Aedes aegypti and *Aedes albopictus*: Life cycle, biology and distribution.

(all diagrams, figures and photographs produced by D. Nimmo)

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i Introduction

The mosquitoes, or Culicidae, are a family of about three and a half thousand species within the order Diptera, the two-winged flies. They are one of the more primitive families of Diptera, being more closely related to midges, gnats and crane flies, for example, than to houseflies and blowflies. Mosquitoes are found throughout the world except in places that are permanently frozen. Three quarters of all mosquito species live in the humid tropics and subtropics, where the warm moist climate is favourable for rapid development and adult survival, and the diversity of habitats permitted the evolution of many species. Mosquitoes are classified into three subfamilies, the largest and most diversified of which is divided into a number of tribes:

Family	**Culicidae:**			
Subfamily		Toxorhynchitinae		
		Anophelinae		
		Culicinae:		
Tribes			Sabethini	
			Culicini;	
Genus			*Coquillettidia*	
			Culex	
			Culiseta	
			Deinocerites	
			Haemagogus	
			Mansonia	
			Orthopodomyia	
			Psorophora	
			Uranotaenia	
			Aedes;	
Species				***aegypti***
				albopictus
				stimulans
				sierrensis etc...

Like other true flies, culicids exhibit 'complete metamorphosis', i.e. the juvenile form passes through both larval and pupal stages. The larvae are anatomically different from the adults, live in a different habitat and feed on a different type of food. Transformation to the adult takes place during the non-feeding pupal stage.

Aedes aegypti (also known as *Stegomyia aegypti* [(1)]), commonly known as the *yellow fever mosquito* (although more appropriately, because it transmits far more of this virus, it should be known as the dengue mosquito), is a mosquito that can transmit dengue fever, Chikungunya, yellow fever, West Nile virus and several other viruses.

Aedes albopictus, commonly known as the Asian tiger mosquito or forest day mosquito, is characterized by its black and white striped legs and small, black and white body. This species is able to survive in a wide range of habitats and conditions. The Asian tiger mosquito has a rapid bite that allows it to escape most attempts by people to swat it. This mosquito has become a significant pest in many communities because it closely associates with humans (rather than living in wetlands), and typically flies and feeds in the daytime rather than at night or at dusk and dawn. It is a container and puddle breeder, needing only a few ounces of water to breed. *Aedes albopictus* can transmit Eastern equine encephalitis virus and dengue fever.

ii The life cycle (overview)

The mosquito goes through four separate and distinct stages of its life cycle: Egg (1), Larva (2), Pupa (3), and Adult (4). In the case of *Aedes* eggs are laid one at a time on a moist surface. Most eggs hatch into larvae within 48 hours if submerged in water. But in the case of *Aedes aegypti* and *Aedes albopictus* the eggs are resistant to desiccation and can survive out of water for up to a year. Both *Aegypti* and *albopictus* can survive in very small pools of water like the rim of a plant container or a coke can. The larvae grow and develop through four instars before developing into pupae. Adult mosquitoes then emerge from the pupae after about 48 hrs. This whole process from egg to adult can take as little as 6-9 days, dependent on temperature. The adult females, after they have mated, then search for a suitable bloodmeal (males do not bloodfeed), *aegypti* has become specialised on feeding on humans, *albopictus* does feed on humans but not as exclusively as *aegypti*. The females develop eggs over the following 2-3 days and then lay them on a suitable moist surface, completing the life cycle.

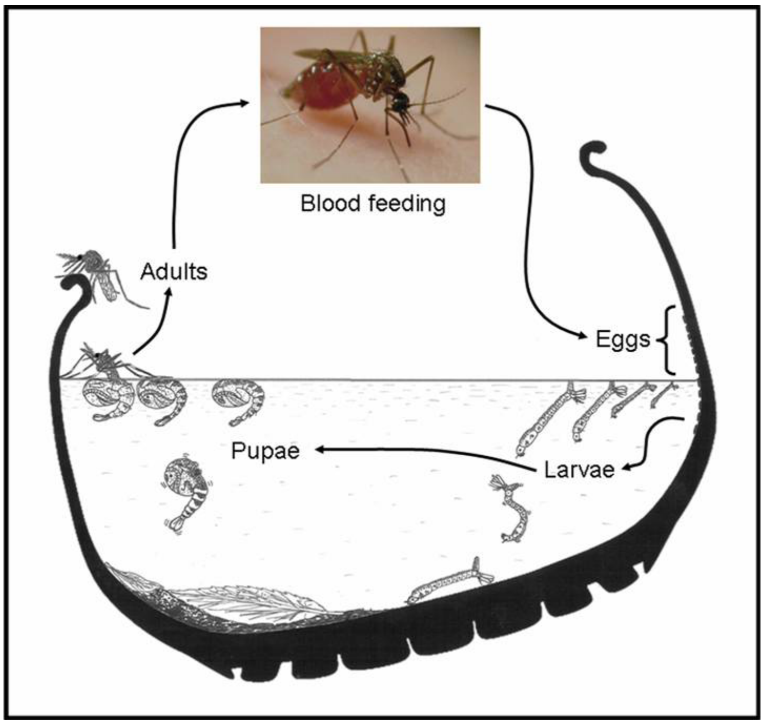


Figure 1; *Aedes* life cycle diagram.

iii

Female mosquitoes lay some 50 to 500 eggs at one time, depositing them on water or

The eggs

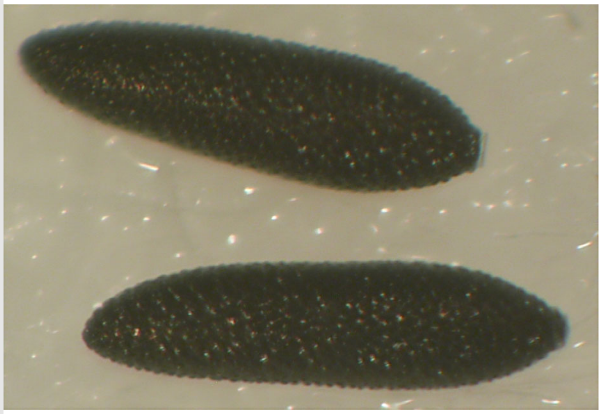


Figure 2; *Aedes aegypti* eggs.

on sites that will be flooded. *Aedes aegypti* and *albopictus* typically lay between 50 and 120 eggs. Each egg is protected by an egg shell. Spermatozoa stored by the inseminated female fertilize the oocytes as they are ovulated, and embryonic development starts almost immediately after the eggs have been laid. Within one to two days to a week or more, depending on temperature, the embryo develops into a fully formed larva. In most species the larva hatches once it is formed, and can survive for a few days at most in the absence of water. Mosquitoes of the tribe Aedini (*Aedes aegypti* and *albopictus*) have water-proofed egg shells capable of resisting desiccation, and fully-formed but unhatched aedine larvae can survive for months or even years in the absence of free water. Aedine species lay their eggs in places that may not be flooded for days, weeks or months. A fall of rain that inundates oviposition sites, or a high tide flooding a salt marsh, stimulates hatching and can lead to an apparent population explosion.

iv
The larvae

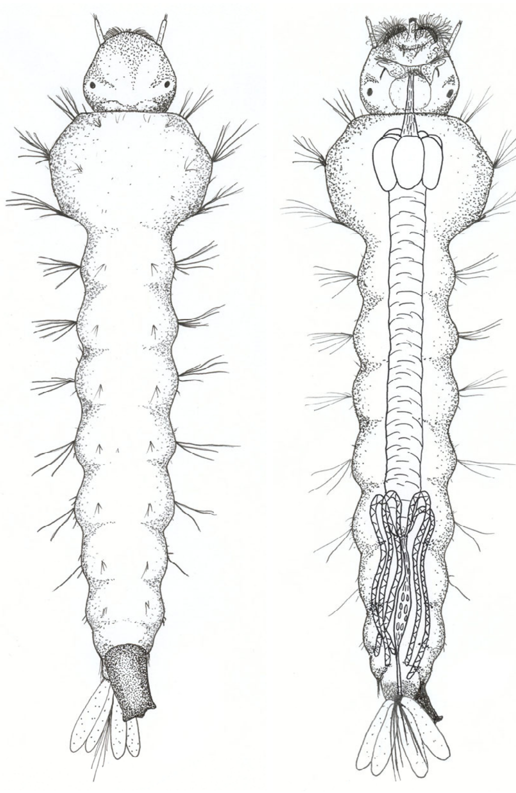


***Figure 3; Aedes aegypti* larvae.**

Mosquito larvae are legless, but they retain a well-formed head and so do not appear maggot-like. The larval habitats are small or shallow bodies of water with little or no water movement typically shallow pools, sheltered stream edges, marshes and water-filled tree holes, leaf axils or man-made containers. The habitats range in size from animal footprints to marshes and rice fields. Most species live in fresh water but a few are adapted for a life in brackish or saline water in salt marshes, rock pools or inland saline pools. All aquatic animals have problems of water and salt balance, whether they live in fresh or salt water, and the means by which mosquito larvae have solved these problems has been the subject of much investigation. In addition to the usual internal organs of ion regulation, mosquito larvae have four external balloon-like anal papillae, which are capable of ion uptake from very dilute solution. When it hatches from the egg the young mosquito larva is fully adapted for living in water, and two features determine its manner of life: use of atmospheric oxygen for respiration and use of water borne

particles as food.
The air breathing habit requires mosquito larvae either to live more or less permanently at the air/water interface, as most anopheline and some culicine larvae do, or to make frequent visits to the water surface. The only functional respiratory openings are a pair of spiracles, near the end of the abdomen, from which air filled tracheae extend to all parts of the body.
The spiracles of culicine and toxorhynchitine larvae are situated at the end of a tube or siphon, and the larvae hang downwards from the surface membrane by their siphons with their spiracles open to the air. The spiracles of anopheline larvae are flush with the dorsal surface of the last abdominal segment, and the larvae lie horizontally below the surface membrane, their spiracles opening through it. Larvae of two culicine genera (Mansonia and Coquillettidia) are able to remain permanently submerged. They live with their respiratory siphons, which have modified saw, like tips, forced into the air-filled tissues that fill the stems and roots of certain aquatic plants.
The characteristic food resource of mosquito larvae is 'particulate matter'. This includes aquatic micro organisms, such as bacteria, diatoms and algae, and also, as an important component, particles of detritus that are largely derived from decayed plant tissues. Such particles provide food for diverse aquatic invertebrates, which filter them from the water by a variety of mechanisms. Mosquito larvae, which live mainly in still water, are exceptional in not relying on natural water currents to bring the particles to them. Through the regular beating of their 'mouth brushes' mosquito larvae generate water currents which flow towards the head, and in a manner that is not well understood they separate particles of a certain size from the water. Anopheline larvae typically feed at the water surface, in a particle-rich layer just below the surface membrane. Culicine larvae feed on particles suspended in the water column, and many supplement this feeding mode by abrading with their mouthparts the layers of organic matter that cover submerged surfaces, so generating new particles. Toxorhynchitine larvae are predatory on small invertebrates, as are a very few species in the other two subfamilies.
The growing mosquito larva moults four times. On the first three occasions that it leaves its cast cuticle the larva appears very much as before. During the period of the fourth moult the imaginal disks develop rapidly, changing the form of the insect crudely to that of an adult, and the organism that leaves the fourth larval skin is a pupa. The rapid growth rates (5-10 days from hatched larvae to adult) of many tropical species permit the exploitation of transient water bodies.

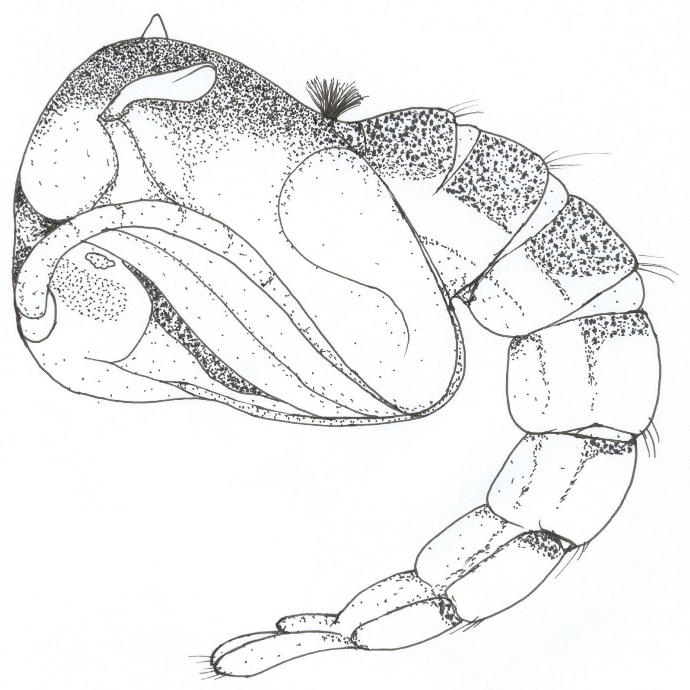
v

The pupae

The pupa remains an aquatic organism. The pupal stage is a resting, non-feeding stage of development, but pupae are mobile, responding to light changes and moving (tumble) with a flip of their tails towards the bottom or protective areas. That it has assumed the form of an adult is largely concealed because the head and thorax, with their elongate appendages are cemented together in the form of a cephalothorax. This process is similar to the metamorphosis seen in butterflies when the butterfly develops - while in the cocoon stage - from a caterpillar into an adult butterfly. The abdomen, which now terminates in two large paddles, has retained the strong larval musculature and is an effective organ of propulsion. An air bubble, which is enclosed

Figure 4;

Aedes aegypti pupa (female).



between the appendages, provides buoyancy, and the pupa floats at the water surface with the top of its thorax in contact with the surface membrane and its abdomen hanging down.

The new form and posture preclude use of the terminal abdominal spiracles for respiration. That function is taken over by the mesothoracic spiracles, which open within large 'respiratory trumpets'. As the pupa floats at the air/water interface the hydrophobic rims of the respiratory trumpets protrude through the surface membrane.

During the pupal stage certain larval organs are destroyed, e.g. the alimentary canal, while replacement adult organs are constructed from undifferentiated embryonic cells. Other organs, including the heart and fat body, are carried over to the adult stage. These final stages of metamorphosis can be completed within one to two days if the temperature is sufficiently high. When the adult is fully formed within the pupal cuticle, the insect rests at the water surface and starts to swallow air. The consequent increase in internal pressure forces a split along the midline of the pupal thoracic cuticle, and the adult slowly expands out of the pupal cuticle and steps on to the water surface.

vi The adults

Like many of the more primitive Diptera, adult mosquitoes have an elongate body and long wings and legs, which provide an aerodynamically stable form. The hind wings are modified as small oscillating sense organs, or halteres, which assist flight control. Like other Diptera, mosquitoes are fluid feeders. Exceptionally among the more primitive Diptera, their mouthparts have evolved into an elongate composite proboscis, half as long as the body, suitable for probing nectaries and, in the case of the female, adapted for piercing skin and imbibing blood from peripheral blood vessels. The outer sheath-like part of the proboscis, the labium, encloses the remaining mouthparts, which have the form of needle-like stylets. Of these, the female's mandibles and maxillae, which are flattened and toothed, can be driven

Figure 5; _Aedes aegypti_ adult.

through tissue by the muscles at their bases, making a channel for other styletized mouthparts which contain canals for the delivery of saliva and the removal of blood. Both males and females use the sugar in plant juices as a source of energy, usually obtaining it from nectaries but sometimes from other sources such as rotting fruit and honeydew. Anopheline and culicine females have a requirement for protein, from which to develop large batches of eggs, and they engorge on vertebrate blood for that purpose. T. oxorhynchitine females feed only on plant juices.

Body odour and carbon dioxide, carried on the wind stimulate sense receptors on the antennae and palps of female mosquitoes, alerting them to the presence of a host. The females respond by flying upwind, which takes them towards the host. Close to the host, visual stimuli and the convection currents of warm moist air that rise from the host provide additional cues. The females of some species are able to detect individual vertebrate hosts at a distance. Anopheles males responded to one calf at a distance of 14m, and to two calves at over 36m. The females of all blood-feeding species show a degree of specificity in their choice of host, whether mammal, bird or cold-blooded vertebrate. Some species are highly specific, feeding predominantly on one or a few host species only, others are less specific. Individual human beings differ in their attractiveness to mosquitoes; the cause of the difference has not been elucidated. Once landed on an appropriate part of the host, the female of Anopheles female drives the styletized feeding components of her mouth, parts into its skin. The saliva that is injected as the mouth, parts penetrate contains a substance that prevents haemostasis, the aggregation of blood platelets that is the host's first defence against the laceration of small blood vessels. The saliva is also the source of immunogens that are responsible for the characteristic skin reactions to mosquito bites. Sooner or later the probing stylets pierce a blood vessel, and the presence of blood is identified from its content of ADP and ATP. If the female is undisturbed, feeding continues until abdominal stretch receptors signal repletion. Within a few minutes gorging mosquitoes can imbibe up to four times their own weight of blood. This provides the protein needed for egg production, but also inflicts upon the mosquito a water load, which renders flight difficult, and potentially toxic amounts of sodium and potassium. The adult excretory system is capable of rapid elimination of water and salts, and diuresis commences while the female is still feeding.

Digestion of blood proteins yields amino acids which are reconstituted in the mosquito's fat body as proteinaceous yolk. This is transported to the ovaries and incorporated into the oocytes, which are matured in a number that matches the provision of yolk. It is a feature of mosquito biology that eggs are not matured continuously but in batches, following the periodic blood meals. Male mosquitoes can be readily distinguished by their large and elaborate antennae, in which rings of fibrils encircle the shaft. These antennae resonate in response to a pure tone of a certain pitch. Female mosquitoes in flight produce a familiar whining sound, the pitch of which reflects the wing beat frequency of the species. That sound activates the antennae of conspecific males, and provides directional indicators which the massive sense organs at the base of the antennae can resolve.

The role of adult male mosquitoes is insemination of females, and when not resting the males are either feeding or exhibiting a behaviour pattern that is likely to bring them into contact with females. One conspicuous manifestation of male behaviour is swarming the localized assembly of from two or three individuals to many thousands of individuals of a single species. Any conspecific female that enters a swarm will be seized immediately by a male. Mating also occurs outside swarms. Inseminated females store sufficient sperm in their spermathecae to fertilize a number of egg batches. A factor called matrone that is transferred in semen renders females unreceptive to males and refractory to further copulation, but its effectiveness may not persist throughout the life of the female.

The behavioural activities of adult mosquitoes-emergence, mating, feeding, and oviposition take place at particular times of day and night, which vary between species. Adults of *Anopheles gambiae*, for example, emerge during the late afternoon and, once mature, mate during a twenty-minute period at dusk. The females take blood meals principally during the four hours after midnight. The timing is not governed directly by light and dark but by endogenous or so-called circadian rhythms, which are reset daily by the change from light to dark at sunset.

When a female has matured a batch of eggs she takes to the wing and responds to stimuli from suitable oviposition sites. For most mosquitoes the oviposition site is a water body with particular characteristics; odour, taste, flow and shade are known to influence different species. The eggs may be dropped individually to float on the water surface, as by females of Anopheles, or packed together to form a floating egg raft, as by Culex. Aedine species deposit their eggs on moist surfaces, often at the edge of a body of water or on an area of soil that will be flooded. By whatever means, the female finds the appropriate habitat, and the larvae hatch into conditions for which they are adapted.

In tropical regions the life span of adult mosquitoes ranges from a few days to several weeks. In temperate regions it is frequently longer, and in species that overwinter as adults the life span of females may approach one year. The females' behavioural responses and physiological processes follow a pattern, the gonotrophic cycle, which starts with response to the vertebrate host and feeding, continues with the digestion of blood and formation of a batch of mature oocytes, and ends with oviposition. Within an hour of completing one gonotrophic cycle a female may commence another. At warmer temperatures, tropical *Anopheles* and *Aedes* oviposit regularly every two or three days.

vii *Aedes aegypti* and *Aedes albopictus* have a global distribution (figures 6 and 7

Distribution

respectively). *Aedes albopictus* is a very recent invader of the New World; it was first detected in America in 1985[2], being transported over from Asia in old used tyres.

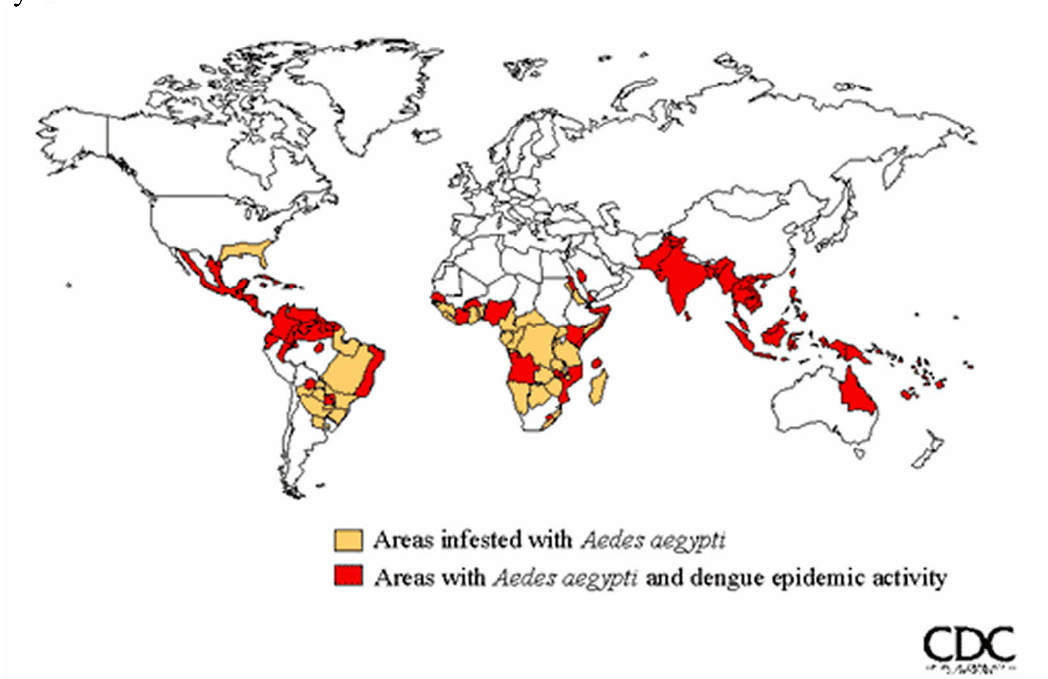


Figure 6; Worldwide distribution of *Aedes aegypti* (CDC).

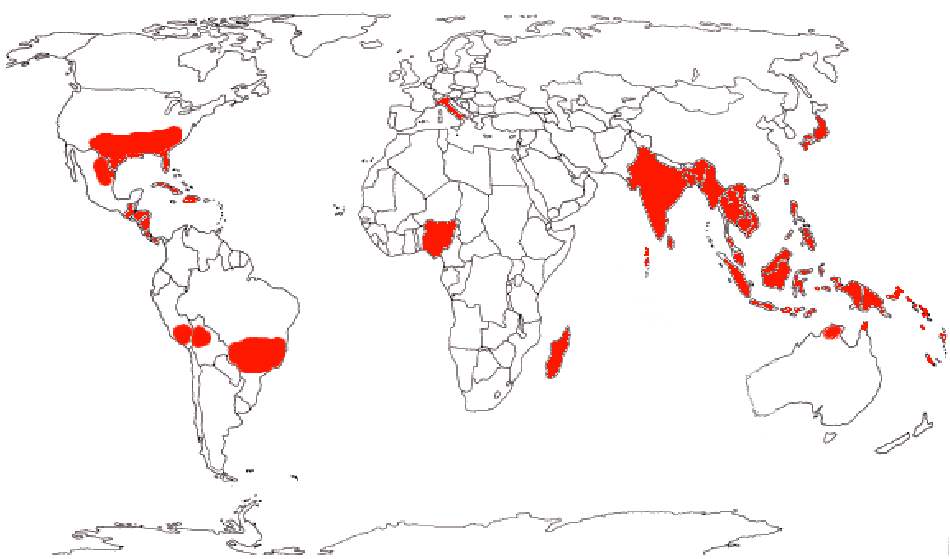


Figure 7; Worldwide distribution of *Aedes albopictus* (adapted from Parola *et al*[(3)])

Appendix 1

References

1 Reinert, J. F., R. E. Harbach & I. J. Kitching (2004). Phylogeny and classification

of Aedini (Diptera: Culicidae), based on morphological characters of all life stages. *Zool. J. Linn. Soc.* **142**: 289–368.

2 NC Department of Environment and Natural Resources, Division of Environmental Health, Public Health Pest Management Section (No date) "Asian Tiger Mosquitoes... Some Facts." Information Pamphlet.

3 Philippe Parola,*†1 Xavier de Lamballerie,‡§1 Jacques Jourdan,¶ Clarisse Rovery,* Véronique Vaillant,# Philippe Minodier,* Philippe Brouqui,*† Antoine Flahault,** Didier Raoult,†‡ and Rémi N. Charrel‡§ Novel Chikungunya Virus Variant in Travelers Returning from Indian Ocean Islands. Emerging Infectious Diseases • www.cdc.gov/eid • Vol. 12, No. 10, October 2006

Appendix 2

Bibliography

Clements A.N. the Biology of Mosquitoes; development, nutrition and reproduction. 2000, Volume 1. CABI Publishing.

http://www.cdc.gov/

http://www.who.int/