

An overview of studies on sex pheromones of insect vectors of pathogenic trypanosomatids of medical and veterinary importance

Uma visão geral dos estudos sobre feromônios sexuais de insetos vetores de tripanossomatídeos patogênicos de importância médica e veterinária

Una visión general de los estudios sobre feromonas sexuales de insectos vectores de tripanosomátidos patógenos de importancia médica y veterinária

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Abstract

Insect vectors of Leishmaniasis, Chagas disease and African trypanosomiasis remain human health, veterinary and economic problems worldwide. Several sex pheromone molecules that contribute to mating behavior have been identified in these vectors. These chemical signals are potential alternatives to traditional chemical insecticides. This review discusses the diversity of sex pheromone molecules and their role in the mating behavior of insect vectors of Leishmaniasis, Chagas disease and African trypanosomiasis. The selection of studies was made based on research and review articles that presented sex pheromone aspects regarding insect vectors. In some species, these molecules have a dual function as serving as sex and aggregation pheromone. We also highlight the current knowledge of these substances as potential vector control tools. The studies revealed that sex pheromone applicability is largely experimental and restricted to some vectors. Based on these limitations, we included updated tables with the chemical identity of several sex pheromone compounds and other relevant information concerning the target species, which can contribute to future studies of control methodologies.

Keywords: Insect vectors; Sex pheromones; Control strategies.

Resumo

Insetos vetores das leishmanioses, doença de Chagas e tripanossomíase africana continuam sendo um problema para saúde humana e veterinária e econômica em todo o mundo. Várias moléculas de feromônios sexuais que contribuem para o comportamento de acasalamento foram identificadas nesses insetos vetores. Esses sinais químicos são potenciais alternativas aos inseticidas químicos tradicionais. Esta revisão discute a diversidade de moléculas de feromônios sexuais e seu papel no comportamento de acasalamento de insetos vetores de leishmanioses, doença de Chagas e tripanossomíase africana. A seleção dos estudos foi feita com base em artigos de pesquisa e revisão que apresentassem aspectos relacionados aos feromônios sexuais nesses insetos vetores. Em algumas espécies, essas moléculas têm a dupla função de servir como feromônio sexual e de agregação. Destacamos também o conhecimento atual dessas substâncias como uma potencial ferramenta de controle vetorial. Os estudos revelaram que a aplicabilidade dos feromônios sexuais é amplamente experimental e restrita a alguns vetores. Com base nessas limitações, incluímos tabelas atualizadas com a identidade química de diversos compostos dos feromônios sexuais e outras informações relevantes sobre as espécies-alvo, que podem contribuir para futuros estudos de metodologias de controle.

Palavras-chave: Insetos vetores; Feromônios sexuais; Estratégias de controle.

Resumen

Los insectos vectores de las leishmaniasis, la enfermedad de Chagas y la tripanosomiasis africana continúan siendo un problema de salud humana, veterinario y económico a nivel mundial. En estos vectores se han identificado varias

moléculas de feromonas sexuales que contribuyen al comportamiento de apareamiento. Estas señales químicas son alternativas potenciales a los insecticidas químicos tradicionales. Esta revisión discute la diversidad de moléculas de feromonas sexuales y su papel en el comportamiento de apareamiento de insectos vectores de Leishmaniasis, enfermedad de Chagas y tripanosomiasis africana. La selección de los estudios se hizo con base en artículos de investigación y revisión que presentaban aspectos de las feromonas sexuales respecto a los insectos vectores. En algunas especies, estas moléculas tienen una doble función como feromona sexual y de agregación. También destacamos el conocimiento actual de estas sustancias como herramientas potenciales para el control de vectores. Los estudios revelaron que la aplicabilidad de las feromonas sexuales es en gran medida experimental y restringida a algunos vectores. Con base en estas limitaciones, incluimos tablas actualizadas con la identidad química de varios compuestos de feromonas sexuales y otra información relevante sobre las especies objetivo, que pueden contribuir a futuros estudios de metodologías de control.

Palabras clave: Insectos vectores; Feromonas sexuales; Estrategias de control.

1. Introduction

Insect vectors of medical and veterinary importance can transmit pathogens to humans and other animals. Many of these insects are members of Diptera and Hemiptera orders with hematophagous habits (Durden & Mullen, 2019). They can host trypanosomatids parasites from *Leishmania* and *Trypanosoma* genera, etiological agents of leishmaniasis and trypanosomiasis, respectively (Maslov et al., 2013; Lukeš et al., 2014). These diseases can cause the death of domestic animals, wildlife and millions people per year, mainly in Latin America, Africa and Asia (Palatnik-De-Sousa & Day, 2011; Alvar et al., 2012; Aregawi, et al., 2019; Lidani et al., 2019; Maggi & Krämer, 2019; Gao et al., 2020).

Leishmaniasis are a group of diseases caused by *Leishmania* protozoan parasites and the transmission occurs through the bite of infected female phlebotomine sandflies (Diptera: Psychodidae). Human Leishmaniasis encompasses different clinical forms: visceral, cutaneous, mucocutaneous, post-kala-azar dermal, and mucosal, according to the parasite specie and its location in the tissues (Burza et al., 2018, WHO, 2022). More than 1 billion people live in endemic areas for leishmaniasis in Asia, Africa, Americas, and Mediterranean region (WHO, 2021). Dogs are the main reservoir of *Leishmania infantum* that causes the visceral form (Moreno and Alvar, 2002). This parasite is potentially fatal to the animal (Ribeiro et al., 2018) and people (Ready, 2014). Other domestic and wild species could maintain the life cycle of *L. infantum* and other *Leishmania* parasites (Quinnell & Courtenay, 2009; Cardoso et al., 2021).

The American trypanosomiasis or Chagas disease is caused by *Trypanosoma cruzi* parasites. Mainly transmitted to humans through feces/urine of triatomines (Hemiptera: Reduviidae) in contact with mucosa or small abrasions in the skin, followed by congenital transmission, blood transfusions, oral mechanisms, and others (WHO, 2021). With an annual incidence of 30,000 cases in America and approximately 6 to 7 million cases worldwide, providing serious consequences for public health (PAHO, 2021). Domestic animals (e.g., dogs and cats) and wild species (e.g., rodents, American marsupials, primates, and bats) are natural reservoirs (Jansen & Roque, 2010; Jansen et al., 2015).

Human African trypanosomiasis or sleeping sickness, the etiological agents are subspecies of *Trypanosoma brucei* that are transmitted through the bite of infected tsetse flies (Diptera: Glossinidae). *Trypanosoma brucei gambiense* causes a chronic form of the disease in West and Central Africa, while *Trypanosoma brucei rhodesiense* is responsible for the acute form in Eastern Africa (Ando et al., 2002; Barrett et al., 2003). Wild and domestic animals are the main parasite reservoirs (CDC, 2020). In the last two decades, vector control programs reduced the cases of Human African trypanosomiasis to less than 1,000 in endemic countries (WHO, 2019a, 2019b).

Additionally, sleeping sickness disease has an animal variant, known as Animal African trypanosomiasis or Nagana. *Trypanosoma congolense*, *Trypanosoma vivax* and *T. brucei* are the main etiological agents, also transmitted by tsetse flies. Wild species are considered reservoirs despite being generally tolerant to the infection (Kasozi et al., 2021). Cases of Nagana are frequently diagnosed in domesticated animals, such as cattle, pigs and horses (Steverding, 2008). Veterinary experts

consider Nagana the major constraint to livestock production in Sub-Saharan Africa (Bekele, et al., 2015).

Over the past years, several sex pheromones of insects, including disease vectors have been identified. They could be characterized by a single compound or, more commonly, a combination of molecules in a precise ratio (Wyatt, 2017). Sex pheromones can be involved in mating recognition, and mate assessment, and distinguishing individuals of different species (Johansson & Jones, 2007; Steiger & Stökl, 2014). Moreover, their production and release are usually age-related, coinciding with the maturation of ovaries/ testicles and in some species, they are associated with the feeding status (Blomquist, et al., 2012).

Historically, the principal method to control insect vectors of human and animal disease is chemical insecticides (Kitchen, et al., 2009). However, most of these products present risks to human health and the environment, as well as, the selection of phenotypically resistant insects (Rivero et al., 2010; Himeidan et al., 2012).

Sex pheromones are species-specific compounds that elicit an appealing potential, and behavioral effect and present a low tendency to select resistance in the target specie (Lorenzo, et al., 2014). The incorporation of these molecules as control tools are alternatives to reduce the impacts of the chemical insecticides (Lorenzo et al., 2014; Müller et al., 2019; Wilson et al., 2020; Wooding et al., 2020).

In this sense, this review discusses the diversity of sex pheromone molecules and their role in the mating behavior of insect vectors of Leishmaniasis, Chagas disease and African trypanosomiasis. We also highlight the current knowledge of these substances as potential vector control tools.

2. Methodology

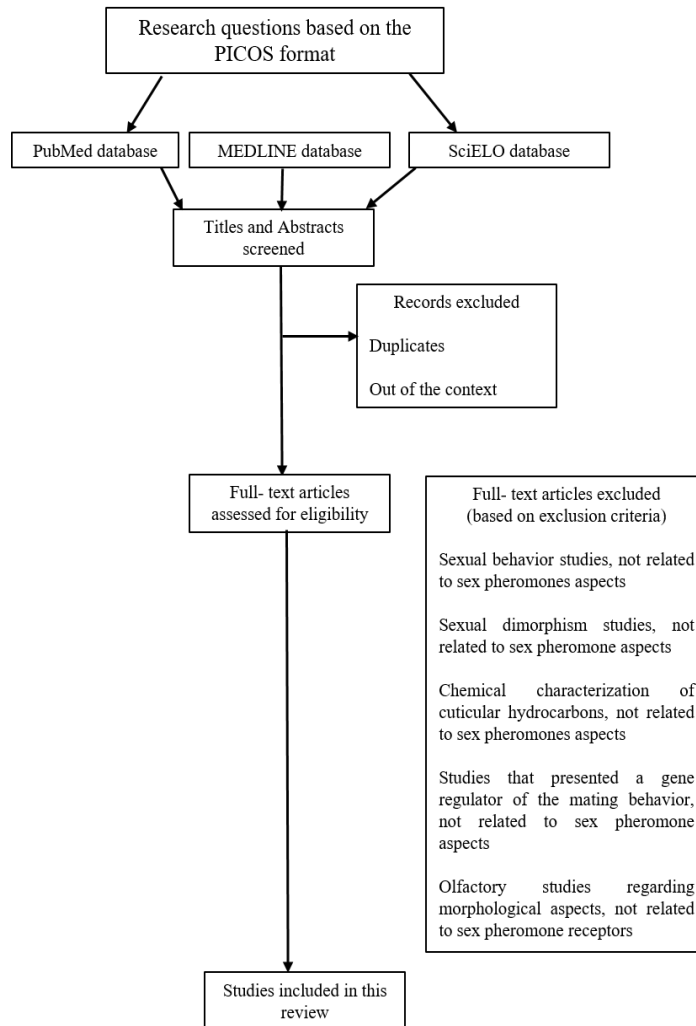
2.1 Research question

The research questions were defined based on the format called PICOS (population, intervention, comparator, outcome, and studies types). Population: families of insect vectors that transmit leishmaniasis and trypanosomiasis. Intervention: production and release of sex pheromones. Comparator: no comparison. Outcome: morphological analysis, behavioral, physiological, chemical, molecular, and insect control studies regarding sex pheromones. Studies types: laboratory and field studies. Then a research question was formulated following the PICOS criteria: “Which are the studies that present morphological, behavioral, physiological, chemical, molecular analysis as well control methodologies regarding sex pheromones in the insect vectors of leishmaniasis and trypanosomiasis?”.

2.2 Literature research and studies selection

An electronic search was conducted in PubMed, MEDLINE and SciELO data-bases from 2020 to 2022, with no publication date restrictions. The following combinations of terms were used in these data-bases: Glossinidae and sex pheromone, Glossinidae sex pheromone gland; Glossinidae contact pheromone; Glossinidae and sexual behavior; Psychodidae and sex pheromone; Psychodidae and pheromone gland; Psychodidae and sexual behavior; Reduviidae and sex pheromone, Reduviidae and sex pheromone gland; Reduviidae and sexual behavior. Due to the great number of results, a screening was realized in the titles and abstracts of the papers. Then, full texts of potentially relevant papers were assessed for eligibility. The study selection was based on the research question. The inclusion criteria were based on research and review articles that presented sex pheromone aspects (such as mating behavior, methods of control, and others) regarding vector insects included in the families Glossinidae, Psychodidae and Reduviidae. The exclusion criteria were established based on research articles that did not present sex pheromone aspects involving these insect vectors.

Figure 1: Fluxogram for the selection of articles. Publications were searched in PubMed, MEDLINE and SciELO database. The studies selection was based on the inclusion and exclusion criteria that followed the research question defined by PICOS format.



Source: Authors.

3. Results and Discussion

1. Subfamily Phlebotominae

Phlebotomine sand flies are insect vectors of medical and veterinary relevance. Females transmit viral agents (Maroli, Feliciangeli, Bichaud, Charrel, and Gradoni, 2013), *Bartonella bacilliformis* (Townsend, 1913; Depaquit et al., 2010) and *Leishmania* parasites (Young & Hertig, 1926; Akhoundi et al., 2016). The major vectors of *Leishmania* species belong to the genera *Phlebotomus* and *Lutzomyia*, which are distributed in the Old and New World, respectively (Akhoundi et al., 2016).

1.1 Site of the sex pheromone production and release

In some species of *Lutzomyia*, males synthesize sex pheromone in glandular cells underlying the abdominal tergites. Cuticular ducts transported these molecules, then they are released in disseminating structures on the cuticular surface (Hamilton et al., 2001; Spiegel et al., 2002). Disseminating structures present different shapes and they are scattered in some abdominal tergites. In *Lutzomyia longipalpis* and *Lutzomyia cruzi*, they are like papules, small round with a central pore, located in the pale spots on tergites IV or III and IV (Spiegel et al., 2002). Papules of *Lutzomyia pessoai* are similar to those

found in *L. longipalpis* and *L. cruzi* although they are distributed from III to VII tergal segments (Ward et al., 1993). Whereas in *Lutzomyia cruciata* the disseminating structures presented a mammiform appearance and they are located in IV-VII tergites (Serrano et al., 2016).

In *L. cruzi* and *L. longipalpis* males, sex pheromone glands cells are composed of a secretory unit, a small reservoir and ducts that connect the reservoir with the papules in the cuticular surface. The gland cells present several lipid droplets and endoplasmic reticulum profiles as well as mitochondria involved in the sex pheromone biosynthesis (Spiegel et al., 2002; Spiegel et al., 2004; Spiegel et al., 2011). In *L. longipalpis*, the gland cell maturation is synchronized with the sex pheromone production reinforcing the role of cytoplasmic organelles in the sex pheromone biosynthesis (Carolina N Spiegel et al., 2011).

Disseminating structures appear to be absent in vector insects of the *Phlebotomus* genus (Ward et al., 1993) and studies regarding morphological/ ultrastructural aspects of the sex pheromone gland cells were not found. Although, some behavioral analyses indicated that males could produce sexual compounds.

1.2 Sex pheromone components

L. longipalpis species complex presents an elaborate pheromone communication, wherein males produce terpenoid compounds that attract conspecific males, acting as an aggregation pheromone, and also attract females to the lekking males, serving as a sex pheromone (Spiegel et al., 2016; De Souza et al., 2017).

There are at least four different sex-aggregation pheromones phenotypes (chemotypes), according to the terpene profile present in these glands (Hamilton, et al., 2004).

Chemotype 1 or (*S*)-9-methylgermacrene-B (9MGB) is the most geographically widespread in Latin America. In Brazil, this chemotype has been observed in several *L. longipalpis* populations in North (Carolina N. Spiegel et al., 2016), Central-West, Northeast (Maingon et al., 2003; Watts et al., 2005) and mainly in Brazil Southeast States (Hamilton et al., 1996a; Hamilton et al., 2005; Araki et al., 2009; Casanova et al., 2015; Spiegel et al., 2016; Galvis-Ovallos et al., 2017). It is also found in Venezuela (Watts et al., 2005), Paraguay (Brazil, et al., 2009), Argentina et al., 2010), Costa Rica (J. G. C. Hamilton, et al., 1996), Honduras (J. G. C. Hamilton, Ward, et al., 1996) and Colombia (J. G. Hamilton & Ward, 1991). Chemotype 2 or (1*S*, 3*S*, 7*R*)-3-methyl- α -himachalene (3M α H) was identified only in Bahia (Northeast region of Brazil) (Hamilton et al., 1996a; Hamilton et al., 1999; Dufour et al., 2012) and Venezuela in *Lutzomyia pseudolongipalpis* populations that they belong to the *L. longipalpis* complex (Watts et al., 2005). Chemotype 3 or cembrene-1 (CEMB-1) is restricted to North (Carolina N. Spiegel et al., 2016), Northeast (Maingon et al., 2003; Watts et al., 2005) and Southeast (Hamilton et al., 2004; Casanova et al., 2015) regions in Brazil. CEMB-1 of *L. longipalpis* population from Sobral (Ceará State- Brazil) was reclassified as a novel diterpene, named Sobralene (Palframan et al., 2018). Chemotype 4 or cembrene-2 (CEMB-2) occurs in Jaíba (Minas Gerais State- Brazil) (J. G. C. Hamilton et al., 2004). A fifth chemotype or (*S*)-9-methyl-germacrene-B+ (9MGB+) was identified by the amounts of specific terpenes present as well as morphological differences in the sex-aggregation pheromone of some *L. longipalpis* populations from Sobral (CE) and Montes Claros (Minas Gerais State- Brazil) (Hamilton et al., 2005; Hickner et al., 2020).

In other *Lutzomyia* species, 9MGB was the major sex pheromone compound in *L. cruzi* (Brazil & Hamilton, 2002; Watts et al., 2005). A mixture of 12 sesquiterpenes was found in male abdominal extracts of *L. cruciata*, although the major component remains unknown (Serrano et al., 2016). In male *L. pessoai* a monocyclic diterpene could act as male sex pheromone (J. G. C. Hamilton & Ward, 1994).

However, more studies are necessary to unveil the chemical identity of the sex pheromone components in other vector species of sandy flies.

1.3 Behavioral and physiological responses to the sex pheromone

Females of *L. longipalpis* feed on a wide range of animals including household animals, livestock and wildlife species. The attraction to these hosts might be regulated by many factors, such as heat and CO₂ and their appealing potential might increase combined with male pheromones (Nigam & Ward, 1991).

Matting assays evaluated behavioral patterns of aggregation and courtship in *L. longipalpis* populations. They revealed that 3M α H produced by males from Jacobina (Bahia State- Brazil) population was able to attract both sexes. In the same study, ascoid sensillum receptor cells in the antennae of males and females responded only to the major component (3M α H) of the sex pheromone gland from Jacobina populations. Suggesting that 3M α H has a dual function in promoting male aggregations as well as serving as a sex pheromone for females (C. N. Spiegel et al., 2005).

Concerning the sex pheromone production and release status in *L. longipalpis* populations, the sex pheromone biosynthesis (9MGB) started around 12 hours after the insect emergence and increased continuously during the first 3 days, stabilizing thereafter, coinciding with the period when males are more able to attract females, in populations from Lapinha (Carolina N Spiegel et al., 2011). Data from Jacobina revealed that 3M α H is produced in 12–14h after emergence increasing gradually and reaching a peak at 7 days (González et al., 2017). While Sobral (possible sobralene chemotype) and Campo Grande (9MGB) populations males presented traces of pheromone at 6–8 h after the emergence. The sobralene peaked in 7 days and 9MGB at 9 days, then sex pheromone production decreased. Additionally, sexually mature males from Jacobina, Sobral and Campo Grande released more sex pheromone when females were close in the first hours of the day. In the light conditions, only Sobral population released more sex pheromone compared to the dark and the compound quantity was the same when they were alone or with females (González et al., 2017). In this sense, the amount of sex pheromone released by *L. longipalpis* populations depends on several factors, such as male age, light / dark condition, and whether females are present.

However, there are few studies regarding behavioral and physiological responses of the sex pheromones in other sand flies species. One of them demonstrated that females of *L. cruciata* were attracted to the male abdominal extracts, suggesting the presence of sex pheromone (Serrano et al., 2006). In *Phlebotomus papatasi*, females were attracted to the compounds released by males (Chelbi, et al., 2011). Females of *Phlebotomus argentipes* were attracted to male extracts. When the male extracts were combined with host odors, the appealing potential increased, indicating that host and males compounds presented a synergistic effect (Kumar et al., 2012).

1.4 Molecular characterization of sex pheromone biosynthesis

Transcriptomic and proteomics approaches revealed genes expressed in the sex pheromone gland of *L. longipalpis* from Lapinha population. Among them, six enzymes of the mevalonate-pathway and the enzymes involved in sesquiterpenoid biosynthesis were identified (González-Caballero et al., 2013; González-Caballero et al., 2014).

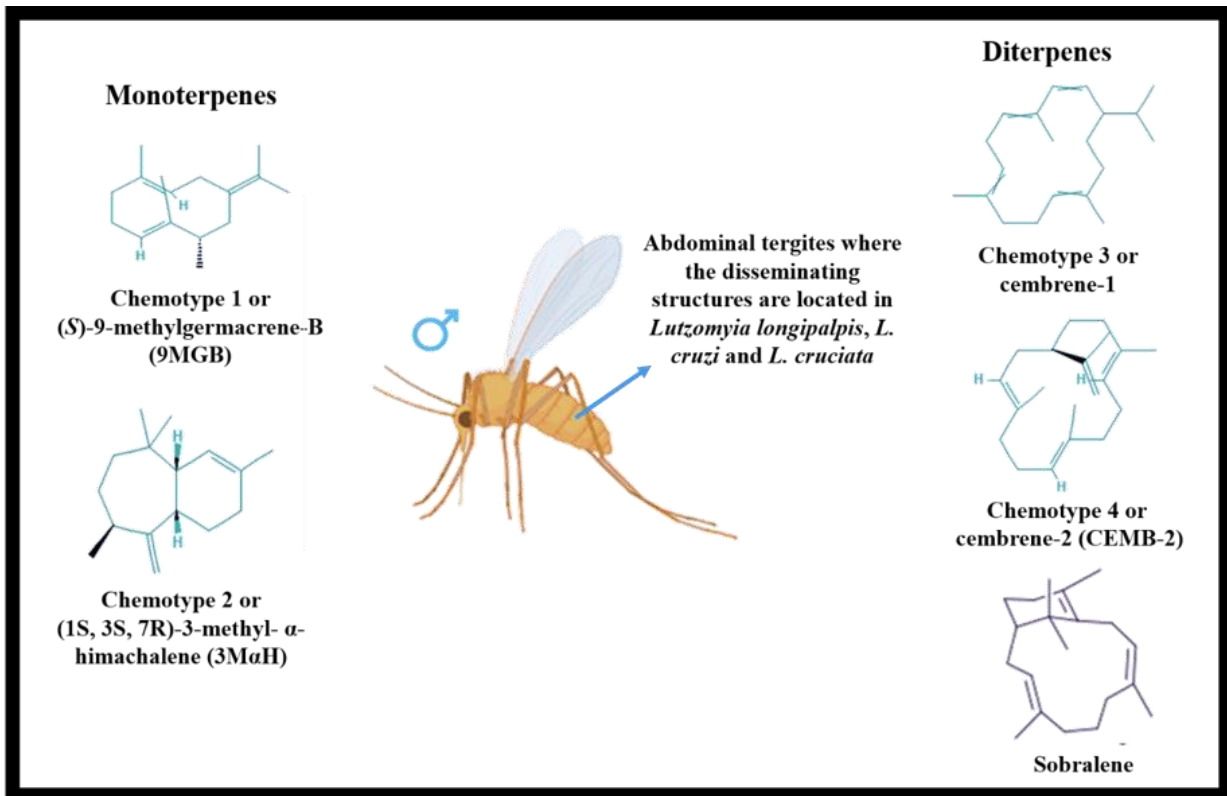
1.5 Practical applications of the sex pheromone as a control strategy

In *L. longipalpis*, a combination of synthetic sex-aggregation pheromone (9MGB) and host odor (chicken) was tested in prototype lures, they were able to attract females and males over the period of several hours at night (Bray et al., 2009). Bray and col. (2014) increased 9MGB concentration and developed a longer-lasting lures in experimental chicken sheds, they attracted female *L. longipalpis* for up to ten weeks and males for up to twelve weeks. Therefore, the sand fly response is significantly related to the quantity of pheromone loaded in the lures (Bell et al., 2018). Besides, males and females were attracted to these longer-lasting lures over distances up to at least 30m in the field, depending on the local environmental and meteorological conditions (González et al., 2020). Co-location of these pheromone baited traps and insecticide was efficient “lure-and-kill” strategy in chicken sheds (Daniel P. et al., 2010). A cluster randomized trial of these lure-and-kill methods

leads to a reduction of *L. longipalpis* at homesteads and the incidence of Canine leishmaniasis in domestic dogs (Courtenay et al., 2019). This intervention also decreased the female vector abundance in neighboring untreated houses and required a lower quantity of insecticide co-located with the synthetic pheromone (Gonçalves et al., 2021). It is important to mention that when sand flies were exposed to the synthetic pheromone in combination with the residual insecticide, they did not present resistance (González et al., 2019). Therefore, these data suggest that the pheromone-based lure-and-kill strategy is considered a potential *L. longipalpis* control tool.

In *P. papatasi*, preliminary field experiments showed that light traps baited with small groups of males and females together were attractive to females. However, further work needs to identify the chemical(s) that are responsible for mediating this attraction and also to determine its potential as a tool for vector control (Chelbi et al., 2011).

Figure 2: Known chemotypes of the aggregation-sex pheromone in males of *Lutzomyia longipalpis* complex. These compounds are produced in glands located in the disseminating structures in the abdominal tergites.



Source: Created in Biorender.com.

Table 1: Overview of the subfamily Phlebotominae.

Vector specie	Vector-borne diseases	Etiological agent	Host	Location	Sex pheromone components	Site of the sex pheromone production and release	Behavioral and/or physiological responses to the sex pheromone	Sex pheromone biosynthesis	Sex pheromone receptors	Practical applications of the sex pheromone in field	References
<i>Lutzomyia longipalpis</i>	Visceral leishmaniasis.	<i>Leishmania (Leishmania) infantum chagasi</i> .	Birds and mammals, including humans.	Latin America.	Sobralene Chemotype 1: 9MGB Chemotype 2: 3MαH Chemotype 3: Cembrene-1 Chemotype 4: Cembrene-2 Chemotype 5: 9MGB+	Sex pheromone gland cells associated with disseminating structures in males in the pale spots in the third and/or forth abdominal tergites.	For females acts as sex pheromone and males acts as aggregation pheromone.	Mevalonate pathway and sesquiterpenoid biosynthesis.	No studies were found. Electrophysiological response in the ascoid sensillum	Long-lasting lure with sex pheromone/ Lures with sex pheromone conjugated with insecticide, as a 'lure-and-kill' strategy	Spiegel et al., 2002; Spiegel et al., 2011; Spiegel et al., 2016; Spiegel et al., 2005; De souza et al., 2017; Hamilton et al., 2004; Hamilton et al., 2005; Maingon et al., 2003; Watts et al., 2005; Hamilton et al., 1996a; Araki et al., 2009; Galvis-Ovallos et al., 2017; Brazil et al., 2009; Salomón et al., 2010; Hamilton et al., 1996c; Hamilton and Ward, 1991; Hamilton et al., 1999; Dufour et al., 2012; Palframan et al., 2018; Nigan and ward, 1991; González et al., 2017; González-Caballero et al., 2013; González-Caballero et al., 2014; Ward et al., 1990; Bray et al., 2009; Bray et al., 2014; Bell et al., 2018; Bray et al., 2010; Courtenay et al., 2019; González et al., 2019.
<i>Lutzomyia cruzi</i>	Visceral leishmaniasis/ Canine leishmaniasis	<i>Leishmania (Leishmania) infantum chagasi</i> .	Birds and mammals, mainly dogs and humans.	Brazil (Cerrado and Pantanal) and Bolivia	9MGB	Sex pheromone gland cells structures in males.	No studies were found.	No studies were found.	No studies were found.	No studies were found.	Spiegel et al., 2002; Spiegel et al., 2016; Spiegel et al., 2004; Brazil and Hamilton, 2002; Watts et al., 2005.

<i>Lutzomyia cruciata</i>	Cutaneous leishmaniasis	<i>Leishmania mexicana</i>	Mammals, mainly humans.	Mexico and Central America.	Mixture of 12 sesquiterpene in males.	There are disseminating structures but the sex pheromone glands were not identified.	Females were attracted to the male abdominal extracts.	No studies were found.	No studies were found.	No studies were found.	Serrano et al., 2016
<i>Phlebotomus papatasi</i>	Cutaneous leishmaniasis	<i>Leishmania major</i>	Mammals, including humans.	North Africa, Eurasia, and India.	No studies were found.	No studies were found.	Females were attracted to the headspace volatiles of small groups of males and males with females.	No studies were found.	No studies were found.	Traps baited with small groups of males and females are attractive to females.	Chelbi et al., 2011.
<i>Phlebotomus argentipes</i>	Visceral leishmaniasis	<i>Leishmania donovani</i> .	Mammals, including humans.	Bangla-desh, India, Nepal and Sri Lanka	No studies were found.	No studies were found.	Virgin females were attracted to males extracts. Addition of host odor in theses extracts increased the attraction.	No studies were found.	No studies were found.	No studies were found.	Kumar et al., 2012

Source: Authors.

2. Family Glossinidae

Tse-tse flies are bloodsucking insects of the genus *Glossina*. Some species are vectors of trypanosome parasites to humans and other animals.

2.1 Site of the sex pheromone production and release

In *Glossina morsitans morsitans*, *Glossina austeni* and *Glossina pallidipes*, sex pheromones components were isolated from the cuticular surface of females (Table 2) (Carlson, et al., 1978; McDowell et al., 1981; Carlson et al., 2000; Carlson et al., 2005).

2.2 Sex pheromone components

Female *G. m. morsitans* produced trimethyl-alkane in the cuticular waxes that act as a contact sex pheromone (Carlson, et al., 1978). Conspecific components (dimethyl-alkanes) were found in females of *G. austeni* and *G. pallidipes* (Huyton et al., 1980; McDowell et al., 1981; Carlson et al., 2000) (Table1). Alkenes were also reported as a contact sex pheromone of *G. austeni* (Carlson et al., 2005) (Table 2).

2.3 Behavioral and physiological responses to the sex pheromone

Males of *G. m. morsitans* attempt to copulate with sex pheromone extract isolated from females et al., 1978). When males and females were treated with tetracycline there is an alteration in the cuticular components. In addition, the relative amount of the female sex pheromone and the mating success also decreased after the treatment. Probably, the microbiota could influence the sex pheromone profile, and consequently the mate choice (Englx et al., 2018).

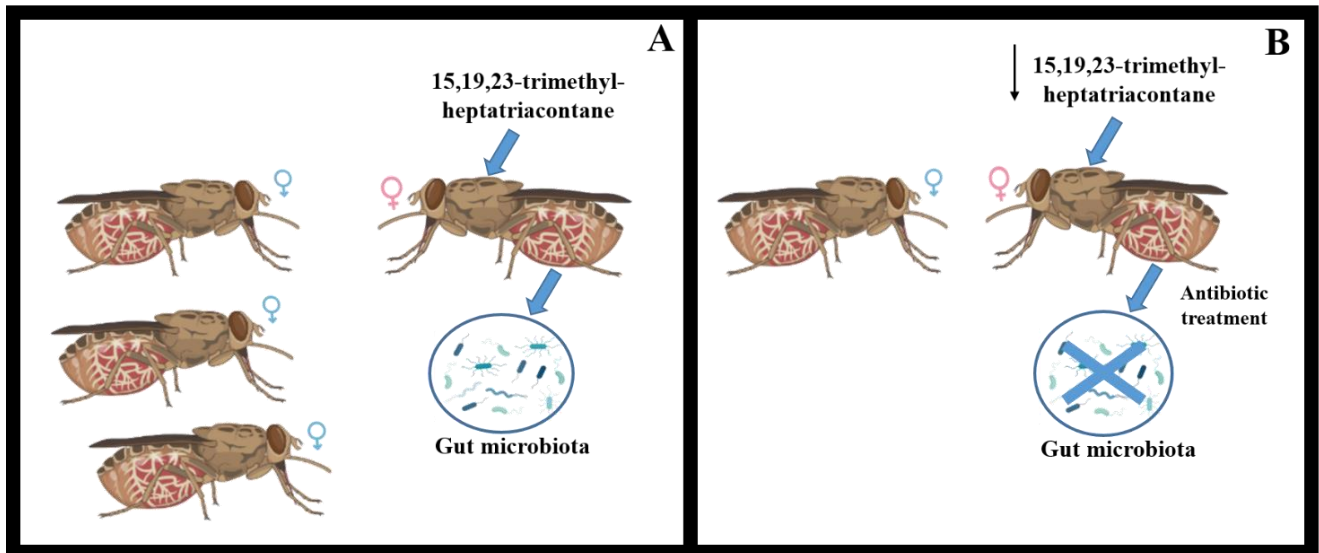
In bioassays, male *G. austeni* showed mating behavior to the synthetic 15, 19-dimethyltriacontane (Huyton et al., 1980). Mating attempts were also observed in contact with other alkene fractions from female's cuticular extract and their synthetic stereoisomers (Carlson et al., 2005).

Female *G. pallidipes* produced the isomers 13,17 dimethylpentatriacontane and 15,19-dimethylpentatriacontane, as components of the contact sex pheromone, that elicited mating behavior in males (McDowell et al., 1981). These behavioral attempts were also detected in presence of the synthetic composition of these molecules (D. A. Carlson et al., 1984).

2.4 Practical applications of the sex pheromone as a control strategy

Preliminary assays co-located the synthetic sex pheromone of *G. m. morsitans* with chemosterilant in traps that elicited males to copulate with the bait and their fertility was reduced (Langley, Coates, Carlson, Vale, & Marshall, 1982).

Figure 3: Mate choice assays in *Glossina morsitans morsitans*. A: Females produced contact sex pheromone (15,19,23-trimethyl-heptatriacontane), a cuticular hydrocarbon that triggers a male sexual behavior. B: In females, the antibiotic treatment reduced the gut microbiota and the contact sex pheromone, as well as affected mate choice behavior in males.



Source: Created in Biorender.com.

Table 2: Overview of the family Glossinidae.

Vector specie	Vector-borne diseases	Etiological agent	Host	Location	Sex pheromone components	Site of the sex pheromone production and release	Behavioral and/or physiological responses to the sex pheromone	Sex pheromone biosynthesis	Sex pheromone receptors	Practical applications of the sex pheromone in field	References
<i>Glossina morsitans morsitans</i>	Nagana and Sleeping sickness	Nagana: <i>Trypanosoma congolense</i> and <i>Trypanosoma vivax</i> Human sleeping sickness: <i>Trypanosoma brucei rhodesiense</i>	Mainly humans, but also other mammals.	Africa	15, 19, 23-trimethylheptatriacontane.	Cuticular surface of females.	Males presented a mating behavior in contact with females cuticular. The microbiota influence in the mate choice	No studies were found.	No studies were found.	Baited traps with synthetic sex pheromone and bisazir, when males tried to copulate their fertility was reduced.	Carlson, Langley and Huyton, 1978; Englx et al., 2018; Langley et al., 1982.
<i>Glossina austeni</i>	Nagana and Sleeping sickness (minor vector)	Nagana: <i>Trypanosoma congolense</i> and <i>Trypanosoma Vivax</i> Sleeping sickness: <i>Trypanosoma brucei rhodesiense</i>	Mainly bushpig, but also other mammals including humans.	Africa	13,17-dimethylpentatriacont-1-ene; 13,17-dimethyltrtriacont-1-ene; 15, 19-dimethyltrtriacontane (possible candidate)	Cuticular surface of females.	Males presented a mating behavior in contact with females cuticular extracts and their synthetic stereoisomers.	No studies were found.	No studies were found.	No studies were found.	Huyton et al., 1980; Carlson et al., 2005.
<i>Glossina pallidipes</i>	Nagana, (mainly cattle) and Sleeping sickness (minor vector).	Nagana: <i>Trypanosoma brucei brucei</i> Sleeping sickness: <i>Trypanosoma brucei rhodesiense</i>	Mammals, including humans.	Africa.	The isomers, 13,17-dimethylpentatriacontane and 15,19-dimethylpentatriacontane	Cuticular surface of females.	Males presented a mating behavior	No studies were found.	No studies were found.	No studies were found.	McDowell et al., 1981; Carlson et al., 1984.

Source: Authors.

3. Subfamily *Triatominae*

Triatomines are hematophagous insects that feed on the blood of vertebrates from different taxa. In mammals, during blood ingestion, these insects can transmit the protozoan *T. cruzi*, the etiological agent of Chagas disease in humans (Chagas, 1909).

3.1 Site of the sex pheromone production and release

Adults of triatomines have a pair of metasternal glands (MGs) in the ventral region of the metathorax (Brindley, 1930; Staddon, 1979; Weirauch, 2006). In *Triatoma brasiliensis* and *Rhodnius prolixus*, the glandular apparatus presents a tubular structure containing secretory cells with canaliculus that fuse with the central duct, which conducts the secretion to a reservoir connected to the exterior by an orifice (Vitta et al., 2009; Lopes et al., 2020). The secretory cells of *R. prolixus*, present a well-developed rough, smooth endoplasmic reticulum, lipids droplet, and several mitochondria scattered in the cytoplasm (Lopes et al., 2020). Probably, these organelles may be involved in the sex pheromone biosynthesis of this vector.

3.2 Sex pheromone components

Alcohols and ketones are the main compounds of MGs in *Triatoma infestans* (Manrique et al., 2006), *T. brasiliensis* (Vitta et al., 2009b) and *R. prolixus* (Pontes et al., 2008) (Table 3). In *T. infestans*, MGs produce at least 6 components and the main constituent is 3-pentanone (Manrique et al., 2006). While MGs of *T. brasiliensis* are sources of 16 compounds, including 3-pentanone (Vitta et al., 2009b), as well as in *T. infestans*. *R. prolixus* release a blend of 12 volatile in their glands (Pontes et al., 2008).

In *Triatoma dimidiata* haplogroups, MGs release alcohols, ketones, and aldehydes (Table 3). Haplogroups 1 and 2 emit 21 components and haplogroup 3 presents 15 compounds. Interestingly, 3-methyl-2-hexanone is the major MGs component in all these groups. (May-Concha et al., 2013; May-Concha et al., 2015).

MGs components of *T. infestans*, *T. brasiliensis*, *R. prolixus*, and *T. dimidiata* appeared to be the same in both sexes (Manrique et al., 2006; Pontes et al., 2008; Vitta et al., 2009b; May-Concha et al., 2013; May-Concha et al., 2015).

Three species of the *phyllosoma* complex (*Triatoma longipennis*, *Triatoma pallidipennis* and *Triatoma phyllosoma*) produce alcohols, ketones, and aldehydes in their MG (Table 3). There are qualitative and quantitative differences in the compounds profile according to sexes. In addition, females of all three species release rose oxide isomers of the monoterpene class (I. J. May-Concha, et al., 2018).

3.3 Behavioral and physiological responses to the sex pheromone

Significant variations in the electrophysiological activity in male *T. infestans* antenna evoked by a mating pair, suggesting that a chemical sex signal could be released during the copula. Behavioral analysis revealed that males aggregate around mating pairs, reinforcing this hypothesis (Manrique & Lazzari, 1995).

Under experimental conditions, 3-pentanone was detected in MGs of *T. infestans* and in the headspace of copulating pairs (Manrique et al., 2006). Probably, this compound was emitted from females that elicited matting behavior and male aggregation. When these glands were occluded, the proportion of mating couples decreased and males did not aggregate (Crespo & Manrique, 2007). In these insects the mating attempts by the male requires contact of the male antennae with the female, the epicuticular lipids seem to trigger this response. Thus, these lipids could act as a contact pheromone (Cocchiaro-Bastias, et al., 2011). However, additional investigations are necessary to confirm the role of these lipids in mating.

T. brasiliensis males presented oriented walk to air currents associated with MGs volatiles from males and females. However, this response was not present when females had their MGs blocked (Vitta et al., 2009b). In the same study, males' antennae responded to several components of female MGs.

In *R. prolixus*, the emission of MGs compounds was detected more frequently in females, mainly during the early hours of the scotophase (Gina B. Pontes et al., 2008). Further, these compounds stimulate males to leave shelters, elicit flight initiation, and oriented walk toward air currents carrying female odors and subsequent aggregation around mating pair (Pontes et al., 2014; Pontes & Lorenzo, 2012; Zacharias et al., 2010). When male or female MGs were blocked, the copulation success decreased (Pontes et al., 2008). By contrast, only the occlusion of female MGs affected the aggregation around mating pairs (Pontes & Lorenzo, 2012). In addition, unfed males did not aggregate around the copulating pairs et al., 1971), indicating a possible role of the sex pheromone in mating assessment (Johansson & Jones, 2007). A synthetic blend of the most abundant compounds released by *R. prolixus* female MGs can be used to attract males (Bohman, et al., 2018). In the same study, a single sensillum recording indicated that *R. prolixus* basiconic chemosensilla have olfactory receptor neurons that respond to female MGs compounds. All these results suggest the involvement of female MGs compounds in the sexual context.

Behavioral analysis of *T. dimidiata* revealed that males were attracted to volatiles released by females; other males, mating pairs, and synthetic compounds formulated from female MGs extract (May- Concha et al., 2013). The synthetics 1-octen-3-ol, octanal, nonanal and decanal evoked high antennal responses in both sexes. These compounds could be found in MGs extracts of all haplogroups. Although, in haplogroup 2 the octanal was produced in only trace quantities and in haplogroup 3 nonanal and decanol were also found in lower amounts (May- Concha et al., 2018).

Virgin adult males of *Triatoma mazzottii* were attracted by extracts of female abdominal waxes (Table 3). Probably, these substances are sex pheromone components, once some males performed copulation movements over a cotton plug that contained the extracts. Moreover, when the male antennae were blocked, they did not show oriented responses in the presence of these substances (Ondarza, et al., 1986).

3.4 Molecular characterization of sex pheromone receptors

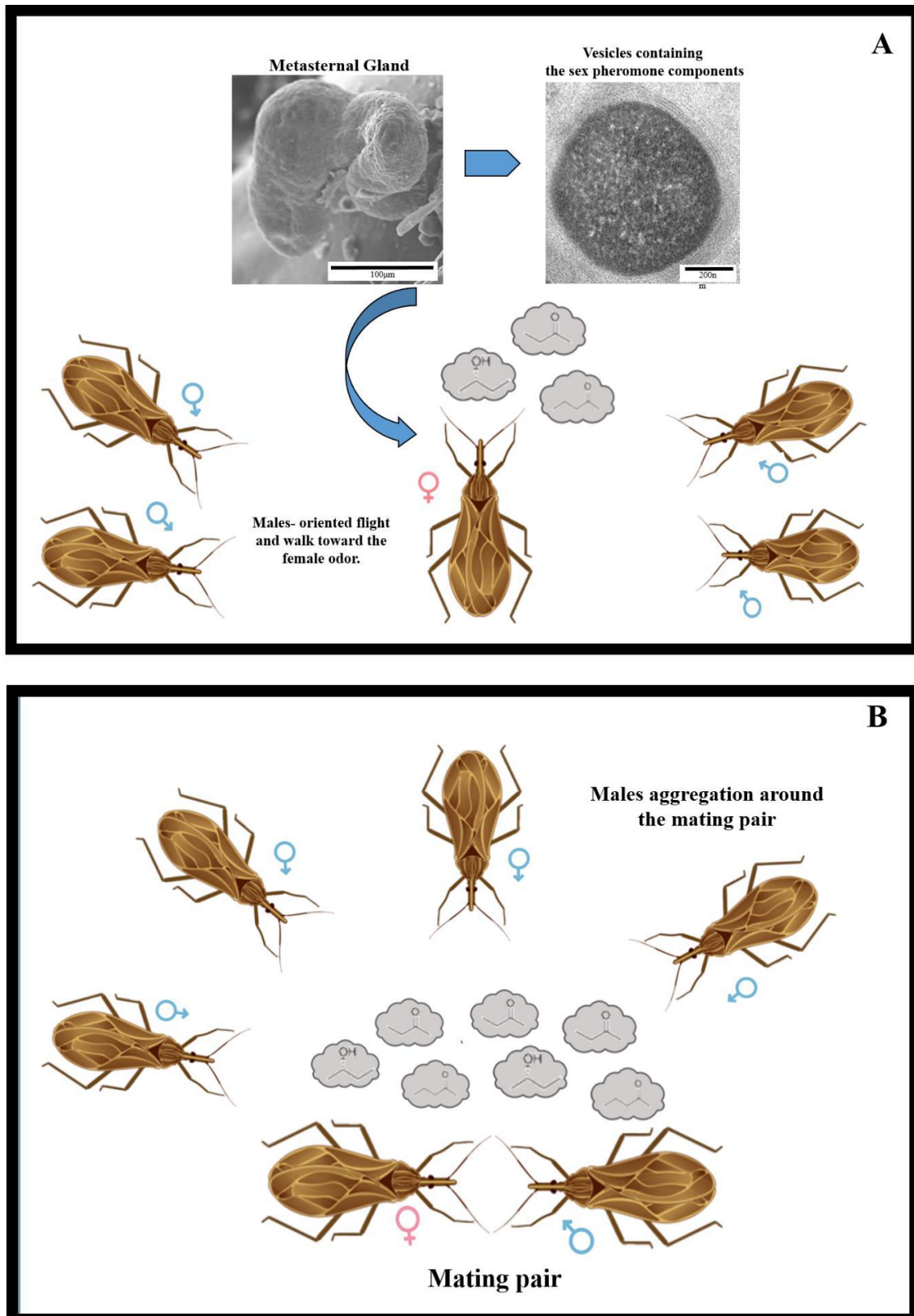
In *T. brasiliensis* antenna and *rostrum* there were several odorant binding proteins (OBPs) and chemosensory proteins (CSPs) genes differentially expressed between sexes. Probably, these genes are involved in sex-specific behavior or sexual dimorphism. OBPs and CSPs genes that are over-expressed only in males could be related to the detection of female sex pheromone (Marchant et al., 2016).

In *R. prolixus* a gene of an OBP (RproOBP27) was expressed only in adult male antennae, which suggests these proteins could play a role in male specific behaviors such as in the detection of female-derived semiochemicals. Silencing RproOBP27 expression in males represented a drastic decrease in the amount of protein circulating in antennae and they were not able to detect females. Based on this behavioral response, RproOBP27 could be involved in the reception of semiochemicals related to mating findings. This hypothesis is further supported by docking analysis that RproOBP27 binds the most abundant components identified in female MGs (Oliveira et al., 2018).

3.5 Practical applications of the sex pheromone as a control strategy

As shown in many studies (Bohman et al., 2018; Lorenzo et al., 2014; Pontes et al., 2008) sex pheromone components are a promising strategies for monitoring and/or controlling triatomines species. However, field bioassays evaluations are needed to develop control tools.

Figure 4: An overview of mating behavior in Triatomine species. Metasternal gland produces vesicles containing the sex pheromone in both sexes. In females, these compounds stimulate males to leave shelters, elicit flight initiation, and oriented walk towards air currents carrying female odors (A) and they aggregate around mating pair (B).



Source: Created in Biorender.com.

Tableau 3: Overview of the subfamily Triatominae.

Vector specie	Vector borne disease	Etiological agent	Host	Location	Sex pheromone components	Site of the sex pheromone production and release	Behavioral and/or physiological responses to the sex pheromone	Sex pheromone biosynthesis	Sex pheromone receptors	Applications of the sex pheromone in field	References
<i>Triatoma brasiliensis</i>	Chagas disease	<i>Trypanosoma cruzi</i>	Mammals, mainly humans.	Semi-arid region of northeastern Brazil.	2-Butanone; 3-Pentanone; (2S)-butanol; 2-Methyl-1-propanol; 3-Pentanol; (2R) - Pentanol; (3R) - Hexanol/ (3S) -Hexanol; (2S)-Methyl-1-butanol; 3-Methyl-2-hexanol; (4R)-Methyl-1-hexanol; 6-Methyl-1-heptanol; (4R)-Methyl-1-heptanol; (1R)-Phenylethan	Metasternal gland associated with disseminating structures, in males and females.	Mate recognition, mate assessment, mating and males aggregation.	No studies were found.	OBPs and CSPs in males antennae	No studies were found.	Vitta et al., 2009; Vitta et al., 2009b; Marchant et al., 2016

<i>Rhodnius prolixus</i>	Chagas disease	<i>Trypanosoma cruzi</i>	Mammals, mainly humans.	Colombia and Venezuela.	2-Butanone; 2-Pentanone; (2S)-Butanol; 2-Methyl-3-buten-2-ol; 3-Methyl-2-butanol; 3-Pentanol; (2S) - Pentanol; (3E) -2-Methyl-3-penten-2-ol; (2S) -4-Methyl-2-pentanol; (3S)-Hexanol; 2-Methyl-1-butanol; (2S/2R)-4-Methyl-3-penten-2-ol.	Metasternal gland associated with disseminating structures, in males and females.	Mate recognition, mate assessment, mating and males aggregation.	No studies were found.	RproOBP2 in males antennae (basiconic chemosensilla)	No studies were found.	Brindley, 1930; Lopes et al., 2020; Pontes et al., 2008; Pontes et al., 2014; Pontes and Lorenzo, 2012; Zacharias et al., 2010; Baldwina et al., 1971; Bohman et al., 2018; Oliveira et al., 2018
<i>Triatoma infestans</i>	Chagas disease	<i>Trypanosoma cruzi</i>	Mammals, mainly humans.	Argentina; Bolivia; Brazil (BA, MG and RS-residual foci). MG and RS-residual foci).	2-Butanone; 3-Pentanone; 3-Pentanol; 3-Hexanol; 2-Methyl-1-butanol and unknown compound.	Metasternal gland. The same compounds in males/females. Not described disseminating	Mate recognition, mate assessment, mating and males aggregation.	No studies were found.	No studies were found.	No studies were found.	Manrique et al., 2006; Sanchez et al 1995; Manrique and Lazzari, 1995; Crespo and Manrique, 2007; Cocchiaro-Bastias et al., 2011.

<i>Triatoma dimidiata</i>	Chagas disease	<i>Trypanosoma cruzi</i>	Mammals, mainly humans.	Latin America	<p>Haplogroup 1 and 2: 3-Methyl-2-pentanone*; 2-Methyl-3-buten-2-ol*; 3-Methyl-2-hexanone* (isomers); 3,5-Dimethyl-2-hexanone*; 3,5-Dimethyl-2-hexanone isomer*; 3-Methyl-2-pentanol; Octanal*; 1-Octen-3-one*; 3-Methyl-2-hexanol*; 4-Methyl-2-pentanol; 6-Methyl-5-hepten-2-one*; 3,5-Dimethyl-2-hexanol (isomers) *; Dodecanal; 2-Nonanol; 3,5-Dimethyl-1-hexene; 1-Octen-3-ol*; Decanal*; Nonanal*; 4-Methyl-1-pentanol.</p> <p>Haplogroup 3: 3-Methyl-2-hexanol isomer</p>	Metasternal gland. Produces the same compounds in males and females. Disseminating structure were not described.	Mate recognition, mate assessment, mating and males aggregation.	No studies were found.	No studies were found.	No studies were found.	May-Concha et al., 2013; May-Concha et al., 2015.
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<i>Triatoma longipennis</i>	Chagas disease	<i>Trypanosoma cruzi</i>	Mammals, including humans.	Mexico	<p>Molecules found in both sexes: 3-Methyl-2-pentanone; 3-Methyl-2-hexanone; 4-Methyl-2-heptanol; 3,5-Dimethyl-2-hexanone; 3,5-Dimethyl-2-hexanone (isomer); 2-Methyl-3-pentanol; 6-Methyl-2-heptanol; 2-Hexanol; 1-Octen-3-one; 3-Methyl-2-hexanol; 3-Methyl-2-hexanol (isomer); 2-Nonanol; 1-Octen-3-ol; 3,5-Dimethyl-1-hexene; Decanal; Isobutyric acid.</p> <p>Molecules found only in females: Rose oxide (isomers).</p>	Metasternal gland. Some compounds were produced exclusively in females gland. Disseminating structure were not described.	No studies were found.	No studies were found.	No studies were found.	No studies were found.	May-Concha et al., 2018
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<i>Triatoma pallidipennis</i>	Chagas disease	<i>Trypanosoma cruzi</i>	Mammals, including humans.	Mexico	<p>Molecules found in both sexes:</p> <p>3-Methyl-2-pentanone; 2-Methyl-3-pentanol; 2-Hexanol; 1-Octen-3-one; 3-Methyl-2-hexanol; 1-Octen-3-ol; Decanal; Propanoic acid; Isobutyric acid; Pentyl Butanoate; 2-Methyl hexanoic acid.</p> <p>Molecules found only in females: Rose oxide (isomers).</p>	Metasternal gland. Some compounds were produced exclusively in female gland. Disseminating structure were not described.	No studies were found.	No studies were found.	No studies were found.	No studies were found.	May-Concha et al., 2018.
<i>Triatoma phyllosoma</i>	Chagas disease	<i>Trypanosoma cruzi</i>	Mammals, including humans.	Mexico	<p>Molecules in both sexes:</p> <p>3-Methyl-2-pentanone; 3-Methyl-2 hexanone; Propanoic acid; Isobutyric acid; Pentyl butanoate;</p>	Metasternal gland. Some compounds were produced exclusively in female gland. Disseminating structure were not described.	No studies were found.	No studies were found.	No studies were found.	No studies were found.	May-Concha et al., 2018.

					2-Methyl hexanoic acid. Molecules only in females: Rose oxide (isomers).						
<i>Triatoma mazzottii</i>	Chagas disease	<i>Trypanosoma cruzi</i>	Mammals, including humans	Mexico	No studies were found.	No studies were found.	Males were attracted by extracts of females abdominal walls.	No studies were found.	No studies were found.	No studies were found.	Ondarza et al., 1986

*Compounds presented in haplogroup 1, 2 and 3 of *Triatoma dimidiata*. Source: Authors.

4. Conclusion

In this review, we summarized the current knowledge of the sex pheromones presented in the insect vectors of Leishmaniasis, Chagas disease and African trypanosomiasis. These chemical signals interfere directly with the behavior and physiology of these vectors. Therefore, sex pheromones represent an alternative to the chemical insecticide. Considering that they present a high specificity, appealing potential, behavioral effect and low tendency to select resistance in target species.

Nevertheless, their practical application is still largely experimental and restricted to some species. Based on these limitations, future multidisciplinary studies are needed to improve the application of sex pheromones-based technologies in the field and expand the knowledge to other insects of medical and veterinary importance. We included updated tables with the chemical identity of several sex pheromone compounds and other relevant information concerning the target species, which can contribute to future studies of control methodologies.

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