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ARTHROPODA

Triatominae (Subfamily): Kissing Bugs

Sue Ann Gardner, compiler

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- Class Insecta
  - Order Hemiptera
    - Suborder Heteroptera
      - Family Reduviidae
        - Subfamily Triatominae

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Chapter 65

Triatominae (Subfamily): Kissing Bugs

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Introduction

Triatomines are insects belonging to the order Hemiptera, suborder Heteroptera, family Reduviidae, and subfamily Triatominae. All members of this subfamily are hematophagous, which is considered to be a recently derived characteristic in evolutionary terms. In relation to the taxonomy and phylogenesis of triatomines, it is interesting that the Hemiptera order has dispersed representatives throughout tropical and temperate regions. In this order more than 80,000 species are known. Traditionally, Hemiptera is divided into two suborders, Homoptera and Heteroptera. Some Homoptera and most Heteroptera are adapted to feeding on plant sap. Some insects of the Heteroptera suborder are predators on insects and on other invertebrates, sucking their hemolymph, while other Heteroptera have become hematophagous, for instance, the Triatominae subfamily (Schofield and Dolling, 1993).

Triatomine Hematophage Biology (Excerpted and adapted from Schofield, 2000a)

Relative to digestion, a whole series of physiological adaptations is required for an obligate hematophage (see Lehane, 1991). Blood is a nutritionally rich resource, but it is highly alkaline, and much of the protein is locked in the blood cells. Consequently, the Triatominae require both a hemolysin to open the blood cells and a system to acidify the blood meal before it can be digested. Species of Reduviidae are derived from plant-sucking Hemiptera which have lost the ability to secrete trypsin, the usual digestive protease, because plant sap has virtually no protein, and plant seeds have potent antitrypsins (Schofield, 1996). Thus, the Reduviidae, including Triatominae, must make use of secreted cathepsins as proteases, which are generally active only at acid pH. Blood is also generally deficient in certain vitamins, particularly folate and B vitamins, so that all obligate bloodsuckers require symbionts to assist in producing these compounds. These symbionts are so important that all other obligate blood-suckers carefully conserve them either intracellularly or in a special organ known as the mycetome. But in Triatominae these symbionts are free in the gut lumen, which is taken as additional evidence that the blood-sucking habit is a relatively recent adaptation (Schofield and Dolling, 1993).

Morphology of a Representative Species, *Triatoma sanguisuga* (Extracted verbatim from Byron and Capinera, 2019)

Eggs

The eggs of *Triatoma sanguisuga* are pearly-white, oval, and approximately 1.5 mm-long. Eggs are indiscriminately deposited individually on the substrate. Once a blood meal is taken, females begin oviposition after 4–6 days, depositing 1–5 eggs per day (Grundemann, 1947). In a study by Hays (1965), female nymphs collected in the field that developed into adults under laboratory conditions each laid an average of 711 eggs in their lifetime. However, the range of eggs laid per female was large (from 312 to 1,166) indicating a need for more research in this area.

Nymphs

According to Grundemann (1947), *Triatoma sanguisuga* goes through 8 instars, determined by measuring the head capsule (because of the swelling associated with blood-feeding, body size is an inaccurate measurement). In a laboratory setting, each instar lasted approximately 41 days. Each molt requires blood-feeding. Development time is directly linked to temperature and host availability.

Adults

Triatoma sanguisuga adults are approximately 19 mm-long, with dark brown to black, flattened bodies and elongate, cone-shaped heads (Griffith, 1947). Antennae are elbowed, with six segments. The head bears a slender beak-like structure used to administer the notorious kiss, or bite. The abdomen is wide, with sides sticking out past the wing margins, displaying 6 reddish-orange spots on each side (Drees and Jackman, 2018) (Figure 2).

History of the Subfamily Triatominae (Extracted from Tartarotti et al.., 2006)

Triatomines probably evolved from Reduviidae predator groups. The Reduviidae early on in their evolution possibly fed on soft forms of invertebrate animals that inhabited vertebrate nests, such as caterpillars, larvae, and spiders. Later they began to attempt perforating the skin of small vertebrates. It is possible that, in the first phase, hematophagy was optional, and, since the saliva of these insects had no anesthetic properties, the triatomines would have been driven to feed on newly born vertebrates, which would be attacked in a special form of predation. Later in this phase, starting with adaptations for hemolysis, the hematophagous process would have begun (Carcavallo et al., 1999).

To avoid the predatory vertebrates in the nests and burrows, it was necessary to make adaptations, such as cryptic behavior and inverse activity pattern, for feeding while the vertebrate is asleep. In predators, the saliva has a proteolytic effect, a characteristic that was lost by most of the hematophagous insects to make it possible to ingest blood by a painless bite. Hematophagy also requires a rapid compensation of the enormous amount of blood that triatomines ingest. The insect therefore excretes great amounts of water and salts immediately to reduce its weight. Another adaptation to hematophagy is the erythrocytic rupture and hemolytic process at the beginning of digestion (Carcavallo et al., 1999). Triatomines are little different from Reduviidae predators, in habitat and forms, which also corroborates the argument that this group is a recent one.

Gorla and colleagues (1997) consider that triatomines are polyphyletic in origin and they believe that hematophagy have appeared recently, associated with the evolution of vertebrate nests. The polyphyletic hypothesis suggests that the adaptative steps from free life predators to hematophagous feeding might have occurred several times, not only among different groups of Reduviidae, but also among other Hemiptera groups. Deep phylogenetic analysis should resolve this question of polyphyly.

This hypothesis may explain the close relationship between genera and species of triatomines associated with certain vertebrates. For instance, *Psammolestes* associated with bird's nests, *Dendrocolaptidae*, *Cavernicola pilosa barber* with Chiroptera, *Microtriatoma* with the biocenosis of the great Bromeliads, *Panstrongylus geniculatus* associated with the *Edentates* (see Figure 1), and some species of the *Triatoma protracta* complex associated with the *Neotoma genus*. The polyphyletic hypothesis also helps to explain most of the anatomical differences found between some tribes and their notable similarity with taxa of other Reduviidae subfamilies. For example, species of *Alberproseniini* possesses morphological characteristics of the Cetherinae and species of *Psammolestes* possesses anatomical characteristics present in the Physoderinae subfamily. Among the most convincing studies, it has been discovered that there are fundamental differences in salivary components between species of Rhodniini and Triatomini, as well as differences in sensorial patterns, suggesting different origins for these two tribes. Therefore, the Triatominae subfamily should be assumed, more correctly, to be a utilitarian group, defined on the basis of their hematophagous habits and adaptations associated to this diet, and not a phylogenetic group of individuals sharing a common ancestry (Carcavallo et al., 1999).

Figure 1. Subfamily Triatominae Jeannel, 1919. Species: *Panstrongylus geniculatus*. Locality: Montebello, Amalfi Municipality, Departmento de Antioquia, Colombia (6°55'58''N; 75°05'30'' W, 18-24 °C). Source: F. Otálora Luna, 2006. License: CC BY-SA 3.0.

Some authors, including Usinger and colleagues (1966) believe, however, that the triatomines represent a monophyletic group and that their hematophagy have appeared only once. Gaunt and Miles (2000) also postulate that the triatomines are of monophyletic origin, based on the appearance of a salivary protein (anti-thrombin).

The monophyletic hypothesis is not only difficult to support, but it also causes problems in the understanding of the insects' distribution, association with animals, source of feeding and adaptation to different habitats. The comparison between population and behavioral parameters, association with vertebrates and habitat, as well as their biogeographical characteristics support the hypothesis that triatomines probably appeared several times within the Reduviidae and that they represent species of polyphyletic origin, based on their apomorphic character with relation to hematophagy (Schofield, 1988; Lyman et al., 1999; Bargues et al., 2000, Marcilla et al., 2001).

Figure 2. Adult *Triatoma sanguisuga*, eastern blood-sucking conenose. Locality: Pryor, Mayes County, Oklahoma, United States. Source: R. Webster, 2012. License: CC BY-SA 4.0.

Biogeographic History (Extracted from Tartarotti et al.., 2006)

The New World is clearly the center of triatomine origin and diversity. Of the approximately 137 triatomine species (Galvão et al., 2003), 105 occur in this area. Of the 14 genera, 12 are found exclusively in America: *Alberprosenia*, *Belminus*, *Bolbodera*, *Cavernicola*, *Dipetalogaster*, *Eratyrus*, *Microtriatoma*, *Panstrongylus*, *Parabelmintos*, *Paratriatoma*, *Psammolestes,* and *Rhodnius*. Only 2 genera, *Linshcosteus* and *Triatoma*, occur in the Old World, and the *Triatoma* is also found in the New World. The *Linshcosteus genus*, with 5 species, is confined to the Indian subcontinent, 7 species of *Triatoma* are present in Southeast Asia, and 1 species, *T. rubrofasciata*, is cosmopolitan in the tropics. Its wide distribution can be explained by marine transport from the 17th century to the early 20th century. This species is also present in the Brazilian northeast (Schofield and Dolling, 1993). *T. rubrofasciata* is considered to be an ancestor of the other 7 *Triatoma* species in Southeast Asia (*T. amicitiae*, *T. bouvieri*, *T. cavernicola*, *T. leopoldi*, *T. migrans*, *T. pugasi*, *T. sinica*) because they share morphological characteristics and are all included in the Rubrofasciata group. Another interesting characteristic that confirms the hypothesis that *T. rubrofasciata* is an older species is related to its painful bite, considered a primitive characteristic (Schofield, 1988).

The almost total absence of triatomines in Africa, except *Triatoma rubrofasciata*, probably brought to African ports by ships, suggests that the hematophagous evolution of Reduviidae in Africa was inhibited by the evolution of the hematophagous Anthocorideos, now known as Cimicidae, which had already occupied the available niches. The high degree of morphological specialization of Cimicidae suggests that they arose prior to the triatomines and that the latter evolved independently in America after the separation of the continents. This hypothesis is better than the view that triatomines may have appeared in Africa and, subsequently, were locally extinguished (Schofield, 2000a).

The dispersion of triatomines by vertebrates was studied on *Rhodnius prolixus* in Central America. It is believed that these insects migrated from South America to Central America, transported by birds. Enzymatic and RAPD (Random Amplification of Polymorphic DNA) analyses corroborated this view, the limited genetic variability denoting the recent origin of populations from South America (Dujardin et al., 1998).

Similarly, the presence of *Rhodnius prolixus* in Mexico is associated with the migration of vertebrates. The expansion and distribution of *T. infestans*, for example, is closely related to human activity (Schofield, 1988). The species is endemic in Bolivia and has been dispersed by human action, their domiciliary invasion obeying an opportunist mechanism provided by the stimulus of shelter and feeding (Forattini, 1980).

Triotamine Phylogeny

In the triatomine group, the Rhodniini, Cavernicolini, Bolboderini, Alberproseniini, and Linshcosteini tribes appear to be monophyletic groups, that is, each tribe possesses an ancester in common, while the Triatomini tribe is considered to be polyphyletic (Lent and Wygodzinsky, 1979; Galvão et al., 2003). The recognition of Rhodiniini as a monophyletic tribe takes into account characteristics of the *Rhodnius* genus not shared with other triatomines, such as, apical antenna insertion, body forms, post-ocular callosities, male genital characteristics, egg surface architecture, and nitroforine presence in the salivary glands. Besides these characteristics, the species of both *Rhodnius* and *Psammolestes* are primarily arboreal in contrast with the terrestrial habits of most of the other triatomines (Schofield and Dujardin, 1999). In addition, studies of sequence of ribosomic RNA mitocondrial and cytochrome B genes cluster *Psammolestes coreodes* with the species *Rhodnius prolixus*, *R. robustus*, and *R. neglectus* (Lyman et al., 1999).

Currently the most widely accepted hypothesis is that triatomines are a polyphyletic group, based on their convergent apomorphic hematophagy characters which have appeared independently several times in Reduviidae. These insects are highly adaptable to different habitats created by the constant expansion by humans and other animals. The hypothesis of a polyphyletic assemblage is corroborated by several studies on the Rhodiniini and Triatomini tribes. Analyses of sequences of mitochondrial (Stothard et al., 1998; Lyman et al., 1999) and ribosomal DNA (Bargues et al., 2000; Marcilla et al., 2002) and analysis of polymorphism length of intergenic transcribed rDNA (Tartarotti and Ceron, 2005), enzymatic studies, morphological analyses and taxonomic (Carcavallo et al., 1999), ecological studies (Schofield, 1988) show the non-monophyletic nature of this group.

Life Cycle: Triatomines as Vector for *Trypanosoma cruzi* (Extracted verbatim from DPDx, 2023)

An infected triatomine insect vector (or kissing bug) takes a blood meal and releases trypomastigotes in its feces near the site of the bite wound (see Figure 3, including life cycle phases numbered in the text). Trypomastigotes enter the host through the wound or through intact mucosal membranes, such as the conjunctiva (1). Common triatomine vector species for trypanosomiasis belong to the genera *Triatoma*, *Rhodnius*, and *Panstrongylus*. Inside the host, the trypomastigotes invade cells near the site of inoculation, where they differentiate into intracellular amastigotes (2). The amastigotes multiply by binary fission (3) and differentiate into trypomastigotes, and then are released into the circulation as bloodstream trypomastigotes (4). Trypomastigotes infect cells from a variety of tissues and transform into intracellular amastigotes in new infection sites. Clinical manifestations can result from this infective cycle. The bloodstream trypomastigotes do not replicate (different from the African trypanosomes). Replication resumes only when the parasites enter another cell or are ingested by another vector. The kissing bug becomes infected by feeding on human or animal blood that contains circulating parasites (5). The ingested trypomastigotes transform into epimastigotes in the vector's midgut (6). The parasites multiply and differentiate in the midgut (7) and differentiate into infective metacyclic trypomastigotes in the hindgut (8).

Triatomine Behavior (Extracted verbatim from Tartarotti et al., 2006)

Primitive predatory behavior still occurs in many triatomine species, including *Triatoma rubrofasciata*, which feeds on caterpillars, *T. rubrovaria* which can feed on spiders and silkworm, and *T. circummaculata*, which feeds on vertebrates' blood and cockroach hemolymph. Young nymphs of *Eratyrus mucronatus* preferentially feed on invertebrate animals, while nymphs in more advanced stages and adults feed on vertebrates' blood. Cannibalistic behavior can be a transitional stage between predation and hematophagy. There are reports of nymphs sucking blood from other nymphs in laboratory colonies. Such cleptohematophagous behavior occurs in *Belminus herreri* which obtains blood from species of recently fed *Rhodnius*. In short, all of these observations suggest that hematophagy is a recent characteristic in triatomines and that adaptations to this habit are still occurring (Schofield, 2000b).

For mammals, the bite from Reduviidae predators tends to be very painful and can cause death, especially by anaphylactic shock in small animals. The same happens in the case of certain triatomines. For instance, the bite of *Panstrongylus geniculatus* in pigs and humans in the Amazon leaves painful lesions and, in the case of *Triatoma rubrofasciata*, there has been at least 1 report of human death (Schofield, 2000b).

Medical Importance (Excerpted and adapted from Barreto Vieira et al., 2018)

Triatominae bugs are the vectors of Chagas disease, a major concern to public health especially in Latin America, where vector-borne Chagas disease has undergone resurgence due mainly to diminished triatomine control in many endemic municipalities. Although the majority of Triatominae species occurs in the Americas, species belonging to the genus *Linshcosteus* occur in India, and species belonging to the *Triatoma rubrofasciata* complex have been also identified in Africa, the Middle East, Southeast Asia, and the Western Pacific. Not all Triatominae species have been found to be infected with *Trypanosoma cruzi*, but the possibility of establishing vector transmission to areas where Chagas disease was previously non-endemic has increased with global population mobility. Additionally, the worldwide distribution of triatomines is concerning as they are able to enter into contact and harbor other pathogens, leading to concern that they could have competence and capacity to transmit them to humans during the bite or after successful blood feeding, spreading other infectious diseases. There are reports suggesting that triatomines may be competent vectors for pathogens such as *Serratia marcescens*, *Bartonella*, and *Mycobacterium leprae*, and that triatomine infection with other microrganisms may interfere with triatomine-*T. cruzi* interactions, altering their competence and possibly their capacity to transmit Chagas disease.

The transmission of Chagas disease by species of Triatominae is very well reported in the literature. Infection with vector-borne *T. cruzi* begins when metacyclic trypomastigotes, which are motile forms of the parasite, penetrate into the vertebrate host through the triatomine feces and urine. Once in the vertebrate host, these forms, which have evolved to survive inside host cells, infect nucleated cells. Within the cell, they differentiate into amastigotes in a phagosomal compartment known as the parasitophorous vacuole, escape to the cytoplasm, and replicate asexually

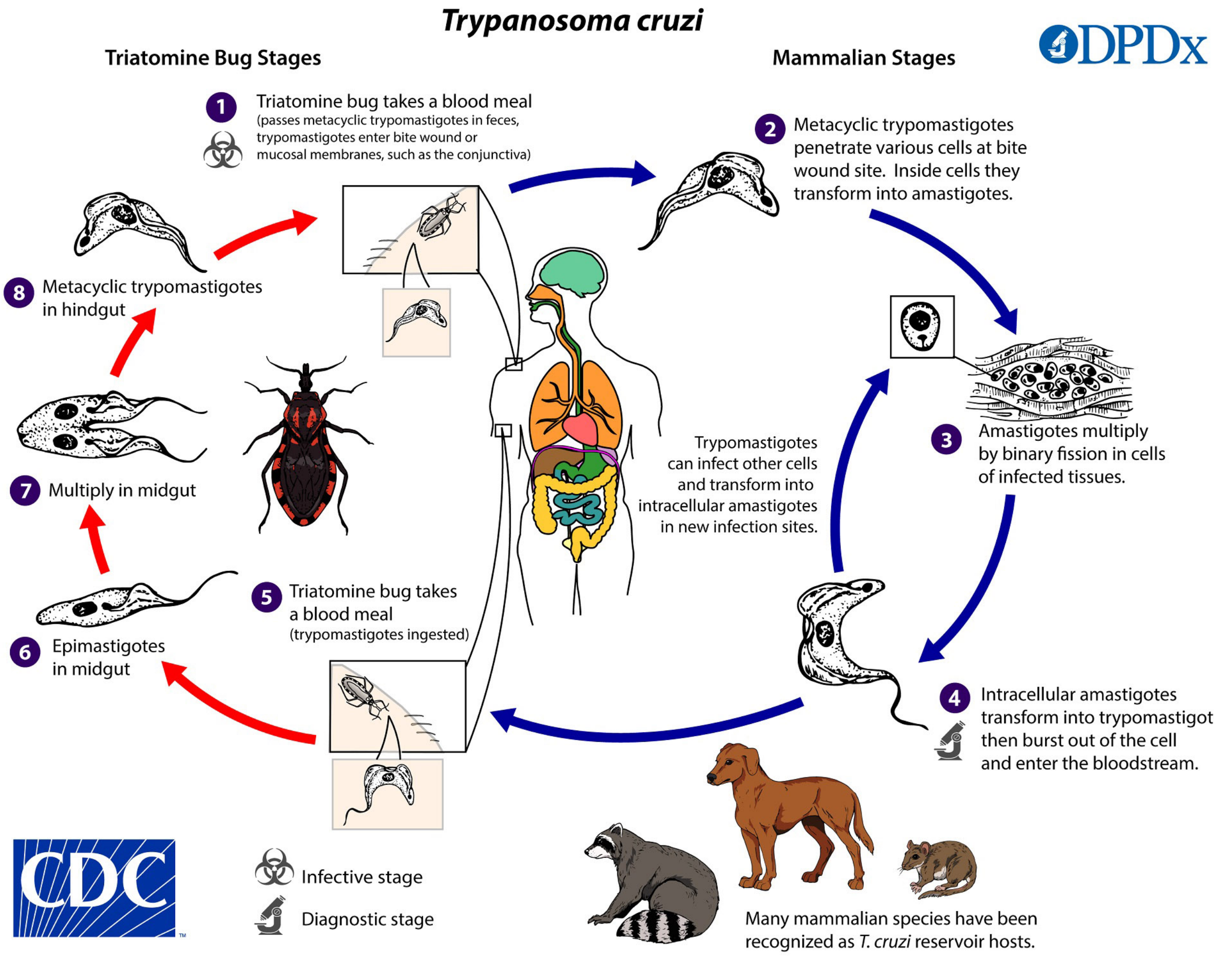

Figure 3. Life cycle of the protozoan parasite, *Trypanosoma cruzi*, the cause of Chagas disease, a zoonotic disease that can be transmitted to humans by blood-sucking triatomine bugs. Source: DPDx, 2023. Public domain.

through longitudinal binary division to form several amastigotes. As the cell becomes full of amastigotes, these convert into trypomastigotes and breach it, invading adjacent tissues and spreading to distant sites through bloodstream and lymphatics. The parasite population expands due to repeated cycles of cell invasion and replication, which lead to immune responses and can give rise to Chagas-associated pathologies (Tyler and Engman, 2001).

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