Chapter 1. Taxonomy, description and distribution of the mosquito Ae. aegypti

This chapter presents the taxonomic classification, nomenclature and systematics of the mosquito species Aedes aegypti and its two sub-species. Then the morphologic features of Ae. aegypti are described at successive stages: Eggs, Larvae (including differences with other mosquito genera), Pupae (showing sexual dismorphism), and Adults that present distinct characteristics of head, thorax and abdomen between male and female individuals. Elements on the origin of mosquito Ae. aegypti, and its current geographic distribution in tropical and subtropical regions of the world, are also provided.

Classification and nomenclature of Aedes aegypti

Classification (Taxonomy)

The family Culicidae is divided into three subfamilies: Toxorhynchitinae, Anophelinae and Culicinae, within which only subfamilies Anophelinae and Culicinae have medically-important mosquito species. The subfamily Culicinae includes over 3 050 species, belonging to 109 genera, of which the most important regarding health issues are the genera *Aedes, Culex, Mansonia, Haemagogus, Sabethes*, and *Psorophora* (Service, 2012; Tyagi, Munirathinam and Venkatesh, 2015).

The systematic classification of *Aedes aegypti* is presented in Table 1.1 and localises this species within the order Diptera, family Culicidae, subfamily Culicinae, tribe Aedini, genus *Aedes*, subgenus *Stegomyia*, and species *Aedes aegypti* (ITIS, 2014; WRBU, 2014).

TAXON	NOMENCLATURE (Authority)
Kingdom	Animalia (Margulis and Schwartz, 1998)
Subkingdom	Bilateria (Hatschek, 1888)
Infrakingdom	Protostomia (Grobben, 1908)
Superphylum	Ecdysozoa (Aguinaldo et al., 1997)
Phylum	Arthropoda (Latreille, 1829)
Subphylum	Hexapoda (Latreille, 1825)
Class	Insecta (Linnaeus, 1758)
Subclass	Pterygota (Lang, 1888)
Infraclass	Neoptera (Martynov, 1923)
Superorder	Endopterygota (Sharp, 1898)
Order	Diptera (Linnaeus, 1758)
Suborder	Nematocera (Berthold, 1827)
Infraorder	Culicomorpha (Wood and Borkent, 1989)
Family	Culicidae (Stephens, 1829)
Subfamily	Culicinae (Meigen, 1818)
Tribe	Aedini (Neveu-Lemaire, 1902)
Genus	Aedes (Meigen, 1818)
Subgenus	Stegomyia (Theobald, 1901)
Species	Aedes aegypti (Linnaeus, 1762)

Table 1.1. Standardised taxonomic hierarchy and nomenclature for Ae. aegypti (Linnaeus, 1762)

Source: ITIS (2014), *Aedes aegypti*, Integrated Taxonomic Information System (database), <u>www.itis.gov/servlet/SingleRpt/SingleRpt?search_topic=TSN&search_value=126240</u>; WRBU (2014), Mosquito Classification Comparison, 2013, The Walter Reed Biosystematics Unit. <u>Subspecies</u>. Human population increase and extension to wild habitats, in addition to the evolution of vector behaviour, are important phenomena that greatly influence the "domestication" and the constitution of subpopulations of many mosquitoes (Powell and Tabachnick, 2013). *Ae. aegypti* presents two subspecies or subpopulations:

- The first subspecies, *Ae. aegypti formosus*, is the ancestor of the domestic form of *Ae. aegypti* and still lives in forests and vegetated ecotones in sub-Saharan Africa (Lounibos, 1981). In addition to its attraction to tree holes for breeding habitats and egg laying, it has a preference for non-human blood as sources of blood meals (required by females for egg production) and feeds on wild animals. Morphologically, this form is much darker than the form adapted to human habitats (McClelland, 1974).
- The second subspecies, *Ae. aegypti aegypti* (often designated by the shorter name *Ae. aegypti*), is found globally in tropical and subtropical regions, typically in association with humans, but is absent from the interior of Africa south of the Sahara (Moore et al., 2013; Powell and Tabachnick, 2013). In contrast to the first subspecies, *Ae. aegypti aegypti* predominantly breeds in artificial containers provided by humans, also breeds indoors, and has a preference for feeding on human blood (Moore et al., 2013).

A third subspecies was previously thought to exist, *Ae. aegypti queenslandensis*, described as a light-coloured form found in the Mediterranean Basin (Mattingly, 1967). However, recent analysis suggests that *Ae. aegypti queenslandensis* is genomically identical to the second subspecies *Ae. aegypti aegypti* (Rašić et al., 2016).

Nomenclature

<u>Common names</u>. The usual common name for *Ae. aegypti* is the "yellow fever mosquito", as it is a principal vector for yellow fever. The closely-related species *Ae. albopictus* is often referred to as "Asian tiger mosquito". In colloquial language, "tiger mosquito" is sometimes used for naming both species indistinctly, drawn from the observation of their striped-colour abdomen.

<u>Synonyms</u>. If two or more names are found to apply to the same species, they are considered synonyms. The name *Ae. aegypti* (Linnaeus, 1762) is now in general use and has been for more than five decades. However, this species has appeared under many other names in the past, among the most cited are (ITIS, 2014; WRBU, 2014):

- *Culex aegypti* (Linnaeus, 1762)
- *Culex excitans* (Walker, 1848) and
- Culex taeniatus (Weidemann, 1828).

Recent studies have resulted in a number of generic and subgeneric changes to the classification of the tribe Aedini in Europe and other regions of the world. Among other changes, the subgenus *Stegomyia* was elevated to the category of genus for the species *Ae. aegypti* and *Ae. albopictus* (*Stegomyia aegypti* and *St. albopicta*, respectively) (Reinert and Harbach, 2005). In practice, it is rarely called *St. aegypti* and is still commonly referred to as *Ae. aegypti*.

Systematics

Ae. aegypti and Ae. albopictus populations seem to have different evolutionary histories, the former originated from Africa and the latter from South-East Asia. For Ae. aegypti, the general structure of the phylogenetic trees based on mitochondrial genes showed that most populations from South America were found to be genetically similar to populations from South-East Asia (Thailand and Viet Nam), except for one sample from Boa Vista (northern Amazonia), which was more closely related to samples from Africa (Côte d'Ivoire and Guinea). This suggests that African populations of Ae. aegypti introduced during the slave trade have persisted in Boa Vista, resisting eradication campaigns (Mousson et al., 2005).

Over the past 50 years, many population genetic studies of *Ae. aegypti* have documented large genetic differences among worldwide populations. Phylogenetic analyses, including through studies involving population genetics of *Ae. aegypti* s.1. using mitochondrial DNA markers, have shown that global collections fell into two clades (Tabachnick and Powell, 1979; Powell, Tabachnick and Arnold, 1980; Tabachnick, 1982, 1991; Lorenz et al., 1984; Wallis, Tabachnick and Powell, 1984; Tabachnick et al., 1985; Muñoz et al., 2013; Moore et al., 2013). One clade contained *Ae. aegypti* from East Africa, South America and the Caribbean, suggesting that these New World populations were derived directly from East African populations. The other clade containing subspecies *Ae. aegypti formosus* from both East and West Africa, suggesting an independent introduction of *Ae. aegypti* to Asia (Moore et al., 2013; Powell and Tabachnick, 2013). Further support for the existence of two principal clades worldwide is provided from studies in Africa (Brown et al., 2011; Delatte et al., 2011) as well as the New World (Bracco et al., 2007; Scarpassa, Cardoza and Cardoso Junior, 2008).

Morphology

Morphologic features have been used in many studies to describe variations among populations of the same species. Morphological characteristics of *Ae. aegypti* life stages are described in greater detail in the following sub-sections.

Eggs

Eggs of *Ae. aegypti* are long, smooth, more or less ovoid shaped, and approximately 1 mm long. They are white in colour when freshly laid but turn black as a result of melanisation about two hours after oviposition (this colour change is not exclusive to *Aedes* mosquito species) (Nelson, 1986; Service, 2012).

Aedes females lay individual eggs in artificial collections of water, often placed at varying distances from the water line. In addition, a female will preferably not lay the entire clutch at a single site, but rather spread the eggs over two or more sites in a practice known as "skip oviposition". Thus, the eggs stand a better chance of survival (Mogi and Mokry, 1980; Chadee, 1997; Harrington and Edmann, 2001; Foster and Walker, 2002). It was observed that eggs may be laid on successive occasions on the same site (Gillet, 1962) or in different sites (Fay and Perry, 1965; Chadee and Corbet, 1987). The practice of skip oviposition indicates the tendency of a female to avoid laying on surfaces that already bear her own eggs or those of conspecifics (Chadee, Corbet and Greenwood, 1990).

Ae. aegypti eggs can dry, survive desiccation, remain intact for several months and hatch when submerged with water. More details relating to their survival under different temperature and humidity conditions are given under the "Life cycle" section in Chapter 2.

Larvae

Ae. aegypti larvae resemble other mosquito larvae in their morphology; in general, they have an ovoid head, thorax, and abdomen of nine segments. The posterior segment (anal) has four lobed gills for osmotic regulation and a short barrel-shaped siphon bearing a single pair of subventral tufts for breathing at the water surface (Figure 1.1) (Nelson, 1986; Clements, 2000; Service, 2012). Additional morphologic characteristics include at least three pairs of setae in the ventral brush, antennae that are not greatly flattened, and a lack of enormous setae on the thorax. These characteristics are sufficient in distinguishing *Aedes* larvae from most others belonging to family Culicidae and subfamily Culicinae (Service, 2012).

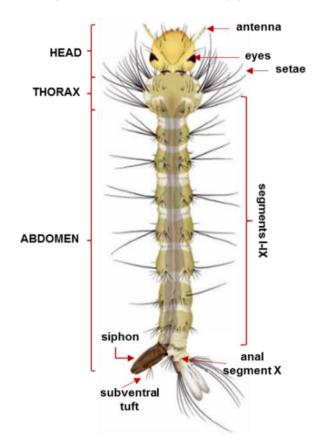
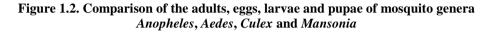


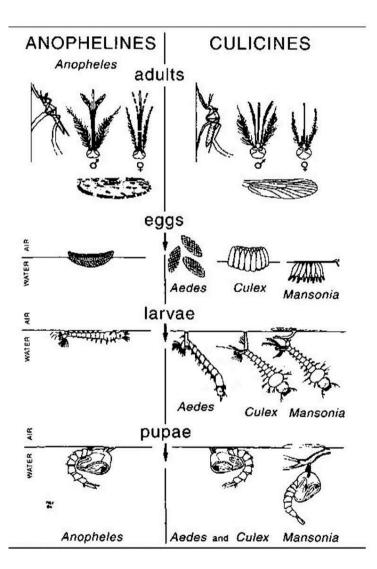
Figure 1.1. Dorsal view of Ae. aegypti larva

Source: Modified from Rueda, L. (2004), "Pictorial keys for the identification of mosquitoes (Diptera: Culicidae) associated with dengue virus transmission", in *ZOOTAXA 589*, Magnolia Press, Auckland, pp. 60.

The resting position at the water surface is also different among the various mosquito species: *Anopheles* larvae lay parallel to the water surface, *Culex* larvae rest at an angle and *Aedes* larvae hang almost vertically (Figure 1.2). The larvae pass through four instars (I, II, III, and IV respectively) with growth and changes in form and size occurring during

their development. The first instar *Ae. aegypti* larva is only about 1 mm in length, whereas in the fourth instar stage it reaches a length of approximately 8 mm (Schaper and Hernandez-Chavarria, 2006; Bar and Andrew, 2013a). Growth and development of larval instars is temperature dependent, however, complex interactions with other factors such as resource availability and intraspecific density also contribute to variation in development rate (Couret and Benedict, 2014). At cool environmental temperatures (around 15°C), *Ae. aegypti* larvae can remain in a particular instar for months, so long as the water supply is sufficient (Foster and Walker, 2002; Bar and Andrew, 2013a; Brady et al., 2013).



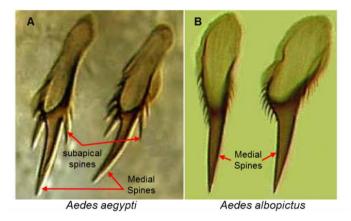


Source: Modified from Warrell, D.A. and H.M. Gilles (eds.) (2002), Essential Malariology, 4th Ed., Hodder Arnold, London, pp. 350.

The most distinguishing characteristics facilitating the differentiation of *Ae. aegypti* larvae from many other species of the *Aedes* genus are the 2 lateral spines on each side of

the thorax and the straight row of 7 to 12 comb scales on the 8^{th} abdominal segment. *Ae. aegypti* exhibits a medial spine with stout, subapical spines (Figure 1.3, panel A) which are absent in *Ae. albopictus* (Figure 1.3, panel B) (Nelson, 1986).

Figure 1.3. Comb scales of *Ae. aegypti* exhibiting a medial spine with stout, subapical spines and of *Ae. albopictus* without subapical spines

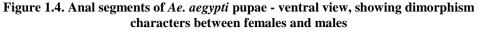


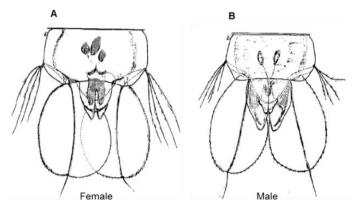
Source: Modified from Rueda, L. (2004), "Pictorial keys for the identification of mosquitoes (Diptera: Culicidae) associated with dengue virus transmission", in *ZOOTAXA 589*, Magnolia Press, Auckland, pp. 60.

Pupae (sexual dimorphism)

The pupa is the stage of the life cycle of mosquitoes that follows the last larval instar and precedes the adult stage. Pupae are comma-shaped, composed of two main sections, cephalothorax (head and thorax fused) and abdomen (Nelson, 1986; Service, 2012). At the base of the cephalothorax of the pupa is a pair of breathing tubes or "trumpets" that pierce the water surface to allow breathing (Nelson, 1986). At the tip of the abdomen there is a pair of oars or paddles used for swimming, which in the female (Figure 1.4, panel A) are wider and overlap, but in the male (Figure 1.4, panel B) are narrow and separated (Vargas, 1968).

Another morphologic difference between female and male pupae is their overall size, with the female usually being larger than the male (Figure 1.4). Since the range in body size between female and male pupae overlaps considerably and can be affected by both biotic and abiotic, including environmental factors such as diet, temperature, rearing conditions, overcrowding, it is deemed necessary to select additional sexually dimorphic characteristics such as the differences in paddles in order to determine the sex of pupae (Vargas, 1968).





Source: Modified from Vargas, V.M. (1968), "Sexual dimorphism of larvae and pupae of Ae. aegypti (Linn.)", Mosquito News, Vol. 28, pp. 374-379.

Adults (male and female)

The body of an adult *Ae. aegypti* mosquito is composed of head, thorax, and abdomen (Figure 1.5). *Ae. aegypti* males and females are similar in appearance except for the differences in size and form of the antennae (males have plumose antennae), maxillary palps (females have shorter palps), abdomen, claws and in scale markings (Bar and Andrew, 2013b). These differences are described in detail below.

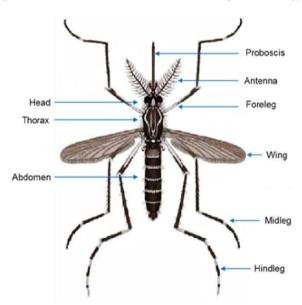


Figure 1.5. Dorsal view of the female mosquito Ae. aegypti

Source: Modified from Rueda, L. (2004), "Pictorial keys for the identification of mosquitoes (Diptera: Culicidae) associated with dengue virus transmission", in *ZOOTAXA 589*, Magnolia Press, Auckland, pp. 60.

Head

In both male and female *Ae. aegypti*, dorsally the head is globular in shape and laterally convex with a vertex that has silvery-white flat scales. The female clypeus has two silvery white dots, whereas the male has no dots. Females have a larger head capsule $(0.55 \pm 0.09 \text{ mm})$ than males $(0.53 \pm 0.06 \text{ mm})$ (Bar and Andrew, 2013b). The head bears several structures critical to the mosquito's ability to feed as well as to act as a vector of human diseases.

<u>Mouthparts</u>. The mouthparts in these mosquitoes include a pair of maxillary palps, which have five white scale bands and are longer $(0.77 \pm 0.06 \text{ mm})$ and more developed in males than in females $(0.53 \pm 0.06 \text{ mm})$ (Bar and Andrew, 2013b). The proboscis is longer in males $(0.76 \pm 0.04 \text{ mm})$ than in females $(0.66 \pm 0.03 \text{ mm})$ (Bar and Andrew, 2013b). However, only in females is this structure adapted for skin penetration to enable blood feeding, even though they may survive in nature by sucking plant juices. The male proboscis is adapted to feed on nectar and plant juices rich in carbohydrates (Clements, 1992).

<u>Antenna</u>. Each antenna of *Ae. aegypti* arises from a globular pedicel, has 13 flagellar segments and a greatly reduced scape. Males have longer antennae $(0.57 \pm 0.03 \text{ mm})$ than females $(0.52 \pm 0.07 \text{ mm})$. The antennal hairs are bushy and plumose in males whereas in females they are smaller and less dense (Nelson, 1986; Bar and Andrew, 2013b).

Thorax

Females of *Ae. aegypti* have a larger thorax measuring 0.50 ± 0.08 mm in length and 0.35 ± 0.07 mm in width while the shorter male thorax is 0.41 ± 0.06 mm in length and 0.29 ± 0.02 mm in width. The thorax of *Ae. aegypti* is black or dark brown coloured and consists of the pro-, meso-, and metathoracic segments, which together bear the wings (one pair), legs (three pairs), and halteres (one pair) (Bar and Andrew, 2013b).

Many, but not all, *Aedes* adults have conspicuous patterns on the thorax formed by white or silver coloured scales (Service, 2012), and these patterns vary between species. An example of the difference across species is the case of *Ae. aegypti* with its typical, white, lyre-shaped markings (Figure 1.6, panel A), compared to *Ae. albopictus* with its median-longitudinal white stripe (Figure 1.6, panel B) (Nelson, 1986). The scutellum in *Ae. aegypti* is three-lobed with each lobe having silvery white scale patches, and a few dark scales at the apex of the midlobe (Bar and Andrew, 2013b).

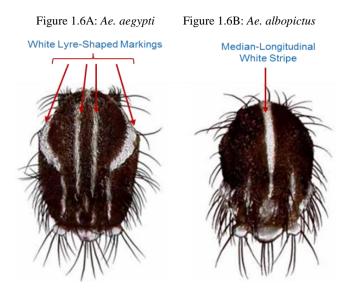


Figure 1.6. Comparative dorsal view of thoracic scutum of Ae. aegypti and Ae. albopictus

Source: Modified from Rueda, L. (2004), "Pictorial keys for the identification of mosquitoes (Diptera: Culicidae) associated with dengue virus transmission", in *ZOOTAXA 589*, Magnolia Press, Auckland, pp. 60.

At the same time, adults of *Aedes* and other Culicinae may be distinguished from adult *Anopheles* mosquitoes by their shorter palps and their resting position which is more horizontal or parallel to the resting surface (Nelson, 1986; Service, 2012).

Abdomen

The abdomen consists of eight segments covered with black and white scales forming distinctive patterns in both males and females. In females, the eighth segment is greatly reduced. The tergites (dorsal portion of each abdominal segment) are dark brown in colour and the first abdominal segment has a patch of pale, median scales. The dorsal side of abdominal segments II through VII has transverse white bands. The size of abdomen in males is larger (length 3.03 ± 0.18 mm and width 0.51 ± 0.07 mm) than in females (length 2.94 ± 0.20 mm and width 0.41 ± 0.06 mm) (Bar and Andrew, 2013b).

The posterior tip of the abdomen is narrow in males while in females it has a broad round shape. *Ae. aegypti* can be differentiated from most of the other Culicinae by their pointed abdomen and the absence of spiracular bristles (Service, 2012).

With age, the lyre-shaped markings on the thorax may disappear, but the distinctive white scales on the pedicel, clypeus, and tip of the palps, and the pattern of white scales on abdominal sternites (ventral plate on each abdominal segment) III-V, usually remain. These characteristics are essential for the identification of *Ae. aegypti* females with damaged morphological structures and to differentiate them from *Ae. albopictus* females (Nelson, 1986; Savage and Smith, 1995).

Origin and current geographic distribution

The likely origin of *Ae. aegypti* is the Ethiopian region of the tropical belt in Africa, from which it has spread to tropical and subtropical regions throughout the world in association with humans (Nelson, 1986; Powell and Tabachnick, 2013). *Ae. aegypti* was probably carried to other continents via trading and transport ships that resupplied in African ports

during the 15th century through to the end of the 17th (Christophers, 1960; Reiter, 1998). These ships carried freshwater reservoirs on board and could maintain breeding colonies of *Ae. aegypti* (Christophers, 1960), so it is probable that the species was introduced to the rest of the world via this means (Tabachnick, 1991).

To date, *Ae. aegypti* is an invasive tropical species worldwide with a cosmopolitan habitat from 40° N to 40° S latitude (a range extending across all or most of the world in appropriate habitats).

Ae. aegypti is usually tolerant to temperatures ranging from 14°C to 30°C (Hemme et al., 2010; Brady et al., 2013, 2014). Under optimal conditions of temperature and humidity, the embryo needs two to three days for full development from oviposition to the next stage of the life cycle. The definition of physiological embryonic parameters within this temperature range correlates with the presence of Ae. aegypti in tropical and subtropical regions of the world (Farnesi et al., 2009). Larval development in Ae. aegypti is a function of temperature, and these effects have been well studied. Temperature also impacts on adult size, dry weight, and ovariole number, all of which decrease as the temperature increases (Christophers, 1960; Rueda et al., 1990). High extreme temperatures alone (> 40° C) are unlikely to limit the species, but low temperatures are a limiting factor. Below 15°C, adult Ae. aegypti mosquitoes become torpid, unable to fly, and can move their limbs only slowly (Christophers, 1960; Rowley and Graham, 1968; Yang et al., 2009). Lower temperatures can slow development to such a degree (where egg-to-adult cycles are longer than 45 days) that the species is prevented from establishing itself in the environment, although human habitations may afford some seasonal protection.

Rain quantity and frequency (precipitation level) is another factor which, combined with temperature, affects the sustainable establishment of the species in a given area.

Global historical collections and laboratory experiments on this well-studied vector have suggested its distribution is limited by the 10°C winter isotherm¹ (Christophers, 1960), while a more recent and complex stochastic population dynamics model analysis suggests the temperature's limiting value to be more towards the 15°C yearly isotherm (Otero, Solari and Schweigmann, 2006). Scholte et al. (2010) indicated that *Ae. aegypti* could not survive winter temperatures in Northern Europe. The predicted global distribution of *Ae. aegypti*, based on occurrence data as well as environmental and land-cover variables, is shown in Figure 1.7 (Kraemer et al., 2015).

Notes

¹ An isotherm is a line on a map or chart of the earth's surface connecting points having the same temperature at a given time or the same mean temperature for a given period.

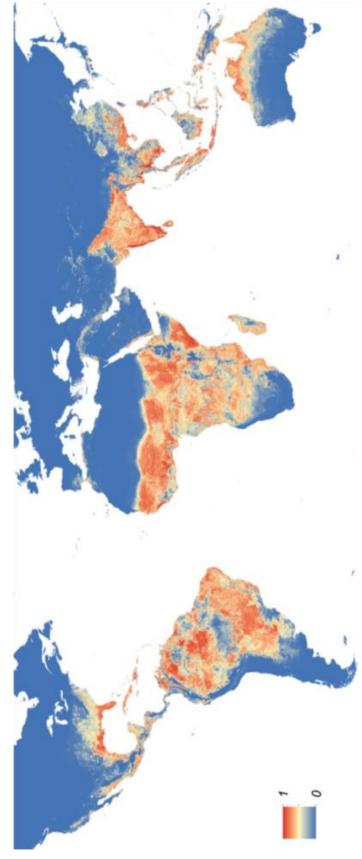


Figure 1.7. Global map of the predicted distribution of Ae. aegypti

Note: The map depicts the probability of occurrence. • Blue (dark grey) = 0 • Red (light grey) = 1 Source: Kraemer, M.U.G. et al. (2015), "The global distribution of the arbovirus vectors Aedes aegypti and Ae. albopictus", eLife, Vol. 4: e08347.

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