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Review

Global Diversity, Distribution, and Genetic Studies of Stable Flies (*Stomoxys* sp.)

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Abstract: In the subfamily Stomoxyinae there are currently 18 recognized *Stomoxys* species, plus two subspecies. Most *Stomoxys* knowledge was gained through studies with *S. calcitrans*, a cosmopolitan species, economic pest, and vector. Other *Stomoxys* spp. are known only from a few trapped adult specimens. Herein, the *Stomoxys* spp. have been grouped by their ecological diversity, global distribution, and phylogeny and phylogeography. Seven species are dependent to some degree on humans and their activities, particularly animal production. Eleven species are dependent on wildlife to some degree for their development, and little is known about their biology in many cases. Global distributions include one cosmopolitan species (*S. calcitrans*), twelve species found only in Africa, four species only in Asia, and one species (*S. sitiens*) in Africa and Asia. Most genetic studies on *Stomoxys calcitrans* showed little variation in North America, possibly due to the adults' long range flight capability. Phylogeographic analysis of *S. calcitrans* showed a differentiation between Oriental populations (first lineage) and populations from Afrotropical, Palearctic, Nearctic, Neotropical and Oceanian regions (second lineage). Genetic studies were followed by sequencing of the *Stomoxys calcitrans* genome and phylogenetic studies of the *Stomoxys* genus using 10 of the known species. Phylogenetic relationships were established.

Keywords: synanthropic species; genetic sequencing; Afrotropical origin; two subspecies

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1. Introduction

The genus *Stomoxys* Geoffroy (1762) belongs to the family Muscidae. Even if for a long time the tribe of Stomoxyini was included within the subfamily Muscinae, today it seems that most entomologists accept the proposal to group the 18 recognized species of the genus *Stomoxys* within the subfamily Stomoxyinae [1]. The *Stomoxys* flies are biting flies, 3–10 mm long, hematophagous, with the appearance of a housefly (*Musca domestica* Linnaeus, 1758) but with an adapted biting mouth apparatus, the proboscis, directed forward in the axis of the body and capable of piercing the skin. The subfamily Stomoxyinae includes ten genera, of which the most important are *Haematobosca* Bezzi, 1907, *Haematobia* Lepeletier et Serville, 1828, and *Stomoxys* Geoffroy, 1762 [1]. Diagnosis between the different species of the genus *Stomoxys* is achieved by different morphological characters, in particular the width of frons in males, the colour of thorax and legs, the nervation of wings, the presence and number of hairs and bristles, and the variability of abdominal patterns. Entomologists use the keys of Zumpt [1]. For example, *S. calcitrans* is 4–7 mm long, and has an abdomen punctuated with black spots of rounded shape and a discontinuous median black line. As keys for males and females are separated, the distinction of sexes is based on the posterior part of the abdomen, modified for copulation and oviposition, and on eye spacing at the apex of the head, smaller in males than in females. The rigid biting apparatus, the proboscis, is composed of three long, strongly sclerotized, nonretractile parts: a labium (lower lip), a

labrum (upper lip), and a hypopharynx forming two tubes. Saliva is injected into the host dermis through the thinner tube represented by the hypopharynx, while blood is drawn through the larger tube formed by the labium and the dorsal part of the hypopharynx. In *Stomoxys* flies, both sexes are hematophagous; blood is necessary for reproduction, but flies can survive by feeding on nectar [2,3].

Knowledge on *Stomoxys* flies has been acquired mainly by studying the only species that is cosmopolitan: *Stomoxys calcitrans* (Linnaeus, 1758), known as the stable fly (Figure 1).

Figure 1. *Stomoxys calcitrans*, known as stable fly, with a cosmopolitan distribution. Photo: Dr Mikel Alexander González, Spain.

This species is the only one of the genus *Stomoxys* that is present on the European and American continents. This knowledge of *S. calcitrans* has been acquired in relation to their impact on the livestock industry. The adults represent a significant nuisance due to the pain of their bite and the possible transmission of pathogens [4]. In the United States Taylor et al. (2012) [5] estimated the economic impact of stable flies on the livestock industry to be USD 2.2 billion per year. Using the same calculation formulas, French livestock farming losses have been estimated to be EUR 145 million per year for the meat industry and EUR 234 million per year for the dairy industry [6]. The health impacts are also very important. *Stomoxys* adults are mechanical vectors of pathogens present in the blood and skin of their hosts, especially livestock, but occasionally humans. Equine infectious anaemia, African swine fever, West Nile, Rift Valley and lumpy skin disease viruses are known to be transmitted by *Stomoxys* flies, while transmission of other viruses is suspected. Rickettsia (*Anaplasma*, *Coxiella*) and other bacteria and parasites (*Trypanosoma* spp., *Besnoitia* spp.) are also transmitted by *Stomoxys* adults. Finally, stable flies were also found to act as an intermediate host of the helminth *Habronema microstoma* and may be involved in the transmission of some *Onchocerca* and *Dirofilaria*. Being cosmopolite, *Stomoxys calcitrans* might have a greater worldwide impact than previously thought on animal and human pathogen transmission [4,7].

The traditional way of controlling these biting flies relies on the use of insecticides, mainly pour-on insecticides on the back of animals, when most of the flies are seen on the lower legs. However, for several years now, breeders have noticed that these products are no longer effective, despite the high frequency of application. This has been confirmed by numerous laboratory studies showing, phenotypically and genetically, that stable flies have become resistant to all available insecticides [8–12]. Other control methods have become necessary.

This review attempts to gather updated information on the diversity, distribution, phylogeny of the genus *Stomoxys* and the phylogeography of the cosmopolitan species *S. calcitrans*.

2. Diversity and Ecological Remarks

The subfamily Stomoxyinae, comprising 10 genera and 49 species, was described as a well-defined and monophyletic taxon by Zumpt (1973) [1]. Four species are divided into two or three subspecies, which represent a total of fifty-four taxa. Since this work, three new species have been described in the genus *Haematobosca* [13–15]. A total of 52 species and 57 taxa are currently recognized (Table 1).

Table 1. List of genera and number of species and taxa known in 2023 in subfamily Stomoxyinae (Diptera: Muscidae).

Genera	Number of Species	Number of Taxa *
Rhinomusca Malloch (1932)	2	2
Neivamyia Pinto & Fonseca (1930)	5	5
Bruceomyia Malloch (1932)	1	1
Parastomoxys Zumpt (1973)	1	1
Prostomoxys Zumpt (1973)	1	1
Stygeromyia Austen (1907)	2	2
Haematobosca Bezzi (1907)	15	15
Haematobia Lepeletier & Serville (1828)	6	9
Haematostoma Malloch (1932)	1	1
Stomoxys Geoffroy (1762)	18	20

* Taxa: species and subspecies.

The 18 species of the genus *Stomoxys* can be easily identified using morphological characters and the key proposed by Zumpt [1]. They can be grouped by their different ecologies:

Seven species are wholly or partly dependent on human activities and on livestock farming [1].

1. *Stomoxys calcitrans* (Linnaeus, 1758), described by Linnaeus from specimens caught in Sweden, has subsequently been found worldwide and redescribed under 32 synonymous names. The first in-depth studies on its biology were conducted in Egypt [16–18]. These authors showed that the developmental media of this species were the dung of cattle or horses, mixed with straw and urine. They do not develop in pure faecal matter. The authors have also shown that they grow very well in decaying plant material. A review on the biology of this species was recently published [7].

2. *Stomoxys niger* Macquart, 1851 was described from specimens from the island of La Réunion (Indian Ocean). Originally described as *Stomoxys nigra*, the name was changed to *S. niger* when it was realized that the name *Stomoxys* was masculine [19]. It was then redescribed under 12 different synonymous names. This species was then divided into two subspecies when Zumpt (1973) [1] suggested that the species *S. bilineata* Grünberg, 1906 should be considered a subspecies of *S. niger*. The two subspecies, henceforth named

S. niger niger Macquart, 1851 and *S. niger bilineatus* Grunberg, 1906, are identified by morphological characters of tibiae coloration [1]. Moreover, while *S. niger niger* appears to be well associated with livestock activities, *S. niger bilineatus* often appears in association with wildlife [20,21]. *S. niger niger* is considered the most common species in Africa. It has been described in many countries on the continent, but also in Madagascar and the Mascarene Islands (Reunion, Mauritius, and Rodrigues). Recently, one of us (GD) has received three specimens from Sao Tomé and Principe. Fiasson (1943) [22] (quoted by [1]) had also described it in Venezuela (South America), but this is obviously an error. This species feeds on cattle, horses, donkeys, and sometimes on humans, and their bite is painful.The subspecies *Stomoxys niger bilineatus* Grunberg, 1906 has been separated from *S. niger niger* on morphological characters, of which the most visible is the coloration of the tibiae. Zumpt (1973) [1] studied specimens from Mali, Ethiopia, Tanzania, Mozambique, Zimbabwe, and South Africa. This species has also been captured in Gabon [20,21,23].

3. *Stomoxys sitiens* Rondani, 1873 was described from specimens from Eritrea, and then redescribed by Brunetti in 1910 under the same name, and by other authors under two other synonymous names with specimens from India and Singapore. This species has since been captured in China [24] and in Thailand [1,25–27]. *S sitiens* is indeed present in both the African continent and Asia. Hafez and Gamal-Eddin (1959) [16,17] showed in Egypt that this species has a similar ecology to *S. calcitrans*. The preimaginal forms are found in the dung of cattle, horses, and donkeys when mixed with straw, but also in decaying vegetation. *S. sitiens* appears to prefer drier, semi-arid environments than *S. calcitrans* [1].

4. *Stomoxys indicus* Picard, 1908 was described as *S. indica* from specimens from the Calcutta region of India. It has been redescribed under eight synonymous names from specimens from Southeast Asia (India, Malaysia, Borneo, Vietnam, Taiwan). This species is found mainly in contact with cattle, but also goats, in the same places as *S. calcitrans*. This species has also been captured in Thailand [26,28,29]. However, it seems (Kano, 1953 [30] cited by Zumpt, 1973 [1]; [26]) that this species has a crepuscular or nocturnal activity. The larvae are found in the dungs of cattle and horses.

5. *Stomoxys bengalensis* Picard, 1908 was described from specimens from India. It was redescribed under a synonymous name in 1910, and is known from the following countries: India, Burma, Vietnam, Malaysia, and Indonesia [1]. It has also been captured more recently in Thailand [26,27]. This species is known to feed on cattle, but its biology is very poorly known.

6. *Stomoxys uruma* Shinonaga and Kano, 1966 was described from specimens from Japan (Ryukyu) and China (Hong Kong). It has also been observed in Thailand [31], Vietnam, and Taiwan. The larval stages are not known and the authors who described it indicate that they feed on cattle and water buffalo. Changbunjong et al. (2012) [32] reported large numbers of *S. uruma* collected in Kho Yai National Park (Thailand).

7. *Stomoxys taeniatus* Bigot, 1888 was described as *S. taeniata* from specimens from South Africa. It was later redescribed under three synonymous names from specimens from Cameroon, Tanzania, Sudan, and Congo. The larval forms are not known and Reid (1956) [33] (quoted by [1]) indicated that specimens captured in Sudan were biting cattle.

Eleven species are known to be wildlife-related or of unknown biology.

8. *Stomoxys omega* Newstead, 1907 was described from specimens from the Congo. These specimens had been captured from a wild buffalo that had just been shot [1]. Zumpt (1973) [1] reported that he examined specimens from the following countries: Liberia, Nigeria, Cameroon, Congo, Uganda, Malawi, and South Africa. This species has been captured in abundance in Gabon in a forested area, far from any livestock [23].

9. *Stomoxys xanthomelas* Roubaud, 1937 was described from specimens from Congo. Zumpt (1973) [1] also indicated its presence in Congo, Uganda, and Tanzania. He specified that its biology is unknown, but specimens were captured in Gabon when Vavoua traps were placed in the canopy 30 m above the ground [34]. Blood meal analysis showed that this species fed on and associated with monkeys. This was confirmed by observing the emergence of adults from chimpanzee faecal material placed in an emergence cage [35].

10. *Stomoxys pallidus* Roubaud, 1911 was described as *S. pallida* from specimens from Benin. It was redescribed from Malawi in 1932 under a synonymous name [1]. Very close morphologically to *S. xanthomelas* because of the yellow coloration of their abdomens, it differs in other characters. It is known from the following countries: Sierra Leone, Liberia, Congo, Uganda, and Malawi [1]. This species, like *S. xanthomelas*, seems to prefer dense forest areas and feeds on antelopes and hippopotami. The biology of this species is very poorly known.

11. *Stomoxys ochrosoma* Speiser, 1940 was described from specimens from Tanzania. Redescribed in 1932 under a synonymous name from specimens from Uganda, this species is easily recognizable by the yellow colour of its entire body. It is also known from Kenya. Concerning its biology, it has been indicated that the females project their eggs on columns of Dorylinae ants. The larvae would thus develop in the anthills of this species [36] (quoted by [1]). Nothing else is known about the biology of this species.

12. *Stomoxys luteolus* Villeneuve, 1934 was previously described as a subspecies of *S. ochrosoma*, but Zumpt (1973) [1] confirms the separation between the two. This species is known only from Congo and Uganda. No information is available on its biology.

13. *Stomoxys stigma* Van Emden, 1939 is a species very close to *S. omega*, described from specimens from Uganda. No information on its biology is available.

14. *Stomoxys transvittatus* Villeneuve, 1916 was described as *S. transvittata* from specimens from South Africa. It is also known from Malawi, Zimbabwe, Kenya, and Congo. *S. transvittatus* was the most abundant species captured in a forested area in Gabon [23]. No information is available on its biology.

15. *Stomoxys pullus* Austen, 1909 was described as *S. pulla* from specimens from India. A very rare species in collections, nothing is known about its biology. This species has been captured more recently in Thailand [32]. In Thailand, most of the specimens were captured in Khao Yai National Park with abundant wildlife, but others were captured in a local beef cattle farm at the border of the National Park.

16. *Stomoxys boueti* Roubaud, 1911 was described from specimens from Benin. This species is morphologically close to the species *S. uruma* from the Oriental Region and is also known from Congo. Some of the known specimens were taken from buffalo, but nothing else is known about its biology [1].

17. *Stomoxys inornatus* Grünberg, 1906 was described as *S. inornata* from specimens from Cameroon. This species, also described under another synonymous name, is widely known from West and Central Africa: Liberia, Nigeria, Uganda, Kenya, Burundi, Rwanda, Congo, and Sudan. This species has been captured more recently in Gabon [37,38]. The biology of this species is unknown.

18. *Stomoxys varipes* Bezzi, 1906 was described from specimens from Eritrea. Very close morphologically to *S. niger*, this species is also known from Ethiopia, Uganda, Kenya, Tanzania, Rwanda, Congo, Zimbabwe, and Malawi. The biology of this species is unknown [1].

3. Distribution

The global distribution of the 18 species of the genus *Stomoxys* can be summarised in the following map (Figure 2).

Additional details to this distribution map are added:

- *Stomoxys calcitrans* is cosmopolitan, present in all the countries where it has been researched. Almost always found in connection with human activities (breeding), it can sometimes be found in littoral tourist destinations where it can feed on people and become an important nuisance [39,40]. This species is thus adapted to all the climates of the planet, from equatorial zones to mountainous zones with altitude or zones close to the poles.

- *Stomoxys sitiens* is present in both the African continent and Asia.

- twelve Stomoxys species are known only from the African continent: *S. omega*, *S. niger*, *S. xanthomelas*, *S. pallidus*, *S. ochrosoma*, *S. luteolus*, *S. stigma*, *S. transvittatus*, *S. boueti*, *S. taeniatus*, *S. inornatus*, and *S. varipes*.

- four *Stomoxys* species are known only from Asia: *S. indicus*, *S. bengalensis*, *S. pullus*, and *S. uruma*.

- *Stomoxys niger*: the indication of its presence in Venezuela by Fiasson (1943) [22] was questioned by Zumpt (1973) [1]. We have contacted entomologists in this country, who have confirmed that they have never seen any species other than *S. calcitrans*; nor have they ever been aware of a publication indicating the presence of *S. niger* in their country.

- *Stomoxys indicus*: known from several Asian countries, its presence on the island of La Reunion (Indian Ocean) has just been recently confirmed (L. Costet, personal communication). The identification of *S. indicus* has been confirmed morphologically by one of us (GD) and genetically (paper in preparation). Only two species (*S. calcitrans* and *S. niger niger*) were known until now on the island of La Reunion [41]. The presence of *S. indicus* confirms the links between India and the Mascarene Islands.

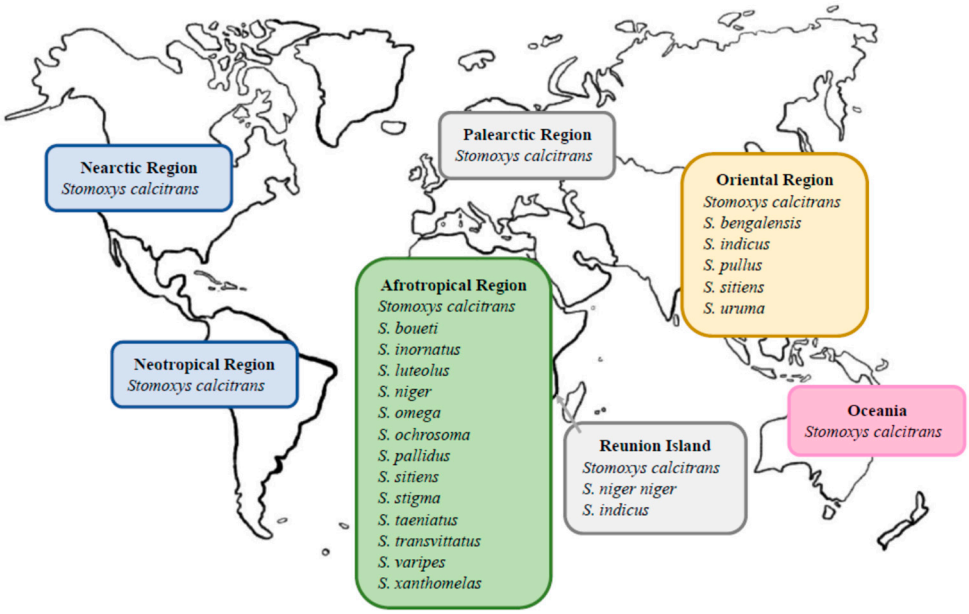

Figure 2. Known distribution of the 18 species of *Stomoxys*.

4. Phylogeography of *Stomoxys calcitrans*

Most studies on *Stomoxys* flies' genetics have been conducted on *Stomoxys calcitrans*. The initial objectives of these studies were to obtain information on population dynamics, the origin of outbreaks, and the identification and geographical distribution of insecticide resistance, to thus develop more effective control strategies. Most studies were conducted at a local level, with only a few at a more global scale. These aspects of *S. calcitrans* genetics were reviewed by Rochon et al. (2021) [7]. Szalanski et al. (1996) [42] observed significant gene flow between populations of *S. calcitrans* from Canada and the USA (Nebraska and Texas). Biochemical and molecular methods showed little variation between these populations, likely related to a bottleneck at the time of the colonization of North America by these flies. This genetic homogeneity is related to the dispersal capacity of these flies [40]. Those results have been confirmed by Kneeland et al. (2013) [43] who, using the amplified fragment length polymorphism (AFLP) method with samples from North America, showed that *S. calcitrans* flies have a high level of gene flow on a continental scale.

Dsouli-Aymes et al. (2011) [44] conducted a phylogeographic analysis to study the population genetic structure of *S. calcitrans* and to trace its global dispersion. They compared twenty populations from the five major zoogeographic regions of the world using mitochondrial (COI-cytochrome c oxidase subunit I, Cyt B-cytochrome B, and ND1-16S-nicotinamide adenine dinucleotide) and nuclear (ITS2-internal transcribed spacer 2) genes. Their results show a differentiation between Oriental populations (first lineage) and populations from Afrotropical, Palearctic, Nearctic, Neotropical and Oceanian regions (second

lineage). These two clades were separated by mean genetic distances of 1.7 to 2.3% [44]. The absence of shared haplotypes between them and the genetic distance suggest that they diverged in allopatry, and that the Oriental lineage has been isolated since 0.7–1 million years ago (mid-Pleistocene) [44]. Oriental populations appear in their work as isolated and not participating in the colonization of other regions. Afrotropical populations seem the source of *S. calcitrans* dispersion to other regions. Tsai et al. (2023) [45] also performed a detailed study of the phylogeography of *S. calcitrans*, using 13 populations from Taiwan, 10 specimens from Poland, and all available data in GenBank and BOLD. They confirmed that the likely origin of S. *calcitrans* is in the Afrotropical region. They also suggested that the differences observed between the phylogroups of the Afrotropical, Oriental and Nearctic regions could be due to the isolation of populations in different refugia during the Pleistocene glaciations. They also showed the influence of transnational livestock trade activities by giving the example of the arrival of stable flies from North America to Taiwan with the importation of cattle. They also indicated by examining intra- and inter-population genetic distances, in agreement with [44,46], that the species *S. calcitrans* may in fact contain several cryptic species. Kneeland et al. (2015) [47] also studied the genetic diversity of *S. calcitrans* on a global scale. Specimens from different biogeographic regions were analysed with the AFLP technique. Their results show a lack of genetic differentiation despite geographical barriers. They did not observe a correlation between geographical origin and genetic distance. This is inconsistent with the results of Dsouli-Aymes et al. (2011) [44], but they had no samples from the Oriental region in their work. These studies eventually led to the sequencing of the *Stomoxys calcitrans* genome [48]. This work has allowed the identification of many gene families, allowing a better understanding of the behaviour of this species, but also consideration of new and more effective control methods, e.g., the use of olfactory attractants or repellents.

5. Phylogeny of Genus *Stomoxys*

Dsouli et al. (2011) [49] were the first authors, to our knowledge, to have studied the phylogeny of the genus *Stomoxys* considering 10 of the 18 known different species. Phylogenetic relationships have been established using maximum likelihood and Bayesian methods from DNA fragments from COI, CytB mitochondrial genes, and ITS2 nuclear genes. A phylogenetic tree inferred from the concatenation of the three genes (totalizing 1635 nucleotide sites) and a chronogram resulting from the relaxed clock Bayesian analysis of the same concatenation are available in their publication [49]. The main results of this work were:

- the genus *Stomoxys* appears as paraphyletic because of the inclusion of the species *Prostomoxys saegerae* (Zumpt, 1969) in the analysis. The phylogenetic tree shows *P. saegerae* as a sister group of *S. varipes*. The monospecific genus *Prostomoxys* was created by Zumpt [1] on a simple morphological character showing maxillary palpi as long as the proboscis, when it is shorter for the genus *Stomoxys*. The authors proposed to reintegrate the species *P. saegerae* into the genus *Stomoxys* [49].

- a deep molecular divergence was observed between the subspecies *Stomoxys niger niger* and *S. niger bilineatus*. The authors proposed that these taxa should be considered as distinct species.

- three distinct lineages were observed within the genus *Stomoxys*, identified by Bayesian phylogenetic analyses. The first lineage includes the species *Stomoxys indicus*, which appears as the sister species to all other *Stomoxys* species. The second lineage groups strictly African species *S. inornatus*, *S. transvittatus*, *S. omega*, and *S. pallidus*. The third lineage includes the cosmopolitan *S. calcitrans*, African species such as *S. varipes*, Oriental species such as *S. bengalensis*, and *S. sitiens*, which is present in Africa and the Oriental region.

- the chronogram gave estimations of the divergence time between taxa. If the divergence time between the *Stomoxys* genus and its Stomoxyinae sister-clade (*Haematobia* and *Haematobosca*) is estimated around 30.8 Mya, the age estimate for the emergence of *S. indicus*

is estimated at about 27 Mya [49]. The placement of *S. indicus* as the sister group to the remaining *Stomoxys* species lets us suggest that this species would be at the origin of the genus *Stomoxys* in the Oriental region.

6. Conclusions

The subfamily Stomoxyinae currently consists of 18 recognized *Stomoxys* species plus two subspecies. When grouped by ecological diversity, seven species are synanthropic to some degree and benefit particularly from animal production. Eleven species are dependent on wildlife to some degree for their development, and little is known about their biology in many cases. Global distributions include one cosmopolitan species (*S. calcitrans*), twelve species found only in Africa, four species found only in Asia, and one species (*S. sitiens*) found in both Africa and Asia.

Little genetic variation is found in North America, possibly because of gene flow from the adults' long range flight capability. Phylogeographic analysis of *S. calcitrans* showed a differentiation between Oriental populations (first lineage) and populations from Afrotropical, Palearctic, Nearctic, Neotropical and Oceanian regions (second lineage). Sequencing of the *Stomoxys calcitrans* genome allows for better fly management opportunities. Phylogenetic studies of the *Stomoxys* genus using 10 of the known species produced phylogenetic relationships among species. These studies let us suppose that the species *S. indicus* would be at the origin of the genus *Stomoxys* in the Oriental region 27 Mya ago.

As most of the knowledge on *Stomoxys* flies has been acquired from the cosmopolitan *Stomoxys calcitrans*, more research on the biology of other species is necessary; not only those species known to be linked with human activities, but also other species which could play a role in the transmission of pathogens between wild fauna and livestock.

At the same time, because of the developing resistance of these flies to available insecticides, more research is also necessary on new and more sustainable control methods: more efficient and specific trapping systems against adult flies, and biocontrols (parasitoids and predators) against preimaginal stages.

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