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The Tabanidae (Diptera) in Brazil: Historical aspects, diversity and distribution

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ABSTRACT. We present an overview of horseflies in Brazil. For this, we compiled and analyzed the data available in the Taxonomic Catalogue of the Brazilian Fauna ("Catálogo Taxonômico da Fauna do Brasil" – CTFB). A total of 496 valid species in three subfamilies and 44 genera are recorded from Brazil, of which 46.3% are endemic to the country. The genera with the highest numbers of described species are: *Tabanus* Linnaeus (15.5%), *Fidena* Walker (12.9%), *Catachlorops* Lutz (9.8%) and *Dichelacera* Macquart (7.8%). The taxonomy of Tabanidae in Brazil began with European researchers in 18th and 19th centuries. Brazilian taxonomists, beginning with Adolph Lutz, started publishing on Tabanidae only in 1907. A total of 50 researchers of different nationalities first authored the description of the Brazilian species. Of these, only seven were women. Approximately 45% of the primary types of Brazilian species are deposited in Europe, 33% in Brazil, 16% in the USA, and other 6% in South American countries or their repository is unknown. In Brazilian collections, 98% of the primary types are distributed in only four collections. Species distribution records in Brazil indicate that the regions with the highest number of recorded species (in the North and Southeast) are those that harbor the main collections of Tabanidae, as well as the states with the highest number of species, namely Amazonas, Pará and São Paulo. The Brazilian Atlantic Forest (233 spp.) and the Brazilian Amazon (222 spp.) are the most diverse regarding the distribution of species in those biomes, although the Brazilian Amazon has a greatest number of endemic species (131 spp.). The taxonomic changes proposed in this work are to revalidate the combination of *Chrysops lynchi* Brèthes, 1910 **stat. reval.**, *Stypommisa serena* (Kröber, 1931) **comb. reval.**, and the *Tabanus ornativentris* Kröber, 1929 **sp. reval.**

KEY WORDS. Brazilian Catalogue, history, horseflies, taxonomy.

INTRODUCTION

Tabanidae, commonly known as horseflies, are cosmopolitan flies in the suborder Brachycera. They inhabit almost all habitats including mangroves, deserts, forests and highlands up to 4,000 meters high (Fairchild 1981). Tabanidae has around 4,650 valid species (Evenhuis and Pape 2021). They are considered potential pests of domestic animals and humans due to the hematophagous behavior of the females of most species. Krinsky (1976), Foil (1989) and Baldacchino et al. (2014) reviewed more than 30 disease agents possibly transmitted by Tabanidae. Recently, molecular tools have expanded the record of pathogens in different species and regions (Bilheiro et al. 2019, Rodrigues et al. 2021, 2022, Ramos et al. 2023). In addition to their medical relevance, tabanids cause indirect economical loss associated with their bites. When they are abundant, they prevent farm workers from doing their jobs. They keep tourists away from vacation spots, and cause great stress on domestic animals, impairing their feed and rest. Some species are floral visitors (Pechuman and Teskey 1989) and a few are pollinators (Johnson and Morita 2006).

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Horsefly larvae are predatory and solitary. They are generally whitish and cylindrical and have 12 segments with some spiniform setae that help in their movement on the substrate. Most species live in environments with some humidity or water, from decomposing logs to waterways. Coscarón and Papavero (2014) published a state-of-the-art paper on the immature horseflies of the Neotropics.

Adult horseflies range from 5 to 25 mm in length and are often showy flies with contrasting colors. Tabanidae is considered a monophyletic group supported by two synapomorphies: cell r4 encompassing the apex of the wing and lower calyptra well developed (Woodley 1989). Additionally, in the hypothetical ground plan of the family, the antennal flagellum has eight segments, while the proximal segments in some subfamilies fuse with the postpedicel so that only three or four segments can be discerned. This apomorphic condition unites Chrysopsinae + Tabaninae and is known as the basal plate.

There are 1,205 species of tabanids described in 65 genera in the Neotropical region (Coscarón and Papavero 2009b, Henriques et al. 2012). Coscarón and Papavero (2009a) provided a richly illustrated key to the supraspecific categories of the region. Knowledge of the Neotropical Tabanidae species is mostly represented by the descriptions of species. A few contributions cover regional sets of species and provide species list and/or keys (Rafael et al. 1991, Barros and Gorayeb 1996, Henriques and Rafael 1999, Krolow et al. 2007, Turcatel et al. 2007, Gorayeb 2008, Lima et al. 2015, Krolow and Henriques 2017, Oliveira et al. 2022, Zamarchi et al. 2023). Exceptions are the reviews of some genera, which provide some basis for the identification and knowledge of distribution and ecology (Henriques and Rafael 1995, Rafael and Ferreira 2004, Henriques and Krolow 2009, 2019, Krolow and Henriques 2010, Turcatel et al. 2010, Krolow et al. 2015, Carmo and Henriques 2019, Turcatel 2019). This situation is no different for Brazil and several genera require taxonomic updating.

Brief history of the taxonomy of Tabanidae in Brazil

Although the oldest species of Tabanidae known for Brazil had their names linked to Linnaeus (1758), De Geer (1776) and Fabricius (1787) in the 18th century, these species were not necessarily described from Brazilian specimens, and their occurrence records for Brazil were made later. Then there was a great increase in the knowledge of horseflies that occur in Brazil from the 19th century onwards. During this period, works carried out by Wiedemann (1819, 1821, 1828, 1830), Macquart (1838a, 1838b, 1846, 1847, 1848, 1850) and Bigot (1892) are noteworthy.

The 20th century was even more productive, and four researchers were very active in Tabanidae: 1) Adolpho Lutz was the first Brazilian to dedicate his work to Tabanidae and describe a species, *Stibasoma willistoni* Lutz, 1907. He published on Tabanidae between 1905 and 1937. His legacy (species lists, taxon descriptions, nomenclatural acts and classification proposals) was summarized in Benchimol and Sá (2005); 2) The German researcher Otto Kröber was a contemporary of Lutz who published several articles between 1925 and 1939; 3) Other notable Brazilian researcher is Mauro Pereira Barretto, who made a significant contribution between 1946 and 1960; 4) The North American researcher Alexander Graham Bell Fairchild dedicated his career to the study of Tabanidae in the Neotropical region. He published for more than 50 years, from 1934 to 1989. Furthermore, his 1981 visit to the Brazilian Northern institutions Museu Paraense Emílio Goeldi, Belém, and Instituto Nacional de Pesquisas da Amazônia, in Manaus, had great influence on and encouraged research on horseflies in the country. His visit resulted in the training of a new generation of researchers who have contributed to the taxonomic knowledge of the group in the region.

Despite some collection gaps and the lack of taxonomic revisions for certain genera, Tabanidae is a well-studied group, and the number of species that will be described for Brazil in the 21st century will probably be much smaller than what was described in the previous century. This work provides an overview of horseflies in Brazil, through the compilation and analysis of data available in the Catálogo Taxonômico da Fauna Brasileira ("Taxonomic Catalog of Brazilian Fauna" – CTFB) (Krolow and Henriques 2023).

MATERIAL AND METHODS

The data used in our analyses was for the most part extracted from the "Catálogo Taxonômico da Fauna Brasileira" and are available at http://fauna.jbrj.gov.br. Data on the gender and nationality of Tabanidae authors, and data on immatures and males of Tabanidae, were obtained from different sources. Data were extracted and compiled in an Excel spreadsheet (Supplementary material Table S1), which was used in part of the analyses and generation of graphs. Only the accumulation curves were generated in the R 4.3.1 program using the tidyverse, magrittr, vegan and janitor packages. The maps were produced using QGIS (version 3.32.3), with the shapefile with Brazil and the Brazilian biome limits being obtained from the Instituto Brasileiro de Geografia e Estatística (IBGE, https://www.ibge.gov.br). The

geographic records listed as "States" and "Biomes" that were marked with "?" or that do not have a defined location are present in the supplementary spreadsheet but were removed from the analyses.

The acronyms of the institutions mostly follow the proposal by Evenhuis (2023): (AMNH) American Museum of Natural History, New York, New York, USA; (ANSP) Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; (CAS) California Academy of Sciences, San Francisco, California, USA; (CMNH) Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; (Coll. Kröber) Personal collection, Germany; (Coll. Guérin-Méneville) Personal collection, France; (CUIC) Cornell University, Ithaca, New York, USA; (CZMA) Coleção Zoológica da Universidade Estadual do Maranhão, Caxias, Maranhão, Brazil; (DZUP) Universidade Federal do Paraná, Coleção Entomológica Padre Jesus Santiago Moure Jesus Santiago Moure, Curitiba, Paraná, Brazil; (FSCA) Florida State Collection of Arthropods, Gainesville, Florida, USA; (HNHM) Hungarian Natural History Museum, Budapest, Hungary; (IBSP) Instituto Butantan, Secretaria de Estado da Saúde de São Paulo, São Paulo, São Paulo, Brazil; (IEAUT) Istituto di Entomologia Agraria della Università di Torino, Turin, Italy; (IOC or FIOC) Fundação Instituto Oswaldo Cruz, Brazil, Rio de Janeiro, Rio de Janeiro, Brazil; (INPA) Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil; (ISTH) Institut für Schiffs und Tropenkrankheiten, Hamburg, Germany; (LACM) Los Angeles County Museum of Natural History, Los Angeles, California, USA; (MACN) Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; (MCZ or MCZC) Harvard University, Museum of Comparative Zoology, USA, Cambridge, Massachusetts, USA; (MHNLS) Museo de Historia Natural La Salle, Caracas, Venezuela; (MLPA) Universidad Nacional de La Plata, Museo de la Plata, La Plata, Argentina; (MLUH) Martin-Luther-Universität, Zentralmagazin Naturwissenschaftlicher Sammlungen, Zoologische Sammlung, Halle (Saale), Germany; (MNHN) Muséum National d'Histoire Naturelle, Paris, France; (MPEG) Museu Paraense Emilio Goeldi, Belem, Pará, Brazil; (MZPW) Polish Academy of Science, Museum and Institute of Zoology, Warszawa [=Warsaw], Poland; (MZUN) Museo Zoologico di Università degli Studi, Napoli [= Naples], Italy; (MZUSP) Museu de Zoologia da Universidade de São Paulo, São Paulo, São Paulo, Brazil; (NHMUK or NHM) The Natural History Museum [formerly British Museum (Natural History)], London, United Kingdom; (NHRS) Naturhistoriska riksmuseet, Stockholm, Sweden; (NMW or NHMW) Naturhistorisches Museum Wien, Wien, Austria; (OSU or OSUC) Ohio State University, C.A. Triplehorn Insect Collection, Columbus, Ohio, USA; (SMF) Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt, Germany; (SMNS) Staatliches Museum für Naturkunde, Stuttgart, Germany; (USNM) National Museum of Natural History, [formerly, United States National Museum], Washington D.C., USA; (UUZM) Uppsala University, Uppsala, Sweden; (ZMAN) Universiteit van Amsterdam, Instituut voor Taxonomische Zoologie, Zoologisch Museum, Amsterdam, Netherlands; (ZMHB) Museum für Naturkunde der Humboldt-Universität, Berlin, Germany; (ZMUC) University of Copenhagen, Zoological Museum, København [= Copenhagen], Denmark; (ZSM) Zoologische Staatssammlung, München [= Munich], Germany.

RESULTS AND DISCUSSION

Brazilian Tabanidae fauna

Brazilian Tabanidae represent about 10% of the world fauna. A total of 496 valid species in three subfamilies, seven tribes (Fig. 1) and 44 genera are recorded from Brazil, with 230 species (46.3%) endemic to the country (Table 1). Tabaninae is the most diverse subfamily with 351 species (70.7%), of which 156 (31.45%) are endemic to Brazil (Fig. 2). The second is Pangoniinae with 113 species (22.78%) and 68 endemic species (13.71%) (Fig. 2). The least diverse is Chrysopsinae with 32 species (6.45%) and six endemic species (1.21%) (Fig. 2).

The most diverse tribes belong to Tabaninae; the first is Diachlorini with 268 species (54.0%) and 138 endemic species (27.82%), the second is Tabanini with 83 species (16.7%) and 18 endemic species (3.63%) (Fig. 3). Next, the tribe Scionini has 77 species (15.5%) and 50 endemic species (10.08%) (Fig. 3). The Rhinomyzini and Scepsini tribes have only one Neotropical representative each, but none endemic to Brazil (Fig. 3).

Tabanus Linnaeus is the most speciose genus with 77 species (15.5%), followed by *Fidena* Walker 64 spp. (12.9%), *Catachlorops* Lutz 49 spp. (9.8%), *Dichelacera* Macquart 39 spp. (7.8%), and *Chrysops* Meigen 31 spp. (6.2%) (Table 1). Another 23 genera have less than 30 species, while 16 other genera are represented by only one species in Brazil (Table 1). Nine genera occur exclusively in Brazil: *Lepmia* Fairchild (2 spp.) and *Protosilvius* Enderlein (6 spp.), and the monospecific genera *Anaerythrops* Barretto, *Elephantotus* Gorayeb, *Erioneura* Barretto, *Leptapha* Enderlein, *Muscotabanus* Henriques & Krolow, *Oopelma* Enderlein, and *Stigmatophthalmus* Lutz.

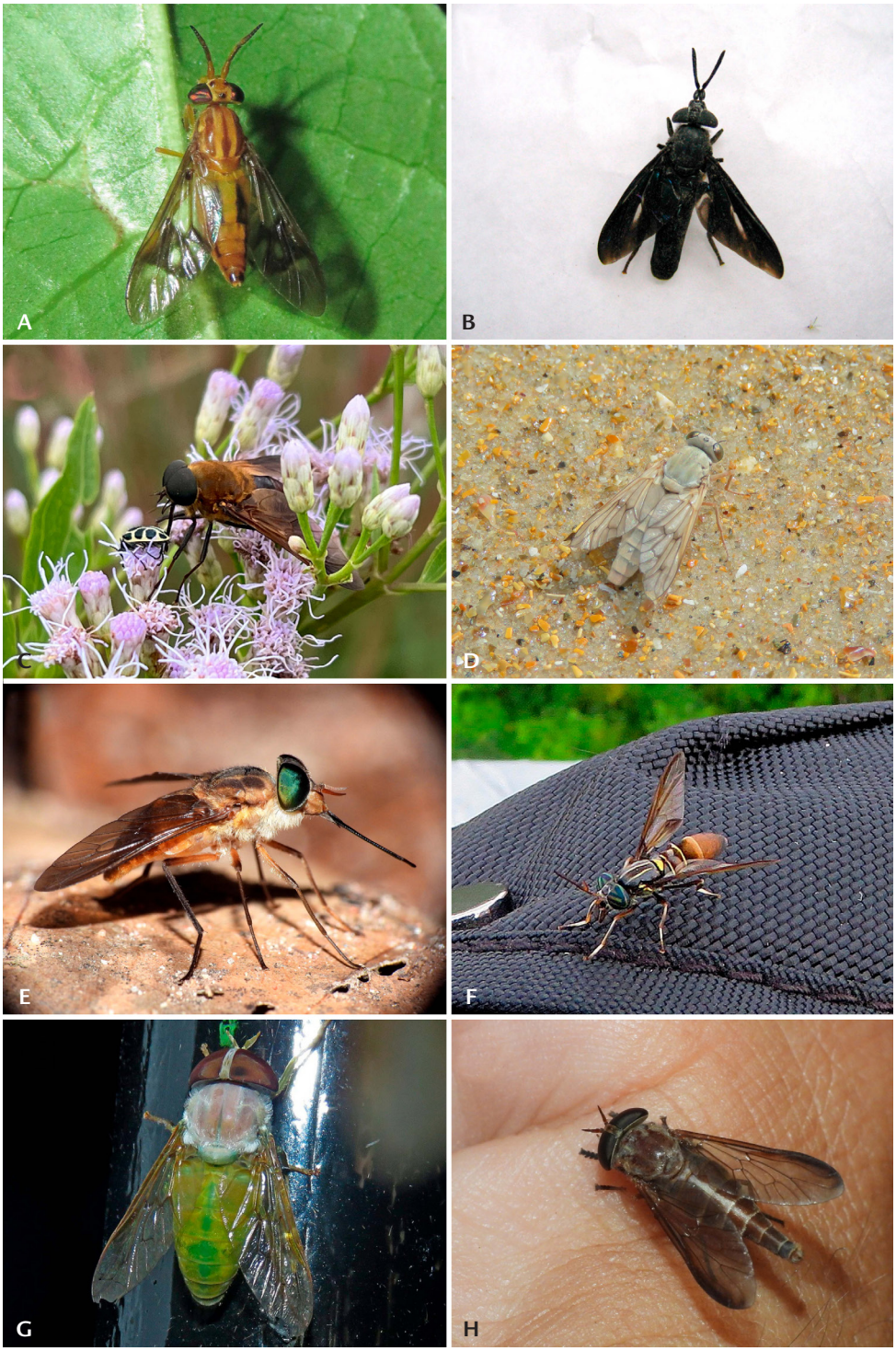
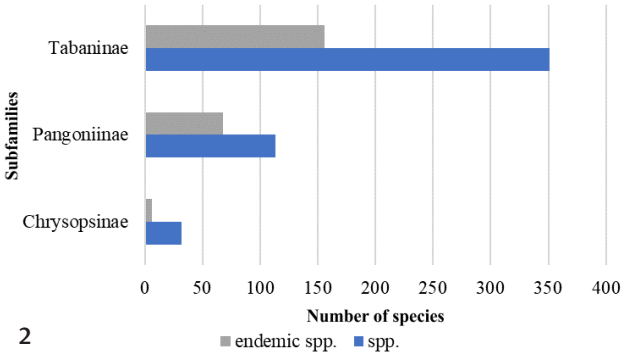


Figure 1. Some Tabanidae of Brazil: (A) Chrysopsini, *Chrysops variegatus*, photo S. Dantas; (B) Rhinomyzini, *Betrequia ocellata*, photo F.F. Xavier; (C) Pangoniini, *Esenbeckia* sp., photo M. Zamoner; (D) Scepsini, *Scepsis appendiculata*, photo D. Luiz; (E) Scionini, *Fidena pseudoaurimaculata*, photo S. Dantas; (F) Diachlorini, *Acanthocera marginalis*, photo S. Dantas; (G) Diachlorini, *Chlorotabanus leucochlorus*, photo S. Dantas; (H) Tabanini, *Tabanus mucronatus*, photo S. Dantas.



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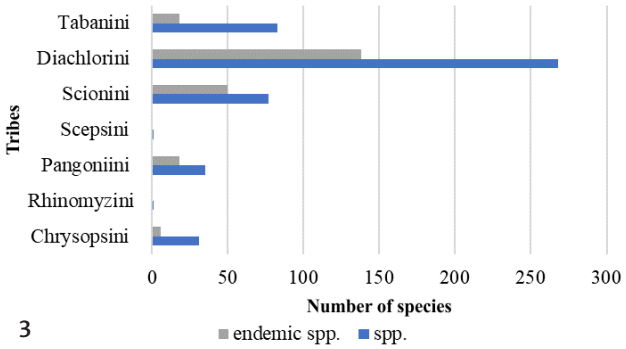

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Figures 2–3. Number of species and endemic species of Tabanidae in Brazil: (2) subfamilies; (3) tribes.

Authors of Brazilian species of Tabanidae

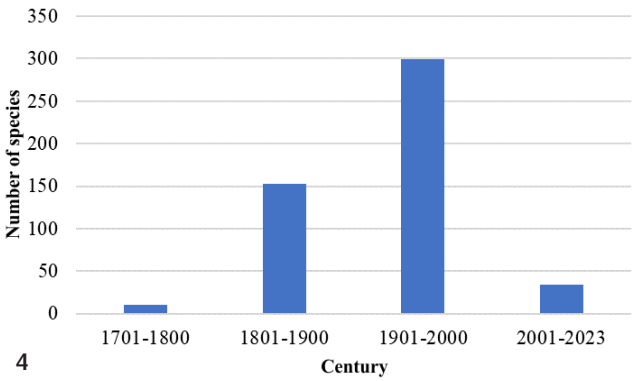
Although the oldest species of Brazilian Tabanidae are credited to Linnaeus, the country name was not specifically mentioned in any of his descriptions. His types were labeled "America meridionali" and "America calidiore" (Linnaeus 1758: 601–602). The first species described from Brazil was *Tabanus longicornis* by Fabricius (1775: 790), currently *Acanthocera longicornis* (Fabricius, 1775). The specimen came from the famous Endeavor expedition and was collected by Mr. Joseph Banks in Ilha Rasa (Rio de Janeiro) (Papavero 1971). Only ten species that are currently recorded in Brazil were described in the 18th century (Figs 4–6).

There was a great increase in the knowledge of horseflies that occur in Brazil in the 19th century, with 153 species described (Fig. 4). The most prolific author of this period was Wiedemann, with 60 described species (Table 2). Most of these species (44) were described in Wiedemann (1828) (Figs 5–7). The second most prolific author of that century was Macquart who described 35 species (Figs 6, 7) between 1838–1850, followed by Bigot (1892) who described 10 species (Table 2).

A total of 299 species with records in Brazil were described in the 20th century, and three researchers were responsible for the description of 186, constituting more

Table 1. Number of subfamilies, tribes, genera, species and endemic species of Tabanidae in Brazil.

Subfamily	Genus	Number of species	Endemic species
Chrysopsinae			
Chrysopsini	*Chrysops* Meigen	31	6
Rhinomyzini	*Betrequia* Oldroyd	1	0
Pangoniinae			
Pangoniini	*Esenbeckia* Rondani	29	12
	Protosilvius Enderlein	6	6
Scepsini	*Scepsis* Walker	1	0
Scionini	*Fidena* Walker	64	42
	Lepmia Fairchild	2	2
	Pityocera Giglio-Tos	7	4
	Pseudoscione Lutz	3	2
	Scione Walker	1	0
Tabaninae			
Diachlorini	*Acanthocera* Macquart	23	14
	Anaerythrops Barretto	1	1
	Bolbodimyia Bigot	1	0
	Catachlorops Lutz	49	35
	Chlorotabanus Lutz	9	4
	Cryptotylus Lutz	4	1
	Dasybasis Macquart	2	1
	Dasychela Enderlein	1	0
	Diachlorus Osten Sacken	28	8
	Dichelacera Macquart	39	21
	Dicladocera Lutz	5	2
	Elephantotus Gorayeb	1	1
	Erioneura Barretto	1	1
	Eutabanus Kröber	1	0
	Lepiselaga Macquart	3	0
	Leptapha Enderlein	1	1
	Leucotabanus Lutz	11	3
	Muscotabanus Henriques & Krolow	1	1
	Myiotabanus Lutz	2	1
	Oopelma Enderlein	1	1
	Pachyschelomyia Barretto	1	0
	Phaeotabanus Lutz	12	3
	Philipotabanus Fairchild	6	3
	Pseudacanthocera Lutz & Neiva	3	2
	Rhabdotylus Lutz	2	0
	Selasoma Macquart	1	0
	Stenotabanus Lutz	25	15
	Stibasoma Schiner	14	9
	Stigmatophthalmus Lutz	1	1
	Stypommisa Enderlein	18	8
	Teskeyellus Philip & Fairchild	1	1
Tabanini	*Phorcotabanus* Fairchild	2	1
	Poeciloderas Lutz	4	0
	Tabanus Linnaeus	77	17
Total	44	496	230



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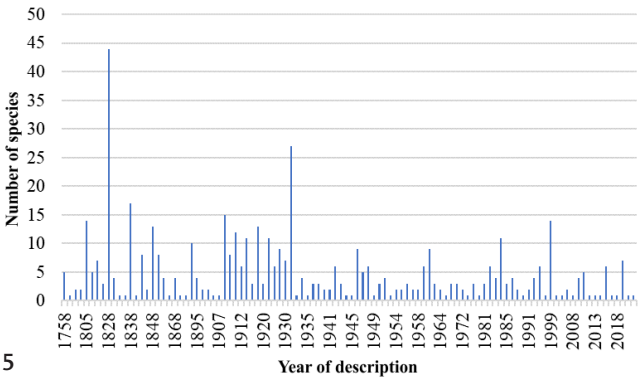

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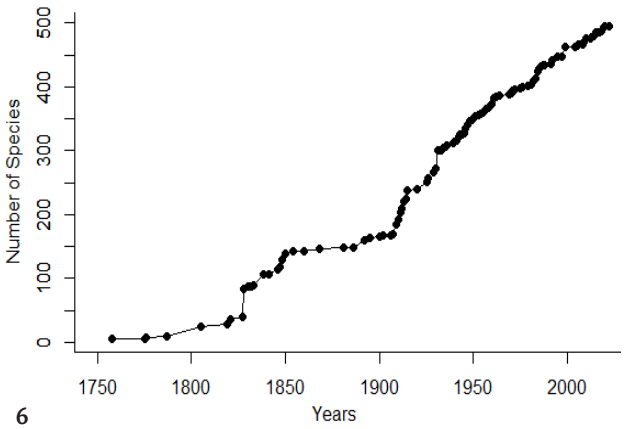
Figures 4–5. Number of Brazilian species of Tabanidae: (4) per century of description; (5) per period of description.



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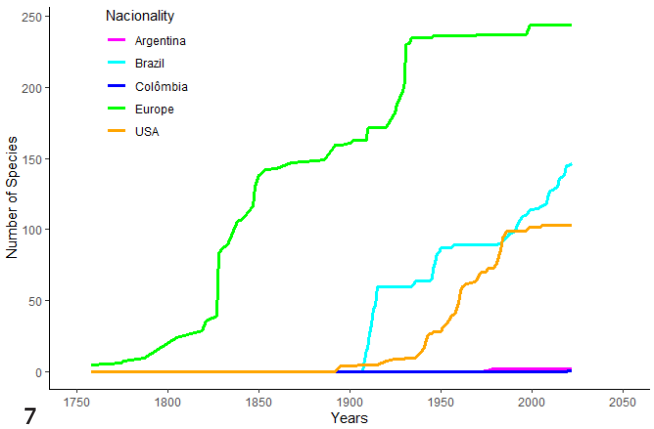

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Figures 6–7. Accumulation curve of Tabanidae species recorded from Brazil by year: (6) based on the year of the description of each species; (7) based on the first record of each species for the country or continent (Europe) and categorized by nationality of the first authors.

than 60% of these species. The first was Fairchild, publishing constantly between the 1930s and 1980s (Fig. 7). He was the first author of 67 species of Tabanidae that are currently valid and with records for the country (Table 2). The second was Adolpho Lutz, who first-authored 63 species between 1907–1936 (Fig. 7), and the third was Kröber, who in the short period of 14 years (1925–1939) was the first author of 56 species recorded in Brazil (Table 2, Fig. 7).

It was only after 1980 that Brazilian researchers became predominant (Fig. 7). Now, we are at the beginning of the 21st century and 34 species of material collected in the country have been described; of these, only one species, *Esenbeckia auribrunnea* Gualdrón-Díaz & Gorayeb, 2020, had a non-Brazilian researcher as the first author (Fig. 7).

The taxonomy of Tabanidae in Brazil began with European researchers who worked alone during the 18th and 19th centuries (Fig. 7), meaning that of all species recorded for Brazil, 163 (32.87%) were described in that period without the presence of any Brazilian researchers (Fig. 4).

North American researchers began working on the group at the end of the 19th century (Fig. 7). The first wave of Brazilian researchers came from the beginning of the 20th century through the work of Adolpho Lutz and his collaborators, Oliveira Castro and Arthur Neiva (Fig. 7). The year 1931 was the most productive of this century, with the description of 27 species of Tabanidae that occur in Brazil (Fig. 5).

A total of 50 researchers of different nationalities first authored the description of the Brazilian species (Table 2, Fig. 8). Europeans were predominant, both in number of authors (23) and in number of species 245 (49.40%). Brazilians were second, with 16 authors and 147 species (29.64%), followed by North Americans with nine authors and 100

Table 2. Nationality and gender of authors (only first author) who described the Brazilian species of Tabanidae.

First Author	Gender	Nationality	Species	Percentage
Fairchild	male	USA	67	13.51
Lutz	male	Brazil	63	12.70
Wiedemann	male	Europe	60	12.10
Kröber	male	Europe	56	11.29
Macquart	male	Europe	35	7.06
Barretto	male	Brazil	24	4.84
Henriques	male	Brazil	22	4.44
Fabricius	male	Europe	17	3.43
Walker	male	Europe	15	3.02
Gorayeb	male	Brazil	11	2.22
Bigot	male	Europe	10	2.02
Brèthes	male	Europe	8	1.61
Philip	male	USA	8	1.61
Wilkerson	male	USA	8	1.61
Chainey	male	Europe	7	1.41
Enderlein	male	Europe	7	1.41
Hine	male	USA	5	1.01
Krolow	male	Brazil	5	1.01
Limeira-de-Oliveira	male	Brazil	5	1.01
Linnaeus	male	Europe	5	1.01
Rafael	male	Brazil	5	1.01
Ricardo	female	Europe	4	0.81
Rondani	male	Europe	4	0.81
Schiner	male	Europe	4	0.81
Williston	male	USA	4	0.81
Burger	male	USA	3	0.60
Carmo	male	Brazil	3	0.60
Pechuman	male	USA	3	0.60
Thunberg	male	Europe	3	0.60
Coscarón	male	Argentina	2	0.40
De Geer	male	Europe	2	0.40
Stone	male	USA	2	0.40
Turcatel	female	Brazil	2	0.40
Barros	male	Brazil	1	0.20
Bassi	female	Brazil	1	0.20
Bequaert	male	Europe/USA	1	0.20
Borgmeier	male	Europe/Brazil	1	0.20
Castro	male	Brazil	1	0.20
Gualdrón-Díaz	female	Colombia	1	0.20
Guérin-Méneville	male	Europe	1	0.20
Guimarães	male	Brazil	1	0.20
Lane	male	Brazil	1	0.20
Lima	female	Brazil	1	0.20
Maldonado Capriles	male	USA	1	0.20
Oldroyd	male	Europe	1	0.20
Penaforte	female	Brazil	1	0.20
Perty	male	Europe	1	0.20
Röder	male	Europe	1	0.20
Summers	female	Europe	1	0.20
Wulp	male	Europe	1	0.20
50			496	100

species (20.36%). Another three species (0.60%) have been described by non-Brazilian researchers from Latin America (Fig. 8).

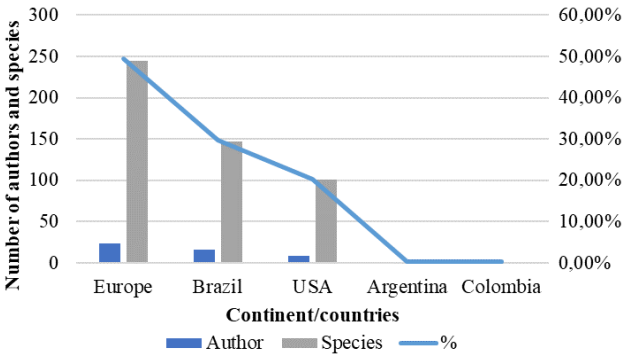


Figure 8. Countries of authors of Brazilian species of Tabanidae by number of described species.

In addition to being a pioneer, Lutz authored the largest number of species described by Brazilians, with 63 species (42.86%) (Table 2). Three other researchers were the first authors on more than 10 new species descriptions: Barretto (24 spp.), Henriques (22 spp.) and Gorayeb (11 spp.), who together represent 38.78% (Table 2). Thus, more than 80% were described by only four researchers.

Only seven women (14%) in a universe of 50 Tabanid researchers (Table 2) have described Tabanid species. The first woman to describe Tabanidae species from Brazil was the European Gertrude Ricardo (four species) (Ricardo 1900, 1902). Then almost a century later, the first Brazilian woman to publish a new species of Tabanidae was Rosângela Maria de Azevedo Bassi (Bassi 1997). In summary, only 11 species known from Brazil were described by female researchers, about 2% of the total (Fig. 9). The underrepresentation of female researchers in a taxon studied for three centuries underscores a prevalent issue within entomology and other scientific fields. In a recent article, Hipolito et al. (2021) showed a generalized gender gap in Brazilian entomology, better explained by a scissor shaped curve: women are the majority in lower positions (Undergraduate to Master programs), but this number falls drastically when permanent and more prestigious positions are taken into account.

Type specimens

The primary types of Brazilian Tabanidae are mostly deposited in European institutions: 226 primary types in 19 institutions (Table 3). This is not a surprise, considering

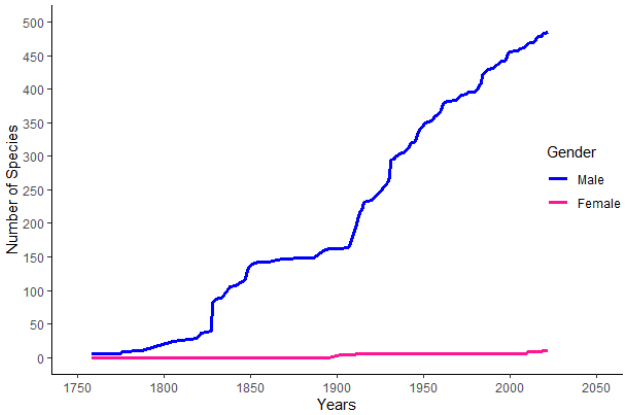


Figure 9. Accumulation curve of Tabanidae species recorded in Brazil per year, based on the first record of each species for the country and categorized by gender of the first authors.

the history of authors and numbers of species described by them. The same pattern was also observed in second and third place, Brazil and the United States, which respectively have 166 primary types in seven collections and 83 primary types in 10 collections (Table 3). The repository institution of 10 primary tabanid types is not known.

Table 3. Location of primary types of Brazilian Tabanidae species by country/region.

Location	Number of collections	Primary of types	Percentage
Europe	19	226	45.56
Brazil	7	166	33.47
USA	10	83	16.73
Argentina	2	10	2.02
unknown	–	10	2.02
Venezuela	1	1	0.20

Despite the gap between specimens held in Brazilian institutions in relation to Europe, three of the first four collections that hold more primary types are Brazilian (Table 4). The collection holding most primary types is FIOC, with 65 primary types of species that occur in Brazil. Next, NHMUK appears with 58, MZUSP with 39 and INPA with 38 primary types. Only seven collections in Brazil house primary types (Fig. 10).

Regarding the primary types, 374 are holotypes, 78 lectotypes, 6 neotypes and 37 represented by syntypes, in addition to one unknown (Table 5). About 95% were described based on females and 5% have been lost or destroyed (Table 5).

Table 4. Primary type deposit location of Brazilian Tabanidae, with acronyms and numbers.

Type location	Acronym	Types
Brazil	FIOC	65
Europe	NHMUK	58
Brazil	MZUSP	39
Brazil	INPA	38
Europe	NMW	37
Europe	ZMHB	35
USA	MCZ	30
Europe	MNHN	24
Brazil	MPEG	21
Europe	ZMUC	20
USA	FSCA	18
Europe	MLUH	11
unknown	unknown	9
USA	AMNH	8
Argentina	MACN	8
USA	USNM	8
USA	CUIC	7
Europe	SMF	6
USA	CAS	5
Europe	Coll. Kröber (destroyed)	5
Europe	NHRS	5
Europe	ISTH (destroyed)	3
Europe	MZPW	3
Europe	HNHM (destroyed)	3
Europe	MZUN	3
Europe	UUZM	3
USA	CMNH	2
Europe	DFS	2
Argentina	MLPA	2
USA	OSU	2
Europe	SMNS	2
Europe	ZSM	2
USA	LACM	2
Europe	*MLUH	1
Europe	*NMW	1
USA	ANSP	1
Europe	Coll. Guérin-Méneville (lost)	1
Brazil	CZMA	1
Brazil	DZUP	1
Brazil	IBSP	1
Europe	IEAUT	1
Venezuela	MHNLS	1
Europe	ZMAN	1
Total	41	496

*Probably lost.

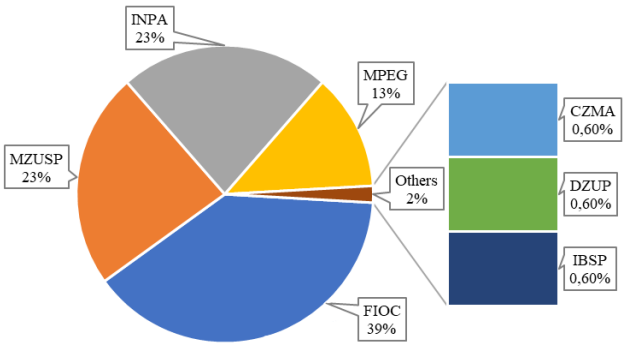


Figure 10. Brazilian collections housing Brazilian primary types of Tabanidae.

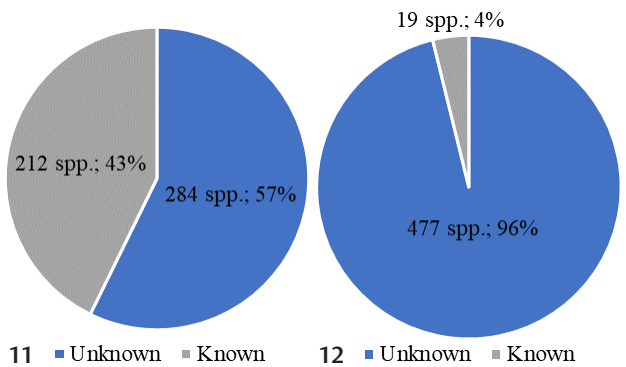
Table 5. Primary type of Brazilian species of Tabanidae with number by sex and condition.

Primary type	Number of types	Female	Male	Lost/destroyed
Holotype	374	351	23	22
Lectotype	78	77	1	–
Neotype	6	6	0	–
Syntype	37	37	4	2
Unknown	1	1	0	1
Total	496	472	28	25

Male and immature specimens

Most horsefly species are only known from females. The males are known for less than half of the species with records in Brazil (Fig. 11). This bias can be explained by the habits and biology of the males, which have shorter lifespans and are less mobile, usually hovering in open areas or canopy, waiting for females to copulate with (Chvála et al. 1972).

Likewise, our knowledge of horsefly larvae is incipient. The larvae are mostly predators and explore several environments, usually aquatic or semi-aquatic. They are usually long lived and have specific habitat restrictions, and are difficult to rear in the laboratory. The larvae of only 19 species with records for Brazil have been described (Fig. 12) (Coscarón and Papavero 2014).



Figures 11–12. Number of Brazilian species of Tabanidae: (11) with males described; (12) with known immature specimens.

Tabanidae distribution

The distribution records of Tabanidae species in the country corroborate the observations of Santos et al. (2020) and Machado and Martins (2022): the regions with more recorded species (in the North and Southeast) are also those housing the main collections of Trichoptera and Neuroptera and, as expected, the states that are thought to be richest in the number of species, namely Amazonas (165 spp.), Pará (149 spp.) and São Paulo (146 spp.). The Northeast region has the lowest number of recorded species and only two states in the region have a truly significant number of species, Bahia (52 spp.) and Maranhão (87 spp.); furthermore, it does not seem coincidental that there is a resident researcher and a reference collection in Maranhão (CZMA). Furthermore, Sergipe is the only state in the country without official records of Tabanidae (Fig. 13).

When Brazil is subdivided into terrestrial biomes, the Atlantic Forest and the Amazon are the most diverse in the number of tabanids, with 233 and 222 species recorded, respectively. The number of endemic species is high in both biomes, and the endemism in the Amazon reaches a high percentage of 59%. The third richest biome is the Cerrado with 147 species; however, the endemicity in this biome is low, with a percentage of 22%. The other three biomes of Caatinga, Pampa and Pantanal are less diverse, and together they do not reach even half the number of species recorded for the Atlantic Forest or the Amazon (Fig. 14).

Update of Brazilian Tabanidae

Anaerythrops Barretto, 1948. Genus wrongly attributed to the article of Barretto (1948c, published in December), the same genus had already been previously published in August 1948 (Barretto 1948b) as *Anerythrops*. However, *Anaerythrops* must be maintained. According to The International Code of Zoological Nomenclature, this is a case of prevailing usage.

Chrysops latitibialis Kröber, 1926 was registered for Brazil in Henriques and Gorayeb (1993), Henriques (1997) and Henriques and Rafael (1999) and reproduced in Coscarón and Papavero (2009b). After further study of the photos of the types made available by the Museum of Comparative Zoology (MCZ), we have concluded that

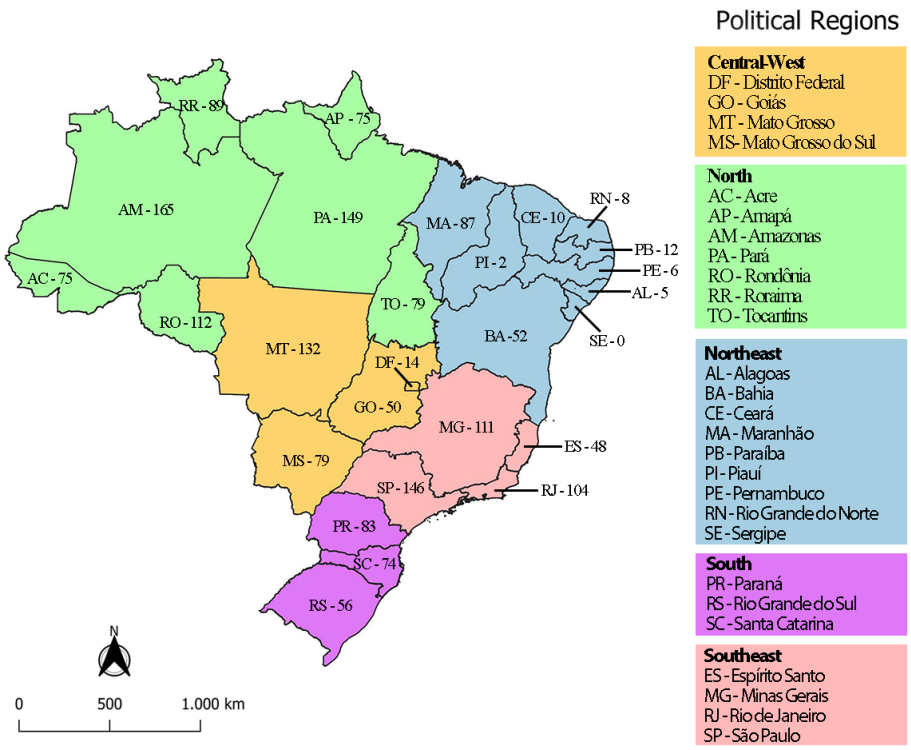


Figure 13. Number of species of Tabanidae recorded for the Brazilian states.

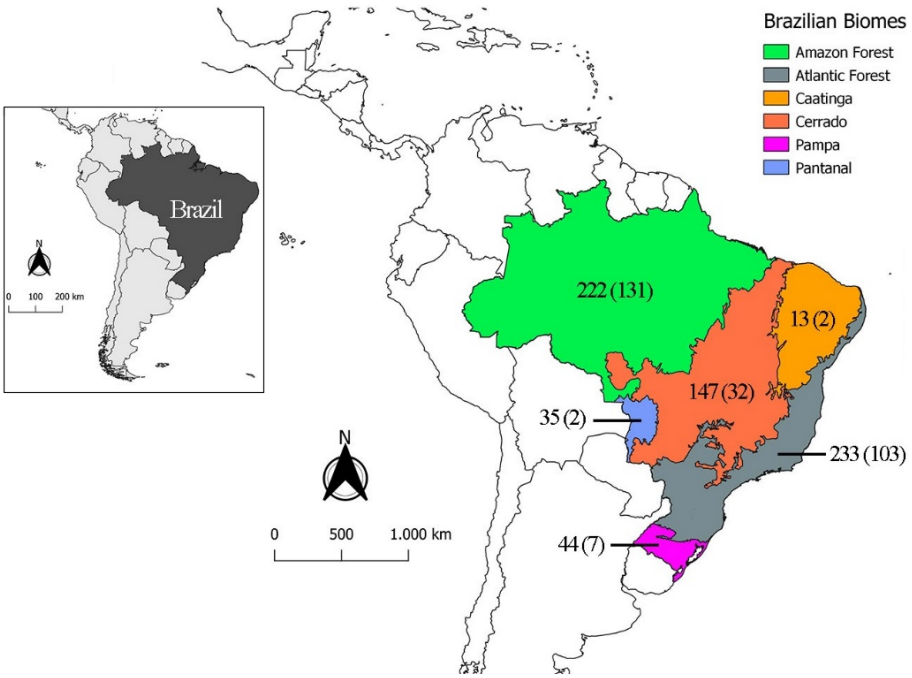


Figure 14. Number of Brazilian species of Tabanidae recorded for terrestrial biomes. The first number represents the total of species and second the number of endemic species.

the Brazilian records are *C. weberi* Bequaert, 1946 (removal of record).

Chrysops lynchi Brèthes, 1910 (stat. reval.). Considered by several authors as a synonym, variety and subspecies of *Chrysops variegatus* (De Geer, 1776), we consider this species as valid due to the great difference in the shape of the scape and the sympatric distribution with *C. variegatus* in the states of Mato Grosso and Mato Grosso do Sul, in Brazil.

Tabanus amazonensis (Barretto, 1948). Species wrongly attributed to 1949 (Barretto 1949), the same species had already been previously published in August 1948 (Barretto 1948a) (year correction).

Stypommisa serena (Kröber, 1931) (comb. reval.) This species, originally described in *Tabanus*, has been allocated in different genera by several authors: as *Stenotabanus* (Fairchild 1964), as *Stypommisa* (Fairchild 1971, Wilkerson 1979, Wilkerson and Fairchild 1985), and as *Phaeotabanus* (Fairchild and Burger 1994, Coscarón and Papavero 2009b). Herein we transfer it again to *Stypommisa* due to the similarity of the structure of the frons, including the frontal callus and banding pattern on the dorsum of the abdomen.

Tabanus ornativentris Kröber, 1929 (sp. reval.). This species was synonymized with *Tabanus ferrifer* Walker, 1850 (= *T. nebulosus* De Geer, 1776) by Fairchild (1943), treated as a subspecies of *T. nebulosus* since Fairchild (1956), and again synonymized with *T. nebulosus* by Coscarón and Papavero (2009b). However, as demonstrated by Coscarón et al. (1998), the immatures and adults of *T. ornativentris* can be differentiated from *T. nebulosus*. Unlike hypothesis of Fairchild (1984), the two morphotypes are not isolated and occur in sympatry in the states of Mato Grosso and Mato Grosso do Sul, Brazil, according to new records Krolow and Henriques (2017) and informed here (Supplementary material Table S1). Therefore, we revalidate the species here.

Future perspectives and gaps

As described, the taxonomy of Tabanidae in Brazil has experienced great advances through the 20th century and the beginning of the 21st century. Nevertheless, the great number of species makes the study of horseflies somewhat challenging and several aspects of the biodiversity of the family remain largely unexplored. There is only one phylogenetic hypothesis for the Tabanidae (Morita et al. 2016). While this hypothesis provides great advancement in our understanding in the evolution of the family and showing that several traditionally recognized groups are not monophyletic (including subfamilies, tribes and genera), the sampling of various genera, including those occurring in the neotropics and Brazil, is still lacking. Several genera in the region are diagnosed based on a handful of discrete, sometimes variable characteristics, blurring the limits among taxa. Despite its abundance, there are no biogeographical hypothesis for the family, and our knowledge about the evolutionary history of Tabanidae in the neotropics is close to non-existent.

Despite important advances in the past few years (Bilheiro et al. 2019, Rodrigues et al. 2021, 2022, Ramos et al. 2023), still little is known about the potential disease agents carried by Tabanidae, and even less so the real capacity of these flies to act as vectors of diseases agents. There are no studies addressing pollination of flowers by Tabanidae in Brazil, or even in the neotropics, despite the importance of this family as pollinators of flowers in other regions (Johnson and Morita 2006).

Even on taxonomical grounds, most species in the country are still identified by old keys, revisions and descriptions, with some of them being more than 30 years old (e.g., Barretto 1948d, Fairchild 1983, Wilkerson and Fairchild 1983). The illustrations of most species are also insufficient, usually limited to drawings and lacking color, which is one of the main characteristics for species identification. Some regions and biomes are also historically neglected, especially in the Northeast and Central West of Brazil.

Future studies in Tabanidae should address these gaps, ideally in an integrative manner. Understanding the evolution of these flies in the neotropics, the biogeographical events which led to its diversification and the parasite carried by these flies are crucial for understanding horsefly biodiversity in a broader sense. These studies must be grounded in a robust taxonomy and classification, only obtained by thorough revisions. When possible, these should be associated with modern imaging and molecular techniques.

Research groups and collections in Brazil

In the past two or three decades, a new generation of scientists have taken on the studies of Tabanidae in the country. In alphabetical order, the major taxonomists who have worked on the family in recent decades are: Antonio Thadeu Medeiros de Barros – Centro de Pesquisa Agropecuária do Pantanal (Embrapa, Corumbá); Augusto Loureiro Henriques – Instituto Nacional de Pesquisas da Amazônia (INPA, Manaus); Daniel Dias Dornelas do Carmo – Universidade de São Paulo – (USP, Ribeirão Preto); Francisco Limeira

de Oliveira – Universidade Estadual do Maranhão (UEMA, Caxias); Inocêncio de Sousa Gorayeb – Museu Paraense Emílio Goeldi (MPEG, Belém); José Albertino Rafael – Instituto Nacional de Pesquisas da Amazônia (INPA, Manaus); Mauren Turcatel – Field Museum of Natural History (FMNH, Chicago, USA), and Tiago Kütter Krolow – Universidade Federal do Tocantins (UFT, Porto Nacional). Important studies of seasonality and abundance have also been conducted, highlighting the laboratories of Antonio Thadeu Medeiros de Barros (Embrapa, Corumbá) and Rodrigo Ferreira Krüger (Universidade Federal de Pelotas).

The location of the major horsefly collections in Brazil are largely dependent on historical factors. Institutions that were founded early in history of Brazil and those with a working specialist tend to be have more specimens. As shown in this work, the largest Tabanidae collection in the country is housed at the Museu de Zoologia da Universidade de São Paulo (MZUSP), which harbors the collection of Mauro Pereira Barretto, followed by the Instituto Nacional de Pesquisas da Amazônia (INPA) and the Museu Paraense Emílio Goeldi (MPEG). Other noteworthy collections are Fundação Instituto Oswaldo Cruz (FIOC), which houses the types of Adolpho Lutz, and Coleção Entomológica Padre Jesus Santiago Moure (DZUP). More recently, two institutions located outside major urban centers have gained prominence due to their regional collections: the well-established Coleção Zoológica da Universidade Estadual do Maranhão (CZMA), and the more recent (just over a decade old) Coleção de Entomologia da Universidade Federal do Tocantins (CEUFT).

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Competing Interests

The authors have declared that no competing interests exist.

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Supplementary material 1

Table S1. Updated taxonomic data on the Brazilian tabanid fauna.

Authors: TK Krolow, DDD Carmo, LP Oliveira, AL Henriques
Data type: species data.

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