?	
66	0	?	?	?	?	?	?	?	0	?	?	?	1	?	?	?	1	?	?	?	
67	0	?	?	?	?	?	1	?	?	?	0	?	?	?	?	?	1	?	?	?	
68	0	?	?	?	?	?	1	1	0	?	0	?	?	?	?	?	1	?	?	2	
69	0	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	1	?	?	?	
70	0	?	?	?	?	?	?	1	2	?	?	?	?	?	?	?	1	?	?	?	
71	0	1	?	?	?	?	?	?	?	?	0	1	0	?	?	?	1	0	0	2	
72	0	?	?	?	?	?	?	0	0	?	?	?	?	?	?	?	1	?	?	?	
73	0	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	1	?	?	?	
74	0	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	1	?	?	2	
75	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	2	
76	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	2	
77	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	2	
78	0	?	?	?	?	?	?	?	?	?	0	0	1	1	0	?	1	0	0	2	
79	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	2	
80	0	1	?	?	?	?	1	0	0	?	0	?	?	0	0	?	1	0	0	2	
81	0	1	1	1	0	0	?	?	0	1	0	?	1	1	?	?	1	?	?	2	
82	0	1	?	?	?	?	1	1	1	?	0	?	0	?	?	?	1	0	0	2	
83	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	2	
84	0	?	?	?	?	?	?	?	?	?	1	1	?	?	0	?	1	0	0	2	
85	0	?	?	?	?	?	?	?	?	?	0	?	?	0	?	?	1	0	0	2	
86	0	?	?	?	?	?	?	?	2	?	?	?	0	?	?	1	1	0	0	?	
87	0	1	?	?	?	?	1	1	2	?	?	0	?	?	0	1	0	1	0	2	
88	0	?	1	?	?	?	1	1	2	?	0	?	1	1	1	1	1	0	0	2	

89	0	?	1	?	?	?	1	1	2	?	0	?	1	?	?	?	1	0	0	2
90	0	?	?	?	?	?	1	1	0	?	?	?	?	?	?	?	1	0	0	?
91	0	?	?	?	?	?	1	1	2	?	0	?	1	?	?	?	1	0	0	?
92	0	?	?	?	?	?	?	1	2	?	0	?	1	?	?	?	1	0	0	?
93	0	?	1	?	1	?	?	0	0	?	0	?	1	?	?	?	1	0	0	?
94	0	?	?	?	?	?	?	?	2	?	0	?	?	?	?	?	1	?	?	?
95	0	1	?	?	?	?	1	1	0	?	0	?	0	0	0	1	1	1	1	2
96	0	1	0	?	0	?	1	1	0	?	0	1	1	1	1	?	1	1	1	2
97	0	?	?	?	?	?	?	0	0	?	0	?	?	?	?	?	1	1	?	?
98	0	1	1	?	?	?	1	1	0	?	0	1	?	1	0	?	1	1	0	2
99	0	?	1	1	1	1	?	?	0	?	0	?	?	1	1	1	1	1	1	2
100	0	?	?	?	?	?	?	?	0	?	?	?	?	?	?	1	1	1	?	?
101	0	?	?	?	?	?	?	?	0	?	0	?	?	?	?	1	1	1	?	?
102	0	?	?	1	?	?	?	?	?	?	?	?	?	?	?	1	1	1	?	?
103	0	?	?	?	?	?	?	?	0	?	?	?	?	?	?	1	1	1	?	?
104	0	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	1	1	?	?
105	0	1	0	0	0	0	1	1	2	?	0	?	?	?	?	?	1	1	0	2
106	0	?	?	?	?	?	?	1	1	?	?	?	1	1	0	1	1	0	0	2
107	0	?	?	?	?	?	?	?	2	?	?	?	?	?	?	1	1	0	0	?
108	0	?	?	?	?	?	?	?	0	?	0	?	?	1	1	1	1	0	0	2
109	0	?	?	?	?	?	1	1	2	?	?	?	?	?	?	?	1	0	0	?
110	0	?	?	?	?	?	?	1	2	?	?	?	?	?	?	0	1	0	0	?
111	0	?	?	?	?	?	?	?	2	?	?	?	?	?	?	1	1	0	?	?
112	0	?	?	?	?	?	?	?	2	?	?	?	?	?	?	1	1	0	?	?
113	0	?	?	?	?	?	?	?	2	?	?	?	?	?	?	1	1	0	?	?
114	0	?	?	?	?	?	1	1	2	?	0	?	?	?	?	1	1	0	0	2
115	0	?	?	?	?	?	?	?	2	?	?	?	?	?	?	1	1	?	?	?
116	0	?	1	?	1	?	1	1	2	?	?	?	?	?	?	1	1	?	?	?
117	0	?	?	?	?	?	?	?	2	?	?	?	1	?	?	1	1	0	0	?
118	0	1	1	?	1	?	1	1	2	?	0	?	0	?	?	1	1	0	0	2
119	0	1	?	?	?	?	?	?	?	?	0	1	0	1	?	?	1	?	0	2
120	0	?	?	?	?	?	1	0	0	?	0	1	1	?	0	1	1	0	0	2
121	0	?	?	1	?	?	?	?	?	?	0	1	?	?	?	1	1	0	0	2
122	0	1	?	?	?	?	?	1	0	?	?	?	1	?	?	?	1	?	?	?
123	0	?	?	?	?	?	?	?	?	?	0	1	0	?	?	1	1	0	0	2
124	0	1	1	?	?	?	1	1	0	?	0	1	0	1	0	1	1	0	0	2
125	0	1	1	1	?	?	1	0	0	?	0	1	0	?	?	1	1	0	0	2
126	0	1	?	?	?	?	1	1	0	?	0	1	1	?	0	1	1	1	0	2
127	0	1	?	?	?	?	1	1	0	?	0	1	0	?	0	1	1	0	0	2
128	0	1	1	?	?	?	1	1	1	?	0	1	0	?	0	1	1	0	0	2
129	0	1	?	?	?	?	1	0	0	?	0	1	0	?	?	1	1	0	0	2

	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
1	0	0	0	-	0	0	1	0	0	0	?	-	0	0	0	?	3	1	0	0

2	0	0	0	-	0	0	0	0	0	0	0	-	2	?	0	?	1	0	0	3		
3	0	0	0	-	0	0	0	?	0	0	0	-	1	0	0	1	3	0	0	0		
4	0	0	0	-	0	0	0	0	0	0	0	-	2	0	0	0	3	0	0	0		
5	1	1	1	2	0	1	?	0	0	0	?	0	2	0	0	?	3	0	0	0		
6	1	1	1	1	0	?	?	?	1	0	?	?	1&2	0	?	?	?	0	0	0		
7	-	1	1	0	0	1	0	0	1	?	0	-	?	0	?	?	1	0	0	2		
8	1	1	1	2	0	1	1	0	0	?	?	?	1	0	0	?	?	0	0	0		
9	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	0	0	0		
10	1	1	1	0&1	0	1	0	1	1	1	?	1	2	0	1	?	3	0	0	0		
11	?	?	?	?	?	?	?	?	?	1	?	1	1	0	?	?	3	0	0	0		
12	1	?	?	?	?	?	?	?	1	1	0	0	1	1	0	1	0	3	0	0	0	
13	?	?	?	?	?	?	?	?	1	1	0	0	1	0	0	1	?	3	?	0	0	
14	1	1	1	1	1	?	?	?	1	1	0	?	1	1	0	1	?	3	0	0	0	
15	?	?	?	?	?	?	?	?	1	1	0	0	1	0	0	1	?	3	0	0	0	
16	?	?	?	?	?	?	?	?	?	1	?	?	0	2	?	?	0	3	0	0	0	
17	?	?	?	?	?	?	?	?	?	1	0	0	1	2	0	?	?	?	0	0	0	
18	1	1	1	?	0	?	?	?	1	1	?	?	2	0	?	?	?	3	0	0	0	
19	?	?	?	?	?	?	?	?	1	1	0	0	1	0	0	0	?	3	0	0	0	
20	?	?	?	?	?	?	?	?	?	1	?	?	0	0	?	?	?	3	0	0	0	
21	1	?	?	?	?	0	?	?	1	?	?	?	0	?	?	?	?	1	0	0	0	
22	1	1	1	1	1	?	?	?	1	1	1	0	1	0	0	?	?	1	0	0	0	
23	1	1	1	1	1	1	0	1	1	0	0	?	1	0	0	?	2	0	0	0	0	
24	1	1	1	0	1	1	0	1	1	0	0	?	0	2	0	0	3	0	0	0	0	
25	1	1	1	0	0	1	0	?	?	0	0	?	1	0	1	?	2	0	0	2	0	
26	1	1	1	1	?	1	0	?	?	?	0	?	?	?	?	?	?	?	?	?	?	
27	1	1	1	1	?	?	?	?	?	1	0	0	?	1	0	?	0	1	0	0	0	
28	?	1	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	
29	1	1	1	0	?	?	0	?	?	1	0	0	?	0	0	?	0	1	0	0	0	
30	1	1	1	1	?	?	?	?	1	1	1	0	?	0	0	?	?	3	0	0	0	
31	1	1	1	1	1	1	?	?	1	1	1	0	?	1	0	?	0	2	0	0	0	
32	1	1	1	1	?	?	?	?	1	1	0	0	?	0	0	0	?	3	0	0	0	
33	1	1	1	1	?	?	?	?	?	1	?	?	0	0	?	?	0	2	0	0	0	
34	1	1	1	0	1	?	0	1	1	0	0	1	1	0	?	?	3	0	0	0	0	
35	1	1	1	0	1	1	?	?	1	1	0	0	?	0	?	?	?	3	0	0	0	
36	?	1	?	?	?	?	?	?	1	1	0	?	1	0	0	0	0	?	?	?	0	
37	?	1	?	?	?	?	?	?	1	1	0	0	1	1	0	0	?	3	?	0	0	
38	1	1	1	0	?	1	1	0	1	0	0	1	1	2	0	1	0	3	0	0	0	
39	1	1	1	?	1	?	?	?	1	1	1	0	1	0	2	0	0	?	0	0	0	
40	1	1	1	?	1	?	?	?	1	1	0	1	1	2	0	1	0	2	0	0	0	
41	1	1	1	?	1	1	0	?	?	1	1	0	?	?	?	0	0	2	0	1	0	
42	1	1	1	0	?	?	?	?	?	1	?	?	?	1	0	0	?	3	0	0	0	
43	1	?	?	?	?	?	?	?	?	1	?	?	?	2	?	?	?	?	?	?	0	
44	1	?	?	?	?	0	?	?	?	1	?	0	?	0	0	?	?	2	0	0	0	
45	?	?	?	?	?	?	?	?	?	0	0	0	?	?	?	?	?	?	?	?	?	
46	1	1	1	1	1	1	0	1	1	1	1	?	0	0	1	0	3	?	0	0	0	
47	1	1	1	1	1	1	0	1	1	1	0	?	1	0	0	1	3	1	0	0	0	
48	1	1	1	1	1	1	0	1	1	1	0	?	1	0	0	1	3	1	0	1	1	
49	1	1	1	?	?	1	0	1	1	1	0	?	2	0	0	1	3	1	0	0	0	
50	1	1	1	0	1	?	?	?	?	?	?	?	0	0	1	1	3	?	0	0	0	
51	1	1	1	1	1	?	?	?	?	1	1	0	?	1	0	?	1	3	?	0	0	
52	?	?	?	?	?	?	?	?	?	?	0	?	0	2	0	?	1	0	0	1	1	
53	1	?	1	-	1	?	?	?	?	1	1	0	?	0	2	?	?	3	0	0	0	
54	?	?	?	?	?	?	?	?	?	?	?	?	0	?	0	2	0	0	3	0	0	0
55	?	?	?	1	?	?	?	?	?	1	1	?	?	0	0	?	?	3	0	0	0	
56	1	1	1	1	1	0	0	1	1	1	0	?	0	0	1	?	3	0	0	0	0	
57	?	?	?	?	?	?	?	?	?	?	1	0	?	1	0	0	0	3	0	0	0	
58	1	1	1	0	1	1	0	1	?	?	?	?	0	0	1	0	?	?	?	?	0	
59	?	?	?	?	?	?	?	?	?	?	?	?	?	2	?	?	?	3	0	0	3	
60	?	?	?	?	?	?	?	?	?	1	?	0	?	2	2	0	0	1	0	0	3	
61	1	1	?	?	?	?	?	?	?	1	0	0	?	0	0	?	0	3	0	0	0	
62	?	1	1	?	?	?	?	?	?	1	?	?	?	0	0	1	?	3	0	0	0	
63	?	1	1	0&1	?	?	?	?	?	1	?	?	?	1	?	?	?	?	?	?	0	0
64	1	1	1	1	1	?	?	?	?	1	?	0	?	0	0	?	?	3	0	0	0	
65	?	?	?	?	?	?	?	?	?	?	?	0	?	2	0	0	?	3	0	0	0	
66	?	?	?	?	?	?	?	?	?	?	?	0	?	0	0	0	?	2	1	1	2	
67	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	?	3	0	0	0	
68	?	?	?	?	?	?	?	?	?	0	0	0	?	0	0	0	?	3	0	0	0	
69	?	?	?	?	?	?	?	?	?	?	?	0	?	0	?	?	?	?	?	0	0	
70	?	?	?	?	?	?	?	?	?	0	0	0	?	0	0	?	?	3	0	0	0	
71	1	1	1	1	1	?	?	?	?	1	0	0	?	?	?	?	?	?	?	?	?	
72	?	?	?	?	?	?	?	?	?	0	0	0	?	0	0	?	0	3	0	0	0	
73	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	
74	?	1	?	?	?	?	?	?	?	?	1	?	?	0	0	0	0	0	?	0	0	
75	?	1	?	?	?	?	?	?	?	?	1	0	?	?	2	0	?	0	3	0	0	1
76	?	1	?	?	?	?	?	?	?	?	1	?	0	?	2	0	?	0	?	0	0	2
77	?	1	?	?	?	?	?	?	?	0	0	?	?	1	0	?	0	4	?	?	0	0

78	1	1	1	1	1	1	?	1	1	0	0	?	0	0	0	0	3	0	0	0	
79	?	1	?	?	?	?	?	?	?	0	1	0	?	0	2	?	0	3	0	0	1
80	1	1	1	0	0	1	0	1	?	1	0	?	0	0	?	0	3	0	0	?	
81	1	1	?	?	?	?	?	1	0	0	0	1	1	0	1	0	?	0	0	?	
82	1	1	1	1	1	1	0	1	1	1	0	?	?	0	?	0	3	0	0	0	
83	?	1	?	?	?	?	?	?	?	1	?	?	?	0	0	?	0	2	0	0	0
84	1	1	1	0	?	?	?	?	?	?	?	?	?	0	0	0	?	?	0	0	0
85	1	1	1	0	1	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?
86	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?
87	1	1	1	1	?	1	0	?	1	0	?	?	0	0	1	?	3	0	0	?	
88	1	1	1	1	?	1	?	?	1	0	?	0	?	0	0	1	?	3	0	0	0
89	1	1	?	?	1	?	?	?	1	1	1	?	?	?	0	?	?	3	0	0	0
90	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?	3	0	0	0
91	?	1	?	?	?	?	?	?	1	?	?	?	?	2	0	?	0	3	0	0	0
92	?	1	?	?	?	?	?	?	?	1	0	?	?	0	0	?	?	3	0	0	0
93	?	1	?	?	?	?	?	?	?	1	0	?	?	2	0	0	?	3	0	0	1&2
94	?	1	?	?	?	?	?	?	?	1	1	0	?	?	?	?	?	?	?	?	0
95	1	1	0	-	0	1	1	1	0	0	0	?	0	?	?	?	?	?	?	?	0
96	1	1	0	-	0	0	?	1	1	?	0	?	?	0	0	?	?	3	0	0	0
97	?	1	?	?	?	?	?	?	1	0	?	?	?	?	?	?	0&1	0	0	0	0
98	1	1	0	-	1	?	?	?	1	1	?	0	?	0	2	0	?	4	0	0	0
99	1	1	0	-	0	1	0	1	1	0	0	?	?	?	?	?	?	3	0	0	0
100	?	1	0	-	?	?	?	?	1	1	0	?	?	?	?	?	?	?	?	?	0
101	?	1	0	-	?	?	?	?	?	1	?	?	?	?	0	?	?	?	?	?	0
102	?	1	0	-	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
103	?	1	0	-	?	?	?	?	?	1	1	0	?	?	?	?	?	3	0	0	0
104	?	1	0	-	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?
105	1	1	0	-	1	1	?	?	?	1	?	?	?	?	?	?	?	3	0	0	0
106	1	1	1	?	?	?	?	?	?	1	?	0	?	0	0	?	?	?	?	?	0
107	?	?	1	?	?	?	?	?	?	1	?	0	?	?	?	?	?	?	?	?	?
108	1	1	1	1	?	1	?	1	1	?	?	?	?	2	0	?	0	?	?	0	0
109	?	?	?	?	?	?	?	?	?	1	0	0	?	?	?	?	?	?	?	?	?
110	?	1	1	1	?	?	?	?	?	1	0	0	?	1	0	?	?	3	?	0	0
111	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
112	?	1	1	?	?	?	?	?	?	1	?	1	?	?	?	?	?	?	?	?	?
113	?	1	1	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	0
114	1	1	1	0	1	?	?	?	1	1	0	0	?	0	0	?	?	?	?	?	0
115	?	?	?	?	?	?	?	?	?	1	?	?	?	0	0	?	?	?	?	?	0
116	?	?	?	?	?	?	?	?	?	1	?	0	?	?	?	?	?	?	?	?	?
117	?	1	1	?	?	?	?	?	?	1	?	0	?	?	1	0	?	?	?	?	?
118	1	1	1	0	1	?	?	?	1	1	?	?	?	?	1	0	?	?	?	?	?
119	1	1	1	0	1	1	?	1	?	?	?	0	?	?	?	?	?	?	?	?	?
120	1	1	1	0	1	?	?	?	?	1	1	0	?	?	?	?	?	?	?	?	?
121	1	1	1	0	1	1	?	1	?	?	?	0	?	?	?	?	?	?	?	?	?
122	?	1	?	?	?	?	?	?	?	?	1	0	?	?	?	?	?	?	?	?	?
123	1	1	1	0	1	0	?	1	?	?	?	0	?	?	?	?	?	?	?	?	?
124	1	1	1	0	1	1	?	1	1	0	1	?	?	?	?	?	?	?	?	?	?
125	1	1	1	0	1	1	0	1	1	0	0	?	?	?	?	?	?	?	?	?	?
126	1	1	1	-	1	1	0	1	1	?	?	0	?	?	?	?	?	?	?	?	?
127	1	1	1	0	1	1	0	1	1	0	0	?	?	?	?	?	?	?	?	?	?
128	1	1	1	0	1	1	0	1	1	?	0	?	?	?	?	?	?	?	?	?	?
129	1	1	1	0	1	1	0	1	1	0	0	?	?	?	?	?	?	?	?	?	?

	81	82	83	84	85	86	87	88	89	90	91
1	1	1	0	0	?	?	?	?	0	?	?
2	?	?	?	0	1	1	0	0	0	2	0
3	0	1	0	?	0	1	0	0	0	1	0
4	1	0	0	?	1	1	0	0	1	0	1
5	0	0	0	?	?	?	?	?	1	?	?
6	1	1	0	?	?	?	?	?	1	?	?
7	0	?	0	?	?	?	?	?	1	?	?
8	2	0	0	0	1	0	0	?	1	2	1
9	0	1	0	?	?	?	?	?	?	?	?
10	0	1	0	0	?	0	?	?	1	?	0
11	0	1	0	1	?	?	?	?	?	?	?
12	?	2	0	0	?	1	?	?	?	?	0
13	1	2	0	?	?	0	?	?	1	0	0
14	1	2	0	0	?	1	?	?	?	?	0
15	0	0	0	0	?	1	?	?	?	?	0
16	0	1	0	0	?	?	?	?	?	?	?
17	0	0	0	?	?	?	?	?	?	?	?
18	1	1	0	0	?	?	?	?	?	?	?
19	1	2	0	0	?	1	?	?	?	?	0
20	1	2	0	0	?	?	?	?	?	?	?

21	0	0	0	?	?	?	?	?	?	?	?
22	0	1	0	?	?	?	?	?	?	?	?
23	1	?	0	0	?	?	?	?	1	?	0
24	0	1	0	0	?	?	?	?	?	?	0
25	0	?	0	1	?	?	?	?	?	?	?
26	?	?	?	?	?	?	?	?	1	?	0
27	0	?	0	0	?	?	?	?	1	?	0
28	?	?	?	?	?	?	?	?	?	?	?
29	0	1	0	0	?	?	?	?	1	?	0
30	1	0	0	0	?	?	?	?	1	?	0
31	0	1	0	0	?	?	?	?	1	?	0
32	0	1	0	0	?	?	?	?	1	?	0
33	0	0	0	0	?	?	?	?	?	?	?
34	1	?	0	0	?	?	?	?	1	?	0
35	1	2	0	0	?	?	?	?	1	?	0
36	1	2	0	0	?	1	?	?	?	?	1
37	1	1	0	0	?	1	?	?	1	1	0
38	1	2	0	0	?	1	?	?	?	?	1
39	0	1	0	0	?	?	?	?	?	?	1
40	0	2	0	0	?	1	?	?	1	?	1
41	2	?	0	0	?	?	?	?	1	?	?
42	1	2	0	0	?	?	?	?	?	?	?
43	0	0	?	?	?	?	?	?	?	?	?
44	0	0	0	?	?	?	?	?	1	?	?
45	?	?	?	?	?	?	?	?	?	?	?
46	0	2	0	0	3	1	0	1	1	1	0
47	0	2	0	0	?	?	?	?	1	?	?
48	0	1	1	1	3	1	0	1	1	0	1
49	0	0	0	1	1	1	0	1	1	0	1
50	0	0	0	1	3	1	0	1	1	0	1
51	1	2	0	0	2	1	0	1	1	0	1
52	0	0	0	1	?	?	?	?	?	?	?
53	0	0	0	0	?	?	?	?	?	?	?
54	0	0	0	0	?	?	?	?	?	?	?
55	1	1	0	0	?	?	?	?	?	?	?
56	0	1	0	0	?	?	?	?	?	?	?
57	1	0	0	0	?	?	?	?	?	?	?
58	?	0	0	?	?	?	?	1	1	0	0
59	?	?	0	?	?	?	?	?	?	?	?
60	?	?	0	0	?	?	?	?	?	?	?
61	0	1	0	?	?	?	?	?	?	?	?
62	?	2	0	0	1	?	0	?	?	?	?
63	1	?	0	0	?	1	0	?	1	?	?
64	1	1	0	?	?	?	?	?	?	?	?
65	1	1	0	0	?	?	?	?	?	?	?
66	?	3	1	?	?	?	?	?	?	?	?
67	1	1	0	?	?	?	?	?	?	?	?
68	0	0	0	0	?	?	?	1	1	?	0
69	?	0	0	?	?	?	?	?	?	?	?
70	1	?	0	0	?	?	?	?	?	?	?
71	?	?	?	?	?	?	?	?	1	1	0
72	1	0	0	0	?	?	?	?	?	?	?
73	?	?	?	?	?	?	?	?	?	?	?
74	0	0	0	0	?	?	?	?	?	?	?
75	1	2	0	0	?	?	?	?	?	?	?
76	1	2	0	0	?	?	?	?	?	?	?
77	0	?	?	?	?	?	?	?	?	?	?
78	2	0	0	0	?	?	?	?	?	?	?
79	1	1	0	0	?	?	?	?	?	?	?
80	0	0	0	0	?	?	?	?	1	?	?
81	0	2	0	0	?	1	?	?	1	?	0
82	0	0	0	0	?	?	?	?	1	?	?
83	1	2	0	0	?	?	?	?	?	?	?
84	?	2	0	0	?	?	?	?	?	?	?
85	?	?	?	?	?	?	?	?	?	?	?
86	?	?	?	?	?	?	?	?	?	?	?
87	1	2	0	0	?	?	?	?	1	?	?
88	0	2	0	0	?	?	?	?	?	?	?
89	0	1	0	?	?	?	?	?	?	?	?
90	0	0	0	0	?	?	?	?	?	?	?
91	0	1	0	0	?	?	?	?	?	?	?
92	1	0	0	?	?	?	?	?	?	?	?
93	0	1	0	0	?	?	0	?	1	0	?
94	0	?	?	?	?	?	1	?	0	2	0
95	1	1	0	0	?	?	?	?	?	?	?
96	0	0	0	0	?	?	?	?	1	?	?

97	0	0	0	0	?	?	?	?	1	?	?
98	0	0	0	0	?	?	?	?	?	?	?
99	0	0	0	0	2	0	0	0	1	0	0
100	0	?	?	?	2	?	?	?	1	0	?
101	1	?	?	?	?	1	0	?	1	2	?
102	?	?	?	?	0	1	?	?	1	0	?
103	1	0	0	0	3	1	0	?	1	2	0
104	?	?	?	?	?	?	?	?	?	?	?
105	0	0	0	?	?	?	?	?	?	?	?
106	1	0	0	0	?	?	?	?	?	?	?
107	?	?	?	?	?	?	1	?	?	?	?
108	0	0	0	0	3	1	0	1	1	0	0
109	?	?	?	?	?	?	?	?	?	?	?
110	0	0	0	0	?	1	1	0	1	2	0
111	?	?	?	?	?	?	?	?	?	?	?
112	?	?	?	?	?	?	?	?	?	?	?
113	1	2	?	?	?	?	?	?	?	?	?
114	0	?	?	?	2	?	0	?	1	0	?
115	0	2	0	0	2	0	0	0	1	0	0
116	?	?	?	?	?	?	?	?	?	?	?
117	1	?	?	?	2	?	?	?	1	0	?
118	0	?	?	?	2	1	1	0	1	2	0
119	?	?	?	?	?	?	?	?	1	?	0
120	?	?	?	?	?	?	?	?	?	?	?
121	?	?	?	?	?	?	?	?	1	?	?
122	?	?	?	?	?	?	?	?	?	?	?
123	?	?	?	?	?	?	?	?	1	?	?
124	?	?	?	?	?	?	?	?	1	?	?
125	?	?	?	?	?	?	?	?	1	?	?
126	?	?	?	?	?	?	?	?	?	?	?
127	?	?	?	?	?	?	?	?	1	?	?
128	?	?	?	?	?	?	?	?	1	?	?
129	?	?	?	?	?	?	?	?	1	?	?

Appendix 2. List of terminal taxa.

N	Terminal (Name)	Author(s), year	Region	Material or literature used
1	<i>Pachyneura fasciata</i>	Zetterstedt, 1838	PAL	Krivosheina 1999; Fitzgerald 2004b; Paramonov & Salmela 2016
2	<i>Hesperinus brevifrons</i>	Walker, 1848	NEA	Hardy 1945, 1981; Iwata & Nagatomi 1981; Fitzgerald 2004b
3	<i>Penthetria neonigrita</i>	Fitzgerald, 2021	NEO	Fitzgerald 2004b, 2021
4	<i>Plecia plagiata</i>	(Wiedemann, 1824)	NEO	Fitzgerald 2004b; Hardy 1945; MZUSP; NHMUK
5	<i>Bibio albipennis</i>	Say, 1823	NEA	Hardy 1945, 1961; Skartveit & Willassen 1996; Fitzgerald 1997, 2004a; https://www.inaturalist.org/observations/232535274
6	<i>Bibio intermedius</i>	Rondani, 1850	NEO	material, Fitzgerald 1997, 2023
7	<i>Bibiodes aestivus</i>	Melander, 1912	NEA	Melander 1912, Hardy 1945, 1981, Fitzgerald 2004b
8	<i>Bibionellus barrettoii</i>	Lane & Forattini, 1948	NEO	Pinto & Amorim 1997, Fitzgerald 2004b, Falaschi et al. 20182 paratypes
9	† <i>Protodilophus semispinosus</i>	Skartveit, 2023	OR	Skartveit 2023
10	<i>D. febrilis</i>	(Linnaeus, 1758)	PAL	Duda 1930, Haenni 1982, Blaschke-Berthold 1994, Skartveit & Willassen 1996, Fitzgerald 2004b, photos MNHN
11	<i>D. antipedalis</i>	Wiedemann, 1818	PAL	Duda 1930, Haenni 1982

12	<i>D. beckeri</i>	(Hardy, 1948)	PAL	Báez 1984, Skartveit & Willassen 1996
13	<i>D. borealis</i>	Skartveit, 1993	PAL	Skartveit 1993, Skartveit & Willassen 1996
14	<i>D. femoratus</i>	Meigen, 1804?	PAL	Haenni 1982, Skartveit & Willassen 1996, photos MNHN
15	<i>D. humeralis</i>	Zetterstedt, 1850	PAL	Haenni 1982, Skartveit & Willassen 1996
16	<i>D. maderae</i>	Wollaston, 1858	PAL	Haenni & Báez 2001
17	<i>D. maghrebensis</i>	Haenni, 1981	PAL	Haenni 1981
18	<i>D. martinovskyi</i>	Haenni & Bosák, 2007	PAL	Haenni & Bosák 2007
19	<i>D. neglectus</i>	Haenni, 1982	PAL	Haenni 1982, Skartveit & Willassen 1996
20	<i>D. oceanus</i>	Haenni & Báez, 2001	PAL	Haenni & Báez, 2001
21	† <i>D. palaeofebrilis</i>	Skartveit, 2009	PAL	Skartveit, 2009
22	<i>D. sardous</i>	Haenni, 2009	PAL	Haenni 2009
23	<i>D. atrimas</i>	Edwards, 1915	AFR	Skartveit & Freidberg, 2023
24	<i>D. baleensis</i>	Skartveit & Freidberg, 2023	AFR	Skartveit & Freidberg, 2023
25	<i>D. bicolor</i>	Wiedemann, 1821	AFR	Skartveit & Freidberg, 2023
26	<i>D. buxtoni</i>	(Hardy, 1948)	AFR	Skartveit & Freidberg, 2023
27	<i>D. capensis</i>	Edwards, 1925	AFR	Skartveit & Freidberg, 2023
28	<i>D. disagrus</i>	(Speiser, 1910)	AFR	Hardy 1951, Skartveit & Freidberg, 2023
29	<i>D. erythraeus</i>	Bezzi, 1905	AFR	Skartveit & Freidberg, 2023
30	<i>D. lucidus</i>	(Hardy, 1948)	AFR	Skartveit & Freidberg, 2023
31	<i>D. malagasicus</i>	Skartveit & Freidberg, 2023	AFR	Skartveit & Freidberg, 2023
32	<i>D. obsoletus</i>	(Hardy, 1951)	AFR	Skartveit & Freidberg, 2023
33	<i>D. paucidens</i>	Hardy, 1962	AFR	Skartveit & Freidberg, 2023
34	<i>D. riftensis</i>	Skartveit & Freidberg, 2023	AFR	Skartveit & Freidberg, 2023
35	<i>D. suberythraeus</i>	Edwards, 1915	AFR	Skartveit & Freidberg, 2023
36	<i>D. bispinosus</i>	Lundström, 1913	PAL	Skartveit & Kaplan 1996, Skartveit & Willassen 1996, Haenni et al. 2023
37	<i>D. clavicornus</i>	Skartveit & Kaplan 1996	PAL	Skartveit & Kaplan 1996, Skartveit & Willassen 1996
38	<i>D. hiemalis</i>	Becker, 1908	PAL	Báez 1984, Skartveit & Willassen 1996; https://www.inaturalist.org/observations/147338848 ; 141411508
39	<i>D. lingens</i>	Loew, 1869	PAL	Skartveit & Kaplan 1996, Skartveit & Willassen 1996, El-Hawagry et al. 2023

40	<i>D. tridentatus</i>	Walker, 1848	PAL	Skartveit & Kaplan 1996, Skartveit & Willassen 1996, Haenni & Marafi 2023, El-Hawagry et al. 2023
41	<i>D. nuptus</i>	Speiser, 1914	AFR	Skartveit & Freidberg, 2023
42	<i>D. vicarius</i>	(Hardy, 1948)	AFR	Skartveit & Freidberg, 2023
43	† <i>D. cerestensis</i>	Nel, Legal & Coster, 2022	PAL	Nel, Legal & Coster, 2022
44	† <i>D. crassicornis</i>	Skartveit, 2009	PAL	Skartveit 2009, 2021
45	† <i>D. succineus</i>	Skartveit 2009	PAL	Skartveit 2009, Fitzgerald & Greenwalt 2022
46	<i>D. bicoloripes</i>	Edwards, 1938	NEO	Edwards, 1938, Hardy 1953 + NHMUK photos, material
47	<i>D. flavicornis</i>	Edwards, 1938	NEO	Edwards 1938 + NHMUK photos, material
48	<i>D. pectoralis</i>	Wiedemann, 1828	NEO	Wiedemann 1828, Hardy 1967, Hardy 1953, material
49	<i>D. trisulcatus</i>	Macquart, 1838	NEO	Edwards 1938, Hardy 1953, material
50	<i>D. sp. nov. A</i>	-	NEO	material
51	<i>D. sp. nov. B</i>	-	NEO	material
52	<i>D. golbachi</i>	(Hardy, 1953)	NEO	Hardy, 1953
53	<i>D. quadridens</i>	(Hardy, 1953)	NEO	Hardy, 1953
54	<i>D. serenus</i>	(Hardy, 1953)	NEO	Hardy, 1953
55	<i>D. inconnexus</i>	(Hardy, 1961a)	NEO	Hardy, 1961a
56	<i>D. segregatus</i>	(Hardy, 1961a)	NEO	Hardy, 1961a
57	<i>D. quinquespinae</i>	(Hardy, 1961a)	NEO	Hardy, 1961a
58	<i>D. espeletiae</i>	Sturm, 1990	NEO	Sturm 1990
59	<i>D. acutidens</i>	Edwards, 1929	OR	Edwards 1929, Hardy 1951, Hardy & Delfinado 1969
60	<i>D. bakeri</i>	(Hardy, 1951)	OR	Hardy 1951, Hardy & Delfinado 1969
61	<i>D. harrisoni</i>	Hardy, 1953	AO	Hardy 1953, Harrison 1990
62	<i>D. tricuspidatus</i>	Hardy, 1982	AO	Hardy, 1982
63	<i>D. varipes</i>	Skuse, 1890	AO	Skuse 1890, Hardy 1951, 1953, 1982
64	<i>D. innubilus</i>	Hardy & Delfinado, 1969	OR	Hardy & Delfinado 1969
65	<i>D. pictilis</i>	Hardy & Delfinado, 1969	OR	Hardy & Delfinado 1969
66	<i>D. crenulatus</i>	Hardy & Delfinado, 1969	OR	Hardy & Delfinado 1969
67	<i>D. scabricollis</i>	Edwards, 1929	OR	Edwards 1929, Hardy 1951, Hardy & Delfinado 1969
68	<i>D. trispinosus</i>	Edwards, 1929	OR	Edwards 1929, Hardy 1951, Hardy & Delfinado 1969
69	<i>D. anomalus</i>	(Hardy, 1942)	NEO	Hardy 1942

70	<i>D. globosus</i>	(Hardy, 1942)	NEO	Hardy 1942
71	<i>D. minimus</i>	(Hardy, 1942)	NEO	Hardy 1942
72	<i>D. ornatus</i>	(Hardy, 1942)	NEO	Hardy 1942, Fitzgerald 2023
73	<i>D. variceps</i>	(Hardy, 1942)	NEO	Hardy 1942
74	<i>D. arizonaensis</i>	(Hardy, 1937)	NEA	Hardy 1945, 1961b
75	<i>D. caurinus</i>	McAtee, 1921	NEA	Hardy 1945
76	<i>D. emarginatus</i>	McAtee, 1921	NEA	Hardy 1945, 1961b
77	<i>D. obesulus</i>	Loew, 1870	NEA	Hardy 1945, 1961b
78	<i>D. occipitalis</i>	Coquillett, 1904	NEA	Hardy 1945, 1961b
79	<i>D. sayi</i>	(Hardy, 1959)	NEA	Hardy 1945, 1961b, Fitzgerald 2004b
80	<i>D. serotinus</i>	Loew, 1862	NEA	Hardy 1945, Skartveit & Willassen 1996, Fitzgerald 2004b
81	<i>D. spinipes</i>	Say, 1823	NEA	Hardy 1945, 1961b, inaturalist: 164264105; 218264979; 226877453; 163906807; 221402799
82	<i>D. strigilatus</i>	McAtee, 1921	NEA	Hardy 1945, 1961b
83	<i>D. tibialis</i>	Loew, 1869	NEA	Hardy 1945, 1961b
84	<i>D. tingi</i>	(Hardy, 1942)	NEA	Hardy 1942, 1945, 1961b
85	† <i>D. idanos</i>	Fitzgerald & Greenwalt, 2022	NEA	Fitzgerald & Greenwalt, 2022
86	<i>D. aberratus</i>	Hardy, 1982	AO	Hardy 1982
87	<i>D. nigrostigma</i>	(Walker, 1848)	AO	Hardy 1951, 1953, Harrison 1990, Fitzgerald 2004b
88	<i>D. crinitus</i>	(Hardy, 1951)	AO	Hardy 1951, 1953, Harrison 1990
89	<i>D. segnis</i>	Hutton, 1901	AO	Hardy 1951, 1953, Harrison 1990
90	<i>D. transvestis</i>	Hardy, 1968	AO	Hardy 1968
91	<i>D. conformis</i>	Hardy, 1968	AO	Hardy 1968
92	<i>D. dichromatus</i>	Hardy, 1968	AO	Hardy, 1968
93	<i>D. multispinosus</i>	(Hardy, 1951)	AO	Hardy 1951, 1968
94	<i>D. longirostris</i>	Macquart, 1850	AO	Hardy 1951, 1982
95	<i>D. arboreus</i>	Fitzgerald, 2004a	AO	Fitzgerald 2004a
96	<i>D. tuthilli</i>	(Hardy, 1953)	AO	Hardy 1953, Harrison 1990; 4658387; 4638259
97	<i>D. exiguus</i>	(Hardy, 1951)	AO	Hardy 1951, 1968
98	<i>D. gracilis</i>	Hardy, 1968	AO	site tbm
99	<i>D. collessi</i>	Hardy, 1982	AO	Hardy 1982
100	<i>D. parvus</i>	Hardy, 1982	AO	Hardy 1982
101	<i>D. pictipes</i>	Skuse, 1889	AO	Hardy 1951, 1982, https://www.inaturalist.org/observations/25985104
102	<i>D. sexspinosus</i>	Hardy, 1982	AO	Hardy 1982
103	<i>D. modicus</i>	Hardy, 1982	AO	Hardy 1982
104	<i>D. discretus</i>	Hardy, 1982	AO	Hardy 1982

105	<i>D. alpinus</i>	Harrison, 1990	AO	Harrison 1990
106	<i>D. proxilus</i>	Fitzgerald, 2004a	AO	Fitzgerald 2004a
107	<i>D. partitus</i>	Hardy, 1982	AO	Hardy 1982
108	<i>D. atripennis</i>	Hardy, 1982	AO	Hardy 1982
109	<i>D. cantrelli</i>	Hardy, 1982	AO	Hardy 1982
110	<i>D. conspicuus</i>	Hardy, 1982	AO	Hardy 1982
111	<i>D. dubius</i>	Hardy, 1982	AO	Hardy 1982
112	<i>D. flavicrus</i>	Hardy, 1982	AO	Hardy 1982
113	<i>D. longipilosus</i>	Hardy, 1982	AO	Hardy 1982
114	<i>D. mc Alpinei</i>	Hardy, 1982	AO	Hardy 1982
115	<i>D. skusei</i>	Hardy, 1982	AO	Hardy 1982
116	<i>D. surrufus</i>	Hardy, 1982	AO	Hardy 1982
117	<i>D. tersus</i>	Hardy, 1982	AO	Hardy 1982
118	<i>D. tetrascolus</i>	Hardy, 1982	AO	Hardy 1982; https://www.inaturalist.org/observations/223685230
119	<i>D. antarcticus</i>	(Walker, 1837)	NEO	Edwards 1930
120	<i>D. calcaratus</i>	Edwards, 1930	NEO	Edwards 1930
121	<i>D. castanipes</i>	(Bigot, 1888)	NEO	Edwards 1930
122	<i>D. dorsalis</i>	(Philippi, 1865)	NEO	Edwards 1930, Hardy 1953
123	<i>D. flavifemur</i>	Edwards, 1930	NEO	Edwards 1930
124	<i>D. flavihalter</i>	Edwards, 1930	NEO	Edwards 1930
125	<i>D. gracilipes</i>	Edwards, 1930	NEO	Edwards 1930, Hardy 1953
126	<i>D. interruptus</i>	Edwards, 1930	NEO	Edwards 1930
127	<i>D. luteus</i>	Edwards, 1930	NEO	Edwards 1930
128	<i>D. patagonicus</i>	Edwards, 1930	NEO	Edwards 1930, Hardy 1953
129	<i>D. tetracanthus</i>	Edwards, 1930	NEO	Edwards 1930

CONSIDERAÇÕES FINAIS

Neste trabalho, quatro espécies são redescritas, três delas com a terminália masculina descrita pela primeira vez (*D. bicoloripes*, *D. pectoralis* e *D. flavicornis*), e três delas com a terminália feminina descrita pela primeira vez (*D. bicoloripes*, *D. pectoralis* e *D. trisulcatus*). Além disso, duas novas espécies foram descritas, incluindo as terminálias masculinas e femininas descritas e ilustradas.

A distribuição geográfica foi expandida para três espécies (*D. bicoloripes*, *D. pectoralis* e *D. trisulcatus*), e o conhecimento sobre a sazonalidade foi expandido para todas as quatro espécies. No contexto brasileiro, apenas três estados possuíam registros para *Dilophus* (Rio de Janeiro, Santa Catarina e São Paulo), e todos eles estão localizados na Mata Atlântica (Falaschi & Schelesky-Prado 2024). Neste estudo, novos registros para

cinco estados são relatados (Goiás, Mato Grosso do Sul, Minas Gerais, Paraná e Rio Grande do Sul), representando também novos registros para os biomas Cerrado e Pampa.

Informações sobre a biologia de Bibionidae, especialmente da fauna Neotropical, são escassas. Aqui, observações sobre o comportamento de visitação de flores e alimentação foram relatados para *Dilophus bicoloripes* e *D. pectoralis*.

A análise cladística resultou em três árvores mais parcimoniosas das quais a árvore de consenso estrito foi discutida (Figura 1A-G). Alguns clados mais inclusivos descritos na literatura foram recuperados, e as relações entre os clados foram as seguintes: *Hesperinus* + (*Penthetria* + (*Plecia* + (Bibionini + Dilophini))).

A monofilia dos Dilophini foi bem suportada (14:1, 32:1, 56:1). No entanto, *Dilophus* não foi recuperado como monofilético, a menos que †*Protodilophus* seja incluído no gênero. Assim, a tribo se torna monotípica novamente. Tanto o “grupo *D. febrilis*” quanto o “grupo *D. bispinosus*” não foram recuperados nesta análise.