

Incriminating leishmaniases vectors in Colombia: An overview and roadmap for future research

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ABSTRACT

A major challenge in defining the vector status of phlebotomine sand flies is selecting the appropriate criteria. Vectors can be graded by importance, with successful transmission as the highest grade. Potential vectors are often identified based on high frequency in transmission foci, anthropophily, and more recently by identification of DNA in field samples. However, a species' ability to transmit a pathogen depends not only on its intrinsic biology of sand fly–*Leishmania* interactions but also on ecological parameters, which are rarely evaluated. This study aimed to analyze the literature data describing characteristics of Colombian sand flies related to their role as vectors of Leishmaniinae parasites. Based on information contained in scientific publications using combinations of five criteria, sand fly species were graded into five levels, and 26 species were considered as potential or proven leishmaniasis vectors in Colombia. Levels one to four refer to potential or suspected status, while level five denotes proven vectors. Studying vectors in a regional context is crucial because species' behaviors vary with environmental and ecological conditions, meaning a species may be a key vector in one area but not in another. A better understanding of vector-parasite interactions will aid in developing innovative control strategies and formulating significant epidemiological perspectives.

1. Introduction

The leishmaniases are caused by a genetically very diverse group of Leishmaniinae trypanosomatids and so far, 21 species have been linked to disease in man (Lainson and Shaw, 2010; Akhouni et al., 2016). The clinical manifestations are broadly classified into two main groups, cutaneous leishmaniasis (CL), that is more common and visceral leishmaniasis (VL). Collectively these diseases are endemic in 99 countries, with an annual incidence of 0.9–1.6 million new cases (OMS 2023). Most of the species associated with the different clinical forms belong to the genus *Leishmania*.

The spectrum of CL clinical manifestations is enormous, ranging from localized ulcerated skin lesions, disseminated papular lesions, diffuse non-ulcerated nodular lesions to mutilating mucocutaneous lesions (Lainson and Shaw, 2010; Murray et al., 2005; Da-Cruz and Pirmez, 2005). In the Americas, leishmaniasis cases are reported in 17 countries, and Colombia has the second-highest number of cases, following Brazil (Organização Pan Americana da Saúde 2021). In 2022,

5154 cases were reported in Colombia, of which 98% were CL (SIVIGILA-INS 2022).

The parasites causing the leishmaniases are transmitted by females of the Phlebotominae subfamily that currently consist of 1060 species worldwide. Of these 555 are registered in the Americas (Galati and Rodrigues, 2023) and 56 have been reported as confirmed or suspected leishmanial vectors (Maroli et al., 2013). A major challenge is choosing the criteria that are used to define vectorial status. This was addressed by group of experts at the Third European Multicolloquium of Parasitology held in 1980 (Killick-Kendrick and Ward, 1981). They considered that vectors could be graded according to their order of importance from being merely suspected to proven. Five grades based on different criteria were chosen. The conclusive criteria for the 5th grade was successful transmission. This has been done for many vectors of the subgenus *L. (Leishmania)* (Adler and Ber, 1941; Lainson et al., 1977; Beach et al., 1984; Svobodová et al., 2006; Maia et al., 2011; Ward et al., 1977), but only once for a parasite of the subgenus *L. (Viannia)* (Ryan et al., 1987).

Although additional criteria have been proposed (Ready, 2013),

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including parameters related to mathematical modeling aiming the evaluation of control measures, they are not strictly related to the vector incrimination but vector capacity in specific focus.

The reporting of insect species as potential vectors in the literature is commonly based on the encounter of species with high frequencies in transmission foci, their anthropophily, and occasionally evidence of natural infection. However, the actual potential of a species to transmit a pathogen depends not only on the vector's intrinsic biology but also on parameters of its vectorial capacity related to its environment (F. Galvis-Ovallos et al., 2017), which are rarely evaluated (Casanova et al., 2009).

There are records of at least 172 sand fly species in Colombia (Bejarano and Estrada, 2016), and 10% of them are considered as possible leishmanial parasite vectors. According to Galati's classification (Galati, 2003), these species belong to the genera *Lutzomyia* França, 1924, *Nyssomyia* Barretto, 1962, *Pintomyia* Costa Lima, 1932, *Psychodopygus* Mangabeira, 1941, and *Bichromomyia* Galati, 2003.

Entomological surveillance is a fundamental part of leishmaniasis control programs, helping to understand the particularities of the dynamics of local transmission. Key information on the capacity of phlebotomine species to transmit a particular agent is essential in defining risk areas and planning containment and control strategies. Although entomological studies associated with leishmaniasis are frequent in Colombia, information on the role of the vectors of the different *Leishmania* is limited (Travi et al., 1988; Alexander et al., 1992; C. Ferro et al., 1995; Santamaría et al., 2006). The present study's aim is to analyze the data used to incriminate Colombian sand flies as vectors of Leishmaniinae parasites to humans.

2. Methodology

2.1. Type of study

A review and critical analysis of the literature on phlebotomines in Colombia.

2.2. Literature search

Original scientific articles published in English or Spanish covering any parameter of vector capacity, including topics related to the investigation of phlebotomine fauna related to studies on any clinical manifestation of leishmaniasis, experimental studies on vector competence, detection of parasites of Leishmaniinae subfamily, or feeding habits were selected. Review articles, predictive or modeling articles on phlebotomine distribution or presence, as well as entomological inventory studies, were excluded (Fig. 1). gray literature was not included. No date limits were applied. Bibliographic searches were conducted in the PubMed, Scielo, and Google Scholar databases. The following terms were used for literature search: "cutaneous leishmaniasis, sand fly species, Colombia", "cutaneous leishmaniasis vectors Colombia", "leishmaniasis endemic focus", "natural infection vector leishmaniasis Colombia", "endemic foci leishmaniasis Colombia", "focus endemics leishmaniasis Colombia". In Scielo, the search included: "leishmaniasis *Lutzomyia* Colombia", "leishmaniasis vectores Colombia", "flebotomos leishmaniasis Colombia", "infección natural vector leishmaniasis Colombia", "natural infection flebotomos leishmaniasis Colombia". And in Google Scholar: "cutaneous leishmaniasis sand fly species Colombia".

A full-text reading of the remaining articles was conducted, and the results were synthesized to include only those related to incrimination parameters. This was followed by a manual search based on the references of these articles that were not part of the initial search. A final search was also performed on Google Scholar, adding 12 more articles to the study. The final list consisted of 51 articles (Fig. 1). When any reference was detected in the analysis of the articles, it was included. No statistical analyses were conducted.

The generic abbreviations followed the proposal by Marcondes

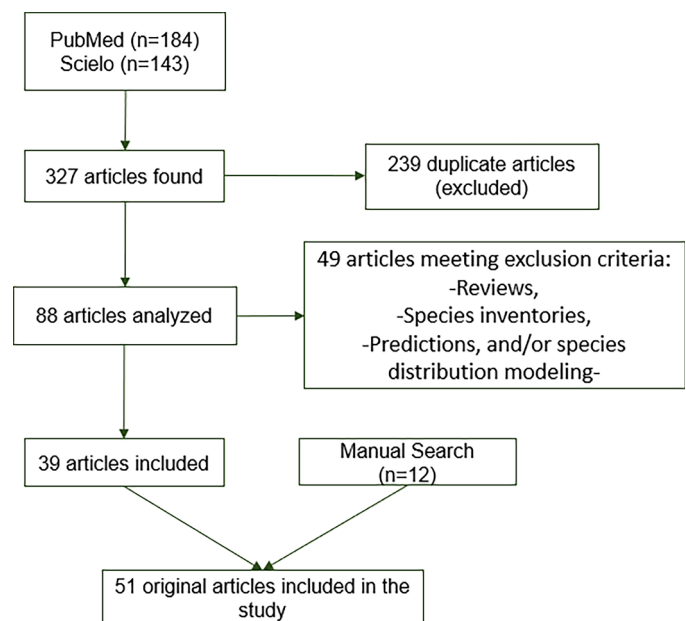


Fig. 1. Search strategy flowchart.

(Marcondes, 2007).

2.3. Definition of adopted criteria for vector classification

In this study concepts such as competence, capacity, susceptibility to infection, or permissive vectors were defined as:

Vector competence is defined by intrinsic mechanisms that allow a species of phlebotomine to support the development of the parasite and transmit it during a new blood intake (Meyer, 1989; Kamhawi, 2002). Some species even allow the development of more than one species of trypanosomatids, known as "permissive vectors" (Kamhawi, 2006; Dos-átlová and Volf, 2012). In this regard, one must be very careful since many records refer to molecular detection and not necessarily to the parasite's development. In their discussion of permissiveness Myskova, Svobodova, (Myskova et al., 2007) indicated that "GalNAC-containing glycoproteins are involved in the novel mechanism of attachment" that they found in the permissive species *Lu. longipalpis* and *Phlebotomus arabicus*. No such studies have been performed with others neotropical species that appear to permissive such as *Ny. trapidoi* and *Pi. (Pif.) evansi* that support the development of parasites belonging to different subgenera. In the present study, we consider a species as permissive if development of one or more parasite species has been confirmed, either through experimental infections, xenodiagnosis, or evidence of flagellates under the microscope.

Vector capacity is defined as the number of potentially infective bites that the population of a particular species would distribute after feeding on an infected host (Smith et al., 2012). Therefore, vector capacity can be described as the ability of the population of a phlebotomine species to transmit the pathogen to one or more host populations, effectively continuing the pathogen transmission. This depends on the adjustment of several factors determined by the landscape, host biology, pathogens, and the vector itself (Reisen, 2010; Galvis Ovallos, 2016). This adjustment and modeling of vector-borne disease transmission have been based on the postulates proposed in Workshop No. 11 "Ecology of *Leishmania*" (Killick-Kendrick and Ward, 1981; Killick-Kendrick, 1990) for the incrimination of a vector, which considers both the intrinsic and behavioral parameters of the vectors and their relationship with the pathogen and the host. These parameters, in an anthropocentric approach, include for the vector population, geographic distribution coinciding with the disease in humans, high density to maintain infection in nature, anthropophily, sufficient survival to ensure the extrinsic

incubation period of the parasite (the time interval between the ingestion of infected blood and the appearance of infective forms of the parasite in the digestive tract), and demonstrated vector competence (Killick-Kendrick and Ward, 1981).

2.4. Classification regarding the vectorial capacity of phlebotomines in transmitting leishmaniasis agents

The selected 51 articles on Colombian leishmaniasis vectors were searched for mention of the criteria related to vector status mentioned below.

The criteria taken into consideration included:

- i) Epidemiological evidence, considered as sand fly species distribution coinciding with human cases.
- ii) Feeding habits, classified based on evidence of the species' anthropophily, either through capture methods or blood source detection.
- iii) Vector competence, refers to the ability of an insect to become infected with a pathogen, support its development or replication, and subsequently transmit it to a new host. Such data was not available and so we considered vector competence had been shown when an article included results of experimental infections.
- iv) Species abundance in active foci.
- v) Detection of natural infections by either presence of flagellates in the intestine, isolation in cultures, or detection of *Leishmania* DNA. We have been conservative in interpreting the importance of the detection of leishmanial DNA since it is known that parasites can survive for up to seven days before being eliminated in an incompatible host (Kamhawi et al., 2000).

Using combinations of these criteria the different phlebotomine species were classified into five groups. We emphasize that the level given to each species only refers to its vectorial status in Colombia. It was not possible to include species survival as it is an aspect rarely assessed.

Level 1 vectors: species lacking demonstration of vector competence, have little evidence of anthropophily, and no evidence of natural infection, it means only parasite DNA detected.

Level 2 vectors: includes species frequently found in high abundance in active leishmaniasis foci, with parasite DNA also detected, but with no evidence of their vector competence.

Level 3 vectors: species for which vector competence has been shown but the detection of natural infection has not been recorded or only through DNA.

Level 4 vectors: these species met four criteria, lacking only demonstrated vector competence, but in all species, it was possible to obtain isolation and identification of the trypanosomatids causing leishmaniasis.

Level 5 vectors: species meeting all established criteria are called confirmed or proven vectors.

Levels 1–4 denote potential or suspected vectors.

3. Results

The database search identified 327 articles. A total of 239 articles were excluded as duplicate studies. The titles and abstracts of the remaining 88 articles were selected for inclusion. Forty-nine articles met some exclusion criteria. In total, 39 articles were retained. After analyzing the articles, an additional search was conducted based on the references cited in the already included articles, resulting in the inclusion of 12 more articles.

Evidence from 51 articles on focal studies of both VL and CL was analyzed (Fig. 1).

3.1. Level 1 vectors

Parasite DNA has been detected in the following 9 species but vector competence has not been demonstrated, and there is little evidence of anthropophily. These species meet a maximum of three criteria.

Bichromomyia flaviscutellata was not found associated with the studied foci. There are records in the Orinoquia region of Colombia, and natural infection with *Leishmania* through molecular methods has been detected (Vásquez-Trujillo et al., 2013). However, there was no information about anthropophily. This species had previously been suggested as a vector of *L. (L.) amazonensis* in French Guiana (Dedet et al., 1985; Rotureau, 2006) and in Brazil (Lainson et al., 1994). Lainson and Shaw (Lainson and Shaw, 1968) had already indicated this species as a vector of *Leishmania* among rodents, emphasizing how unattractive it is to humans. Another study conducted in Amazonas State, Brazil (Arias et al., 1987), concluded that although the species participates in the transmission of the *L. (L.) amazonensis* amongst rodents it did not play a fundamental role as a vector because it was not anthropophilic. However, the species in Amazonas is *Bi. olmeca nociva*. In Pará State *Bi. flaviscutellata* was found to be anthropophilic in habitats with high sand fly populations (Shaw et al., 1972) and its proven vectorial status was confirmed by transmission experiments (Ward et al., 1977). In contrast *Bi. olmeca olmeca* found in Yucatán (Mexico), mistakenly identified as *Bi. flaviscutellata* (Young and Duncan, 1994), was found (Biagi et al., 1967) to be susceptible to *L. (L.) mexicana*, was highly anthropophilic and very abundant in the endemic region, making it a proven vector.

Bichromomyia olmeca bicolor, reported in a *L. (V.) panamensis* CL foci in Choco (Duque et al., 2004) and Antioquia (Posada López et al., 2014), was not a dominant species in both cases.

Micropygomyia (Micropygomyia) cayennensis cayennensis has been found in mixed foci of VL and CL in the Atlantic region but always at low frequencies (Cortés and Fernández, 2008; Travi et al., 1996; Cochero et al., 2007). Montoya-Lerma, Cadena (Montoya-Lerma et al., 2003) recorded the presence of flagellates in this species, and Cochero, Anaya (Cochero et al., 2007) detected trypanosomatid DNA. Meanwhile, González, León (González et al., 2018) identified *L. (V.) panamensis* DNA and molecular evidence that females fed on humans, but without showing a feeding preference, as the number of females was low. In addition to *Mi. cayennensis cayennensis* not being abundant in the studied foci, studies demonstrating its vector competence and anthropophily are lacking.

Nyssomyia antunesi was found as an abundant species in CL foci in Meta, where it was also detected with *Leishmania* DNA (Vásquez-Trujillo et al., 2013; Vásquez-Trujillo et al., 2008). In Brazil, it was associated as a possible vector of *L. (L.) infantum chagasi* in a focus on Marajó Island, Pará, through the finding of suprapyloric infection (Ryan et al., 1984). Silveira, Ishikawa, (Silveira et al., 2002) described *L. (V.) lindenbergi* for the first time in an CL focus in soldiers in Belém do Pará, proposing that its probable vector was *Ny. antunesi*, based on its abundance and anthropophily in this focus. In Rio Branco, Acre state, *Ny. antunesi* was detected with *L. (V.) braziliensis* DNA (de Ávila et al., 2018), and in Rondônia with *L. (V.) naiffi* (Silva et al., 2021).

Nyssomyia umbratilis, in Colombia, has a restricted distribution in the Amazon (Wolff et al., 2003), but it rarely coincides with active foci of CL transmission. Isolates of *L. (V.) guyanensis* were obtained from females of this species in the Amazonas department (Young et al., 1987). In Brazil, the species has been more extensively studied and is recognized as a vector of *L. (V.) guyanensis* (Ready et al., 1985). It is also recognized as a vector in French Guiana, Suriname (Brazil et al., 2015), and Venezuela (Felicangeli et al., 1985). Therefore, although *Ny. umbratilis* is a proven vector of *L. (V.) guyanensis* in other countries, in Colombia, there is still not very strong evidence of its role as a vector, possibly due to the low proportion of recorded CL cases attributed to *L. (V.) guyanensis* (Ramírez et al., 2016) and its more restricted distribution in the Amazonian areas where the disease is less common.

Pintomyia (Pif.) torvida was found in an CL focus in Cundinamarca,

and positive results of experimental infection with *L. (V.) braziliensis* were obtained (Santamaría et al., 1999).

Pintomyia (Pif.) youngi is an anthropophilic and dominant species associated with an CL focus in Valle del Cauca (Alexander et al., 1995). This species supported the development of *L. (L.) infantum chagasi* in experimental infections carried out in dogs diagnosed with VL (B.L. Travi et al., 2002).

In Venezuela, it was suggested as a possible vector of *L. (V.) braziliensis* (Maingon et al., 1994), and Rojas and Scorza (Rojas and Scorza, 1989) were able to infect females through xenodiagnosis in lesions produced by *L. (V.) braziliensis*, demonstrating its competence. Given the results of experimental infections we consider this could be a permissive vector.

Pintomyia (Pif.) serrana is an anthropophilic species associated with a CL focus in Norte de Santander, where it occurs at low density (Alexander et al., 1992; Alexander and Young, 1992). In addition to its distribution mainly in municipalities in the Andean region (Bejarano and Estrada, 2016), there is little information.

Psathyromyia (Psathyromyia) shannoni is rarely found in VL foci (Travi et al., 1996; González et al., 2018), and more frequently in CL foci. It has typically been designated as an anthropophilic species because it is easily captured with Shannon traps, although there is no additional evidence of its anthropophily. In the studies where it was reported, it was not abundant, representing less than 10% of the total number of collected insects (Alexander et al., 1992; Alexander et al., 1995; Alexander and Young, 1992; Cárdenas et al., 1999). Although species found in Shannon traps typically have a fairly anthropophilic behavior, in this case, the presence of the species may be related to the location of the trap, as they are normally installed outside the home, farther from houses, and generally in less disturbed areas.

Travi, Ferro, (B.L. Travi et al., 2002) achieved experimental infection with *L. (L.) infantum chagasi* in xenodiagnosis with poly-symptomatic dogs, with negative results in oligo-symptomatic ones, suggesting the species as permissive for the development of this *Leishmania*.

In a study carried out in Arboledas, Norte de Santander, flagellates were observed in the digestive tract of some females, however, it was not possible to associate them with any of the reference strains of *Leishmania* from the New World, using isoenzyme profiles (Young et al., 1987). Observation of flagellates in this species was not possible later. Although direct observation of the parasite in the intestine of sand flies is less and less used, the same negative result was obtained with molecular methods currently most used.

3.2. Level 2 vectors

The species categorized in this group are often found in high abundance in active foci of leishmaniasis, natural infection has only been detected through molecular methods, but there is no evidence of their vector competence.

Nyssomyia yuilli yuilli has been associated with endemic foci of CL in the Andean region of the central part of the country, where it always appears among the most frequent species (Santamaría et al., 2006; Posada López et al., 2014; Sandoval et al., 2006; Martínez Dueñas et al., 2019; López et al., 1996; L. Posada-López et al., 2023), and in foci of VL with lower frequencies (Sandoval et al., 2006). Infection by *L. (V.) panamensis*, as well as its preference for humans for blood-feeding, has also been detected through the amplification of different molecular markers (Santamaría et al., 2006; L. Posada-López et al., 2023).

Pintomyia (Pif.) longiflocosa, associated with CL foci in Tolima (Cárdenas et al., 1999; Pardo et al., 2006; Ferro et al., 2011) and Norte de Santander (Cárdenas et al., 2005), has been very abundant in these foci (frequencies above 80% among the collected sand flies), recognized as an anthropophilic species and found naturally infected with DNA from *Leishmania (Viannia)* and *L. (V.) guyanensis* (Ferro et al., 2011).

Pintomyia (Pif.) quasitownsendi, associated with CL foci in Santander and Cundinamarca. Moreno, Guzmán-Rodríguez (Moreno

et al., 2020) confirmed anthropophily and detected *Leishmania (Viannia)* DNA by molecular methods in this species.

Warileya rotundipennis, although rarely collected in domestic environments, was found in an CL focus in Risaralda, where it predominated, and in addition to natural infection through the detection of *Leishmania* DNA, humans were confirmed as the most frequent blood source (Moreno et al., 2015).

3.3. Level 3 vectors

In this category, there are five species for which vector competence has been demonstrated both in experimental infections using chicken membrane and xenodiagnosis, with different *Leishmania* species. However, natural infection by traditional parasitological methods was negative in all cases, and only in *Pi. (Pif.) townsendi* and *Pi. (Pif.) pia*, DNA of *L. (L.) amazonensis* (Hoyos et al., 2020) and *L. (V.) panamensis* (López et al., 2021), respectively, was detected. Even though these species are susceptible to infection by *Leishmania* spp., there is still no evidence that they are involved in the transmission cycle.

Lutzomyia (Lut.) lichyi, although not a dominant species in any of the studies, was found in CL foci caused by *L. (V.) panamensis* and *L. (V.) braziliensis* in Valle del Cauca (Alexander et al., 1995; Warburg et al., 1991; Montoya et al., 1990) and Norte de Santander (Cárdenas et al., 2005). It has been experimentally infected with *L. (V.) braziliensis* (Warburg et al., 1991) and is a highly anthropophilic species (Alexander et al., 1995).

Pintomyia (Pif.) colombiana, associated with CL foci, was the dominant species (100%) in a focus produced by *L. (L.) mexicana* in Nariño. In this study, they also achieved a positive experimental infection with the same species of the parasite (Montoya-Ilerma et al., 1999). *Pi. (Pif.) colombiana* was also recorded at lower frequencies in other foci in Tolima (Pardo et al., 2006; Ferro et al., 2011) and Valle del Cauca, where *L. (V.) panamensis* and *L. (V.) braziliensis* were identified in patients (Alexander et al., 1995). It is a very anthropophilic species and has been experimentally infected with *L. (V.) panamensis* and *L. (V.) braziliensis* (Warburg et al., 1991; Montoya et al., 1990).

Pintomyia (Pif.) nunexzovari was associated with CL foci in Tolima, although it was not a dominant species in these foci (Pardo et al., 2006; Cárdenas et al., 2005), and it was shown to be susceptible to experimental infection with *L. (V.) braziliensis* (Santamaría et al., 1999). This species was suggested as the likely vector of *L. (L.) amazonensis* (Martínez et al., 1998; Torrez et al., 1998) and *L. (V.) braziliensis* (Le Pont and Desjeux, 1984) in Bolivia.

Pintomyia (Pif.) pia was found in CL foci in Tolima and Valle del Cauca, always at low density. It was naturally found infected with DNA from *L. (V.) panamensis* (López et al., 2021) and susceptible to infection by *L. (V.) braziliensis* (Warburg et al., 1991).

Pintomyia (Pif.) townsendi, in an CL focus produced by *L. (L.) amazonensis* in Valle del Cauca, was the most abundant species, and DNA of the same *Leishmania* species registered in the focus was detected (Hoyos et al., 2020). In other foci produced by *L. (V.) braziliensis* and *L. (V.) panamensis*, its vector competence was demonstrated through experimental infection (Warburg et al., 1991; Montoya et al., 1990).

3.4. Level 4 vectors

Pi. (Pif.) spinicrassa, *Ps. panamensis*, and *Lu. (Helcoctomyia) hartmanni* are included in this category, meeting four criteria of vector capacity, with only vector competence yet to be demonstrated.

Lutzomyia (Helcoctomyia) hartmanni, found in foci of LT caused by *L. (V.) braziliensis* and *L. (V.) panamensis* in Boyacá (Santamaría et al., 2006) and Choco (Duque et al., 2004), in both studies with low densities, but there is at least one record in the articles highlighting its anthropophilic behavior. It has also been detected with natural infection by trypanosomatids, both through parasitological examination and parasite isolation (Travi et al., 1988; Alexander et al., 1992; Young et al., 1987;

Kreutzer et al., 1991). *Lu. (Hel.) hartmanni* had previously been identified as a vector of *Endotrypanum colombiense*, as parasites were isolated, contributing to the description of this parasite species (Kreutzer et al., 1991).

Pintomyia (Pif.) spinicrassa is associated with foci of LT in Norte de Santander, where it has been a dominant species (Ovallos et al., 2013). Flagellates of *L. (V.) braziliensis* were isolated from its digestive tract (Alexander et al., 1992), and DNA of the same *Leishmania* species was also detected (Sandoval-Ramírez et al., 2020). It was considered the main vector of *L. (V.) braziliensis* in an LT focus in Norte de Santander (Arboledas), where its population densities were maintained throughout all months of the sampling year. Additionally, promastigotes were observed in the digestive tract of some females (Young et al., 1987).

Psychodopygus panamensis is not normally a dominant species in focus studies. It has rarely been found in foci of VL in the Atlantic region of the country, Córdoba (González et al., 2018), Sucre (Bejarano et al., 2002), and Bolívar (Ardila et al., 2019), and more frequently in CL foci. From this species, an isolation of the *L. braziliensis* complex was obtained in culture, but it was not possible to differentiate between *L. (V.) braziliensis* and *L. (V.) panamensis* with the molecular methods used at this time (Travi et al., 1988). DNA of *L. (L.) amazonensis* (López et al., 2021), the *L. guyanensis* complex (Hoyos et al., 2022), and *L. (V.) panamensis* (Santamaría et al., 2006; González et al., 2018) has been detected. Jaramillo and Travi (Jaramillo et al., 1994) attempted experimental infection with parasites from the *L. braziliensis* complex, with negative results. The species has a wide distribution and, although it may not play a significant role in the transmission of the disease in humans, it may be involved in maintaining the parasites in transmission foci.

In Panama, this species has been extensively studied and incriminated as a vector of *L. (V.) panamensis* (Christensen and Herrer, 1973; Christensen, 1972), and it has been associated with more conserved areas (Valderrama et al., 2011).

3.5. Level 5 proven vectors

A total of 35 articles were found, supporting the status of proven vectors for five sand fly species in Colombia:

Lutzomyia (Lutzomyia) longipalpis, found as the dominant species in some VL foci, primarily in Santander (Sandoval et al., 2006; Flórez et al., 2006) and Cundinamarca (C. Ferro et al., 1995; C. Ferro et al., 1995), has also been found in CL foci but with low frequency (B.L. Travi et al., 2002). The competence of *Lu. longipalpis* for *L. (L.) infantum chagasi* was confirmed by obtaining isolates from the insect (C. Ferro et al., 1995; C. Ferro et al., 1995) and natural infection with the same species (Montoya-Lerma et al., 2003). Travi, Ferro (B.L. Travi et al., 2002) also conducted xenodiagnosis in dogs, both polysymptomatic and oligosymptomatic, with positive results in both cases.

The species has shown permissiveness to *L. (V.) braziliensis* (Alexandre et al., 2020), but percentage of infections was less than other species, such as *Lu. lichi* (Warburg et al., 1991). Due to the ease of maintaining this species in laboratory conditions and its abundance in various locations in Brazil, it is a widely studied species in terms of vectorial capacity (F. Galvis-Ovallos et al., 2017).

Given the extensive genetic diversity of this species (Vigoder et al., 2015) there could be different levels of susceptibility.

Lutzomyia (Tricholateralis) gomezi was first recorded in Colombia by Barreto (1969) in Meta and a location on the Pacific coast, and 50 years later, it is a widely distributed species in the country, found in 28 of the 32 departments (Bejarano and Estrada, 2016), demonstrating a significant capacity to adapt to highly anthropized environments (González et al., 2018). It has been recorded in endemic CL foci, mainly produced by *L. (V.) panamensis* and *L. (V.) braziliensis*, in Antioquia (Posada López et al., 2014), Boyacá (Santamaría et al., 2006), Chocó (Duque et al., 2004), Meta (Vásquez-Trujillo et al., 2013), Córdoba (Hoyos et al., 2022; Vivero et al., 2017), Nariño, Cauca (Travi et al., 1988) and Norte de Santander (Alexander et al., 1992;

Sandoval-Ramírez et al., 2020). It has also been found in mixed CL and VL foci in Bolívar (Cortés and Fernández, 2008; Ardila et al., 2019; Cortés, 2006), Córdoba (González et al., 2018), Santander (Sandoval et al., 2006), and Sucre (Bejarano et al., 2002). In some of these studies, it was notably abundant (Vélez et al., 1991). *Lu. (Trl.) gomezi* is a highly anthropophilic species, a characteristic mentioned in all studies (Travi et al., 1988; Alexander et al., 1992; Santamaría et al., 2006; González et al., 2018; Sandoval-Ramírez et al., 2020; Vélez et al., 1991). Its vector competence was demonstrated by the isolation of parasites in culture, at that time referred to as the *L. braziliensis panamensis/L. braziliensis* complex by Travi, Montoya (Travi et al., 1988). With the same parasite from this *Leishmania* complex, Jaramillo, Travi (Jaramillo et al., 1994) achieved experimental infection, demonstrating its development in this sand fly. Experimental infection in this sand fly was also possible with *E. colombiense* (= *L. colombiense*) (Kreutzer et al., 1991). Natural infection was also evidenced through the detection of DNA from *L. (V.) panamensis* (Santamaría et al., 2006; González et al., 2018; Sandoval-Ramírez et al., 2020; Hoyos et al., 2022), *L. (V.) braziliensis* and *L. (L.) infantum chagasi* (Sandoval-Ramírez et al., 2020).

In Panama, Christensen, Fairchild (Christensen et al., 1983) demonstrated that it is susceptible to infection with strains of the *L. mexicana* complex and was also found infected with *L. (V.) naiffi* (Azpúrua et al., 2010), but most studies indicate it as a vector of *L. (V.) panamensis* (Christensen and Herrer, 1973; Christensen et al., 1983; Miranda et al., 2009) and emphasize its adaptability in fragmented environments (Valderrama et al., 2011).

Nyssomyia trapidoi is an anthropophilic species associated with CL foci, where, although not dominant, it has a high frequency (Santamaría et al., 2006; Duque et al., 2004; Posada López et al., 2014; Sandoval et al., 2006; Martínez Dueñas et al., 2019). Its vector competence was suggested by the isolation of *L. (V.) braziliensis* in culture (Travi et al., 1988). In 1981, strains of *Leishmania* were already isolated from females of this species (Morales et al., 1981), later identified as *L. (V.) panamensis* (Young et al., 1987). This species was also susceptible to experimental infection with *L. (V.) braziliensis*, *L. (V.) panamensis* (Jaramillo et al., 1994), and *E. colombiense* (Kreutzer et al., 1991).

Nyssomyia trapidoi is also present in Central American countries (Guatemala, Honduras, Nicaragua, and Costa Rica) and Ecuador (Galati, 2021), but it is primarily in Panama where more studies have been conducted incriminating it as a vector of *Leishmania* (Christensen et al., 1983; Azpúrua et al., 2010; Miranda et al., 2009), and highlighting its ability to adapt to environments with higher anthropogenic activity (Valderrama et al., 2011).

Pintomyia (Pifanomyia) evansi is commonly associated with drier biomes and regions (Bejarano and Estrada, 2016). It is mainly found in VL foci. It is a proven vector of *L. (L.) infantum chagasi*, as Travi, Montoya (Travi et al., 1996) had found flagellates of this species in females collected in Córdoba and obtained high infection rates in xenodiagnosis performed on sick dogs (Montoya-Lerma et al., 2003; B.L. Travi et al., 2002). It has also been considered a permissive species for infection by other *Leishmania* species, with isolates of *L. (V.) braziliensis* (Bejarano et al., 2012) and susceptibility to infection by *L. (L.) mexicana* and *L. (L.) amazonensis* (Vivenes et al., 2005). It has been found naturally infected with *L. (L.) infantum chagasi* (González et al., 2018; López et al., 2021) and *L. (V.) braziliensis* using different molecular markers (Bejarano et al., 2012).

Travi, Vélez (Travi et al., 1990) found promastigotes in the hindgut and stomodeal valve, suggesting this species as the main vector of *L. (L.) infantum chagasi* in the absence of *Lu. longipalpis*.

Pintomyia (Pif.) ovallesi, in Colombia, has a more restricted distribution in the Andean region (Bejarano and Estrada, 2016), where it is found in foci of CL in Santander, Norte de Santander, and Cundinamarca (Alexander et al., 1992; Alexander and Young, 1992; Sandoval et al., 2006). *L. (V.) braziliensis*, *L. (V.) panamensis* and *L. (L.) amazonensis* DNA has been found in wild caught flies (Sandoval-Ramírez et al., 2020), and it had previously been infected with *L. (V.) braziliensis* under laboratory

conditions (Santamaría et al., 1999).

4. Discussion

Having a clear consensus of the sand fly species involved in the transmission of cutaneous and visceral leishmaniasis undoubtedly enhances the effectiveness of disease surveillance programs. Based on the information contained in scientific papers using combinations of 5 criteria sand fly species were graded into 5 levels and 26 species were considered as potential or proven leishmaniasis vectors in Colombia. Levels one to four refer to potential or suspected status while level 5 denotes proven vectors. Five species matched the requirements of a proven vector. *Lu. (TrL.) gomezi* and *Ny. trapidoi* are the vectors of both *L. (V.) panamensis* and *L. (V.) braziliensis* while *Pi. (Pif.) ovallesi* is a vector for *L. (V.) braziliensis*. *Lu. longipalpis* along with *Pi. (Pif.) evansi* are the two proven vectors for *L. (L.) infantum chagasi*.

In addition to the proven vectors, it was possible to potentially identify permissive vectors of *E. colombiensis* (*Ny. trapidoi* and *Lu. gomezi*), *L. (V.) braziliensis* (*Lu. longipalpis*, *Pi. pia*, *Pi. nuneztovari*, *Lu. lichyi*, *Pi. columbiana*, *Pi. townsendi*, and *Pi. torvida*), *L. (L.) mexicana* (*Pi. columbiana*), and *L. (L.) infantum chagasi* (*Pa. shannoni* and *Pi. youngi*). However, the level of development of the parasite in these species was not always observed so one cannot rule out sink infections that would not become established to transmissible levels. Nonetheless the knowledge that they have the attributes of potential, but unproven vectors is important in surveillance programs, as these species could be responsible for establishing new transmission foci (Volf and Myskova, 2007). The expansion of a permissive vector can completely alter the severity of an epidemiological situation. New entomological research on the vector competence of these species will add weight to their vectorial importance.

Pa. (Psa.) shannoni is recorded in various active foci but at low frequency. Information about natural infection refers to a report of flagellates that could not be identified (Morales et al., 1981), although with positive results for experimental infection by *L. (L.) infantum chagasi* (Warburg et al., 1991), there is no evidence indicating that the species participates in the transmission of leishmaniasis.

Ny. umbratilis is the proven vectors of *L. (V.) guyanensis* (Ready et al., 1986) in Brazil. In Colombia, perhaps due to the low frequency of cases attributed to these *Leishmania* species (Ramírez et al., 2016; Correa-Cárdenas et al., 2020), these sand flies are rarely associated with active foci of leishmaniasis. However, *Ny. umbratilis* has been found infected by *L. (V.) guyanensis* through traditional parasitological methods (Young et al., 1987), and *Leishmania* DNA has been detected in *Ny. antunesi* (Vásquez-Trujillo et al., 2013; Vásquez-Trujillo et al., 2008). It has been suggested this species could be a vector of *L. (V.) lindenbergi* (Silveira et al., 2002) as it was the dominant sand fly in an endemic focus in Brazil. Therefore, both have a clear potential to be considered vectors; however, the evidence in the country remains scarce.

Santamaría, Castillo (Santamaría et al., 1999) considered *Pi. (Pif.) torvida* as the primary vector, as they found infective forms of the parasite in experimental infection. These results are important, but the species remained in this group due to a lack of further studies. *Pi. (Pif.) youngi* and *Pi. (Pif.) serrana* also met few criteria. Although Travi, Ferro (B.L. Travi et al., 2002) observed that *Pi. (Pif.) youngi* is susceptible to infection by *L. (L.) infantum chagasi*, more studies are needed to provide stronger evidence of its potential as a vector.

Mi. (Mic.) cayennensis is repeatedly named as a possible vector of *Leishmania* agents, but in the analyzed articles, we found the detection of flagellates that could not be identified (Montoya-Lerma et al., 2003) and the detection of DNA of *L. (V.) panamensis* (González et al., 2018).

The *Bichromomyia* genus includes species widely studied in other countries, and their potential as vectors of different *Leishmania* species has been proven (Killick-Kendrick, 1999; Brillhante et al., 2015), but evidence of this nature is scarce in Colombia. Species of leishmaniasis agents less common in the country, as expected, have fewer studies, and

suspected vectors remain unknown (Table 1).

The preliminary analysis of the articles identified through different searches allowed us to detect species repeatedly indicated as vectors or of "medical importance". However, we found that in some studies, this capacity is attributed to certain species based on inconsistent citations or only brief comments in the introduction. Just as the abundance of a species is not in itself a sufficient criterion for its incrimination as a vector (Killick-Kendrick, 1990).

Natural infection by DNA detection is not a sufficient criterion either and may not necessarily be correlated with the epidemiological problem of leishmaniasis. This type of finding can only indicate vector-reservoir contact and does not provide evidence for the development or survival of the parasite within the insect.

Recent studies on vector characterization have been mainly based on molecular methods (Sandoval-Ramírez et al., 2020), to the detriment of longitudinal ecological studies, which offer the possibility of highlighting various characteristics of vector populations, such as seasonality, species behavior concerning humans, preferences and feeding habits, as well as the detection of blood sources. There is complexity in determining the importance of natural infections recorded only by molecular methods without more extensive ecological and epidemiological studies.

Every criterion is pivotal in determining a species epidemiological importance, but a crucial one is anthropophily. Its evaluation is difficult due to ethical considerations but feeding habits can be determined via blood meal analysis. Finding engorged females is difficult and results can be biased by sampling in different environments. For instance, blood meals of a highly anthropophilic species in a sylvatic environment will be negative for human blood. In an endemic leishmaniasis foci in eastern Colombia (Sandoval-Ramírez et al., 2020) an analysis of the blood meals of phlebotomine associated with *L. (L.) amazonensis* infections indicated feeding interactions between man, pigs and birds (orioles). They are not reservoirs of this species, suggesting that they were becoming infected in another environment. Those who are unfamiliar with *Leishmania* zoonotic cycles might justifiably consider that either man, wild birds or pigs are the source of the *L. (L.) amazonensis* infections. This is an example of the difficulties of interpreting blood meal analysis results. This same study (Sandoval-Ramírez et al., 2020) showed that 9/11 species fed on man and the predominant anthropophilic ones were two grade 5 vectors *Lu. gomezi* and *Pi. ovallesi* and one grade 4 vector *Pi. spinicrassa*.

Our review has highlighted gaps, especially in endemic sand flies of the country. Endemic species deserve special attention, such as species of the genus *Pintomyia*, subgenus *Pifanomyia*, which have a markedly Andean distribution and have the potential to act as vectors. Several parameters were found throughout the review, but the shortage of studies in this group is evident. Particularly, the species: *Pi. columbiana*, *Pi. quasitownsendi*, *Pi. longiflocosa*, *Pi. torvida*, *Pi. townsendi*, which are endemic to Colombia; *Pi. youngi*, also recorded in Venezuela and Costa Rica, and *Pi. spinicrassa*, recorded in Venezuela.

There is good evidence that special attention should be given to permissive species belonging to the genera *Lutzomyia*, *Nyssomyia* and *Pintomyia*. It highlights their actual and potential importance as vectors of zoonotic cutaneous leishmaniasis. While certain sand fly species reported in Colombia have also been documented in other countries (Table 1), understanding their specific role at the local level requires thorough investigation, taking into account the complex dynamics of transmission influenced by local landscape and ecological interactions.

The study of vectors in the regional context is important because species can have different behavioral dynamics depending on the peculiarities of the environment, local ecological conditions, and diversity. A particular species may be a definitive vector in one area but not necessarily play the same role elsewhere. Since the effective transmission of the pathogen does not depend entirely on the sand fly but rather on a set of components triggering it, these differences in behavior and the environment interfere with vectorial capacity (Reisen, 2010; F. Galvis-Ovallos et al., 2017). Another relevant aspect is when a broad

Table 1
Species of leishmaniasis agents and their associated sand fly species in Colombia and other countries where has been reported.

Parasite species	Sand fly species	Proven (P) or Suspected (S) vector	
		Colombia	Others countries
<i>E. colombiensis</i>	<i>Lu. gomezi</i>	S	PA, VE (Kreutzer et al., 1991; Delgado et al., 1993)
	<i>Lu. hartmanni</i>	S	PA, VE (S) (Delgado et al., 1993)
	<i>Ny. trapidoi</i>	S	
	<i>Ps.</i>	...	PA, VE (S) (Kreutzer et al., 1991; Delgado et al., 1993)
<i>E. equatoriensis</i>	<i>Lu. hartmanni</i>	S	EC(S) (Furuya et al., 1998)
	<i>Bi.</i>	...	BO, BR, EC, GF, PY, VE (P) (Killick-Kendrick, 1999)
<i>L. (L.) amazonensis</i>	<i>flaviscutellata</i>	...	BR(S) (Killick-Kendrick, 1999)
	<i>Bi. reducta</i>	...	VE(S) (Nieves and Pimenta, 2000)
	<i>Mg. migonei</i>	...	BO(S) (Killick-Kendrick, 1999)
	<i>Pi.</i>	...	
<i>L. (L.) infantum chagasi</i>	<i>nuneztovari</i>	P	
	<i>Lu. longipalpis</i>	P	AR, BO, BR, CR, SV, GU, GY, HN, MX, NI, PY, SU (P) (Killick-Kendrick, 1999)
<i>L. (L.) mexicana</i>	<i>Pi. evansi</i>	P	VE (S) (Felicangeli et al., 1999)
	<i>Ny. ylephiletor</i>	...	GU(S) (Killick-Kendrick, 1999)
	<i>Pi.</i>	S	
<i>L. (V.) braziliensis</i>	<i>columbiana</i>	P	
	<i>Lu. gomezi</i>	P	
	<i>Lu. lichi</i>	S	
	<i>Lu. longipalpis</i>	S	
	<i>Ny. trapidoi</i>	P	
	<i>Pi.</i>	S	
	<i>columbiana</i>	S	
	<i>Pi. evansi</i>	S	
	<i>Pi.</i>	S	
	<i>nuneztovari</i>	S	
	<i>Pi. ovallesi</i>	P	VE(S) (Felicangeli et al., 1988)
	<i>Pi. pia</i>	S	
	<i>Pi. spincrassa</i>	S	
	<i>Pi. torvida</i>	S	
	<i>Pi. townsendi</i>	S	
<i>Pi. youngi</i>	...	VE(S) (Hernández et al., 2006)	
<i>Ps. c. carrerai</i>	...	BR (S) (Grimaldi et al., 1989)	
<i>Ps. davis</i>	...	BR(S) (Grimaldi et al., 1991)	
<i>Ps.</i>	S		
<i>panamensis</i>	S		
<i>L. (V.) guyanensis</i>	<i>Ny. umbratilis</i>	S	BR (P) (de Souza et al., 2017; Ready et al., 1986)
<i>L. (V.) lainsoni</i>	<i>Th. ubiquitalis</i>	...	BR, PE (P) (Silveira et al., 1991)
<i>L. (V.) lindenbergi</i>	<i>Ny. antunesi</i>	...	BR (S) (Silveira et al., 2002)
<i>L. (V.) naiffi</i>	<i>Lu. tortura</i>	...	EC (S) (Kato et al., 2008)
	<i>Ps. ayrozai</i>	...	BR(S) (Lainson and Shaw, 1989)
<i>L. (V.) panamensis</i>	<i>Lu. gomezi</i>	P	PA (P) (Christensen et al., 1983)
	<i>Mi.</i>	S	
	<i>cayenensis</i>	S	
	<i>Ny. trapidoi</i>	P	PA (P) (Christensen et al., 1983)
	<i>Ny. yuilli yuilli</i>	S	
	<i>Ny. ylephiletor</i>	...	PA (P) (Christensen et al., 1983)
	<i>Pi. ovallesi</i>	S	
	<i>Pi. spincrassa</i>	S	
	<i>Ps.</i>	S	PA (P) (Christensen et al., 1983)
	<i>panamensis</i>	S	

Bi= Bichromomyia; E = Endotrypanum; L. = Leishmania; Lu. = Lutzomyia; Mi. = Micropogomyia; Mg= Migonemyia; Ny= Nyssomyia; Pi= Pintomyia; Pa= Psathyromyia; Ps= Psychodopygus; V= Viannia.

AR= Argentina; BO= Bolívia; BR= Brasil; CR= Costa Rica; EC= Ecuador; GF= Guiana Francesa; GU= Guatemala; GY= Guiana; HN= Honduras; ME= Mexico; NI= Nicaragua; PA= Panamá; PE= Peru; PY= Paraguai; SU= Suriname; SV= El Salvador; VE= Venezuela.

distribution is attributed to a species when, in fact, it represents a taxon represented by two or more species, as is the case with *Pa. (Psa.) shannoni* (Sábido et al., 2016), with a more restricted distribution.

Studies on vectors employing single methodological approaches should be conducted with caution. However, research adopting an integrative methodological approach plays a crucial role in understanding the dynamics of leishmaniasis transmission, providing a deeper knowledge of vectors. Improving the understanding of the interaction between the vector and the parasite will undoubtedly contribute to the development of innovative control strategies, as well as the formulation of substantial epidemiological perspectives.

The classification of the vector potential of Colombian sand flies was based on evidence collected in scientific articles, and all analyses were conducted concerning transmission to humans. It is possible that some of the mentioned species are likely the main vectors of the zoonotic cycle, but we cannot assume this.

A limitation of this study lies in the non-inclusion of gray literature, inherent to its nature as a review. Nevertheless, the main output of this research, the list of vectors for leishmaniasis agents in Colombia, provides crucial information. This can be utilized by both researchers and entities responsible for surveillance programs, facilitating the quicker identification of potential risk areas.

Given the variety of infected species with parasites such as *L. (V.) braziliensis* and *L. (V.) panamensis*, it is plausible that the wild enzootic cycles are maintained by more than one sand fly species. For example, some of these species may play a fundamental role in maintaining while others contribute to transmission but not maintenance. A major question is which of these species is relevant to zoonotic transmission? In a recent review on reservoir status (Shaw et al., 2023) it was concluded that a mosaic of wild animals maintains the enzootic cycle. The “primary reservoir” ($R_0 > 1$) refers to host(s) that perpetuate the enzootic cycle and “secondary reservoir” ($R_0 < 1$) increases transmission but does not participate in maintenance. Could such a principal apply to vectors? In this context bridging the gap between wild and peri-domestic transmission could be a sand fly that is not a primary vector. A possible example of that is the potential role of *Ps. ayrozai* in bridging this gap in a *L. (V.) panamensis* endemic focus of cutaneous leishmaniasis in the Andean region of Colombia (L. Posada-López et al., 2023). Finally, it is important to note that the vector capacity parameters included in this study vary across local areas and are influenced by different ecological factors (such as landscape, host diversity, and climate) and sociocultural factors (such as anthroponotic activities) that affect transmission dynamics (F. Galvis-Ovallos et al., 2017). Therefore, the species classified in this study should be evaluated based on local evidence to support decision-making in the development of prevention and control measures.

CRedit authorship contribution statement

Laura Posada-Lopez: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Eunice AB Galati:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis. **Jeffrey Shaw:** Writing – review & editing, Visualization, Validation. **Fredy Galvis-Ovallos:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no competing interests.

Data availability

No data was used for the research described in the article.

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