Chapter 4

Tabanids in South America

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Abstract

The text provides information on taxonomy, morphological data, distribution, and bionomy on most recorded species of tabanids in South America. The distribution parameters of species according to classification by biogeographical regions are used. An appendix indicating the main studies about tabanids according to the countries of their origin is still offered.

Keywords: insect vector, horsefly, Neotropical region, taxonomy, bionomy

1. Introduction

The species of family Tabanidae Latreille, 1802, commonly known in South America as "mutucas," "botucas," "mbutú," "colihuacho," and "moscas de los caballos", comprises more than 4400 worldwide species, absent only in the regions of higher altitudes and eternal snows [1, 2], with more than 1800 species present in the Neotropics [3]. They are the largest bloodsucking Diptera, reaching up to 25 mm, with a robust body and some with well-developed proboscis, an aspect that causes respect and fear. Females often require blood meal for maturation of eggs, at least after the first posture, so they are considered autogenous, partially autogenous, or nonautogenous [4]. Males are phytophagous, but females, always in search of blood, repeatedly attack humans, domestic and wild animals, among primates, rodents, alligators, snakes, turtles, and birds, especially during the drier seasons [5–8]. Tabanids are known worldwide for its painful sting and are mechanical and biological vectors of several helminths, viruses, bacteria, and protozoa, etiologic agents of diseases that can affect humans and wild and domestic animals [9–11]. Tabanids have the characteristics necessary for a good mechanical vector: interruption of hematophagism, high mobility, and large mouthparts that can carry blood [10]. The painful tabanid sting is recognized as a determining factor to interrupt blood meal. The sting causes reactions in the host,

such as muscle tremors, tail movement, hit with the head, and kick in order to make the tabanid fly away [12]. But the presence of tabanid predators as the solitary sand wasps *Stictia punctata* (Fabricius) and *Stictia signata* (Linnaeus) (Hymenoptera: Crabronidae) plays an important epidemiologic role: the wasps catch tabanids and take them away, before and during the blood meal, and in this last case, causing interrupted hematophagism [13]. Around the world, more and better evidence has been gathered to assess the importance of tabanids in an epidemiological context. Several studies show a correlation between the time of increased activity of horseflies and the appearance of diseases in animals and man. The season of year in which the vectors are more common means increased health risk to animal populations and exposed human [9, 10, 14, 15]. In Neotropics, tabanids occur mainly in tropical rainforest, deciduous forest, wet savannah, and grassland meadows; they appear to be rare or absent in open savannah, oak forest, tropical dry forest, and seaside mangroves [16]. According to Raymond, there is greater number of species and greater possibility of finding rarer species in the ecotone areas [17].

The classification adopted by most current authors about Neotropical tabanids is the proposal by Mackerras [18], which divided the Tabanidae family into three subfamilies, Chrysopsinae Blanchard, 1840, Pangoniinae Rondani, 1856, and Tabaninae Latreille, 1802, mainly based on genitalia morphology.

The subfamily Chrysopsinae, with species that are an intermediate between Pangoniinae and Tabaninae, is divided into three tribes: Bouvieromyiini Séguy 1930 the more primitive, but with relatively specialized species; Chrysopsini Blanchard, 1840 with fairly structurally uniform species, and few genera but numerous species; and the tribe Rhinomyzini Enderlein, 1922 with only a very specialized species in the Neotropics. The subfamily Pangoniinae, in the Neotropical region, is divided into the tribes Mycteromyiini Coscarón and Philip, 1979, Pangoniini Rondani, 1856, and Scepsini Bequaert, 1930, all with more primitive as specialized species, and Scionini Enderlein, 1922, with only one primitive and anomalous species. The Tabaninae subfamily consists of three tribes, Diachlorini Lutz, 1909, Tabaninae Latreille, 1802, and Haematopotini Bequaert, 1930; the latter does not have representatives in the Neotropics. The Diachlorini tribe has primitive species and specialized species and the largest number of species in the Neotropics. Tabanini tribe also brings together both primitive and specialized species, but not as much as those belonging to tribe Diachlorini; most species is found only in one genus (*Tabanus* Linnaeus) [19, 20]. The terms "primitive" and "specialized" refer to the position of key characters: the most primitive are the ones that are closer to the conditions found in presumably ancestral forms, such as Nematocera, specializing more away from them, either by reducing and increasing the structural complexity.

2. Morphology of tabanids

Tabanids belong to the Suborder Brachycera, characterized by short antennae with three (up to five) segments and the adults emerge from the puparium by a T-shaped slot. The species of family Tabanidae have head wider than thorax and frons may have one or more callus; generally adjacent eyes (holoptics) in males and separated (dicoptics) in females; subcallus generally inconspicuous, but sometimes well-developed, smooth and shiny; antennal flagellum with first major flagellomere and 4–8 apical flagellomeres; maxillary palps with two segments; blood-sucking mouthparts with mandibles and stiliform maxiles of most females adapted to

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puncture the skin of the host; thorax with prominent notopleural lobes; legs with apical spurs in the median tibiae, and may be absent in hind. Wings with veins R_4 and R_5 limiting its apex; radial basal, basal medium, and discal cells large; posterior cubital cell usually closed near the edge of the wing; membranous wings with varying patterns. Male with gonocoxite fused with hiparium and single or partially divided gonostile; epandrium whole or divided; 10th tergite absent and flattened cerci; females usually with 10th tergite divided, 8th sternite is a shield-shaped enclosure and one-segmented [21, 22] (**Figure 1**). About the morphology of tabanids, Barretto's studies must be emphasized, mainly that external morphology of *Poeciloderas quadripunctatus* [23]. The studies of Iide, about the morphology of *Tabanus importunus* [24] and species of *Fidena* (*Fidena*) [25–28] are still used as a reference in morphology studies.

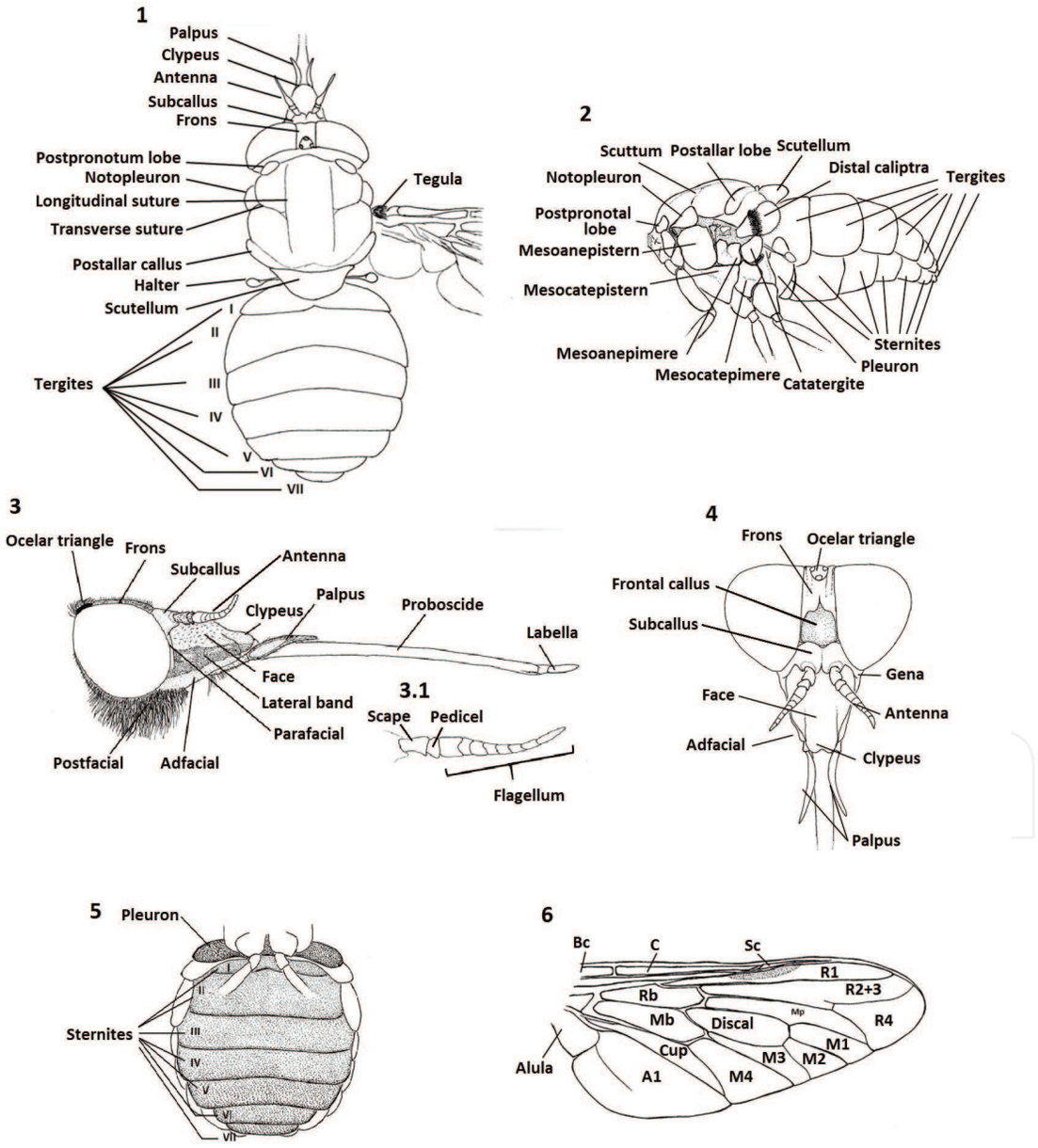

Figure 1. Main parts of a tabanid body (Genus *Fidena*). 1 – Dorsal view of body; 2 – Lateral view of thorax and abdomen; 3 – Lateral view of head; 3.1 Antenna; 4 – Frontal view of head; 5 – Ventral view of abdomen; 6 – Wing: Bc – Basal costal cell; C- Costal cell; Cup – Cubital posterior cell; Mp – Medial posterior cell; M1, M2, M3, M4 – Medial cells; R1, R2+3, R4 – Radial cells. According MacAlpine. Figures used with permission of Gorayeb.

3. South-American tabanids

Studies of tabanid species in South America began in the second half of the nineteenth century, with foreign researchers, some of which have never been on the continent. These studies were in full descriptions of native species, and were based on specimens deposited in private collections, museums, or European universities, sent by professional collectors [1]. These early records were made by Linnaeus, Scopolli, Strom, DeGeer, Fabricius, Thunberg, Meigen, Latreille, and Palisot Beauvois. More extensive studies on tabanofauna South America were performed by several authors. Wiedemann described a large number of species from South-American continent. Walker studied and described several species of South-American tabanid specimens deposited in British Museum and Saunders collections. Kröber was in Argentina and Bolivian Chaco regions, collecting dipterous between 1925 and 1926; he also studied the taxonomy and described several species of South-American tabanids from specimens deposited in museums and research institutes in Europe. It should be mentioned that an important study by Martins [29] on tabanids from Minas Gerais state, Brazil, located in provinces of Cerrado (Chacoan sub-region) and Parana Forest (Parana subregion) revealed the occurrence of 9 genera and 42 species of Pangoniinae, and 12 genera and 52 species of Tabaninae (the most common genera *Chrysops*, with 15 species and *Tabanus*, with 18 species). Descriptions of species carried out at this time are mostly considered insufficient to identify the species currently collected, if holotypes or paratypes are missing for comparison. Thus, many of these species were re-described, using more specific characters, which previously were not valued.

The first tabanid catalog of South America was published by Hunter in 1901 [30], naming 319 species; in separate listing, Hunter lists 64 South-American species described by Walker and another list with 62 species described by Wiedemann, Macquart, and Walker, but without information of locations from where they were collected, presumably from South America. Kröber, in 1934, published another catalog that included species of tabanofauna from South and Central America, Mexico, and the West Indies, which listed 861 South-American species [31]. In 1969, Fairchild [19] published an excellent study of the Neotropical tabanids, with key to genera and subgenera, containing information on the geographical distribution and morphology. Two years later, the same author published his catalog about tabanids from South of the United States, listing 707 species recorded in South America [32]. These Fairchild publications served as the basis for the manual to identify genera and subgenera published by Coscarón and Papavero in 1993 [33], as well as for a new catalog on tabanids from South of the United States, by Fairchild and Burger in 1994 [34]. More recently, in 2009, Coscarón and Papavero [20] published a new catalog of the Neotropics, including the species of Central America, southern part of Mexico and Baja California peninsula, southern Florida, all Caribbean islands, and South America. In the same year the authors also published a new illustrated manual for identification of the subfamilies, tribes, genera, and subgenera of Neotropical tabanids [35]. After the publications of Coscarón and Papavero [20] several species have been described in Neotropics and South America, giving rise to the addendum of 11 new taxa to the catalog [36]. And even after this publication, other species have been described from South America. *Pityocera* (*Pseudelaphella) ecuadorensis* Krolow and colleagues [37] was described from coastal zone of Arid Ecuador province; *Protosilvius*

gurupi Rafael, Marques, and Limeira-de-Oliveira [38], *Muscotabanus rafaeli* Henriques and Krolow, *Pityocera* (*Pseudelaphella*) *pernaquila* Gorayeb and Krolow [37], *Elephantotus tracuateuensis* Gorayeb, *Dasybasis antillanca* González [39], all from Brazilian Amazonian Subregion. *Stenotabanus clavijoi* Gorayeb, Gómez and Velásquez-de-Rios was described from Venezuelan Amazonian Forest [40] and *Dasybasis collagua* González from Chilean Andean region [39]. *Dichelacera matogrossensis* Henriques and Krolow, *Pityocera* (*Pseudelaphella*) *barrosi* Gorayeb and Krolow [37], and *Pityocera* (*Pseudelaphella*) *gorayebi* Limeira-de-Oliveira and Krolow [37] were described from midwest Brazilian Cerrado and *Pityocera* (*Pseudelaphella*) *rhinolissa* Krolow and Henriques [37] from midwest Brazilian Cerrado and Bolivia (central Bolivian Plateau). *Dichelacera walteri* Guimarães, Gorayeb and Carvalho was described from southeast coast, Brazilian Atlantic Forest province [41]. Most studies on tabanids in South America are morphological, with few others about biology, behavior or seasonality, as will be seen by studying the main species of the genera represented in the South America.

South America has 11 major biomes: rainforest spanning the Amazon Forest and Atlantic Forest; the fields and southern savannas; the flooded fields (Pantanal); the montane camps; deserts and scrublands; tropical and subtropical conifers forests (Araucaria Forest); temperate forest; dry tropical forest; mangroves; Mediterranean shrub; and coastal areas of salt marshes. The tabanofauna is found in all biomes, except at higher altitudes, because of the restrictions imposed by low temperatures. In South America, tabanids are found in virtually all habitats and environments from the beaches of coastal areas, salt marshes, mangroves, salt lakes, Chilean and Peruvian deserts, southern grasslands, savannas and scrublands, rain forests, plains, up the slopes the mountains in the line of snow in the Andes [4]. Certainly the habitat of tabanids is also influenced by the food source, e.g., the arboreal fauna of the Neotropical mammals determines that a large number of tabanid species live in that habitat. Fairchild observed the preference of *Philipotabanus inauratus* Fairchild, *Stibasoma apicimacula* Fairchild, *Stenotabanus jaculatrix*, *Stenotabanus maruccii* (Fairchild), *Stibasoma fulvohirtum* (Wiedemann), *Tabanus defilippii* Bellardi, *Dichelacera crocata* Fairchild, *Catachlorops umbratus* Hine and *Stibasoma panamensis* Curran, by treetops of rainforest [42]. Generally, tabanids prefer defined habitats, although a few species widely distributed can be found in many environments, especially those altered by human activity, such as agriculture and livestock [19].

From many studies conducted over the years, it has been possible to map, at least to some degrees, the biogeographical distribution of main tabanids genera of South America; however, there is no study on biogeographic distribution that contemplate tabanids, except that of Fairchild [19]. To characterize the tabanid distribution in South America, a proposal has been elaborated bringing together the studies of Fairchild [19] and Morrone [43, 44], and their divisions of the Neotropical region in biogeographic subregions. The proposal of Morrone is based on previous studies of panbiogeography and cladistic analysis of insect fauna of Latin America [44]. Thus, an attempt to join the proposed biogeographical models and current knowledge about tabanids in South America is presented here.

According to Morrone [44], in a biogeographical context, South America is characterized as consisting of three regions: Neotropical, South American transition zone, and Andean regions (**Table 1**). **Neotropical region** extends from north-central Mexico to Argentina, comprises the

Region/transition zones	Subregion	Dominion	Provinces
Neotropical	Caribbean	North-western South America	Choco (1)
			Maracaibo (2)
			Venezuelan Coast (3)
			Trinidad and Tobago (4)
			Magdalena (5)
			Venezuelan Llanos (6)
			Cauca (7)
			Galapagos Islands (8)
			Western Ecuador (9)
			Arid Ecuador (10)
			Tumbes-Piura (11)
	Amazonian		Napo (12)
			Imeri (13)
			Guyana (14)
			Humid Guyana (15)
			Roraima (16)
			Amapa (17)
			Varzea (18)
			Ucayali (19)
			Madeira (20)
			Tapajos-Xingu (21)
			Para (22)
			Pantanal (23)
			Yungas (24)
	Chacoan		Caatinga (25)
			Cerrado (26)
			Chaco (27)
			Pampa (28)
	Parana		Brazilian Atlantic Forest (29)
			Parana Forest (30)
			Araucaria angustifolia Forest (31)
South-American transition zone			North Andean Paramo (32)
			Coastal Peruvian Desert (33)
			Puna (34)

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Region/transition zones	Subregion	Dominion	Provinces
			Atacama (35)
			Prepuna (36)
			Monte (37)
Andean region	Central Chilean		Coquimbo (38)
			Santiago (39)
	Sub-Antartic		Juan Fernandez Islands (40)
			Maule (41)
			Valdivian Forest (42)
			Magellanic Forest (43)
			Magellanic Paramo (44)
			Malvinas Islands (45)
	Patagonian		Central Patagonia (46)
			Subandean Patagonia (47)

Table 1. Biogeographical classification of South America, adapted from Morrone [44].

Caribbean, Amazonian, Chacoan, and Parana subregions. **Caribbean subregion** from South America, with Northwestern South American dominion, comprises the provinces of Choco, Maracaibo, Venezuelan Coast, Trindad and Tobago, Magdalena, Venezuela Lannos, Cauca, Galapagos Islands, Western Ecuador, Arid Ecuador, and Tumbes-Piura, where some species of genera *Lepiselaga*, *Chrysops*, *Esenbeckia*, *Selasoma*, *Stibasoma*, *Dichelacera*, *Acanthocera*, and *Tabanus* occur. **Amazonian subregion** is the largest subregion of Neotropics, extending from Brazil, the Guyanas, Venezuela, Colombia, Ecuador, Peru, Bolivia, Paraguay, to Argentina. This subregion comprises 13 provinces: Napo, Imeri, Guyana, Humid Guyana, Roraima, Amapa, Varzea, Ucayali, Madeira, Tapajos-Xingu, Para, Pantanal, and Yungas. The tabanid species occurring in these provinces belong mainly to genera *Chrysops*, *Esenbeckia*, *Fidena*, *Boliviamyia*, *Catachlorops*, *Chlorotabanus*, *Cryptotylus*, *Dasychela*, *Diachlorus*, *Dichelacera*, *Lepiselaga*, *Leucotabanus*, *Phaeotabanus*, *Pityocera*, *Poeciloderas*, *Pseudacanthocera*, *Selasoma*, *Stenotabanus*, *Stibasoma*, *Stypommisa,* and *Tabanus.* There are four provinces assigned to **Chacoan subregion**: Caatinga, Cerrado, Chaco, and Pampa. There are no published records for tabanids in Caatinga province, except the fossil *Cretotabanus stonemyomorphus* Martins Neto and Santos [45]. Limeira-de-Oliveira informed that he had captured specimens of *Chrysops*, *Pityiocera*, *Catachlorops*, *Diachlorus*, *Dichelacera*, *Leucotabanus*, *Phorcotabanus*, *Poeciloderas*, and *Tabanus* in states of Piauí and Ceará, Brazil (personal communication). In other three provinces (Cerrado, Chaco, and Pampa), species of genera *Chrysops, Scaptia, Esenbeckia, Fidena, Acanthocera, Catachlorops, Chlorotabanus, Diachlorus, Dasybasis, Dichelacera, Lepiselaga, Leucotabanus, Phaeotabanus, Phorcotabanus, Stenotabanus, Stypommisa, Poeciloderas,* and *Tabanus* occur. **Parana subregion** comprises three provinces: Brazilian Atlantic Forest, Parana Forest, and *Araucaria augustifolia* Forest. The species reported to this subregion belong to genera *Chrysops, Esenbeckia, Fidena, Scaptia, Scepsis, Acanthocera, Catachlorops, Chlorotabanus,*

Dichelacera, *Diachlorus*, *Lepiselaga*, *Leucotabanus*, *Phaeotabanus*, *Pseudacanthocera*, *Rhabdotylus*, *Stigmatophtalmus*, *Poeciloderas,* and *Tabanus*. The **South American transition zone** extends along the highlands of Andes between Venezuela, northern Chile, and western Argentina, and comprises six provinces: North Andean Paramo, Coastal Peruvian Desert, Puna, Atacama, Prepuna, and Monte, where tabanids species of genera *Dasybasis*, *Esenbeckia*, *Fidena*, *Scione*, and *Tabanus* occur. The **Andean region** extends from central Chile and Patagonia, along the high mountain ranges of Venezuela, Colombia and Ecuador, through the coastal desert and Puna of Peru, Bolivia, northern Chile and Argentina, to Argentine-Chilean Patagonia. Andean region consists in three subregions: **Central Chilean subregion** with the provinces of Coquimbo and Santiago with species of *Veprius*, *Protodasyapha*, *Esenbeckia*, *Scaptia*, *Mesomyia*, *Mycteromyia*, *Dasybasis*, and *Tabanus*. **Subantartic subregion**, with the provinces of Juan Fernandez Islands, Maule, Valdivian Forest, Magelanic Forest, Magelanic Paramo, and Malvinas Islands, with tabanids species belonging to genera *Parosca*, *Silvestrielus*, *Scaptia*, *Acellomyia*, *Agelanius*, *Dasybasis, Scaptioides*, *Pseudoscione*, *Haematopotina*, *Poeciloderas* and *Tabanus*. **Patagonia subregion** is divided in two provinces: Central Patagonia and Subandean Patagonia, where species of genera *Scione*, *Scaptia*, *Acellomyia*, *Agelanius*, *Caenopangonia*, *Chrysops*, *Dasybasis*, *Haematopotina*, *Nubiloides*, *Protodasyapha*, *Scaptioides*, *Silvestriellus*, *Veprius,* and *Tabanus* occur (**Figure 2**). There is no doubt that there are species within genera that are ubiquitous, and there are genera with species more restricted to specific habitats. This issue was discussed by Fairchild in 1969 [19], but lacks a more current study on biogeography of tabanids in Neotropics.

Despite the tendency to turn the habitat as the determining factor for tabanid distribution, most authors use the politics division, by countries and their states and provinces, as the distribution paradigm. So, by the end of the chapter, the authors provide (as an Appendix), the main studies on tabanofauna of South-American countries.

Following, the list of subfamilies, tribes, genera, and more registered species of South-American tabanids, offering information on morphological characteristics, distribution, and the most important references of each taxa.

3.1. The subfamily Chrysopsinae (Blanchard, 1840)

This is underrepresented in number of species, except for those belonging to the genus ***Chrysops*** Meigen, 1803, which has a worldwide distribution. The females of this subfamily have a simple pointed genitalia style, simple caudal ends of spermathecal ducts, without cup-like expansions, ocelli, and eyes nearly always patterned with contrasting colored bands or spots. The subfamily is represented by two tribes in the tropical region: **Bouvieromyiini** Séguy, 1930 and **Chrysopsini** Blanchard, 1840 [19].

3.1.1. Tribe Bouvieromyiini (Séguy, 1930)

This comprises primitive and specialized species, with the following characteristics: first antennal segment hardly longer than width, antennae shorter than antero-posterior thickness of head, callus variable, narrower than frons, and eyes with a transverse band [19]. In South

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Figure 2. Distribution of genera of tabanids according to occurrence of species in regions and subregions of South America. Neotropical Region: Caribbean, Amazonian, Chacoan and Parana subregions; South American Transition Zone; Andean Region: Central Chilean, Subantartic and Patagonian subregions. Adapted with permission of Morrone [43, 44].

America especially in Chile and Argentina, only the primitive species can be found. Other primitive species occur in eastern Nearctic region, temperate South Africa, Northeast Asia and Japan, and eastern and southeastern Australia. The more specialized representatives occur in the Old World tropical and southern Africa, Madagascar, Seychelles, Indonesia, New Guinea, and Australia with few species in India and Southern China. The South-American species of Bouvieromyiini tribe are species that occur in the temperate regions of central Chile and Southeast Argentina (Chacoan subregion), and belong to the single subgenus of tribe.

3.1.1.1. Genus Pseudotabanus (Ricardo, 1915)

This genus comprises only three species in the subgenus Coracella (Philip, 1960).

3.1.1.1.1. Subgenus Coracella (Philip, 1960)

Pseudotabanus (Coracella) araucana Coscarón, *Pseudotabanus (Coracella) carbo* (Macquart), and *Pseudotabanus (Coracella) rubricornis* (Kröber). The first species occurs in Chile and Argentina [46] and the latter two only in Chile [34]; *Pseudotabanus (Coracella) araucana* is considered by Coscarón and Papavero [20] as *araucanus*. Coscarón [47] reviewed the subgenera *Coracella*, as belonging to the genus *Mesomyia* Macquart 1850, which continued to appear [46] until the research publication by Fairchild and Burger [34], in which *Coracella* is considered as subgenus *Pseudotabanus*; in the same study, Coscarón [47] described *Pseudotabanus (Coracella) araucana* and provided a key to separate the three species.

3.1.2. Tribe Chrysopsini Blanchard, 1840

This comprises less restrictive species in habitats, and are separated from Bouvieromyiini by first antennal segment longer than width, near always at least twice as long as width, the third with basal plate and four annuli, antennae longer than width of head, callus generally as wide as high or wider, eyes speckled or with a specific pattern of spots and bars [19]. Most species occur in tropics in South America and Africa, but they are well represented in the Nearctic and Palearctic regions, but few eastern, Australian, or Chilean species. Only two genera are present in the Neotropics, ***Chrysops* Meigen**, 1803 and ***Silvius* Meigen**, 1820, but only the first is present in South America.

3.1.2.1. The genus Chrysops Meigen, 1803

It is represented worldwide and brings together 75 species in Neotropics, from Mexico to Argentina, of which 52 are South American [20]. In epidemiological and diagnosis of tabanofauna studies, the *Chrysops* species are more reported in South America. *Chrysops variegatus* (DeGeer) in Paraguay is a possible vector of the equine disease "mal de caderas," caused by *Trypanosoma evansi* [48]. It was the most abundant species observed in a survey performed in Aregua, central Paraguay [49]. Rafael and collaborators [50] captured *C. variegatus* on Maraca Island, Amazonian subregion, Guyana province. Bermúdez and Bermúdez described the larvae and pupae of *Chrysops variegatus* collected between March and April, in tropical area of high humidity and temperatures, associated with aquatic plants *Pondeteria sagitata* Presl and *Sagittaria* sp., in the livestock region of Mexico [51]. The species (as *variegata*) was the second-most collected species after *Lepiselaga crassipes* (Fabricius) in areas of ecotone between secondary forest and pastures, in northern Colombia, Caribbean subregion [52]. The species was also collected in eastern Amazon, in areas of primary forest and pasture [53] and in Brazilian northern Amazon, also in primary forest but at 1200 meters of altitude, border Brazil-Venezuela [50]. In a survey conducted during 1995–1996 in Central Amazon four species of *Chrysops* were found, and the most abundant species was *Chrysops formosus* Kröber; the other species were *Chrysops incisus* Macquart, *Chrysops ecuadoriensis* (Enderlein), and *Chrysops variegatus* (DeGeer) [54]. It also occurs in central Amazon, Brazil, in primary forest and "campinaramas" ground

level, and in forest canopy, 40 meters high, Amazonian Subregion, Varzea province [55–57]; the species was also observed in transition zone between the savannah and the Brazilian Amazon forest [58] and in Caatinga (Limeira-de-Oliveira, in personal communication). *Chrysops variegatus* also occurs in coastal highlands of southeast Brazilian Parana subregion [59], but was not recorded in Brazilian southern Pampa [60]. Buestán captured *Chrysops variegatus* in coastal zone of Ecuador, Western and Arid provinces, and Caribbean subregion [61]. *Chrysops varians* Wiedemann is another wide distributed species and has been captured from savannah of French Guiana [17], in pasture area in western Amazon [53], in the transition zone between the savannah and eastern Brazilian Amazon forest [58], in highlands of southeast Parana subregion [62, 63], and in southern Pampa, province of Chaco subregion, in Brazil [60]. On Marambaia Island, southeast Parana subregion, Brazilian Atlantic Forest province, *Chrysops variegatus* and *Chrysops varians* were observed flying around the head and curling themselves on the hair of people who walk through forests or sandbanks [64, 65].

3.2. Subfamily Pangoniinae (Rondani, 1856)

This comprises the more primitive species of tabanids. They are characterized by ninth tergite undivided in both sexes, caudal ends of spermathecal ducts without cup-like expansions, usually with 7–8 annuli in third antennal segment, ocelli and hind tibial spurs present [19]. Species are distributed in four tribes, all represented in Neotropics [20].

3.2.1. Tribe Mycteromyiini (Coscarón and Philip, 1979)

This was created from genus *Mycteromyia* Philippi, 1865, characterized by elongated body, grayish or yellowish to brown, elevated ocelli at vertex, frons about as wide as high, no callus, but some rugosities above subcallus, face conically produced, wing elongated, accentuated clouds on crossveins, first posterior cell closed and petiolate [19]. The tribe is currently divided in four genera.

3.2.1.1. Genus Caenopangonia (Kröber, 1930)

This was recently placed within this tribe, with small to medium yellowish-brown species, dichoptic eyes in both sexes, widened frons, strong scutal vittae, wings with spotted crossveins, palpi small subcilindrical with reduced apical pits [66]. The genus comprises five species occurring in Central Chile and Midwest Argentina. The former genus comprised three species: *Caenopangonia aspera* (Philip), *Caenopangonia brevirostris* (Philipp) and *Caenopangonia hirtipalpis* (Bigot). Two new species from Chile, *Caenopangonia cerdai* Krolow, Henriques and González and *Caenopangonia coscaroni* Krolow, Henriques and González, were recently described and a key for identification of current species was provided [67].

3.2.1.2. The genus Mycteromyia (Philippi, 1865)

This appears in Coscarón and Papavero's catalog [20] and comprises three Chilean species: *Mycteromyia conica* (Bigot), *Mycteromyia etcheverryae* Coscarón and Philip and *Mycteromyia obscuripennis* (Philippi). However, in Coscarón and Philip revision [68], *Mycteromyia obscuripennis* does not appear to be included in the genus, as well as in the tabanid list of

Chile of Coscarón and González, in 1991 [46] or in the catalog of Fairchild and Burger [34]. Coscarón and Papavero [20] reported Kröber [31, 69] as the reason to keep the species in the genus. *Mycteromyia* sp. was captured in a survey performed in summer of 1971, in province of Coquimbo, Chile (Andean region, Central Chilean subregion) [70]. González conducted morphological studies of the mouthparts of *Mycteromyia conica* Bigot using scanning electron microscopy [71].

3.2.1.3. Genus Promycteromyia (Coscarón and Philip, 1979)

This brings together nine species, endemic to Chile, mainly in Andean region, Central Chile subregion [20, 34, 46]. *Promycteromyia cinerascens* (Bigot), a Chilean species, is the most well studied in the genus (as *Mycteromyia*) [68, 72].

3.2.1.4. Genus Sivestriellus (Brèthes, 1910)

This genus is with four more specialized species, which are distributed to Chile and Argentina in provinces of Pampa (Chacoan subregion) and Central Patagonia (Patagonian subregion) [20, 68].

3.2.2. The tribe Pangoniini (Rondani, 1856)

This has 130 Neotropical species, more or less restricted in habitats and is considered the most ancestral species between tabanids [19, 72]. They have naked eyes, prominent appendix in fork R4 vein, face not produced conically and proboscis rarely exceeding the length of the head, as frequent in Scionini [19]. With the exception of the species of *Esenbeckia*, specimens of this tribe are rarely collected and do not seem to be very active bloodsuckers [73]. The tribe has 14 genera in which the majority is in South America.

3.2.2.1. Genus Esenbeckia (Rondani, 1863)

This brings most tribe species, occurring throughout South America and is considered the most specialized among Pangoniini [19]. They are medium to large, slender and robust specimens, usually narrow frons, with or without a slender to clavate callus, bare eyes, usually with long proboscis and small compact labella, body pilosity short to sparse, often pattern wings [19]. The genus *Esenbeckia* is divided in five subgenera [20].

3.2.2.1.1. Subgenus Esenbeckia (Rondani, 1863)

It was reviewed by Wilkerson and Fairchild in 1985 [74], and brings together 51 species in the tropical region: *Esenbeckia (Esenbeckia) rafaeli* Limeira-de-Oliveira does not appear in Coscarón and Papavero catalog [20, 36, 75]. From neotropical species, only *Esenbeckia (Esenbeckia) illota (Williston)* do not occurs in the South America. In Amazonian subregion, *Esenbeckia (Esenbeckia) prasiniventris* (Macquart) was collected in forest in Roraima province [50], *Esenbeckia (Esenbeckia) matogrossensis* Lutz, in eastern Amazonian forest, Para province [53], and *Esenbeckia (Esenbeckia) clari* Lutz (as *lemniscata* Enderlein) in Pantanal

province [76]. *Esenbeckia (Esenbeckia) osornoi* Fairchild was recorded in Cerrado province of Chacoan subregion, state of Tocantins, Brazil [77]. *Esenbeckia* (*Esenbeckia*) *lugubris* (Macquart) a large, glossy and dark-colored fly, with a powerful flight, and painful sting was by the first time reported in Atlantic Forest, from specimens collected on Marambaia Island, Rio de Janeiro state, Brazil [65].

3.2.2.1.2. The subgenus Ricardoa (Enderlein, 1922)

This comprises 38 species distributed in Central America and Mexico and will not be treated here [20].

3.2.2.1.3. The subgenus Proboscoides (Philip, 1943)

This comprises 11 species, all occurring in South America and ranging from Panama to Paraguay. Fairchild and Wilkerson [78] provided a key to females of 11 species of *Proboscoides*. They are not common in collections and there is much interspecific variation. The species mentioned in more recent studies are *Esenbeckia (Proboscides) farraginis* Fairchild and Wilkerson, collected in Central Brazil, Chacoan subregion, Cerrado province [77]; and *Esenbeckia (Proboscoides) suturalis* (Rondani), which occur in northern and eastern Amazon forest [50, 53].

3.2.2.1.4. The subgenera Astomyia (Burger, 1999) and Palassomyia (Fairchild, 1969)

They are monotypic with both endemic species of Chile. *Esenbeckia* (*Astomyia*) *media* Burger was proposed from a specimen deposited in Arthropod Collection of the State of Florida, with label written by Fairchild reading "*Esenbeckia (Astomyia) media* n. sp., n. subg.", leading to the conclusion that the author planned to propose these new taxa. However, Fairchild did not accomplish his purpose and Burger, describing the species, preserved the names suggested [79]. *Esenbeckia (Palassomyia) fascipennis* (Macquart) seems to be the least specialized among the genus *Esenbeckia* [19].

3.2.2.2. Genus Protosilvius (Enderlein, 1922)

This comprises five species, all occurring in Brazil and is a part of a more primitive group among *Pangoniini* [19]. They are species smaller in size, with slender, long wings, narrow forehead without callus, short proboscis, naked eyes, and has a third antennal segment with a variable number of segments [19]. The species occur only in Brazil, mainly in southeast Cerrado, Atlantic forest and Parana subregion, with one species in Amazon Basin [38]. There is record of a misidentified specimen of *Protosilvius termitiformis* Enderlein, in Paraná state [11, 38].

3.2.2.3. Genus Veprius (Rondani, 1863)

This has five species present in Central Chile and Midwest Argentina. They are flies with head almost twice broader than height, black eyes with no band and abundant pilosity, eyespots present, broad forehead with an inconspicuous or absent callus, third antennal segment

basal plate and set aside 4-style, big and little labela sclerotized [19, 71]. These species occur in Central Chile and West Argentina [80]. Gonzáles described the male and re-described the female of *Veprius fulvus* Coscarón, Philip and Fairchild [80].

3.2.2.4. Genus Protodasyapha (Enderlein, 1922)

This comprises species similar to those in genus *Veprius*, but with 8-annulate antennae, subulate, the basal plate consolidated, and pilose eyes, sometimes pilosity is sparse [19]. The genus has been reviewed by Coscarón [72] and meets four species in two subgenera.

3.2.2.4.1. Subgenus Curumyia (Coscarón 1976)

It has only one species *Protodasyapha (Curumyia) lugens* (Philippi) occurring in Chile and Argentina [20].

3.2.2.4.2. Subgenus Protodasyapha (Enderlein, 1922)

This contains three endemic species from Central Chile [72]. González described the larvae and pupae of *Protodasyapha (Protodasyapha) hirtuosa* (Philippi) and compared with others Pangoniini species from Australia and North America; the larvae were found 3–5 cm beneath the soil surface of a *Lithraea* forest, on a steep and humid hillside [81].

3.2.2.5. Genus Fairchildimyia (Philip and Coscarón, 1971)

This comprises only two species that occur in Midwest Argentina. Coscarón considered that this genus and *Chaetopalpus* Philippi, 1865, form a monophyletic branch in Pangoniini [72]. The species have dark eyes, subulate antennae, frons with a circular-shaped callus, palpi with a short apical segment, sternite 8 of female very wide basally [19]. Chainey and Hall provided a picture of the front view of male head of *Fairchildimyia penai* Philip and Coscarón, comparing it with *Boliviamyia fairchildi* Chainey and Hall, the species described in that paper [73].

The other genera of Pangoniini are all monotypic: *Archeomyotes* Philip and Coscarón, 1971, *Austromyans* Philip and Coscarón, 1971 *Chaetopalpus* Philippi, 1865, each with an endemic species of Chile [20]. The recent genus *Boliviamyia* Chainey and Hall has only one endemic species from Bolivia, *Boliviamyia fairchildi* Chainey and Hall [73].

3.2.3. Tribe Scepsini (Bequaert, 1930)

It has only the genus *Scepsis* Walker, 1850 with a single Neotropical species, *Scepsis appendiculata* Macquart, which appears in catalogs as *Scepsis nivalis* Walker [20, 31, 34, 82]. This is a slender-body fly, with whitish milky wings, atrophied mouthparts, and wide frons without callus in both sexes [19]. The species is found on sand beaches, from coast of Rio de Janeiro state (Brazil) to probably northern Argentina [19]. The species has nonhematophagous habits and can be considered autogenous. Turcatel have reports with specimen coming from Guarapuava, inside the Paraná state, Brazil, plateau region of mixed rain forest, putting in doubt the information of collection [11]. The species was observed on Marambaia Island, Rio

de Janeiro, southeastern Brazil, on the white sand beaches, it has a short and low flight, not reaching more than 25 cm height and 1.5 cm away [64, 65].

3.2.4. Tribe Scionini (Enderlein, 1922)

This species have robust bodies, well-developed ocelli, no frontal callus, pilose eyes, long proboscis, and short palpi [19]. The tribe comprises over 280 species in 17 genera, austral in distribution, occurring in Australia, New Guinea, New Zealand, and South America [66].

3.2.4.1. Genus Pseudomelpia (Enderlein, 1922)

First recognized as subgenus of *Scaptia* [66], it has only the species *Pseudomelpia horrens* (Enderlein), with little body densely hairy, with robust and cylindrical palp, basal antennal ring, partial and irregularly fused with the basal plate [66]. Both male and female are nectar feeding [83]. The species is endemic to Chile, from Santiago to Maule province, Central Chilean and Subantartic regions [66].

3.2.4.2. Genus Osca (Walker, 1850)

This comprises 11 species previously placed in subgenus *Scaptia*, all from southeastern South American, in temperate regions and at high altitudes in Ecuador, Peru, Bolivia, and Chile [20, 66]. They are moderately size flies similar to *Tabanus*, with short proboscis, palpi over half length of proboscis, and antennae with eight annuli [19]. González and Sanhueza using scanning electron microscopy, conducted detailed studies of the morphology and structure of the oral armor of *Osca varia* Walker (who does not have mandibles), *Osca lata* (Guérin-Meville), and rufa *Osca rufa* (Macquart) (all as *Scaptia* (*Scaptia*) (the latter two with mandibles with marginal teeth, suggesting bloodsucking habits) [84]. Larvae of *Osca lata* (Guérin-Méneville) (as *Scaptia* (*Scaptia*) were found under fallen logs in Puyehue forest area in the Patagonian, Subantartic subregion, Valdivian Forest province, Chile [85].

3.2.4.3. Genus Lepmia Fairchild, 1969

This species have moderate-size body and thick proboscis, small and reduced labella, face bulging and few projected, palpi usually short, broad, with extensive bare area [19]. The genus currently comprises six species [66]: two original species and four transferred from subgenus *Scaptia* (*Pseudoscione*) [66]. Pino and colleagues performed a survey during summer of 1971 in province of Coquimbo, Chile (Andean region, Central Chilean subregion) and found *Lepmia atra* (Philippi), as *Scaptia* (*Pseudoscione*), one of the most abundant species [69]. *Lepmia seminigra* (Ricardo), as *Scaptia (Lepmia)*, was collected in sandbank, during early afternoon, in Parana subregion, southeast Brazilian Atlantic Forest province; the species has a powerful flight that produces loud [65].

3.2.4.4. Genus Parosca (Enderlein 1922)

This comprises medium-size species, face conspicuously projected, diverging frons, proboscis long and slender with thick labella, broad palpi extensively flattened triangular dorsally

rotate [19]. Three species are included in genus, all transferred from *Scaptia* (*Pseudoscione*) [66]. The terrestrial larva of austral horsefly *Parosca latipalpis* (Macquart), as *Scaptia* (*Pseudoscione*), was identified by molecular techniques and described from specimens found 2–3 cm below of the soil surface and associated with larvae of Coleoptera, Lepidoptera, and Diptera in southern Chile, Osorno, and subantartic subregion [86].

3.2.4.5. Genus Pseudoscione (Lutz, 1918)

This comprises nine species from the former subgenus *Scaptia* (*Pseudoscione*) [66]. They are from small to medium size stout species, with pale markings along sutures of scutum (like *Scione*), with wing cell M_3 open [66]. They are predominantly Patagonian, occurring in Chile, Argentina, also Brazil [87]. Coscarón reviewed the former subgenus *Pseudoscione*, and offered a key to 15 species (not for the sixteenth species), with its redescriptions and figures [66, 88]. The genus *Pseudoscione* includes the species of former subgenus *Scaptia* (*Pseudoscine*), excluding those transferred for *Lepmia* and *Parosca* [66]. Pino and collaborators performed a survey during summer of 1971 in province of Coquimbo, Chile (Andean region, Central Chilean subregion) and found *Pseudoscione dorsoguttata*, as *Scaptia (Pseudoscione*), one of the most abundant species [70].

3.2.4.6. Genus Scione (Walker, 1850)

This comprises 41 recognized species uniformly mottled, small and slender body, and well-projected face, undeveloped labella, slender legs, cloud marks on wing veins, closed R_3 and M_3 cells [19, 66]. They are considered typically Andean species [88], occurring mainly in the mountainous regions of northwest South America, Venezuela, and Bolivia. Coscarón reviewed the genus and re-described *Scione claripennis* Ricardo and *Scione flavohirta* Ricardo, both the Andean region Argentina, also describing the male of the second species [88]. *Scione aurulans* (Fairchild), *Scione ablusus* Fairchild, and *Scione flavohirta* Ricardo, all were recorded to feed on man, with the latter also recorded to feed on cattle [89, 90]. There is no current formally review of the genus over 80 years, and lacks descriptive and uniform descriptive characters [66].

3.2.4.7. The genus Fidena (Walker, 1850)

This comprises currently 99 species, characterized by medium to large stout body, face shining and snout-like, proboscis extremely long and slender, reduced labella and widely open wing cell M_3 [19, 66]. The species of this genus are considered difficult to study, by the large number of taxa, few males have been described, great variability of characteristics and lack studies of immature stages [91]. *Fidena* species are widely distributed in South America, mainly mountains of southeastern Brazil and just off the subandean region [66]. They are separated into four subgenera.

3.2.4.7.1. Subgenus Fidena (Walker, 1850)

This comprises 94 species, with flattened palpi without subcallus, scuttum without strong vittae, femora, and tibiae without long hairs, wing cell R5 usually closed without long petiole; they occur in South America from Colombia to Argentina, predominantly in Brazil [66]. The

Brazilian species *Fidena (Fidena) rufohirta* (Walker) has a proboscis as long as the body length. IIde performed morphological studies on *Fidena (Fidena) nigripes* (Röder), *Fidena (Fidena) brachycephala* Kröber, *Fidena (Fidena) florisuga* Lutz, *Fidena (Fidena) rufibasis* Kröber, and *Fidena (Fidena) fusca* (Thunberg), that are very useful to study external anatomy of the group [25, 26, 28, 37]. Coscarón redescribed females of *Fidena (Fidena) abominata* Philip, *Fidena (Fidena) atripes* (Röder), *Fidena (Fidena) latifrons* Kröber, *Fidena (Fidena) longipalpis* Enderlein, *Fidena (Fidena) neglecta* Kröber, *Fidena (Fidena) nigripes* (Röder), *Fidena (Fidena) ochrapogon* Wilkerson, *Fidena (Fidena) opaque* (Brèthes), and *Fidena (Fidena) sorbens* Wiedemann, so as males of these species, except *atripes* and *ochrapogon* [91]. *Fidena (Fidena) fusca* Thunberg is reported from mountainous regions of Parana subregion, southeastern Brazil [92, 93]. *Fidena (Fidena) auripes* (Ricardo), *Fidena (Fidena) eriomeroides* Lutz, and *Fidena (Fidena) aurulenta* Gorayeb, were captured in the western Amazon [53]. Rafael and collaborators report *Fidena (Fidena) schildi* (as *childi*) in Sierra de Pacaraima, northern Brazilian Amazon region [50]. Coscarón described the male *Fidena* (*Fidena*) *haywardi* Philip, a species from foothills of Argentine Andes, Puma subregion [88]. *Fidena (Fidena) pseudoaurimaculata* (Lutz) was collected in "campinarama" and canopy forest of Central Amazon Forest province [54, 94]. *Fidena (Fidena) freemani* Barretto, *Fidena (Fidena) analis* (Fabricius), and *Fidena (Fidena) loricornis* Kröber were also reported in the Central Amazon Forest [54, 56, 57, 95]. Records of *Fidena* species in the Amazonian subregion broaden the distribution of this group, in addition to the highlands of Parana and Subandean region [88]. Larvae and pupae of *Fidena (Laphriomyia) rufopilosa* (Ricardo) were found in phytotelmata of terrestrial bromeliads *Canistrum lindenii* (Regel) Mez, *Nidularium innocentii* Lemaire e *Vriesea friburgensis* (Mez), that grow on granitic rocks in secondary Atlantic forest, Brazilian southeast [96]. *Fidena (Fidena) longipalpis* Enderlein was captured in Planalto Serrano and coastal zone Parana subregion, and pampas of Chaco subregion, of southern and south-eastern Brazil [59, 60, 63]. Buestán collected *Fidena (Fidena) aureopygia* Kröber (as *aureopigia*) above 2000 m altitude in the Andean Cordillera in the transition zone between the humid forests of Chocó and the dry forests of southern Ecuador [97]. Lima reports the occurrence of *Fidena (Fidena) bistriga* Fairchild and Rafael, *Fidena (Fidena) castanea* (Perty), *Fidena (Fidena) fumifera* (Walker), and *Fidena (Fidena) lissorhina* Gorayeb and Fairchild in the state of Tocantins, Central Brazil, Chacoan subregion, Cerrado province [77]. Cárdenas and collaborators collected *Fidena (Fidena) rhinophora* (Bellardi) between 500 and 2000 m on both sides of the Andes, in misty rainforest in Ecuador [98–100]. Guimarães and collaborators collected *Fidena (Fidena) winthemi* (Wiedemann) in ecotone between Atlantic forest sandbank and rain forest in Parana subregion, in the southeast Brazilian Atlantic Forest Dominion [65].

3.2.4.7.2. Subgenus Laphriomyia (Lutz, 1911)

This comprises three species with femora and tibiae densely covered by long and conspicuous hairs [35]. There are three recognized species: *Fidena* (*Laphriomyia*) *kroeberi* Fairchild (previously in subgenus *Fidena*), *Fidena* (*Laphriomyia*) *mirabilis* Lutz, 1911 (subspecies of *rufopilosa* [20] or *rufopilosus* [11]), *Fidena* (*Laphriomyia*) *polidetarsis* Kröber (a synonym of *silvatica*) were elected as species of this subgenus [66]. They occur in Peru, Bolivia, and Brazil [66]. *Fidena* (*Laphriomyia*) *kroeberi* Fairchild was captured in both the ground level and canopy of western and central Amazonian Forest [53, 94].

3.2.4.7.3. Subgenus Leptofidena (Kröber 1930)

This also has only one species, with palpi thick, swollen and with a deep lateral concavity, frons with a protuberance callus-like, closure of wing cell R_3 with a long petiole [19, 66]. The species *Fidena* (*Leptofidena*) *morio* Wulp occur in Subandean region, western Argentina, and had the male described by Coscarón [20, 88].

3.2.4.7.4. Subgenus Neopangonia (Lutz, 1909)

This has only one species, with hairy face, with long and conspicuous hairs, scutum with a strong pattern, and wing cell R_5 broadly open [35]. *Fidena* (*Neopangonia*) *pusilla* Lutz occurs only in Brazilian Atlantic Forest province, Parana subregion, southeastern Brazil [20].

3.2.4.8. Genus Pityocera (Giglio-Tos, 1896)

This species has a body from small to medium-size, with antennal flagellum with tufts of hairs on one or more flagellomeres, face projected and shiny, proboscis equal to or longer than body's length [19]. They occur in northern South America [20]. Krolow and collaborators reviewed the genus in 2015, when five new species were also described [37]. The genus comprises 10 species in three subgenera.

3.2.4.8.1. Subgenus Elaphella (Bezzi, 1913)

This has only one species from Subcaribbean and north Amazonian subregions, *Pityocera (Elaphella) cervus* (Wiedemann) [20]. The species has first flagellomere long and finger-like projection, long projections on dorsal surfaces of the second to sixth flagellomeres, and wing with stump vein on M_1 [66].

3.2.4.8.2. Subgenus Pityocera (Giglio-Tos, 1896)

This species has pectinate antennae, with first six antennal flagellomeres with long projections on both dorsal and ventral surfaces, seventh and eighth fused, long and finger-like. The single species, *Pityocera (Pityocera) festai* Giglio-Tos (*festai* according to Coscarón and Papavero and Fairchild; and *festae* according to Lessard and Krolow [20, 37, 66, 101] occur from Panama to Ecuador, Caribbean subregion, and feeds on man [19, 101].

3.2.4.8.3. Subgenus Pseudelaphella (Kröber, 1930)

This currently has eight species after the review of Krolow and collaborators [37], but only three appear in Coscarón and Papavero's catalog [20]; in these species lack the dorsal projections on antennal segments, but there is a dense dorsal patch of hairs on enlarged first annulus of third segment [19]. They occur in Ecuador, Bolivia, and Brazil, in Amazon basin [66]. The new review of Lessard on Tribe Scionini [66] did not include the new species described by South-American authors, which are not mentioned by Coscarón and Papavero [20]: *Pityocera* (*Pseudelaphella*) *barrosi* Gorayeb and Krolow and *Pityocera* (*Pseudelaphella*) *gorayebi* Limeira-de-Oliveira and Krolow, both described from Brazilian Cerrado [37], *Pityocera* (*Pseudelaphella*)

pernaquila Gorayeb and Krolow, from Central and Oriental Brazilian Amazon [37] *Pityocera* (*Pseudelaphella*) *rhinolissa* Krolow and Henriques, from Central Brazilian Cerrado and Bolivian eastern plateau [37], and *Pityocera* (*Pseudelaphella) ecuadorensis* Buestán and Krolow, from coastal zone of Ecuador [37].

According to Lessard, the current genus *Scaptia* Walker, 1859 comprises only species occurring in Australia [66]. But in this text, the records of species of *Scaptia* are preserved as in major original references.

3.3. Subfamily Tabaninae

Neotropical species can be separated from the other subfamilies species by the absence of hind tibial spurs and functional ocelli, male with genitalia style truncate, ducts of spermathecal with cup-like extensions on caudal ends, eyes plain or with horizontal stripes [19]. Tabaninae are divided in two tribes: **Diachlorini** Lutz, 1909 and **Tabanini** Latreille, 1802. In neotropic species, the presence or absence of strong setae on basicosta to separate Tabanini from Diachlorini is often unreliable. In addition, others characters are used, as the sclerotized labella and vestiges of ocelli, which are common in Diachlorini but nearly unknown in Tabanini [19].

3.3.1. Tribe Diachlorini (Lutz, 1909)

This includes more than half of Neotropical Tabaninae, gathering nearly 600 species in 39 genera [20]. The reading of specialized literature to study this tribe, which has a large variety of species, both primitive and specialized, is strongly recommended. The more primitive species are dull colored, from small to medium size, occurring in colder areas and include species of genera *Dasybasis* e *Stenotabanus*; the remaining species are considered more specialized, mostly, are strictly tropical [19]. Trojan [102] published study of South-American Diachlorini distribution and considered that these species "are generally restricted to the northern part of the continent", occupying the Caribbean Archipelagos, limited by Andes in eastern border, and from Santa Catarina state in Brazil to Chaco and Salta in Argentina, in South border. Following some considerations about the main genera, which include the most common species recorded in surveys conducted by South-American researchers.

3.3.1.1. The genus Acanthocera (Macquart, 1834)

This comprises 28 species resembling wasps (Hymenoptera: Vespidae). They have slender and medium-sized body, antennae very long, first antennal segment at least 1,5 times the length of the second, and third always longer than the first and second together, vestigial or absent ocelli, partially sclerotized labella, palpi slender or swollen, slender abdomen with narrowed second tergite [103, 104]. Fairchild redefined the characteristics of the genus and provided a key to 16 species then known [103]. In catalog of Coscarón and Papavero [20] 20 species are listed, and it do not mention the study of Henriques and Rafael [104], where they described *Acanthocera* (*Nothocanthocera*) *distinta* Henriques and Rafael, transferred 11 species from the genus *Nothocanthocera* to genus *Acanthocera*, synonymized *Acanthocera* (*Acanthocera*) *lutzi* to *Acanthocera* (*Acanthocera*) *coarctata*, and the subgenus *Acanthocera* (*Mimodynerus*) Enderlein to *Acanthocera* (*Acanthocera*) Macquart. The species of *Acanthocera* are difficult to capture because

they inhabit the canopy of forest [104]. The species of genus *Acanthocera* are currently distributed in four subgenera.

3.3.1.1.1. Subgenus Acanthocera (Macquart, 1834)

This subgenus has 16 species that have at least a tubercle or dorsal angle on antennal basal plate, usually a fairly long tooth or slender spine, frons rarely as wide as high, generally narrower [104]; the subgenus comprises 10 species in South America. *Acanthocera* (*Acanthocera*) *longicornis* (Fabricius), one of the most recorded species in studies, was captured in an ecotone area between rainforest and sandbanks on Marambaia Island, Rio de Janeiro, and in coastal zone in Parana subregion, Brazilian Atlantic Forest province [59, 64, 65].

3.3.1.1.2. Subgenus Nothocanthocera (Fairchild, 1969)

This comprises 12 species with short basal antennal segment, bare or partially bare frontoclypeus and gena, not wholly sclerotized labella, usually pale scutellum, without diagonal wing band, often resembling wasps [19, 104]; 11 species occurring in South America and one in Central America [104]. *Acanthocera* (*Nothocanthocera*) *distincta* Henriques and Rafael, was omitted by Coscarón and Papavero, from Amazonian forest, Amazonian subregion, Imeri province [36, 104].

3.3.1.1.3. Subgenus Polistimina (Fairchild 1969)

This has the single species *Acanthocera (Polistimina) politiformis* Fairchild, described from a male specimen from Amapa, northern Brazil [104]. The female was also described from Amapa: this red-yellowish species resembles wasps of the genus *Polistes* (Hymenoptera) [104]. The immature stages of *Acanthocera (Polistimina) vespiformis* Burger inhabit the tunnels opened by beetles in the trunks of guanandi *Callophyllum brasiliense* Cambess. The larva transforms sap that flows through these tunnels into a sticky mass with bad smell that attracts flies, which are trapped and are predated by the larvae, which are always found in tunnels less than 2 m above ground [105].

3.3.1.1.4. Subgenus Querbetia (Fairchild, 1964)

It is accepted by Fairchild [32], Moucha [82], Fairchild and Burger [34], Coscarón and Papavero [20] but is not mentioned by Henriques and Rafael in their revision of the genus [104]. These are species with bare eyes, frons less than twice as high as basal width, with basal callus as wide as frons, antennae with first segment very greatly inflated and shiny, labella extensively sclerotized and shiny, basicosta lacking strong setae [19]. There are two species *Acanthocera (Querbetia) chaineyi* Fairchild and Burger from Ecuador and Peru, and *Acanthocera (Querbetia) inopinata* (Fairchild), in Peru and Bolivia [20].

3.3.1.2. Genus Agelanius (Rondani, 1863)

This comprises 12 species, and it is considered as a part of the most primitive group within the tribe Diachlorini [106]. They are brown medium-size species, narrow frons, frontal callus

not touching eyes, which are pilose and without bands, without dorsal prolongation on basal flagellomere, palpi slender and elongate, bare subcallus, and with abundant setae on basicosta, so that is difficult to use keys to separate the group [19]. They are similar to *Dasybasis* and differ from it by narrower frons, ridge-like or clavate callus and vestigial ocelli at vertex [19]. The genus is endemic to southern South America, Subandean Patagonia province, and occurs in Peru, southern Chile, and Argentina [34, 106]. During the last decade, González described *Agelanius verai* González [106], *Agelanius fuscus* González [107], *Agelanius burger* González [108], and *Agelanius chiloensis* González [109] all from Central Chile, Andean subregion. He also described the immature stages of *Agelanius fuscus*, which were found 5–10 cm beneath soil surface in forest of roble beech *Nothofagus obliqua* (Mirb.) Oerst [106] and the immature stages of *Agelanius cortesi* (González) collected beneath the soil surface near a small stream and with abundant *Gunnera chilensis* Lam. (giant-rhubarb) [110].

3.3.1.3. Genus Bolbodimyia (Bigot, 1892)

This comprises 13 species from which nine occurring in South America [20]. They are black or black and yellow, with subcallus and first antennal segment swollen and black shiny, wings wholly black, except the hyaline apex, vein R_4 strongly curved, swollen tibiae [19, 111]. Theses species are infrequently collected [112]. Stone reviewed the genus and provided a key to identification of 10 species then known [112]. Gómez and collaborators recorded *Bolbodimyia brunneipennis* Stone, *Bolbodimyia celeroides* Stone, *Bolbodimyia nigra* Stone and *Bolbodimyia philipi* Stone from Venezuela, and provides a key to the identification of five species reported in the country [111].

3.3.1.4. Genus Catachlorops (Lutz, 1913)

This comprises 66 species, characterized by small size body, frons narrow, frontal callus ridge-like or clavate [19]. Kröber [113] reviewed the genus and Barretto [23] provided a key to the females in Brazil and described the males of several species. Coscarón also reviewed the genus, re-described three species and described two new from Argentina [114]. The last reference to genus was made by Turcatel, when reviewed the records of species from Parana region, southeastern Brazil [11]. The species are distributed in six subgenera.

3.3.1.4.1. Subgenus Amphichlorops (Lutz, 1913)

This has seven species resembling to those in *Catachlorops*, from which are separated by yellow and fuses wings, often darker apical half [19]. All species occur in South America. *Catachlorops (Amphichlorops) flavus* Wiedemann was collected in area next to marsh and woodland in the evening, on Marambaia Island, Brazilian southeast, Parana subregion, Brazilian Atlantic Forest province [65]. They are well distributed in South America occurring in Colombia, Ecuador, Brazil, Peru, Bolivia, Paraguay, and Argentina [20].

3.3.1.4.2. Subgenus Catachlorops (Lutz, 1913)

This has 27 species occurring in South America [20]; they have small and medium-sized body, slender, callus usually clavate, brown to black tinted, black wings with a large rounded

patch in discal cell, and hyaline apex [19]. *Catachlorops* (*Catachlorops) halteratus* Kröber and *Catachlorops* (*Catachlorops*) *rufescens* (Fabricius) inhabitat primary Amazonian Forest, Central Amazon subregion, Varzea province and the first was collected in February and from June to December, and the last, in April and from June to October [95]. *Catachlorops* (*Catachlorops) leptogaster* Barretto was collected in area next to marsh and woodland after 17:00 h, on Marambaia Island, Parana subregion, Brazilian Atlantic Forest province [65].

3.3.1.4.3. Subgenus Hadrochlorops (Fairchild, 1969)

This consists of six species characterized by large and stout body, hyaline wings faintly tinted, brownish or with dark cross veins margins [19]; they occur in Bolivia, Argentina and Brazil [20].

3.3.1.4.4. Subgenus Psalidia (Enderlein, 1922)

This has 13 species of which 7 occur in South America [20]. They are species with very slender palpi, very long antennal tooth, often curved in apex, first posterior cell closed, coarctate or slightly narrowed discal cell, wings always hyaline at base [19]. *Catachlorops* (*Psalidia*) *overali* Fairchild and Rafael was captured in canopy of "terra firme" Amazonian Forest, Central Amazon, subregion, Varzea province [94]. In the same region, *Catachlorops* (*Psalidia*) *rubiginosus* (Summers) occurs from June to November [95].

3.3.1.4.5. Subgenus Psarochlorops (Fairchild, 1969)

This has species related to *Psalidia*, but with the wing pattern reduced to an irregular small band bellow stigma and clouds around cross veins and fork of third vein [19]. This subgenus comprises nine species, and only one does not occur in South America [20]. *Catachlorops* (*Psarochlorops*) *difficilis* (Krober) inhabits the primary Amazonian Forest, Central Amazon subregion, Varzea province, and is collected from September to November [95].

3.3.1.4.6. Subgenus Rhamphidommia (Enderlein, 1922)

This species is characterized by clavate or ridge-like frontal callus, as wide as base frons, flagellum with hook-like projection, labella partially or wholly sclerotized, abdomen with median triangular spots most of tergites, wing with an irregular diagonal dark band [19, 115]. Four species occur in southeast South America, in Brazil and one of them, *Catachlorops (Rhamphidommia) potator* (Wiedemann), also in northern Argentina [20]. Henriques and Krolow described *Catachlorops (Rhamphidommia) dubius* Henriques and Krolow, the first species of the subgenus in Amazonian subregion, Madeira province, and provided a key to determine the species within subgenus [115].

3.3.1.5. Genus Chlorotabanus (Lutz, 1909)

This was created to *Tabanus mexicanus* Linnaeus, without providing a description or point type species, not meeting the rules of the International Code of Zoological Nomenclature [116]. The same paper was reprinted in 1911, keeping the faults [117]. In 1913, Lutz published

a paper entitled "On the Systematics of horseflies, subfamily Tabaninae", republished in 1914 [118, 119]. This issue was currently discussed by Krolow and Henriques [120] and Guimarães et al. [121]. The date of 1913 was accepted for *Chlorotabanus* by Borgmeier [122] and Kröber [31], as well Fairchild [32]. Barretto was the first author to question the validity of the name [123]. Fairchild and Burger [34] also elected the year 1913 to designate the date of *Chlorotabanus*, in which were followed by Coscarón and Papavero [20, 33], but not in their last manual [35]. *Chlorotabanus* species are crepuscular and nocturnal, greenish pale color, without frontal callus, sclerotized labella, and unicolor eyes [19]. Coscarón completed the diagnosis of the genus adding features of gentitalia [72]. The genus appears in Coscarón and Papavero catalog comprising six species [20]; but Krolow and collaborators, in an excellent review, pointed 11 valid species, from which ten occur in South America, and one species in the United States, described three new species, and described the males of *Chlorotabanus leucochlorus* Fairchild and *Chlorotabanus flagellatus* Krolow and Henriques [57]. *Chlorotabanus inanis* (Fabricius) and *Chlorotabanus mexicanus* Linnaeus occur in savannah in French Guyana [17]. In Central Amazonian, Varzea dominion, *Chlorotabanus inanis* was observed in two periods of activity: in the morning, between 05:20 and 05:50 h, and at afternoon, between 17:45 and 18:20 h [124]. *Chlorotabanus inanis* was also captured on Maraca Island, Amazonian subregion, Guyana province, and in the state of Tocantins, Brazilian Chacoan subregion, Cerrado province [50, 77]. Guimarães and collaborators reported *Chorotabanus inanis* on Marambaia Island, Parana subregion, southeast Brazilian Atlantic Forest province; they observed that females prefer to feed on legs of horses, and when feeding, they become seemingly indifferent to the environment and are easily captured [65]. The species seems to be bivoltine, and appears from April to May and from October to December [64].

3.3.1.6. Genus Cryptotylus (Lutz, 1913)

This consists of five species with one subspecies, greenish color, with reduced or absent frontal callus, antennae with strong dorsal angle or tooth, labella wholly sclerotized and clear wings; they seldom attack man and are crepuscular and nocturnal species [19]. They are present in northern Amazonian subregion and one species in Chacoan subregion, in Paraguay and Argentina [20]. Fairchild provided a good key for species of the genus [125]. Philip and Fairchild reviewed the genus as a subgenus of *Chlorotabanus* [126]. Coscarón elected the key features for the diagnosis of genus adding feature of genitalia [72]. Gorayeb and Fairchild provided a new key for the genus and described *Cryptotylus firkin* Gorayeb and Fairchild, from Amazonian subregion, province of Para [127]. Coscarón and collaborators collected larvae of *Cryptotylus unicolor* (Coscarón and Poi of Neif) on *Pistia stratiotes* Linnaeus, in ponds in a region of dry forest, northeastern Argentine, province of Formosa, Argentine Chaco [128].

3.3.1.7. Genus Dasybasis (Macquart, 184)

This is one of the most numerous in tropical fauna, with 70 valid taxa, all present in South America, and also is well represented in of southeastern Subantartic subregion, Chile and Argentina, along Andean region [19, 129]. The genus comprises species that represent part of the most primitive group among Diachlorini [19]. They are species with callus filling the

generally broad frons, or rarely reduced or absent, no tubercle at vertex, or at least, without vestigial ocelli, antennae without tooth, clear wings or clouded crossveins, and pollinose body [19]. The genus was reviewed by Coscarón and Philip in 1967, when the authors redescribed the female *Dasybasis mendozana* (Macquart) that occurs in the Andean pre-cordillera region in Argentina [130]; the male was described by Coscarón [131]. Coscarón also described the larva and pupa of *Dasybasis nigra* (Enderlein), collected at dry season, found in small pits, remaining a dry creek, in Patagonian Subregion, Central Patagonian province [132]. An unidentified species of *Daybasis* was found during a survey performed during summer of 1971 in province of Coquimbo, Andean region, Central Chilean subregion [70]. *Dasybasis fairchildi* Coscarón and Philip had described immature stages from specimens collected in cold water streams in the Peruvian Andean highlands, at 1 cm deep in the sand or among the roots of the vegetation [133]. González described the immature stages of *Dasybasis (Dasybasis) nigrifrons* (Philippi), and *Dasybasis bruchi* (Brèthes) from moss of wetlands in Central and northern Chile [134]. The same author also described the immature stages of *Dasybasis pruinivitta* (Kröber) and *Agelanius cortesi* (González) from the same region [110, 135].

3.3.1.8. Genus Dasychela (Enderlein, 1922)

This consists of nine brown species, with a protuberant face and very long proboscis, tri- or biramous antennae with one or two long and slender dorsal spines with erect hairs and bare eyes [19]; they occur in southeastern South America [20]. Two subgenera are recognized.

3.3.1.8.1. Subgenus Dasychela (Enderlein, 1922)

This has six species, five of which occur in South America in Colombia, Ecuador and Brazil [20].

3.3.1.8.2. Subgenus Triceratomyia (Bequaert, 1937)

This has two species occurring in Ecuador, Peru e Bolivia.

3.3.1.9. Genus Diachlorus (Osten Sacken, 1876)

This comprises flies usually yellow and black colored, wings with a dark pattern, dark band in apex, colored eyes with patches and bands similar to *Chrysops*, variable frons, frontoclypeus bare and shiny [19]. These small flies occur in all South America, except in Chile [20]. *Diachlorus* has 29 species of which only *Diachlorus ferrugatus* (Fabricius) does not occur in South America (Central and North America). The first key to the genus was Kröber's [136], and currently the most elaborated study of the genus is Fairchild's, in which the author provided a key to identification of 23 species [137]. Coscarón added genitalia characteristics to the key characters for diagnosis of species [72]. Wilkerson and Fairchild provided a revised key and described five new species from South America [138]. *Diachlorus jobbinsi* Fairchild, *Diachlorus bicinctus* (Fabricius), and *Diachlorus curvipes* (Fabricius) are well distributed in northern and central Brazilian Amazonian region, in primary forest or varzea, level ground or canopy forest [50, 95]. *Diachlorus bivittatus* (Wiedemann) is a very aggressive species, and

was the most abundant species in survey performed on Marambaia Island, Parana subregion, southeast Brazilian Atlantic Forest province. The species presented two generations per year (bivoltine) [64, 65]. *Diachlorus distinctus* Lutz was also found in that survey and has morphological and ethological similarities with *Diachlorus bivittatus* [65].

3.3.1.10. Genus Dichelacera (Macquart, 1838)

This comprises small to medium size species, with slender body, callus almost always as broad as frons, eyes usually with a single band, and labella wholly sclerotized [19]. According to Coscarón and Papavero [20] there are 80 valid species; but further studies increased this number to 83, with the descriptions of *Dichelacera matogrossensis* Henriques and Krolow, 2015 [139], *Dichelacera (Dichelacera) gemmae* Limeira-de-Oliveira and Gorayeb [140], and *Dichelacera (Dichelacera) walteri* Guimarães, Gorayeb and Rodrigues-Guimarães [41]. They are divided into four subgenera.

3.3.1.10.1. Subgenus Desmatochelacera (Fairchild, 1969)

This has only two species of which one occur from Costa Rica to Ecuador and one in Colombia and Peru [20].

3.3.1.10.2. Subgenus Dichelacera (Macquart, 1838)

This currently has 65 valid species after the revision of the genus *Acanthocera* by Henriques and Raphael and description of new species [41, 104, 139]. A total of 48 species occurs in South America. This subgenus is the largest in number of species, and characterized by labella wholly sclerotized, eyes nearly always with bands, callus more or less square, as wide as frons; all species are small to medium size [19]. *Dichelacera amazonenses* Henriques, *Dichelacera cervicornis* (Fabricius), *Dichelacera damicornis* Fabricius), *Dichelacera marginata* Macquart, *Dichelacera paraensis* Henriques, *Dichelacera trisuca* Fairchild and Philip, *Dichelacera villavoensis* Fairchild and Philip, are well distributed species in several environments in northern, central and eastern Amazonian subregion [54–57, 94, 95]. The type species of *Dichelacera* (*Dichelacera*) *matogrossensis* were collected in Chacoan subregion, Brazilian, Cerrado province [139]. Barros recorded the occurrence of *Dichelacera scutellata* Williston in Brazilian Pantanal, Amazonian subregion [76]. *Dichelacera alcicornis* (Fabricius) was the most abundant species collected in highlands of southeast Parana subregion [62, 63]. *Dichelacera (Dichelacera) walteri* Guimarães, Gorayeb and Rodrigues-Guimarães was described from specimens collected from August to September, on forest sandbanks from Marambaia Island, Parana subregion, Brazilian Atlantic Forest province, Rio de Janeiro [41]. *Dichelacera (Dichelacera) alcicornis* was also collected in the same place [65]. This last species was also recorded from Chacoan subregion, Pampa province, southern Brazil [60].

3.3.1.10.3. Subgenus Idiochelacera (Fairchild, 1969)

It has only one species, *Dichelacera (Idiochelacera) subcallosa* Fairchild and Philip that occurs from Costa Rica to Peru [20].

3.3.1.10.4. Subgenus Orthostyloceras (Lutz, 1933)

This comprises three species: *Desmatochelacera* (*Orthostyloceras*) *ambigua* (Lutz and Neiva) and *Desmatochelacera* (*Orthostyloceras*) *nubiapex* Fairchild and Philip occurring in Brazil, and *Desmatochelacera* (*Orthostyloceras*) *aurata* Wilkerson, occurring in Colombia [20].

3.3.1.11. Genus Dicladocera (Lutz, 1913)

This comprises 32 Andean species [19], although the Coscarón and Papavero catalog [20] also suggests Brazilian species are included in the genus; most species is distributed between Colombia and Peru [20]. This genus includes species with long antennal tooth, short proboscis, soft and pollinose labella, some setae on basicosta, eyes often pilose and wings with a dark band with a fenestrae on discal cell [19]. In Ecuador, *Dicladocera macula* (Macquart) was recorded in both side of Andean cordillera between 1600–3400 m, in montane forest, paramo and Andean shrubs [98]. Coscarón re-described the female e described the male of *Dicladocera nubipennis* (Rondani), a species from Argentine Subandean subregion [141].

3.3.1.12. Genus Lepiselaga (Macquart, 1838)

This has four small and robust species of black color, glossy palps, wings with black pattern with contracted discal cell, in two subgenera [19].

3.3.1.12.1. Subgenus Lepiselaga (Macquart, 1838)

This has the single *Lepiselaga (Lepiselaga) crassipes* (Fabricius), which occurs from Mexico to northern Argentina [20]. This is a very well-studied species. Lutz observed larvae of *Lepiselaga crassipes* (Fabricius) on moorhen lettuce, *Pistia stratiotes* Linnaeus in southeast Atlantic Brazilian Forest [142]. Later, Fairchild suspected that the larvae of the species also found on *Pistia* in mangroves in Panama Canal Zone, would be dependent on a more complex environment, formed by a maze composed of floating debris, mats of filamentous algae, *Salvinia* (water fern) and small specimens of *Pistia* [143]. *Lepiselaga crassipes* was also found in Central Amazon Subregion, Varzea province [55, 95] In a survey conducted in Pantanal, Brazilian Chaco subregion, the species was the fourth most abundant, occurring throughout the year, but more often in September and October [76]. The species also occurs in the transition zone between Cerrado and Pantanal, Brazil [144].

3.3.1.12.2. Subgenus Conopesalaga (Barretto, 1949)

This comprises three species with forehead as wide as high, or wider, inflated notopleurals lobes [19], which are distributed from Western Colombia to Argentina [20].

3.3.1.13. The genus Leucotabanus (Lutz, 1913)

This comprises 15 small- to medium-sized species, which have frons narrow to moderate, vertex with prominent tubercle, nearly always with vestiges of ocelli, callus clavate or ridge-like,

basicosta sparsely or abundantly setose, usually black and shiny [19]. Eleven species occur in South America [20]. The genus has been well studied by Fairchild: in 1941 [145] he reviewed the genus and provided a key to 11 species with figures of eight; in 1953 [146], he reviewed the genus again and updated the key to 15 species; and, in 1985 [147] he updated the studies with a discussion of genus taxonomic position and offered a key to females of 18 species. Godoi and Rafael [148] described the immature stages of *Leucotabanus albovarius* (Walker) from specimens collected in rotten wood of the palm *Bactris gasipaes* Kunth (Arecaceae); they observed the adults active throughout the year in open areas and in primary Amazonian Forest, Central Amazon subregion, Varzea province [95]. *Leucotabanus exaestuans* (Linnaeus), a widely distributed species, is collected in the same environment all year long; it attacks horses and other animals on the head, near base of the ear [53, 95]. *Leucotabanus janinae* Fairchild is another species collected in the same environment from July to December, as well as *Leucotabanus palculus* Fairchild, but collected from July to December [95]. Specimens of *Leucotabanus sebastianus* Fairchild were captured next to marsh and rain forest area, on Marambaia Island, Parana subregion, Brazilian Atlantic Forest province [65].

3.3.1.14. The genus Myiotabanus (Lutz, 1928)

This comprises four species, three occurring in South America [20]; they are small species, with unusually long proboscis, small and partly sclerotized labella, inflated and short palpi [19]. They are similar to sarcophagids flies [149]. In 2004, Rafael and Ferreira reviewed the genus and provided a key to known species [148]. Coscarón and collaborators found larvae of *Myiotabanus barrettoi* Fairchild on *Pistia stratiotes* Linnaeus, in northeastern Argentine, province of Formosa, Argentine Chaco, region of dry forest [150].

3.3.1.15. Genus Phaeotabanus (Lutz, 1913)

It has 15 medium to large flies, greenish when alive or recently dead, unicolor eyes, narrow frons, slender callus, labella sclerotized, antennal plate with an obtuse dorsal angle, wings with dark markings [19]. The majority of species occurs in Brazil [20]. *Phaeotabanus cajennensis* (Fabricius), a large widely distributed species in South America, was captured in Trinidad using traps baited with white mice [151]. The same species was captured in canopy of "terra firme" Amazonian Forest, Central Amazon subregion, Varzea province [94]. *Phaeotabanus cajennensis* was also captured in ecotone between sandbank and rainforest and *Phaeotabanus limpidapex* (Wiedemann), and *Phaeotabanus litigiosus* (Walker) (more abundant from 17:00 to 19:00 h) were captured next to marsh and rain forest area on Marambaia Island, Parana subregion, Brazilian Atlantic Forest province [65]. This last species was also captured on Mel Island, coastal zone of Parana subregion, southeast Brazilian [152]. *Phaeotabanus limpidapex* was also captured at coastal zone of Parana subregion [59]. *Phaeotabanus fervens* (Linnaeus) feeds on caiman, in Pantanal and Central Amazon [95, 153]. The species occur in primary forest in areas of "campinas" and "campinarana", as well as in open areas near rivers and small stream banks, in Central Amazonian subregion, Varzea province [55, 95]; but according to Ferreira-Keppler and collaborators, it is active preferentially in "clareira" than forest [56]. The species was found also on Maraca Island, Amazonian subregion, Guyana province [50]. Other species captured

in primary Amazonian Forest are *Phaeotabanus innotescens* (Walker) and *Phaeotabanus nigroflavus* (Kröber), both commonly collected near surface of water during drier months [95].

3.3.1.16. Genus Philipotabanus (Fairchild, 1943)

It comprises 29 species that are small to medium size flies, slender, narrow to very narrow frons, with clavate to threadlike callus, tubercle at vertex, unicolor eyes and palpi nearly always slender [19]. An excellent review with dichotomous key for the three subgenera and eleven species of genus *Philipotabanus* from records in Amazon was provided by Henriques [154].

3.3.1.16.1. Subgenus Melasmatabanus (Fairchild, 1964)

This has four species and one subspecies, similar to *Philipotabanus*, with a solid wing pattern, without fenestrae around cross veins, with the species all black [19]. All species occur in South America: they are largely distributed and can be seen from Panama to Midwest Brazil, in Andean areas, Amazonian Forest, and Cerrado [20]. Gorayeb and Rafael provided a key to females of species and subspecies of the genus and described *Philipotabanus* (*Melasmatabanus*) *pictus* Gorayeb and Rafael, from specimens collected in Pantanal subregion, Rondonia state, Brazil [155].

3.3.1.16.2. Subgenus Mimotabanus (Fairchild, 1964)

This comprises nine species with eight occurring in South America, Colombia, Ecuador and Peru; similar to foregoing group, they have solid wing pattern or a reduced shade below stigma, broader frons, clavate callus, and stouter palpi [19, 20]. The subgenus was first characterized by Fairchild in 1964 in a key for four species, and in 1975 the author reviewed the genus and provided a key to eight species than known [156]. The last species described for the genus was *Philipotabanus (Mimotabanus) tanypterus* Wilkerson, 1979. Lima reports the occurrence of *Philipotabanus* (*Mimotabanus*) *henriquesi* Limeira-de-Oliveira, Gorayeb and Rafael, from Brazil, in Chacoan subregion, Cerrado province [77].

3.3.1.16.3. Subgenus Philipotabanus (Fairchild, 1943)

This comprises 16 species with frons always narrow to very narrow, palpi slender, eyes bronzy in life, dark wing pattern, with hyaline fenestrae around crossveins and fork of third vein [19]. The genus is represented in Central America, but there are eight South-American species seen from Colombia to Bolivia and northern Amazon region [20]. *Philipotabanus* (*Philipotabanus*) *stigmaticalis* Kröber is a widely distributed species in Amazon Basin, more frequently captured in canopy of primary Amazonian Central Forest, Varzea province and is active throughout the year [94, 95]. Henriques described *Philipotabanus (Philipotabanus) obidensis Henriques, 2006* from eastern Peru and Bolivia, Puna subregion [154].

3.3.1.17. Genus Stenotabanus (Lutz, 1913)

This comprises 74 very small to medium size species, difficult to characterize, bare eyes with at least two transverse bands, moderate to broad frons, and callus as wide as frons [19]. Seven subgenera are currently recognized [20, 157]. Fairchild provided a key to the genera [158].

3.3.1.17.1. Subgenus Aegialomyia (Philip, 1941)

This has 25 species, but only four in South America [20]. *Stenotabanus (Aegialomyia) tobagensis* Fairchild occurs in Trinidad, Antillean dominion, and was observed attacking man on beach and caiman [159], *Stenotabanus (Aegialomyia) aberrans* Philip, described from Ecuador (northwestern South American dominion, Magdalena province), *Stenotabanus (Aegialomyia) geijskesi* Fairchild, from Suriname (Humid Guyana province) and Brazil (Para province, Amazonian subregion), and *Stenotabanus (Aegialomyia) ixyostactes* (Wiedemann), from Brazil (Chacoan subregion, Cerrado province) [20, 160].

3.3.1.17.2. Subgenus Brachytabanus (Fairchild, 1942)

This has three South-American species occurring in Colombia, Venezuela, Bolivia and Argentina, with one of them also occurring in Costa Rica and Panama [20]. *Stenotabanus (Brachytabanus) longipennis* Kröber, attracted by light in Colombia, *Stenotabanus (Brachytabanus) platyfrons* Fairchild, from Argentina, and *Stenotabanus (Brachytabanus) sphaeriscapus* Wilkerson, from Bolivia [20, 89, 156].

3.3.1.17.3. Subgenus Cretotabanus (Fairchild, 1969)

This has only one species, *Stenotabanus (Cretotatabanus) cretatus* Fairchild, recorded from eastern and central Amazonia, that appears before the rainy season and is collected preferably near the ground [55, 95].

3.3.1.17.4. Subgenus Melanotabanus (Lutz e Neiva, 1914)

This subgenus comprises two species from southeast Brazil: *Stenotabanus (Melanotabanus) brunnipes Kröber,* 1929 and *Stenotabanus (Melanotabans) fuliginosus* (Lutz & Neiva), 1914.

3.3.1.17.5. Subgenus Stenochlorops (Fairchild, 1969)

There are four Brazilian species: two from Amazon and two from Cerrado. *Stenotabanus (Stenotabanus) bequarti* Rafael, Fairchild and Gorayeb, occurs only in Amazon, along Rio Negro and its black water tributaries, flying during drier months [95].

3.3.1.17.6. Subgenus Stenotabanus (Lutz, 1913)

This has 59 species seen from Mexico to Argentina, Antilean and some in USA; 26 species are recorded from South America [156, 160]. They are small to very small species, with parallel-sided frons, round or square callus as wide as frons, middle frons with dark hair patch, eyes with two bands; it is the largest subgenera in South America [19, 20]. *Stenotabanus (Stenotabanus) obscurus* Kröber is a widely distributed species, occurring from Costa Rica to Argentina; Coscarón redescribed the female and described the male [161].

3.3.1.17.7. Subgenus Wilkersonia (Fairchild and Burger, 1994)

This has a single species, *Stenotabanus* (*Stenotabanus*) *roxannae* Wilkerson, from Caribbean subregion, Chocó, Colombia [20].

3.3.1.18. The genus Stibasoma (Schiner, 1867)

This comprises 19 species that are similar to bees of the genera *Centris* Fabricius, *Bombus* Latreille, *Xylocopa* Latreille and *Euglossa* Latreille [11]. They have robust bodies, with variable colors, very pilose legs, short antenna with a long dorsal spine, inflated palpi, sclerotized labella and fringed tibiae [19]. The genus was early studied by Ricardo [162] when it comprised six species, and by Knab, in 1913, who provided a key to 10 Neotropical species [163]. Coscarón completed the diagnosis of the genus adding genitalia features [72]. All species of the genus are recorded only from South America [20]. More recently, the genus was reviewed and two new species were described from southeast Brazilian Atlantic Forest: *Stibasoma manauensis* Turcatel, Rafael and Carvalho, and *Stibasoma ruthae* Turcatel, Rafael and Carvalho [164]. The larvae of the species in this genus are usually found in water of phytotelmata of bromeliads (Bromeliaceae). *Stibasoma flaviventre* Macquart and *Stibasoma venenata* Osten Sacken develop in arboreal bromeliads and S*tibasoma fulvohirtum* (Wiedemann) in terrestrial bromeliads, as found in Panama [165]. *Stibasoma fulvohirtum* (Wiedemann), *Stibasoma festifestivum* (Wiedemann), *Stibasoma flaviventre* (Macquart), and *Stibasoma currani* Kröber are the most common species appearing in surveys performed in Amazon [54–56, 94, 95].

3.3.1.19. Genus Rhabdotylus (Lutz, 1913)

This appears in Coscarón and Papavero's catalog [20] as a subgenus of *Stibasoma*, but Trojan, in 1998, revalidated the genus, based on characteristics of body pilosity and leg structure [166]. The genus comprises four species from which three are recorded from South America, and one has unknown distribution [20]. *Rhabdotylus planiventris* (Wiedemann) and *Rhabdotylus viridiventris* (Macquart) were captured in an ecotone area between sandbank and rain forest, on Marambaia Island, Parana subregion, southeast Brazilian Atlantic Forest province [65].

3.3.1.20. Genus Stigmatophthalmus (Lutz, 1913)

It has only one species, *Stigmatophthalmus altivagus* Lutz, which occurs in southeast Brazil, and was collected in mountainous region (800–2150 m above sea level), and in an ecotone area between the sandbank and rain forest on Marambaia Island, coastal zone in Parana subregion, and southeast Brazilian Atlantic Forest province [65, 167].

3.3.1.21. Genus Stypommisa (Enderlein, 1914)

This comprises 34 species, mostly small and slender, frons near always narrow, callus drop-shaped, marked tubercle at vertex, short proboscis, soft labella, palpi somewhat slender, clouds on crossveins, or anterior or posterior infuscation, and third appendiculate vein forked [19, 20]. The species can be seen from Nicaragua to Argentina, and only two species do not occur in South America [20]. Fairchild and Wilkerson reviewed the genus in 1986, including 28 species then known and provided a key to 26 of those species [168]. Coscarón elected genitalia features as key characters for define the genus [72]. *Stypommisa grandicolor* (Lutz) was the third most abundant species in the Central Amazon in a study conducted using Malaise trap in tropical forest [54]. *Stypommisa captiroptera* (Kröber), *Stypommisa glandicolor* (Lutz), and

Stypommisa modica (Hane) are widely distributed and fairly common species captured in surveys carried out in several environments in Amazon [54–57, 94, 95].

Recently, Brazilian researchers proposed the following two new genera within tribe Diachlorini.

3.3.1.22. Genus Muscotabanus (Henriques and Krolow, 2013)

This has the species *Muscotabanus rafaeli*, which was proposed from unidentified specimens from Entomological Collection of the National Research Institute Amazon, all collected in the Central Amazon [169].

3.3.1.23. Genus Elephantotus (Gorayeb, 2014)

The species *Elephantotus tracuateuensis* Gorayeb is described from specimens collected on the edge of a mangrove forest, coastal area of Brazil's western Amazon, near nests of *Eudocimus ruber* (Linnaeus) (scarlet ibis), *Nycticorax nycticorax* (Linnaeus) (socó sleeper) and *Ardea alba* (Linnaeus) (great egret) [170].

Others genera in the tribe Diachlorini are under-represented in more current surveys, and have no economic or sanitary importance.

3.3.2. Tribe Tabanini (Latreille, 1802)

With 207 Neotropical species characterized by setose basicosta, labella wholly pollinose, without ocelli [19, 36] There are some groups of species of *Leucotabanus*, *Stypommisa* e *Tabanus* (those with long antennal spine) difficult to place because the setose basicosta. These problems can be solved by the study of Fairchild [19]. In Neotropics, Tabanini comprises five genera, but only three with South-American species.

3.3.2.1. Genus Phorcotabanus (Fairchild, 1961)

With two South-American species, this can be seen from Colombia to Argentina [20]. *Phorcotabanus cinereus* (Wiedemann) occurs in Central Amazon, and was captured in "clareira," being the most abundant among the tabanid species captured in canopy of the forest [56].

3.3.2.2. The genus Poeciloderas (Lutz, 1921)

This comprises nine species, all endemic of South America; they are mainly observed in south temperate or Andean region, but not in Chile, although *Poeciloderas quandripunctatus* (Fabricius) is well distributed from Mexico to Argentina [20]. It is a fairly homogeneous group, with closely related species and very similar to those of genus *Tabanus*. This group is understudied and lacks higher setting to characterize the species in the genus [19]. Coscarón and Fairchild reviewed the genus in Argentina and provided a key to the four species in that country [171]. The more common species captured in current surveys is *Poeciloderas quandripunctatus* on Central Amazon and on Maraca Island, Amazonian subregion, Guyana province [50, 56]. The species was also captured in Tocantins, Brazil, Chacoan subregion, Cerrado

province [77], and in southeastern Brazilian coastal zone and plateau, Parana subregion [59, 63]. The species was also collected in open meadows, from 10:00 h until ca. 16:00 h, during the sunniest and hottest hours of the day, on Marambaia Island, Parana subregion, southeast Brazilian Atlantic Forest province [65]. This species is recognized having a wide distribution for all Neotropics.

3.3.2.3. Genus Tabanus (Latreille, 1802)

This comprises world-wide distributed species with bare eyes, no tubercle at vertex, short proboscis, soft labella, setose basicosta, basal plate of third antennal segment with an acute or obtuse angle, rarely with a tooth or spine; in tropical species the wings can be tinted, spotted on crossveins, margined brown veins, entirely dark or black, but never banded [19]. Coscarón and Papavero [20] listed 191 species in tropical region, of which 110 occur in South America: in their catalog lacks *Tabanus bibanda* considered *nomen nudum* [37], recorded in the southeastern Brazilian plateau, Parana Forest province, Parana subregion [61]. Fairchild [172] reported *Tabanus nereus* Fairchild and *Tabanus eldridgei* Fairchild in mangrove areas of Colombia and Ecuador, and introduced the measure of "frontal index," as a morphological key feature to tabanid identification. Coscarón reviewed the genus and provided good illustrations to identify 16 Argentine species [173]. In 1983, Fairchild published an excellent study of the *Tabanus lineola* complex, providing keys to males and females of South America species *Tabanus campestris* Brèthes, *Tabanus colombensis* Macquart, *Tabanus commixtus* Walker, *Tabanus curtus* Hine, *Tabanus eldridgei* Fairchild, *Tabanus guapiensis* Wilkerson, *Tabanus nereus* Fairchild, *Tabanus occidentalis* Linnaeus *Tabanus penai* Philip, *Tabanus secundus* Walker (as *stenocephalus* Hine), *Tabanus Triangulum* Wiedemann, *Tabanus vittiger* Thomson, *Tabanus wilkersoni* Fairchild, and *Tabanus wokei* Fairchild [174]. Fairchild also offered a very relevant study of the larger species of *Tabanus* of eastern South America [175]. *Tabanus importunus* Macquart, *Tabanus occidentalis* Linnaeus and *Tabanus pungens* Wiedemann were reported as occurring in French Guiana, in pasture area, transition zone between savannah and eastern Brazilian Amazon forest [176]. *Tabanus aaptus* Fairchild, Tabanus *augustifrons* Macquart, *Tabanus antarticus* Linnaeus, *Tabanus callosus* Macquart, *Tabanus claripennis* Wiedemann, *Tabanus discus* Wiedemann, *Tabanus importunus* Wiedemann, *Tabanus lineifrons* Lutz, *Tabanus nebulosus* DeGeer, *Tabanus nematocallus* Fairchild, *Tabanus occidentalis* Linnaeus, *Tabanus piceiventris* Rondani, *Tabanus sannio* Fairchild, *Tabanus trivittatus* Fabricius, and *Tabanus unimacula* (Kröber) were recorded on Maraca Island, Amazonian subregion, Guyana province [50]. Several surveys conducted since 1999 till 2010, revealed that *Tabanus amapaensis* Fairchild, *Tabanus amanuensis* (Barretto), *Tabanus angustifrons*, Macquart, *Tabanus antarticus* Linnaeus, *Tabanus callosus* Macquart, *Tabanus claripennis* (Bigot), *Tabanus crassicornis* Wiedemann, *Tabanus discus* Wiedemann, *Tabanus importunus* Wiedemann, *Tabanus lineifrons* Lutz, *Tabanus nematocallus* Fairchild, *Tabanus occidentalis* Linnaeus, *Tabanus piceiventris* Rondani, *Tabanus pungens* Wiedemann, *Tabanus sannio* Fairchild, *Tabanus sextriangulus* Gorayeb and Rafael, *Tabanus trivittatus* Fabricius, and *Tabanus xuthopogon* Fairchild, are the most common species in central Amazon [54, 55, 57, 95]. *Tabanus importunus* Wiedemann is reputed as the most important vector in the Pantanal, Chaco subregion, Midwestern Brazil, being most abundant in November. It is the most common species in the region, followed by *Tabanus occidentalis* Linnaeus, a common species found in September and December, by *Tabanus*

claripennis Bigot, more abundant during July to October [76]. A survey performed in Areguá, Paraguay, Chacoan subregion, Pampa province, found *Tabanus triangulum* Wiedemann, *Tabanus secundus* Walker (as *stenocephalus* Hine), *Tabanus occidentalis* Linnaeus, and *Tabanus pungens* (Wiedemann) among the most abundant species [49]. A survey performed in Tocantins, Brazil, Chacoan subregion, Cerrado province found *Tabanus antarcticus* Linnaeus, *Tabanus* cf. *cicur* Fairchild, *Tabanus fuscofasciatus* Macquart, *Tabanus glaucus* Wiedemann, *Tabanus importunus* Wiedemann, *Tabanus mucronatus* Fairchild, *Tabanus occidentalis* var. *dorsovittatus* Macquart, *Tabanus occidentalis* var. *modestus* Wiedemann, *Tabanus palpalis* Brèthes, and *Tabanus xuthopogon* Fairchild [77]. The pupae of *Tabanus triangulum* Wiedemann and *Tabanus platensis* Brèthes, and larvae of *Tabanus nebulosus ornativentris* Kröber on *Pistia stratiotes* Linnaeus were respectively collected in Santa Fé, Buenos Aires and Formosa, Argentina, Chacoan subregion, Pampa province [132]. *Tabanus angustus* Macquart takes place in the hills of Argentine Pampean subregion [131]. In southeastern Brazilian plateau, Parana Forest province, occur *Tabanus fuscus* Wiedemann, *Tabanus colombensis* Macquart, *Tabanus eldridgei* Fairchild, *Tabanus nebulosus ornativentris* Kröber, and *Tabanus wokei* Fairchild [63]. *Tabanus augustus* Macquart, *Tabanus claripennis* (Bigot), *Tabanus fuscus* Wiedemann, and *Tabanus triangulum* Wiedemann were captured in coastal zone of Parana state, Brazilian Atlantic Forest [59]. *Tabanus claripennis* (Bigot), *Tabanus discus* Wiedemann, *Tabanus fuscus* Wiedemann, *Tabanus importunus* Wiedemann, *Tabanus obsoletus* Wiedemann, *Tabanus occidentalis* Linnaeus, *Tabanus pungens* Wiedemann, and *Tabanus triangulum* Wiedemann were collected in several environments on Marambaia Island, Parana subregion, southeast Brazilian Atlantic Forest province [65].

4. Tabanids and diseases

There are few studies concerning transmission of diseases caused by tabanids in South America. Most of the researchers have the scope of knowing the species found in different environments, seasonal fluctuation, and biotic and abiotic factors that affect the behavior of tabanid populations. The first author to relate tabanids with animal disease in South America was Lutz. He pointed the tabanids as the main mechanical vector of *Trypanosoma evansi*, the etiological agent of "mal-de-caderas" or "surra" of equines [176]. Tabanids have been recorded as an important mechanical vector of *Trypanosoma vivax* in South America [177]. Raymond found *Trypanosoma vivax* was transmitted by *Tabanus importunus* between zebu bulls by interrupted blood meal, in French Guiana [17]. In Colombia, three specimens of tabanid (without identification) were found infected with flagellates morphologically compatible with *Trypanosoma vivax* [52], and in a livestock region, was found a strong positive correlation between incidence of *Trypanosoma vivax* in cattle and tabanid population [14]. An experimental essay demonstrated that *Tabanus nebulosus* is able to transmit *Trypanosoma vivax* between cattle, when interrupted blodmeal is resumed within 10 minutes or less [14]. *Cryptotylus unicolor* was able to transmit experimentally *Trypanosoma vivax* between the livestock [178]. Monzón and collaborators recorded equine trypanosomiases transmitted by *Tabanus* sp. in Argentina [180]. Tabanids have been recorded as an important mechanical vector of *Trypanosoma evansi* in Brazilian and Bolivian Pantanal [179]. Outbreaks of the cattle disease

caused by *Trypanosoma evansi* have been associated with the rainy season when tabanids are more abundant [15]. The most important vector of trypanosomiasis of cattle in Pantanal is *Tabanus importunus* and it is more abundant during the rainy season, from September/October to January [181–185].

Due to major environmental changes imposed by human productive activity, new interactions between agents, vectors, and hosts have occurred. A specimen of *Tabanus importunus* was found infected with a *Leishmania* sp.: the diagnosis was performed using DNA amplification technique, in São Paulo, Brazil [186]. *Borrelia burgdorferi* was found naturally infecting tabanids on Marambaia Island, Rio de Janeiro, southeast Atlantic Brazilian Forest (no published data from Guimarães et al). *Tabanus* sp. was reported as vector of human botfly, *Dermatobia hominis* Linnaeus Jr., in Rio Grande do Sul, Brazil [187]. In Ecuador it was reported the transmission of the botfly by *Chrysops varians* [188].

The following is offered as an Appendix, in which the main studies performed in South-American countries are presented.

Appendix

In this study of South American tabanids, the authors included Trinidad, because of its geographic proximity to South America mainland and by the affinity of its tabanofauna with that of South America, it is considered to be in Caribbean subregion [189]. For this aspect, Panama should also be included, but studies on tabanids in that country are very extensive and we chose to omit them. Still, many species that occur in Panama also occur in South America Caribbean subregion.

The first studies on the tabanofauna **Trinidad** were from Bequaert, which listed 23 species belonging to the genera *Chrysops* (five species), *Esenbeckia*, *Selasoma*, *Stibasoma* (two species), *Dichelacera*, *Tabanus* (12 species) and *Acanthocera* [189]. In 1944, Bequaert brought the number of species as 31, 29 in Trinidad and two in Tobago, adding a species of the genus *Lepiselaga*, four in genus *Tabanus* and *Diachlorus* [190]. Callan increased the number of species to 34, registering a species for each genus of *Tabanus* (*Chlorotabanus*), *Stibasoma,* and *Fidena* [191]. Fairchild and Aitken added 11 species, describing *Acanthocera trinidadensis* and *Stibasoma flaviventre*, and corrected previous errors in identification, bringing to 45 species in Trinidad [158]. The record of *Phaeotabanus cajennensis* on the island rose to 46 species of tabanids in Trinidad [151].

About horseflies in **Guyanas**, Desquesnes and Rocque published an important compilation of knowledge on biology, sanitary importance, and control of tabanids [192]. In **French Guiana**, a survey performed by Raymond found some differences in relative abundances of tabanids as the environment: in savannah, the most abundant species were *Tabanus importunus*, *Tabanus occidentalis* var. *dorsovittatus*, *Tabanus wilkersoni*, and *Chlorotabanus mexicanus*; in the rain forest the most abundant species were *Phaeotabanus cajennensis*, *Chlorotabanus inanis*, *Stenotabanus cinereus*, and *Tabanus occidentalis*. Raymond also noted that in ecotone environments, there is a greater variety of species and greater chance of finding rare species [17]. In **Surinam** the available information

on tabanid is the Coscarón and Papavero catalog which list *Tabanus antarcticus* and *Tabanus nebulosus*; and the site InsectoidInfo points *Chlorotabanus inanis* as occurring in that country [20, 193]. In **Guyana** the tabanofauna is very diverse, with species in several genera, but information is restricted to catalogs [30, 32, 34, 82].

Studies on tabanids from **Colombia** were very profitable after 1940s. In 1946, Bequaert published a catalog of Colombian tabanids listing 129 species with their respective localities, and provided a key to the genera [194]. A list of 39 species of tabanids collected from Valle del Cauca, Pacific Ocean coast, was published in 1969 [195]. In 1979, Wilkerson published a list of 158 species of tabanids from Western Colombian in which are described 31 species, one subspecies and one subgenus; he also provided a checklist of 226 Colombian species [196]. During years 2000–2001 Orozco collected tabanids in eastern plains of southeast Colombia, Amazonian subregion, and recorded 64 species in 14 genera (*Catachlorops*, *Chlorotabanus*, *Cryptotylus*, *Chrysops*, *Dasychela*, *Diachlorus*, *Dichelacera*, *Fidena*, *Leucotabanus*, *Phaeotabanus*, *Pityocera*, *Poeciloderas*, *Stypommisa,* and *Tabanus*) [197]. In studies in Antioquia, Colombia, western region of Andes, Caribbean subregion, were recorded *Lepiselaga crassipes*, the most abundant species, followed by *Chrysops variegatus* (as *variegata*), *Tabanus occidentalis*, *Tabanus claripennis*, *Tabanus importunus*, *Tabanus albocirculus*, and *Tabanus nebulosus*. The authors also found three specimens of tabanid (without identification) infected with flagellates morphologically compatible with *Trypanosoma vivax* [52]. In 2016, Wolf and Miranda-Esquivel published the more currently catalogue in which are listed 256 species of Colombian tabanids [198].

In **Venezuela** the first list containing 31 species of tabanid was prepared by Pechuman [199]. The list was supplemented by Stone in 1944 which reported 52 species in 18 genera, and provided a key to the species of the genus *Cryptotylus* [200]. In savannah of the Venezuelan Caribbean subregion it was found the most abundant species *Tabanus pungens*, *Tabanus claripennis*, *Tabanus antarticus*, *Tabanus nebulosus*, *Chrysops venezuelensis* and *Esenbeckia prasiniventris*; the authors also emphasized the importance of tabanids in the transmission of bovine trypanosomiasis in the region [201]. Gorayeb and collaborators recorded 16 species to Venezuela, among the genera *Fidena* (four species), *Catachlorops*, *Diachlorus* (three species), *Dichelacera*, *Dicladocera*, *Leucotabanus*, *Philipotabanus Stenotabanus*, *Stypommisa* (three species) from deposited material the Museum of Agricultural Zoology, Institute Francisco Fernández Yépez of the Central University of Venezuela [202]. In 2005, it was published a list of 20 species of tabanids from Caribbean subregion, northern Venezuela [203]. In 2010, Gómez and collaborators reviewed some species of genus *Bolbodimyia* and provided a key to the recorded five species of this genus in Venezuela [111].

In 1968, Patrick and Hays published a tabanids list of eastern **Ecuador**, with 27 species among genera *Esenbeckia*, *Elaphela*, *Fidena*, *Chrysops*, *Diachlorus*, *Dichelacera*, *Lepiselaga*, *Chlorotabanus* (two species), *Stibasoma*, *Stenotabanus, Stypommisa* (three species), *Philipotabanus*, *Leucotabanus*, *Phaeotabanus* (two species), and *Tabanus* (nine species) collected in 1965–1966 in light areas of tropical forest next Limoncocha, Napo province, Amazonian subregion [204]. Buestán conducted a survey in coastal zone of Ecuador, Western and Arid provinces, Caribbean subregion of Ecuador, and found the most abundant species *Tabanus pungens*, followed by *Tabanus colombensis*, *Tabanus occidentalis*, *Tabanus albocirculus,* and *Lepiselaga crassipes* [61]. Fairchild and

León in 1986 published a revisional list of 81 species of tabanids of Ecuador, providing references of original descriptions, geographical data and a key to determine the genera [205]. In 2005, Cárdenas and Vieira published a list of 42 new records, updating the knowledge of Ecuadorian tabanofauna, with 181 species [206]. In 2007, Buestán and colleagues published a list rising to 204 tabanids species of Ecuador, providing species morphological data and information about the collections environments [207]. In 2009, Cárdenas, Buestán and Dangles published studies on the diversity and distribution of tabanofauna of Ecuador and a catalog listing 198 species; in this study, the authors discussed the distribution of *Chrysops varians tardus*, *Dicladocera macula* and *Fidena rhinophora* using georeferenced localities and niche modeling analyses [99]. More recently, Cárdenas studied the distribution of tabanids according to altitudes and climatic factors, finding that most specimens have their activities limited by extremes temperature and humidity [98, 100].

In **Peru**, the first specific publication on Peruvian tabanofauna was Soukoup's in 1945, which listed 81 species in the country [208], most of them were already mentioned in Kröber's catalog of 1934 [31]. In 1951, Kröber reported the result of the expedition held in southern Peru, adding 14 species to those known [209]. Philip published two lists of species, mostly from Peru, from specimens collected during an expedition of California Academy of Science to west coast of South America [210, 211]. Carrasco in 1972, published a list of 163 tabanid species of which 29 were collected from southern Peru, distributed mainly in the genera *Esenbeckia* (seven species), *Fidena* (five species), *Phaeotabanus* (five species), *Scaptia* (five species), *Scione* (20 species), *Chrysops* (12 species), *Stenotabanus* (12 species), *Dasybasis* (19 species), *Dicladocera* (12 species), *Stypommisa* (eight species), and *Tabanus* (31 species) [212]. Wilkerson and Fairchild in 1985 provided a checklist of 228 species known from Peru, with a key to subfamilies, tribes and genera. The list includes 73 tabanid species which were collected in lowland forest, southeast Peru, Amazonian subregion, Pantanal province, considered by authors as a site of great diversity in tabanids [74].

In **Brazil**, last years of 1900, a new generation of researchers in tabanids brought new knowledge of tabanofauna almost in the entire country. Gorayeb, in 1985, conducted a survey in the western Amazon and recorded 15 species of *Tabanus*, four *Chrysops*, four *Fidena*, three *Catachlorops*, seven *Diachlorus*, four *Dichelacera*, three *Phaeotabanus*, and four species of *Stypommisa* [53]. In surveys conducted in Central Amazon, between 1982 and 2007, using Malaise traps at ground level and hanging traps on water depth and 25 and 40 m high, 60 species belonging to the following genera of tabanids were collected: *Tabanus* (29 *species*), *Chrysops* (seven species), *Diachlorus* (six species), *Leucotabanus* (five species), *Fidena* (four species), *Phaeotabanus* (four species), *Stibasoma* (four species), *Dichelacera* (two species), and *Stypommisa* (three species) [54–57, 94, 95, 213–215]. One of the most abundant collected species in these surveys was *Phorcotabanus cinereus* (Wiedemann), which also occurs in Brazil's eastern savannah, and in the Argentine Chaco [54, 56, 57, 94, 95, 213–215]. In northern Amazon border with Colombia were recorded 20 species of *Tabanus*, two *Esenbeckia*, one *Fidena*, two *Chrysops*, and 13 *Diachlorini* (in genera *Catachlorops*, *Diachlorus*, *Dichelacera*, *Leucotabanus*, *Phaeotabanus* and *Stypommisa* [50]. In a study conducted in Central Amazonian subregion, Varzea province, were caught *Stenotabanus cretatus*, *Stenotabanus bequarti* Rafael, Fairchild and Gorayeb, *Phaeotabanus nigriflavus*, and *Tabanus occidentalis* feeding on caiman

Caiman crocodilus (L.) and anaconda *Eunectes murinus* (Linnaeus) [7]. In Pantanal, Brazilian Amazonian subregion, Barros recorded 10 species of *Tabanus*, and others in several general; most abundant species were *Tabanus importunus*, *Tabanus claripennis*, *Tabanus occidentalis*, *Lepiselaga crassipes*, and *Chrysops* sp. [76]. In Chaco subregion, in Cerrado of the Brazilian Midwest, two species were recorded in *Esenbeckia*, four *Fidena*, six *Catachlorops*, two *Dichelacera*, three *Stypommisa*, and 11 species of *Tabanus* [77]. *Tabanus occidentalis*, *Lepiselaga crassipes*, *Tabanus importunus*, *Tabanus claripennis,* and *Tabanus sorbilans* were the most abundant species recorded in the transition zone between Cerrado and Pantanal, Amazonian subregion [144]. In Parana subregion, a survey performed in Atlantic Forest, Marambaia Island, and southeastern Brazil, recorded 31 species of tabanids of genera *Chrysops* (two species), *Esenbeckia*, *Scepsis*, *Fidena*, *Scaptia*, *Acanthocera*, *Catachlorops* (two species), *Chlorotabanus*, *Diachlorus* (three species), *Dichelacera* (two species), *Leucotabanus*, *Phaeotabanus* (three species), *Rhabdotylus* (two species), *Stigmatophtalmus*, *Poeciloderas*, *Tabanus* (eight species); the most abundant species was *Diachlorus bivittatus* [64, 65]. Also in Parana subregion, southeastern Brazilian plateau, were recorded species of *Acanthocera* (three), *Chrysops* (six), *Dichelacera* (three), *Diachlorus*, *Fidena* (two), *Lepiselaga*, *Phaeotabanus*, *Poeciloderas,* and *Tabanus* (eight) [59, 63]. Dutra and Marinoni captured *Catachlorops furcatus* Wiedemann, *Catachlorops fuscinevris* (Macquart), *Chlorotabanus inanis*, *Chrysops* sp., *Diachlorus bivitattus*, *Dichelacera alcicornis*, *Phaeotabanus litigiosus*, *Poeciloderas quadripunctatus*, *Pseudacanthocera sylverii* (Macquart), *Stenotabanus* sp., and *Tabanus occidentalis* on Mel Island, coastal zone of Parana subregion, Brazilian southeast: the most abundant species was *Dichelacera alcicornis* [152]. Survey conducted between 1995–1997, using Malaise traps, southern Chacoan subregion, Pampa province, Brazilian far south, resulted in a list of 30 species, mainly representatives of *Chrysops* genera (seven species), *Dichelacera* (three species) and *Tabanus* (seven species) [60]. The first published study on seasonal fluctuation in Brazil, is Bouvier's, in 1952, which studied 52 species of tabanids and its seasonal variation in the northwest region of São Paulo, Brazil, Parana Subregion, Brazilian Atlantic Forest province [216].

In **Bolivia**, Chainey and colleagues published a preliminary list and a key to 32 genera and 167 species of tabanids, they also report tabanid collections in lowlands and mountainous areas, including grasslands, forests and wetlands, Chacoan subregion, eastern Bolivia; in this region, during August and October, cattle must be gathering in tight groups to reduce tabanid hematophagism impact on beef and milk yields [90]. Chainey and Hall proposed new genus and species, *Boliviamyia fairchildi* from specimens collected in the forest of the Bolivian southwest, Amazon subregion of Bolivia [73]. Coscarón re-described *Dichelacera boliviensis* (Brèthes) and *Dichelacera micracantha* Lutz from Bolivia [217]. Wilkerson provided a key of species of *Stenotabanus (Brachytabanus)* and described *Stenotabanus (Brachytabanus) sphaeriscapus*, from Bolivia [218]. Gutiérrez and Rumiz in 2002 conducted a great study to assess the degree of specialization relative to habitat of four groups of insects: among tabanids, *Pseudacanthocera brevicorne* (cerrado), *Tabanus sorbilans* (fields), *Phaeotabanus fervens* (riparian forest), and *Tabanus nebulosus* (woods gallery) were more specialized as the habitat; *Tabanus occidentalis* (cerrado, fields, riparian galleries and semi deciduous forests), and *Lepiselaga crassipes* (cerrado, fields, riparian forests and semi deciduous) were less demanding species as the habitat use [219].

About tabanids from **Chile**, Macquart, Rondani and Walker were the first researchers of Chilean tabanofauna [46]. They also highlights the work of Philippi, with the publication of a list of Chilean tabanids in 1865 [220]; the catalog "Insects Diptera of Chile," by Reed in 1888, which lists 61 species of tabanids in Chile [221]; and the works of Enderlein and Kröber who reviewed and published studies on the Chilean species [32, 69, 222]. It should be noted Pine work that offers an excellent review of studies in Chile about tabanids [223]. In 1968, Philip reviewed the types of 28 Chilean species previously described by Philippi in 1865 [221, 224]. In 1973, the first study on tabanid ecology in Chile was published, from collections made using Manitoba trap in north coast of Center-Chilean subregion, recording species of the genera *Scaptia* (three species), *Mycteromyia,* and *Dasybasis* [70]. And in 1991, Coscarón and González published a list of 110 species of Chilean tabanids in 16 genera, with geographical distribution, bibliography, and a key to subfamilies, genera and subgenera [46]. The most recent studies on Chilean tabanids concern the description of *Dasybasis elquiensis* [134]; redescription of male and female of *Scaptia (Pseudoscione) varies* (Walker) and the male's description of *Scaptia (Pseudoscione) atra* (Philippi) [91]; description of female and male redescription of *Dicladocera hoppi* Enderlein [225]; descriptions of adults and immature stages of *Agelanius fuscus* [107]; adult female of *Agelanius verai* and *Agelanius chiloensis* [106, 109]; description of immature stages of *Scaptia (Scaptia) lata* [85], *Dasybasis pruinivitta* [135], and *Agelanius cortesi* [110]; and description of *Dasybasis antillanca* and *Dasybasis collagua* [40]. Studies in wetlands ("humedales") in Chilean Andes in Centro-Chilean subregion, determined that the order Diptera is the most abundant among insects collected by Malaise trap, and in this Order, Tabanidae is the second group most abundant, after Tipulidae [226].

The study of tabanids in **Argentina** have been very fruitful, especially the works of Coscarón that since the beginning of 1960s has been studying the morphology, taxonomy and biology of the group. In addition to describing various species of several genera, Coscarón revised *genera Dicladocera* Lutz in Argentina [141] and *Lepiselaga* Macquart [227], the subgenus *Mesomyia (Coracella)* Philip [47], genera *Dichelacera* Macquart [214], *Stenotabanus* Lutz and *Myiotabanus* Lutz [161], *Catachlorops* Lutz [114], *Leucotabanus* Lutz, *Pseudacanthocera* Lutz, *Bolbodimyia* Bigot and *Pachyschelomyia* Barretto [228], *Diachlorus* Osten Sacken, *Stibasoma* Schiner, *Stypommisa* Enderlein, *Cryptotylus* Lutz and *Chlorotabanus* Lutz [229], *Tabanus* Linnaeus [173], *Chrysops* Meigen [230], *Phaeotabanus* Lutz and *Acanthocera* Macquart [231], *Scione* Walker [88], *Fidena* Walker [91], *Poeciloderas* Lutz [171], the subgenus *Scaptia* (*Lepmia*) Fairchild [232], the genus *Dasybasis* Macquart [130], the tribe Mycteromyiini [68], and the subgenus *Scaptia* (*Scaptia*) Walker [233]. He also studied the immature stages of several species in several genera [85, 128, 132, 133, 149, 234–237]. In 2002, Coscarón compiled an illustrate key to larvae and pupae of Argentine tabanids [238]; and in 2014, Coscarón and Papavero published another more elaborated key to tabanids immature stages of Neotropical tabanids [239]. In 2016, Dufek and colleagues published a study about the tabanids from west Argentina, Chaquean subregion, reporting species of *Chrysops* (four), *Fidena*, *Lepiselaga*, *Diachlorus*, *Dichelacera*, *Phaeotabanus*, *Phorcotabanus*, *Poeciloderas* (two species) and *Tabanus* (five species) [240]. In 1951 and 1953, Hack provided good morphological studies of Argentine tabanids [241, 242]. There is only one list of tabanids from Argentina published by Coscarón (1998) in which he listed 350 species [243].

Tabanids studies in **Paraguay** are still incipient. The first study of Paraguay tabanofauna was performed by Kröber, who described three species of *Poeciloderas*, all currently synonymized, and two species transferred to the genus *Tabanus* [244]. Tabanids were implicated by Russo in transmission of *Trypanosoma equinun* to equine population in Paraguay since 1954 [245]. In 1977, Coscarón summarized available literature on tabanids in Paraguay [246]. Strickman [48] collected tabanids during 1978–1980, in south-central Paraguayan region, Chaquean subregion: nine species of *Tabanus*, five species of *Chrysops*, two *Dichelacera*, two *Diachlorus*, two *Stypommisa*, and one for each genus *Acanthocera*, *Lepiselaga* and *Poeciloderas*. The same author studied the seasonal variation and climatic factors on the bionomics of *Chrysops variegatus*, in central Paraguay, in an area adjacent to a lake, consisted of a sandy and woody strip, bordered by the lake and a grassy swamp [49]. The author also points the species as a possible vector of the equine disease 'mal de caderas,' caused by *Trypanosoma evansi* [48]. No other record of Paraguayan tabanids was found in literature.

Bibliographic information about the tabanids from **Uruguay** is only available in the catalogs of Kröber [31], Fairchild [32], Moucha [82], Fairchild and Burger [34], and Coscarón and Papavero [20]. A list of 21 species of tabanids within the genera *Chrysops* (three species), *Esenbeckia*, *Fidena*, *Acanthocera*, *Catachlorops* (two species), *Dasybasis* (two species) *Lepiselaga*, *Poeciloderas*, *Stenotabanus*, *Stibasoma*, and *Tabanus* (six species) is available at the site "InsectoidInfo" [247].

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