

Chapter 15

Diversity and Distribution of the Arthropod Vectors of the Gulf of Guinea Oceanic Islands



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Abstract The known arthropod vector species on the Gulf of Guinea islands belong to orders Diptera and Ixodida. Among the Diptera, the family Culicidae (mosquitoes) has the most species, 34 (6 endemic), Ceratopogonidae has 13 (all in the genus *Culicoides*), Tabanidae has 6, and Simuliidae has 3 (1 endemic). Ixodida has only 4 species. Most vector species and associated diseases are shared with mainland Africa. Some of these include (1) the human malaria vector *Anopheles coluzzii*, (2) yellow fever and dengue vector *Aedes aegypti*, and (3) the spotted fever group rickettsiae and Q fever vector *Amblyomma* spp. However, there is a considerable lack of information on the natural cycles of many vector-borne diseases that might

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impact local fauna, for which there may be some endemic pathogen lineages. Increased trade by air and sea should compel authorities to remain vigilant, to keep unwanted vectors and diseases at bay. Entomological diversity data remains scarce for Annobón and for the forested interior of the islands, where future sampling efforts may uncover new endemic species.

Keywords Biting midges · Diptera · Flies · Infectious diseases · Mosquitoes · Ticks

Introduction

The discipline of medical entomology originated in the late nineteenth and early twentieth centuries (Service 1978), when P. Manson and R. Ross discovered the obligatory development of specific life stages of the human pathogenic filarial, *Wuchereria bancrofti* Cobbold, 1877, and avian malaria *Plasmodium* parasite in the mosquito *Culex quinquefasciatus* Say (Ross 1911). This discipline aims at studying insects and other arthropods that affect the health of humans, domestic animals, and wildlife (hereafter called vectors). Vector biology can be subdivided into medical (emphasis on human), veterinary (domestic animals), and wildlife disciplines (Edman 2009). However, these are often intertwined, since many vectors transmit infectious agents that cause similar diseases in both humans and animals (zoonoses). A large diversity of pathogens is transmitted by hematophagous arthropods (insects or ticks), including filariae (i.e., worms), protozoa (e.g., malaria), bacteria, and viruses (e.g., dengue, yellow fever, or Zika). Of all the arthropods, the Order Diptera contains the most species that transmit pathogens to humans and wildlife, including one of the most studied families, the Culicidae (mosquitoes).

Recent mosquito surveys on Comoros (Mayotte Island: Le Goff et al. 2014), Seychelles (Le Goff et al. 2012), and Mariana Islands (Guam: Rueda et al. 2011) reveal high numbers of species but few single-island endemics. By contrast, São Tomé and Príncipe harbor six endemic mosquito species (Ramos et al. 1994; Ribeiro et al. 1998; Loiseau et al. 2019) and this high level of mosquito endemism (23%) is especially unusual considering the proximity of the islands to the mainland. In comparison, the Galapagos, Hawaii, and Canary archipelagoes do not harbor endemic mosquito species (Baez 1987; Carles-Tolra 2002; Bataille et al. 2009), while the Azores and Madeira have only one each (Ribeiro and Ramos 1999). Other Dipteran families containing disease vector species, such as Simuliidae and Ceratopogonidae, have been less studied on the Gulf of Guinea oceanic islands, probably due to their lower diversity and lesser medical importance.

In this chapter, we present an overview of the known biodiversity of arthropod vectors and their associated diseases on the Gulf of Guinea oceanic islands. We describe the microhabitats of Culicidae and Simuliidae species and propose future directions that might help in documenting and describing new vector species from the archipelago.

Diversity, Endemism, and Disease Ecology

All vector species on the Gulf of Guinea oceanic islands are Diptera or Ixodida arthropods.

Class Insecta

Order Diptera

The order Diptera is composed of two suborders, Nematocera and Brachycera (Pape et al. 2011). More than 150,000 species have been described, including numerous hematophagous insects able to transmit infectious diseases. Diptera species known as vectors in the Gulf of Guinea islands belong to five families.

Suborder Nematocera

Family Culicidae

Globally, Culicidae includes 3578 mosquito species and subspecies, in 42 genera (Walter Reed Biosystematics Unit 2001). Seven hundred and ninety-five species are known to occur in the Afrotropics (i.e., 22% of the mosquito diversity; Rueda 2008). Culicidae is one of the most studied Diptera families, both worldwide and in the Gulf of Guinea oceanic islands. Hence, for this group, we detail relevant expeditions, from the early twentieth century, which relied mostly on collecting immature stages, to more recent collections, which used both immature and adult decoy trapping.

Early Expeditions (1932–1964)

Published records dating back from the Percy Sladen and Godman Trust expeditions in 1932 and 1933 (Edwards 1934) recorded five species on São Tomé (*Anopheles gambiae* Giles, 1902, *Uranotenia micromelas* Edwards 1934, *Aedes nigricephalus* Theobald, 1901; *Culex fatigans* Wiedemann, 1828 and *Culex tamsi* Edwards, 1934) and two on Príncipe (*Aedes aegypti* Linnaeus, 1762 and *Eretmapodites chrysogaster* Graham, 1909). Two species described from material collected on this expedition, *U. micromelas* and *Cx. tamsi*, are still considered endemic to São Tomé and Príncipe. Based on samples collected during expeditions between 1952 and 1955, 15 additional species were reported for São Tomé and Príncipe (Gândara 1956). During the program to eradicate tsetse flies on Príncipe (see section on Tabanidae), nine species of mosquito were found, four of which were new to the islands, including *Aedes* (*Aedimorphus*) larvae that were not identified to species (Pinhão and Mourão 1961). A few years later, an intensive survey of mosquito larvae at

14 sites on São Tomé (Mourão 1964) collected five additional species (*Uranotaenia balfouri* Theobald, 1904, *Aedes metallicus* Edwards, 1912, *Aedes circumluteolus* Theobald, 1908, *Toxorhynchites brevialpis* Theobald, 1901 and *Culiseta fraseri* Edwards, 1914).

Further Expeditions in the Second Half of the Twentieth Century

An updated list of Príncipe Island mosquito species, based on specimens collected during an expedition in 1986, added seven species (*Ae. nigricephalus*, *Culex antennatus* Becker, 1903, *C. decens* Theobald, 1901, *C. nebulosus* Theobald, 1901, *C. quinquefasciatus* Say, 1826, *U. micromelas* and *U. principensis* da Cunha Ramos, 1993) to the seven previously recorded (Ramos et al. 1989). Then, two new species were described: *Toxorhynchites capelai* Ribeiro, 1991 (Ribeiro 1993), and *Aedes (Aedimorphus) gandarai* Ramos, Capela and Ribeiro, 1994 (Ramos et al. 1994). A few years later, the list of mosquito species increased to 14 on Príncipe and 26 on São Tomé (Ribeiro et al. 1998), including 6 São Tomé endemics, and 1 endemic to both islands (Appendix). The genus *Culex* is represented by the most species, 14, followed by *Aedes*, with 6.

On São Tomé and Príncipe Islands, the only current known vector of human malaria is *Anopheles coluzzii* Coetzee and Wilkerson 2013, previously known as *An. gambiae* M form. *An. coluzzii* is abundant in urban and village settings in coastal areas on both islands. The lower abundance and the possible absence of *An. coluzzii* inland and at elevations above 200 m (Pinto et al. 2000a, b), despite an abundance of semi-permanent pools for immature development, is likely due to much lower human population densities in these areas. After intensive indoor residual spraying campaigns, which started in 2005, the overall prevalence of malaria in children under 9 years old was reduced from 30.5% to 8.3% after the first round, and to 2.1% after the second (Tseng et al. 2008; Teklehaimanot et al. 2009). Prevalence has remained low (~1%; Chen et al. 2019), but active surveillance and mosquito control to prevent malaria outbreaks is ongoing (Lee et al. 2010). The only other *Anopheles* species present on São Tomé, but not on Príncipe, is *An. coustani* Laveran, 1900; however, its role as a secondary malaria vector is not known.

Lymphatic filariasis, a human parasitic infection, is caused by nematodes (*Wuchereria bancrofti* Cobbold, 1887, *Brugia malayi* Brug, 1927 and *B. timori* Partono, 1977), which are transmitted through the bite of infected *Ae.*, *Cx.*, *An.* and *Mansonia* mosquitoes (Chandy et al. 2011). The last report of the presence of *W. bancrofti* on São Tomé dates from 1956 and on Príncipe from 1958 (Fraga de Azevedo et al. 1960). The insecticide spraying that led to the eradication of *Glossina palpalis palpalis* Robineau-Desvoidy, 1830 on Príncipe (see below), probably also impacted mosquito populations, which likely led to eliminating lymphatic filariae on that island (Fraga de Azevedo et al. 1960). Further surveillance might be needed as positive serological tests for lymphatic filariasis have been reported on São Tomé in recent years (Fan et al. 2013; WHO 2019).

Recent Surveys (Within First Quarter of the Twenty-First Century)

Collections performed by the authors on São Tomé and Príncipe in 2016, 2017, and 2019 added four species to the documented diversity (*Ae. albopictus* Skuse, 1894, *Ae. tarsalis* Edwards, 1927, *U. bilineata* Theobald, 1909, and *U. connali* Edwards, 1912). These surveys were primarily focused on collecting mosquito vectors known to transmit wildlife pathogens, especially to birds. At least eight genera of mosquitoes (*Aedes*, *Aedeomyia*, *Anopheles*, *Culex*, *Coquillettia*, *Culiseta*, *Mansonia*, and *Uranotaenia*) can transmit avian malaria (Valkiūnas 2004). Avian malaria has had devastating effects on the endemic bird populations of Hawaii (Fonseca et al. 2000), demonstrating the pernicious nature of introduced diseases on isolated animal populations. São Tomé and Príncipe birds are not heavily infected with *Plasmodium*, exhibiting an average prevalence of around 12% (Reis et al. 2021); however, the birds appear to be carrying *Plasmodium* lineages that originate from the mainland, particularly in lowland bird populations (Reis et al. 2021). Numerous mosquito species may be vectors of avian malaria in the Gulf of Guinea oceanic islands, but their vector competence has not yet been assessed and will be an important future research direction for monitoring the population health of the endemic avifauna.

The highly anthropophilic *Ae. albopictus* (invasive tiger mosquito), likely introduced to the Gulf of Guinea during the last 10 years, is now very widespread on both islands and is of considerable human biting nuisance (Reis et al. 2017; Loiseau et al. 2019). Along with *Ae. aegypti*, *Ae. albopictus* is considered an urban cycle vector (Kamgang et al. 2019b) of Yellow Fever, Dengue, Zika and Chikungunya viruses, which actively circulate in neighboring African mainland countries (Paupy et al. 2010; Braack et al. 2018; Kamgang et al. 2019a). Periodic outbreaks of Yellow Fever occur in neighboring mainland countries, namely in Cameroon, Gabon, and Angola (Chippaux and Chippaux 2018). One study estimated that currently there are between 51,000 and 380,000 severe cases of yellow fever annually in Africa, resulting in an estimated 19,000–180,000 deaths (Garske et al. 2014). Dengue virus strains, in the same *Flavivirus* genus as Yellow Fever virus (Daep et al. 2014), are now probably one of the most important arboviruses, since globally they infect over 100 million people annually, resulting in an estimated 500,000 severe Dengue cases (WHO 2014). A serological survey on pregnant women has actually demonstrated the circulation of this virus on the islands (Yen et al. 2016). No major outbreak of Dengue has been recorded on the islands until a recent one in São Tomé in 2022. In addition, nine resident mosquito species found in São Tomé and Príncipe (Ribeiro et al. 1998) are known as vectors of numerous other arboviruses (e.g., *Alphavirus*, *Flavivirus*, or *Phlebovirus*) in the Afrotropics.

Currently, both Anophelinae and Culicinae subfamilies are present in the Gulf of Guinea islands, as well as the only Culicidae genus that is endemic to Africa, *Eretmapodites* Theobald, 1901. There are 35 resident *Culicidae* species: 31 on São Tomé and 15 on Príncipe (Appendix). To our knowledge *Ae. indet* (Pinhão and Mourão 1961) has not been collected in the last 70 years, and its current presence on the islands is questionable. We have not included *An. funestus* s.l. Giles, 1900, *An. paludis* Theobald, 1901, and *An. pharoensis* Theobald, 1901 (Mesquita 1946, 1952)

in the current list of species, because malaria control campaigns in the 1980s are thought to have eradicated them (Pinto et al. 2000a). The only publication on the mosquitoes of Annobón was about malaria transmission and genetic population structure of *An. coluzzii* in Equatorial Guinea (Moreno et al. 2007).

Family Simuliidae

Among the 2200 species of black flies described around the world, 214 are present in the Afrotropical region (Currie and Adler 2008), including many that transmit pathogens that affect humans (e.g., filarial disease onchocerciasis; Crosskey 1990), poultry (Alder and McCreadie 2019), and wild birds (Valkiūnas et al. 2004). Onchocerciasis (river blindness) is limited to sub-Saharan Africa and is widely known in southern Cameroon and on Bioko Island, where it is transmitted by species of the complex *Simulium damnosum* Theobald, 1903 (Post et al. 2003). Currently, this vector species does not occur on the Gulf of Guinea oceanic islands (Mustapha et al. 2004), and no cases of Onchocerciasis have been reported. The avian parasites *Leucocytozoon*, closely related to avian malaria, are present, especially in highland and forest birds of São Tomé and Príncipe (Reis et al. 2021). However, the vector competence of black fly species for *Leucocytozoon* spp. remains unknown on the islands.

Black flies were first documented at one site on São Tomé in 1988 (Grácio 1988). Extensive sampling of 71 sites on São Tomé reported the presence of two species: *Simulium (Pomeroyellum) alcocki* Pomeroy, 1922, and *S. (Anasolen) dentulosum* Roubard, 1915, the latter being the most abundant (Grácio 1999). In 1998, the São Tomé endemic *S. (Pomeroyellum) santomi* Mustapha, 2004 was added to the list (Mustapha et al. 2004). On Príncipe, only *S. dentulosum* is confirmed. No effort has been made to sample black flies on São Tomé or Príncipe during the last 20 years, and it has been suggested that they are absent from Annobón (Mustapha et al. 2004).

Family Ceratopogonidae

This family of biting midges includes 6206 species in 112 genera and has a diverse fossil record (around 300 species; Borkent and Dominiak 2020). Many species of Ceratopogonidae are important pollinators, and only four genera are known to have species that feed on blood of vertebrates, including humans (Borkent 2004): *Austroconops* Wirth and Lee, 1958, *Culicoides* Latreille, 1809, *Forcipomyia* (subgenus *Lasiohelea*) Meigen, 1818 and *Leptoconops* Skuse, 1889. *Austroconops* is the only genus that is not known to play a role in pathogen transmission, while *Culicoides* is the most important in this regard (Borkent 2004). *Culicoides* includes 1347 described species, and the assessment of this diversity has received much attention in Africa because of their status as vectors of human filarial nematodes (Agbolade et al. 2006), and of several viruses responsible for animal diseases, such as Bluetongue (Mellor 1990) and African Horse Sickness (Mellor et al. 2000; Mellor

and Hamblin 2004). *Culicoides* are also known vectors of avian malaria-like parasites of the genera *Haemoproteus* (*Parahaemoproteus*) and *Leucocytozoon* (*Caulleryi*) (Valkiūnas 2004). On São Tomé, approximately 20% of the birds are infected with these parasites, with a higher prevalence in shaded plantations (Reis et al. 2021). Among the species of *Culicoides*, several can transmit *Haemoproteus*, but vector competence of *Culicoides* species remains unknown.

The first four species of *Culicoides* recorded on São Tomé were collected during the Percy Sladen and Godman Trust expeditions in the 1930s (Edwards 1934), and identified as *C. austeni* Carter, Ingram and Macfie, 1920, *C. distinctipennis* Austen, 1912, *C. citroneus* Carter, Ingram and Macfie, 1920 and *C. grahamii* Austen, 1909. A three-year study of insects in cocoa plantations identified 25 species of Ceratopogonidae, including only one *Culicoides* species: *C. imicola* Kieffer, 1913 (Wirth and Derren 1976). This fifth species recorded on the island is a known primary vector of Bluetongue and African Horse Sickness viruses, largely distributed in Africa, Asia, and Europe (Guichard et al. 2014). *C. distinctipennis*, *C. milnei* Austen, 1909 and *C. imicola* were later mentioned as present on São Tomé (Glick 1990), the latter being the sixth *Culicoides* species recorded on the island. Since the mid-1970s, there has been no evaluation of the diversity of *Culicoides* on São Tomé and Príncipe Islands, and the number of species is thus likely underestimated. There are 156 species formally described in the Afrotropical region (Labuschagne 2016), including high diversities on neighboring mainland African countries, such as Nigeria (Dipeolu 1976) and Cameroon (Callot et al. 1965; Wanji et al. 2019). Gabon is an exception since only six species have been described so far, probably due to very few studies carried out in that country (Delécolle et al. 2013; Augot et al. 2017). In 2019, nine species of *Culicoides* were found in the southeast of São Tomé, along transects from the center of an oil palm plantation to the native forest. While morphological and molecular investigations are ongoing, it is likely that seven species will be added to the records for the island (Appendix). From the four species first recorded for the island (Edwards 1934), only *C. citroneus* and *C. distinctipennis* were found recently. Surprisingly, no endemic *Culicoides* species have been found yet. Considering sampling bias in these islands, it is likely that future studies in different habitat types, especially deeper in the native forest, or in coffee and cocoa plantations, will reveal the presence of endemic *Culicoides* species. Future surveys will most certainly also increase the number of *Culicoides* species on Príncipe and Annobón, as well as clarify their ecology.

Suborder Brachycera

Family Tabanidae

Worldwide, there are currently close to 4400 species and subspecies, and 144 genera of Tabanidae described (Mullens 2019). Tabanid flies of the genera *Tabanus*, *Chrysops*, and *Hybomitra*, commonly known as horseflies and deerflies, are of economic, medical, and veterinary importance (Nevill et al. 1994). However, they

tend to be less studied than other Dipteran families (Baldacchino et al. 2014). Tabanid flies serve as biological vectors (pathogens replicate and develop within the fly), and as mechanical vectors (pathogens are transmitted without amplification and development within the fly via contaminated blood on mouthparts) of several wildlife and livestock pathogens, such as *Trypanosoma* spp. (Nevill et al. 1994), *Babesia* spp., and *Theileria* spp. (Taioe et al. 2017), filarial nematodes, and numerous viruses and bacteria (Baldacchino et al. 2014). In forested Central Africa, tabanid flies of the genus *Chrysops* also infect humans with *Loa loa* Cobbold, 1864, which causes African eye worm (Mullens 2019). This pathogen has not been reported in São Tomé and Príncipe.

Six species in the genus *Tabanus* have been recorded on São Tomé and Príncipe: *T. biguttatus* Wiedemann, 1830; *T. congoiensis* Ricardo, 1908; *T. obscurefumatus* Surcouf, 1906; *T. taeniola*, Palisot de Beauvois, 1806; *T. principis* Bequaert, 1930 (Bequaert 1930) and *T. monocallus* (Travassos Santos Dias 1955), the last two being endemic to the Gulf of Guinea islands. No new tabanid flies have been recorded on the archipelago in recent years.

Family Glossinidae

Glossinidae includes the single genus *Glossina* with 23 species, 6 of which are further divided into 14 subspecies, all but one found in Africa (Krinsky 2019). The genus is divided into three groups based on their ecological preferences: the savannah flies (subgenus *Morsitans*), the forest flies (subgenus *Fusca*), and the riverine flies (subgenus *Palpalis*). Species found in sub-Saharan Africa are vectors of the *Trypanosoma* parasites that cause sleeping sickness in humans (Welburn et al. 2001) and trypanosomiasis in livestock (Meyer et al. 2016) and can have severe impacts on domestic cattle production (De Geier et al. 2020).

The first known introduction of the tsetse fly, *G. p. palpalis*, occurred on Príncipe Island in 1825 (Fraga de Azevedo et al. 1956). At the end of the nineteenth century and beginning of the twentieth century, it became a significant health issue for cocoa plantation workers and local inhabitants, forcing important prophylactic measures between 1911 and 1914, which included hunting for flies, swamp drainage, clearance of vegetation and slaughter of wild pigs, stray dogs, and civets (Bruto da Costa 1913). The prevalence of *Trypanosoma* dropped dramatically (Bruto da Costa 1913), and in 1914 the tsetse fly was considered eradicated in Príncipe (Figueiredo Moura da Silva 2019). In 1956, entomologists rediscovered large numbers of tsetse fly on Príncipe (Tendeiro 1956) and suggested it had been reintroduced from Bioko Island. Although no cases of trypanosomiasis were found in humans, animals or in the tsetse flies, important measures were applied again to eradicate the tsetse flies, including trapping flies, insecticide spraying, clearing of vegetation, and killing of wild pigs, monkeys, and dogs (Fraga de Azevedo et al. 1956). Eradication was effective by July 1958.

Order Siphonaptera

Two flea species, *Ctenocephalides felis* Bouché, 1935 (cat flea; Family Pulicidae) and *Tunga penetrans* Linnaeus, 1758 (chigoe flea; Family Tungidae), occur in São Tomé and Príncipe. A high percentage of dogs seem to have cat fleas infected with *Rickettsia felis*, an emerging human pathogen often causing febrile illness, while just over 3% of humans had antibodies against this bacterium (Tsai et al. 2020).

Class Arachnida

Order Ixodida

The Ixodida contains three families: Ixodidae, Argasidae, and Nuttalliellidae (Nicholson et al. 2019). The Ixodidae or hard-bodied ticks include 15 genera and 707 species, while the Argasidae or soft-bodied ticks contain about 190 species, and the Nuttalliellidae only one species. Worldwide, they are the most important disease vectors in the veterinary field and are second only to mosquitoes in public health importance (Nicholson et al. 2019). Ticks are ectoparasites that blood-feed on mammals, birds, reptiles, and amphibians, but unlike the short blood-feeding periods (at most a few minutes) of Diptera, hard-bodied ticks attach and stay on their hosts for several days. They are implicated in the transmission of numerous infectious diseases caused by pathogens, such as bacteria (e.g., *Rickettsia*, *Borrelia*, *Coxiella*; Parola et al. 2013), viruses (e.g., Crimean–Congo hemorrhagic fever virus, Tick-borne encephalitis virus; Hoogstraal 1979) and protozoa (e.g., *Babesia*; Nelder et al. 2016).

Family Ixodidae

Four species of hard-bodied ticks have been recorded through the years from São Tomé and Príncipe. *Amblyomma astrion* Dönitz, 1909 and *A. splendidum* Giebel, 1877, were collected on São Tomé, and *A. splendidum* on Príncipe (Tendeiro 1957). Subsequently, *Rhipicephalus decolaratus* (Koch, 1844) was collected on both islands (Travassos Santos Dias 1988). In the early 1980s, numerous adult cow and calf deaths on São Tomé were attributed to neurological complications, likely caused by heartwater, a tick-borne rickettsial disease of domestic and wild ruminants transmitted by *A. astrion* (Uilenberg et al. 1982). In 2016, *A. variegatum* Fabricius, 1794, was collected from cattle in the Agua Grande district on São Tomé (Hsi et al. 2020). A serological survey demonstrated the presence of Spotted fever group rickettsiae and Q fever (*Coxiella burnetti*) antibodies in people, which could explain continued reports of febrile illness in São Tomé human residents not due to malaria (Hsi et al. 2020).

Family Argasidae

To date, *Ornithodoros capensis* Neumann, 1901 is the only soft tick species reported for the islands (Travassos 1988). It is an ectoparasite of seabirds in the tropics and subtropics, and was collected in the nests of Brown Noddy *Anous stolidus* (Linnaeus, 1758), Black Noddy *A. minutus* (Boie 1844), and Sooty Tern *Onychoprion fuscatus* (Linnaeus, 1766), during an expedition to Tinhosas (small islets south of Príncipe) in 1970 (Travassos 1988). A recent census of seabird nests on these islets did not report ectoparasites (Valle et al. 2016; Bollen et al. 2018), but they may not have explicitly searched for them.

Distribution, Biology, and Habitat Specificity

In this section, we describe the habitat types and preferred environmental conditions of Culicidae and Simuliidae species, based on the observations of AJC and on the literature (Mourão 1964; Grácio 1999).

Mosquito Habitat and Distribution on São Tomé and Príncipe

Anthropophilic Mosquitoes

Mosquito species that regularly blood-feed on humans include disease vector species – *Ae. aegypti* (Fig. 15.1.1), *Ae. albopictus* (Fig. 15.1.2), *An. coluzzii* (Fig. 15.1.5), *Cx. quinquefasciatus*, and *Ae. circumluteolus* – and species not implicated as disease vectors – *Ae. nigricephalus* and *E. chrysogaster* (Fig. 15.1.3).

Immatures of *An. coluzzii*, vectors of malaria, are found mostly on the coast. They develop in direct contact with clear or eutrophic groundwater, in swamps, and in temporary pools, such as in roadside ditches, depressions in pathways, and between households (Fig. 15.2.1). Blood index values and low sporozoite rates in *An. coluzzii* sampled in 1997 and 1998 on São Tomé (Sousa et al. 2001) indicate that they are meso-endemic, feeding predominantly on dogs, followed by humans, and then pigs. In recent collections by AJC, *An. coluzzii* were also attracted to chicken.

Cx. quinquefasciatus (*Cx. fatigans* in Mourão 1964), a vector of filarial nematodes, is very common in urban areas. It bites humans at night inside homes, and often rests indoors or underneath houses along with *Anopheles* mosquitoes. They represent the majority of mosquitoes in the city of São Tomé (Mourão 1964). Immatures of *Cx. quinquefasciatus* are often found in very high numbers in unmaintained sewage systems and in artificial containers, such as barrels, gutters, tubs, or vats of water.

Ae. aegypti and *Ae. albopictus*, vectors of numerous viruses, primarily bite humans during the day. They have spread worldwide and become cosmopolitan



Fig. 15.1 Pictures of mosquito species: (1) *Aedes albopictus* (female); (2) *Aedes aegypti* (female); (3) *Eretmapodites chrysogaster* (female); (4) *Toxorhynchites brevipalpis* (male); (5) *Anopheles coluzzii* (female). Photo credits; Nil Rahola

(Paupy et al. 2009; Brown et al. 2011; Kraemer et al. 2019). Historically, they both laid eggs in tree cavities (e.g., *Erythrina* sp., *Chlorophora* sp.), but now they are considered container-breeding mosquitoes, as immatures often develop in discarded plastics, tires, and other rubbish that hold water, and in unused cisterns. Still, both species lay eggs in the abundant supply of tree cavities, as well as in fallen banana leaves, in São Tomé and Príncipe. In the past, *Ae. aegypti* was the most collected species (Mourão 1964), but its abundance seems to have decreased since *Ae. albopictus* became established in São Tomé and Príncipe (Reis et al. 2017), as in other parts of the world (Bargielowski and Lounibos 2016). The distribution of *Ae. aegypti* has now contracted into small enclaves, mostly at higher elevations on São Tomé, and is rarely collected on Príncipe.



Fig. 15.2 Examples of microhabitat of Culicidae: (1) Typical roadside ditch located on Príncipe with large numbers of *Anopheles coluzzii* larvae. Arrow points to fourth instar larva; (2) Typical slow-moving river edge on Príncipe supporting large numbers of *Uranotaenia micomelas* and *Culex decens* larvae; (3) Preferred daytime resting location for *Cx. cinerellus*, *Cx. nebulosus* and multiple *Uranotaenia* species in crab holes in road embankment in Alto Douro, São Tomé. Arrows point to *Culex* mosquitoes; (4) *Cx. cambournaci* larvae in water-filled *Heliconia rostrata* flower in Botanical gardens on São Tomé. Arrow points to larvae. Photo credits: Anthony Cornel

Ae. circumluteolus is localized and infrequently captured (human-biting at Mucumbli, São Tomé), and represents the only typical floodwater *Aedes* species on São Tomé, even though immatures have been found in ground pools and in artificial containers (Mourão 1964). This species is a known vector of significant arboviruses, such as Rift Valley Fever, Wesselsbron, Bunyamwera, and Pongola viruses in Africa (Braack et al. 2018).

Finally, *E. chrysogaster*, another pernicious daytime human blood-feeding mosquito, lays eggs opportunistically in trash, but mostly in natural containers, such as plant leaf axils, especially in fallen banana and palm leaves, or cocoa and coconut

shells. This species is present everywhere on the islands but is not known to transmit diseases in São Tomé and Príncipe.

Opportunistic Mosquitoes

Ae. nigricephalus, an opportunistic blood feeder, bites humans during the day and does not disperse far from brackish water estuaries and mangroves, where immatures develop in crab holes. *Cx. cinerellus* Edwards, 1922 is also specialized to develop in brackish water crab holes (Hopkins 1952).

Immatures of other abundant mosquito species, which are more likely to feed on birds, and only seldom feed on humans, such as *Cx. decens*, *Cx. antennatus*, and *Lutzia tigripes* (de Grandpré & de Charmoy, 1901) also occur in temporary water bodies. *Cx. decens* can be abundant on São Tomé (Mourão 1964), and its larvae were frequently found in artificial containers. On Príncipe, large numbers of larvae were found along slow-moving rivers (Fig. 15.2.2).

Immatures of other species that seldom bite humans (e.g., *Ae. tarsalis*, *Ae. gandarai*, *Culex macfieii* Edwards, 1923, *Cx. nebulosus*) and nectar feeders (*Toxorhynchites capelai* and *T. brevipalpis*; Fig. 15.1.4), develop in tree holes and less so in banana or plant leaf axils. Rotting coconut fruits serve as significant sites for the development of *Cx. (Culiciomyia) nebulosus*, while adults primarily rest in crab holes (Fig. 15.2.3). Interestingly, immatures of *Cx. cambournaci* Hamon & Gandara, 1955 are often found in large numbers in the flowers of *Heliconia* species, which have been introduced from the neotropics as ornamentals (Fig. 15.2.4).

The immatures of other species including *Cx. annulioris* Theobald, 1901, *Cx. invidiosus* Theobald, 1901, *Cx. thalassius* Theobald, 1903, *Cx. tamsi*, *Culiseta fraseri*, *L. tigripes*, *Ur. capelai*, *Ur. principensis*, *Ur. balfouri* Theobald, 1904, *Ur. bilineata* and *Ur. connali* are typically found in river seepages, and rocky and thickly vegetated vernal pools. All these opportunistic mosquitoes are potential vectors of avian *Plasmodium*.

Black Fly Habitat and Distribution on São Tomé

Immature Simuliidae filter-feed in flowing waterways. Stream size, water velocity, and seston load are important factors that influence the distribution of black-fly species (Palmer and Craig 2000; Adler and McCreadie 2019). Interestingly, *S. alcocki* and *S. dentulosum* are not concomitant on São Tomé (Grácio 1999), *S. alcocki* is restricted to the northern interior part of the island, while *S. dentulosum* was more widespread. Their niches tend to show ecological allopatry with *S. dentulosum* found in rivers from sea level to 400 m, while *S. alcocki* occurs from 200 to 900 m above sea level. *S. alcocki* immatures tend to be restricted to the first 10 cm of the water column, whereas *S. dentulosum* are found anywhere from close to the surface to 50 cm below the surface. Finally, *S. dentulosum* seems to

prefer streams or rivers with weak water flow (78 cm/s, 87% of oxygen on average), contrary to *S. alcocki* which prefers faster water flow (122 cm/s, 98% of oxygen on average; Grácio 1999). Re-sampling the same sites would be ideal to evaluate if the habitat and microhabitat specificity of these two species have changed over time. We suspect *S. alcocki* as the main vector of *Leucocytozoon* spp. in birds, since both vectors and parasites are found in greater abundance at higher elevations.

Directions for Future Disease Insect Vector Research

Sampling Effort in Diverse Habitats and Specific Vector Families

Among all expeditions and surveys that aimed to collect vectors, we discern two major sampling paucities. First, the forested interior of São Tomé, in the Obô Natural Park, and the forested south of Príncipe are poorly studied. The main reason is probably accessibility, since reaching remote native forest requires long walks and camping. While mosquitoes have been quite well sampled along the entire coast, and also in some parts of the interior of the islands, other families such as Ceratopogonidae or Tabanidae have been sampled in few sites, and do not include all habitat types found on the islands. Second, Annobón has been poorly sampled for all groups. Although the island is small (17 km²) and more isolated, we estimate that some of its arthropod vectors are not yet described. We believe that the Gulf of Guinea oceanic islands are still full of surprises and that all three islands have the potential to hold undescribed arthropod vectors.

Surprisingly, there are no records of louse flies (family Hippoboscidae) and sand flies (family Psychodidae, subfamily Phlebotominae) on the islands. Louse flies, also known as bird flies, flat flies, or ked flies (Reeves and Lloyd 2019), are vectors of *Haemoproteus* parasites in Columbidae birds (Valkiūnas 2004), which have been detected in the blood of *Columba larvata* and *C. malherbii*, both on São Tomé and Príncipe (Loiseau et al. 2017; Reis et al. 2021). Thus, the presence of louse flies on São Tomé and Príncipe islands is highly suspected, even though no record has been published yet. Collection of louse flies can only be done on live birds, or by checking livestock coats. It is also somewhat surprising that no sand fly species have been found on any of the islands, although no surveys have specifically searched for them. Surveys should be done preferentially during the rainy season since these insects are highly seasonal, with abundance peaks during or right after rain (Munstermann 2019). *Leishmania* parasites, transmitted by sand flies, are present in Central Africa (Alvar et al. 2012) but have never been reported on the islands, supporting the hypothesis that these vectors might be absent.

New Complementary Tools to Evaluate Vector Diversity

Skilled entomologists can identify species morphologically, if they have access to updated descriptions and identification keys (Hajibabaei et al. 2007). Distinguishing characters, especially subjective ones that are used in identification keys, at the different stages (i.e., eggs, larvae, and adult specimens) are perceptively difficult for non-experts, particularly in the tropics where the diversity is often high and many species are similar. Recent developments in molecular identification techniques, coupled with reduced sequencing costs can help overcome these identification difficulties, and even reveal cryptic biodiversity. Identification of species using metabarcoding approaches on environmental DNA (eDNA) (Boerlijst et al. 2019; Krol et al. 2019) and on bulk samples (Batovska et al. 2018) is an appealing option, but it is worth noting that sequences belonging to unknown taxa are still a common problem in eDNA barcoding. Surveys of mosquito diversity using these techniques require a sound reference database, which in turn demands a considerable amount of a priori taxonomic work. This can be achieved by sequencing samples from the field and from natural history museums that have been identified by experienced entomologists.

Because dipping methods traditionally used to survey larvae may not always reflect adult diversity found with traps, determining and comparing species diversity across different types of samples (water, soil, or bulk samples) using metabarcoding might be a useful complementary approach. eDNA and bulk sample metabarcoding also show a high potential to become helpful monitoring tools to evaluate changes in relative abundance and species diversity in relation to habitat change and to detect invasive vector species in routine surveys. In addition, novel trap designs as well as visual and chemical lures to attract insects, including vector species, are always under development and may also increase surveillance and biodiversity determinations.

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Appendix

List of the arthropod vectors of the Gulf of Guinea Oceanic Islands of Príncipe (P) and São Tomé (ST).

Entomological data are almost non-existent for Annobón. Beside the record of *Anopheles coluzzii* on Annobón, and the absence of Simuliidae, we cannot state if

other vector species are present or absent. Status of each species was defined as resident (R), endemic (E), introduced (I), or no data (?)

Higher Taxonomy	Subgenus/Group	Species	P	ST
ORDER DIPTERA				
Family Culicidae				
<i>Anopheles</i> Meigen, 1818	<i>Anopheles</i>	<i>Anopheles coustani</i> Laveran, 1900		R
	<i>Cellia</i>	<i>Anopheles coluzzii</i> (<i>Anopheles gambiae</i> M form) Coetzee & Wilkerson, 2013	R	R
<i>Aedes</i> Meigen, 1818	<i>Aedimorphus</i>	<i>Aedes nigricephalus</i> Theobald, 1901	R	R
		<i>Aedes</i> sp. indet	E	
	<i>Catageomyia</i>	<i>Aedes tarsalis</i> Edwards, 1927		R
	<i>Polyleptomyia</i>	<i>Aedes gandarai</i> Ramos, Capela & Ribeiro, 1994		E
	<i>Neomelaniconion</i>	<i>Aedes circumluteolus</i> Theobald, 1908		R
	<i>Stegomyia</i>	<i>Aedes aegypti</i> Linnaeus, 1762	R	R
<i>Aedes albopictus</i> Skuse, 1894		I	I	
<i>Culex</i> Linnaeus 1758	<i>Culex</i>	<i>Culex annulioris</i> Theobald, 1901		R
		<i>Culex antennatus</i> Becker, 1903	R	R
		<i>Culex decens</i> Theobald, 1901	R	R
		<i>Culex invidiosus</i> Theobald, 1901		R
		<i>Culex quinquefasciatus</i> Say, 1826	R	R
		<i>Culex tamsi</i> Edwards, 1934		E
		<i>Culex thalassius</i> Theobald, 1903		R
	<i>Culiciomyia</i>	<i>Culex cambournaci</i> Hamon & Gándara, 1955		E
		<i>Culex cinerellus</i> Edwards, 1922		R
		<i>Culex macfieii</i> Edwards, 1923		R
		<i>Culex nebulosus</i> Theobald, 1901	R	
	<i>Eumelanomyia</i>	<i>Culex inconspicuus</i> Theobald, 1908	R	R
		<i>Culex rima</i> Theobald, 1901		R
		<i>Culex micolo</i> Ribeiro, Cunha Ramos & Capela, 1998		E
<i>Culiseta</i> Felt, 1904	<i>Theomyia</i>	<i>Culiseta fraseri</i> Edwards, 1914		R
<i>Eretmapodites</i> Theobald, 1901		<i>Eretmapodites chrysogaster</i> Graham, 1909	R	R
<i>Lutzia</i> Theobald, 1903	<i>Metalutzia</i>	<i>Lutzia tigriceps</i> De Grandpré & De Charmoy, 1900	R	R
<i>Toxorhynchites</i> Theobald, 1901	<i>Afrorhynchus</i>	<i>Toxorhynchites capelai</i> Ribeiro, 1993		E
		<i>Toxorhynchites brevipalpis conradti</i> Gruenberg, 1907	R	
<i>Uranotaenia</i> Lynch Arribálzaga, 1891	<i>Pseudoficalbia</i>	<i>Uranotaenia capelai</i> Ramos, 1993		E
		<i>Uranotaenia micromelas</i> Edwards, 1934	E	E
		<i>Uranotaenia principensis</i> Ramos, 1993	E	
	<i>Uranotaenia</i>	<i>Uranotaenia balfouri</i> Theobald, 1904		R
		<i>Uranotaenia bilineata</i> Theobald, 1909		R
		<i>Uranotaenia connali</i> Edwards, 1912		R

(continued)

Higher Taxonomy	Subgenus/Group	Species	P	ST
Family Simuliidae				
<i>Simulium</i> Latreille, 1802	<i>Pomeroyellum</i>	<i>Simulium alcocki</i> Pomeroy, 1922		R
		<i>Simulium santomi</i> Mustapha, 2004		E
	<i>Anasolen</i>	<i>Simulium dentulosum</i> Roubard, 1915	R	R
Family Ceratopogonidae				
<i>Culicoides</i> Latreille, 1809	–	<i>Culicoides citroneus</i> Carter, Ingrain et Macfie, 1920	?	R
	Subgenus <i>Avaritia</i>	<i>Culicoides grahamii</i> Austen, 1909	?	R
		<i>Culicoides imicola</i> Kieffer, 1913	?	R
		<i>Culicoides trifasciellus</i> Goetghebuer, 1935	?	R
	Subgenus <i>Meijerehelea</i>	<i>Culicoides distinctipennis</i> Austen, 1912	?	R
		<i>Culicoides enderleini</i> Cornet & Brunhes, 1994	?	R
	Group Milnei	<i>Culicoides austeni</i> Carter, Ingram and Macfie, 1920	?	R
		<i>Culicoides hortensis</i> Khamala, 1991	?	R
		<i>Culicoides krameri</i> Clastrier, 1958	?	R
		<i>Culicoides milnei</i> Austen, 1909	?	R
		<i>Culicoides quinquelineatus</i> Goetghebuer, 1934	?	R
	Group Neavei	<i>Culicoides neavei</i> Austen, 1912	?	R
	Group Nigripennis	<i>Culicoides sp.</i>	?	R
Family Tabanidae				
<i>Tabanus</i> Linnaeus 1758	Group Tabanini	<i>Tabanus biguttatus</i> Wiedemann, 1830		R
		<i>Tabanus congoiensis</i> Ricardo, 1908		R
		<i>Tabanus obscurefumatus</i> Surcouf, 1906		R
		<i>Tabanus taeniola</i> , Palisot de Beauvois, 1806		R
		<i>Tabanus principis</i> Bequaert, 1930	E	
<i>Tabanus monocallosus</i> Travassos Dias, 1955		E		
ORDER IXODIDA				
Family Ixodidae				
<i>Amblyomma</i> Koch, 1844		<i>Amblyomma astrion</i> Dönitz, 1909		R
		<i>Amblyomma splendidum</i> Giebel, 1877	R	R
		<i>Amblyomma variegatum</i> Fabricius, 1794		R
Family Argasidae				
<i>Ornithodoros</i> Koch, 1837	Subgenus <i>Alectorobius</i>	<i>Ornithodoros capensis</i> Neumann, 1901	*	

a Found on Tinhasas Islands

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