Biology, ecology, and systematics of Triatominae (Heteroptera, Reduviidae), vectors of Chagas disease, and implications for human health[1]

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Abstract: The members of the subfamily Triatominae (Heteroptera, Reduviidae) are vectors of *Trypanosoma cruzi* (CHAGAS 1909), the causative agent of Chagas disease or American trypanosomiasis. As important vectors, triatomine bugs have attracted ongoing attention, and, thus, various aspects of their systematics, biology, ecology, biogeography, and evolution have been studied for decades. In the present paper the authors summarize the current knowledge on the biology, ecology, and systematics of these vectors and discuss the implications for human health.

Key words: Chagas disease, Hemiptera, Triatominae, *Trypanosoma cruzi*, vectors.

Historical background

The first triatomine bug species was described scientifically by Carl DE GEER (1773), (Fig. 1), but according to LENT & WYGODZINSKY (1979), the first report on aspects and habits dated back to 1590, by Reginaldo de Lizárraga. While travelling to inspect convents in Peru and Chile, this priest noticed the presence of large hematophagous insects that attacked at night. In subsequent reports, various travelers and naturalists also mentioned the presence of these insects in South America. One of the most celebrated reports was by Charles Darwin, during his trip to South America on the H.M.S. Beagle in 1835, when he wrote: "One which I caught at Iquique, (for they are found in Chile and Peru) was very empty. When placed on a table, and though surrounded by people, if a finger was presented, the bold insect would immediately protrude its sucker, make a charge, and if allowed, draw blood. No pain was caused by the wound. It was curious to watch its body during the act of sucking, as in less than ten minutes it changed from being as flat as a wafer to a globular form..." (DARWIN 1871; LENT & WYGODZINSKY 1979).

American trypanosomiasis or Chagas disease was discovered in 1909 under curious circumstances. In 1907, the Brazilian physician Carlos Ribeiro Justiniano das Chagas (1879-1934) was sent by Oswaldo Cruz to Lassance, a small village in the state of Minas Gerais, Brazil, to conduct an anti-malaria campaign in the region where a railway was being built. The young doctor (28 years old) stayed in the area for about one year, during which time a railroad engineer, Cantarino Mota, alerted him to the presence of hematophagous insects referred to locally as "barbeiros" (the local term for triatomines) (Fig. 2). Alerted to the presence of these insects inside the human dwellings, the doctor decided to investigate the possibility that they might transmit some parasite to humans, since besides malaria, he had detected clinical signs that were difficult to interpret. The local population complained about an uncomfortable feeling referred to as "baticum" (a folk term for palpitation, literally meaning "drumming" or "pounding"), and Chagas observed arrhythmia and signs

[1] This paper is dedicated to Ernst Heiss on the occasion of his 70th birthday.

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Fig. 1: Male of *Triatoma rubrofasciata* (DE GEER 1773), the first species described.

of heart failure among local residents, along with reports of unexplained sudden death. Upon dissecting the triatomines he found flagellates in their intestinal tract. Believing that they belonged to *Trypanosoma minasense*, which infected black tufted-ear marmosets (*Callithrix penicillata*) in the same region, he sent several triatomine specimens to Oswaldo Cruz in Rio de Janeiro to feed on uninfected marmosets. Several weeks later he returned to Rio de Janeiro to discover a new trypanosome in the blood of one of the animals. As a tribute to his mentor he named the species *Trypanosoma cruzi*. He then returned to Minas Gerais to attempt to identify the parasite's vertebrate host. After numerous negative blood samples, he found an infected cat. Some 30 days later he returned to the house where he had discovered the infected animal and found a little girl named Berenice, just two years old, who was febrile and presented circulating forms of *T. cruzi* in her bloodstream.

From 1909 to 1912, Chagas described a new disease, its causative agent, natural reservoirs, and the vector, a fact unparalleled in international medicine to this day and a milestone in the history of medicine, since the discovery was made in the inverse order as compared to the usual (where the discovery of a disease generally precedes that of its causative agent). As a result of his work, in 1912 Chagas received the Schaudinn Award from the Institute of Tropical Diseases in Hamburg, Germany (CHAGAS FILHO 1968). Thus, one and the same researcher, in inverse order and in a short space of time, discovered a new disease that would later bear his last name, first recognizing the vector, next the parasite and reservoirs, and finally the clinical disease in humans (CHAGAS 1909). Chagas' discovery was overlooked by the Brazilian scientific community, as represented by the National Academy of Medicine, and was treated with disbelief for more than 20 years, because some scientists questioned the very existence of the disease. It was in Argentina in 1935 that Salvador Mazza submitted studies on the disease to the Annual Meeting of the Argentine Society of Tropical Medicine and, together with Cecílio Romaña, gave a new dimension and credibility to the problem (CHAGAS FILHO 1968).

For more than one century, since the first description by De Geer, triatomines were studied merely from a descriptive point of view. However, beginning in 1909, when Chagas discovered the disease, and due its newly acquired relevance to human health, studies began on the clinical form of the disease, the protozoan, and the vertebrate hosts, as well as the vector biology and transmission mechanisms. Advances in vector taxonomy began with Arthur Neiva, one of the most important scientists in this phase, who, in 1911, began describing various species, culminating with the publication of his dissertation "Revisão do gênero *Triatoma* Lap." in 1914. Important monographs were published subsequently by PINTO (1925) and DEL PONTE (1930), in addition to other extensive studies published by NEIVA & LENT (1936, 1941), USINGER (1944), ABALOS & WYGODZINSKY (1951), and RYCKMAN (1962), culminating in the grand work by LENT & WYGODZISNKY (1979).

Trypanosoma cruzi and Chagas disease

Chagas disease or American trypanosomiasis was primarily a zoonosis, a parasitic disease of wild animals transmitted by sylvatic species of triatomine bugs. The adaptation of some triatomine species to human dwellings was secondary, as was the parasite's domiciliary cycle. American trypanosomiasis is now an endemic disease affecting mostly Latin America, primarily in rural populations of Central and South America, where it is an important public health problem. According to World Health Organization, an estimated 100 million people are at risk of the disease, with 18 million currently infected (DIAS & COURA 1997). Currently there is no vaccine or effective cure for chronic Chagas disease.

Trypanosoma cruzi, the etiological agent of the disease, is a flagellate protozoan of the order Kinetoplastida, family Trypanosomatidae. It is some 20-thousandths of a millimeter in length and has an elongated body with an undulating membrane allowing its movement in the bloodstream.

Unlike other diseases transmitted by hematophagous insects, in this case infection does not occur through the insect's saliva. When the triatomine bug bites, it defecates during or right after bloodsucking, eliminating infective forms of the parasite in its feces. These forms can penetrate actively either through the bite's orifice, the mucosa, or small wounds and scratches on the skin. Vector-borne transmission is the most important form of transmission, but it can also take place through transfusion, transplacentally, through organ transplants, accidental ingestion of triatomines, laboratory accidents, or even inadequate handling of infected animal carcasses.

Animals infected with *T. cruzi* are always mammals, as the parasite cannot develop in the blood of birds, reptiles, or amphibians. A triatomine bug that has sucked the blood of a mammal (including a human) infected with *T. cruzi* acquires the infection and the protozoan then reproduces, multiplying in the insect's digestive tract and producing the infective forms which are expelled in the feces. Infection remains in the insect throughout its lifespan and can occur both in the nymphs and adults. If the insect sucks infected blood early in life (1st instar nymph), it acquires the infection and will remain infected throughout its life. Only the eggs are not affected, so the second generation remains uninfected until its first ingestion of infected blood (i.e. there is no transovarian transmission). Therefore triatomine bugs reared in the laboratory with blood from uninfected animals can be used safely in experiments. After biting and sucking the blood of humans or animals, the satiated triatomine bug defecates close to the site of the bite, and these feces can contain the infective form of *T. cruzi*. The parasites quickly penetrate into the bloodstream through the triatomine's bite, some minor wound, or through the mucosa (of the eyes, nose, or mouth). Upon entering the bloodstream the parasites are transported to the muscles or organs (mainly the heart and digestive tract), where they multiply and cause lesions. Penetration of *Trypanosoma cruzi* through the skin can cause a local reaction known as a chagoma, and another important sign is unilateral bipalpebral swelling, leaving the patient's eye practically closed. This is the so-called Romaña's sign, named after its discoverer, an Argentine physician.

Fig. 2: *Panstrongylus megistus* (Burmeister 1835), the triatomine species in which Chagas found *Trypanosoma cruzi*.

There are three distinct phases in the disease: acute, indeterminate, and chronic. In the acute phase (3-4 weeks), the infection varies from an asymptomatic to a severe and fatal form, the latter mainly in children or debilitated individuals, characterized by high fever, while other symptoms like diarrhea and vomiting can appear when the digestive tract is affected. The indeterminate phase is characterized by low parasitemia without clinical signs, which can persist or evolve into a chronic disease. The chronic form normally appears 10 to 15 years after the acute phase, and Chagasic cardiopathy is the most common manifestation, the digestive form producing visceromegalies, especially megaesophagus and megacolon.

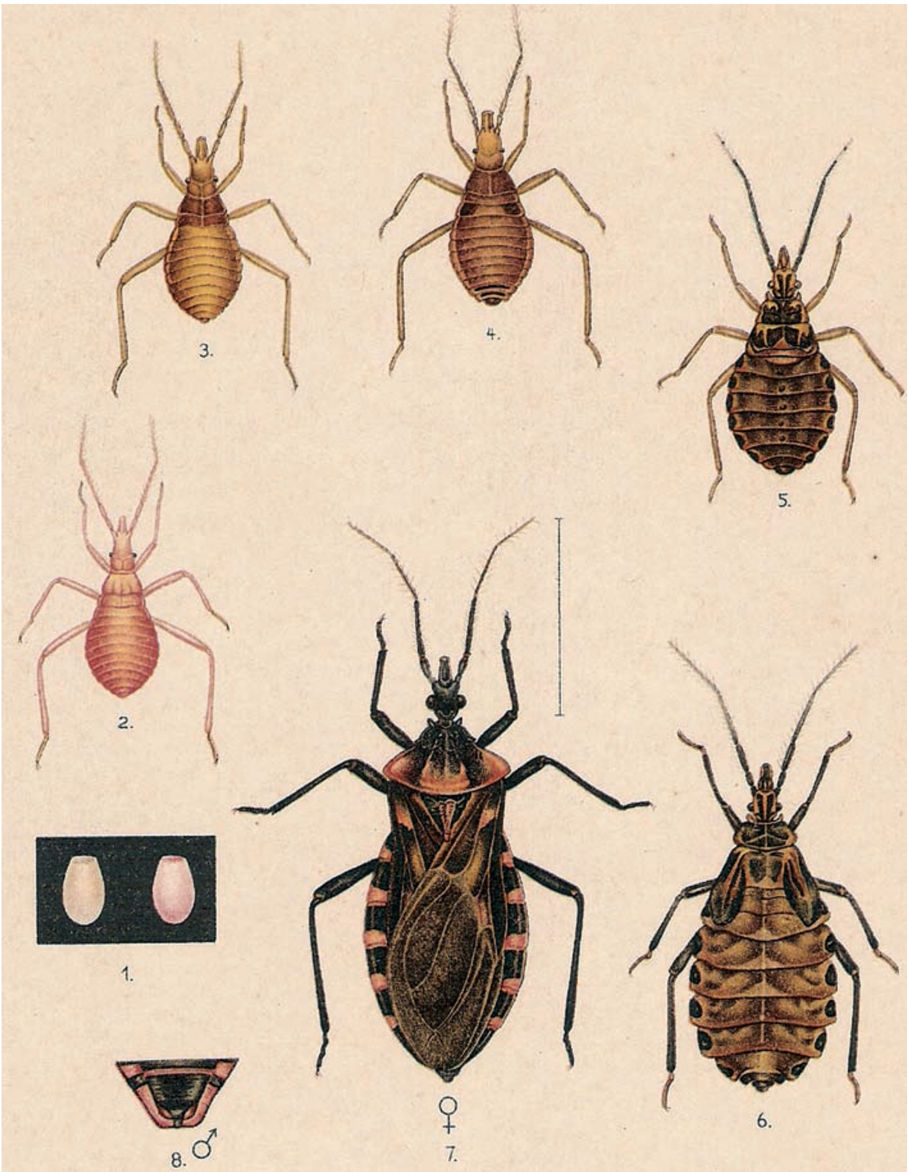

Fig. 3: Eggs, nymphs and female of *Panstrongylus megistus* (BURMEISTER 1835).

Chagas disease vectors

Members of the Triatominae are hemimetabolous insects whose development from egg to adult includes five nymphal stages (Fig. 3). They are obligatory hematophagous insects in all phases of their development. The amount of blood ingested varies according to the species as well as in relation to the stage, and generally the 4th and 5th instar nymphs are the ones that feed the most. In general most species are nocturnal, and during the day they remain in their resting places, although they may sometimes go out to suck blood during the day under adverse conditions. In colonies reared in the laboratory, the bugs seek food sources in broad daylight.

When they finish a meal their body changes appearance, since the volume of blood ingested is so great that the abdomen dilates considerably, giving them a globose appearance by stretching the intersegmental and connexival membranes. Some species may defecate while feeding, while others defecate soon afterwards or even abandon the food source and defecate far from the sucking site. This fact characterizes the various species as either good or bad transmitters of the disease, as the infective forms of *T. cruzi* are expelled in the feces of the infected bugs.

These insects generally suck the blood of their victims at night, while they are asleep. The bites generally occur on uncovered parts of the body. That is why the popular name for the triatomine bug in Brazil is "barbeiro" (barbeiro being "barber" in Portuguese). The sleeping persons are unaware of the bugs, because the bites are generally painless due to the anesthetic and anti-clotting action of the saliva. Cases of hypersensitivity can occur, but are rare.

Triatomines are vector insects and parasites with slow development, whose life-cycle can range from 3-4 months for *Rhodnius prolixus* STÅL up to two years for *Panstrongylus megistus* (BURMEISTER). They live in protected environments, the resting places of their hosts, which can be either sylvatic or domestic animals or humans. Of the known species, about a dozen are epidemiologically important, since they have become domiciliated due to manmade disequilibria in nature (LENT & WYGODZINSKY 1979).

Triatominae external morphology. Most triatomine species can be identified on the basis of their external morphology. The general appearance of triatomines is similar to that of other reduviids, and the general morphology is shown in Fig. 4. Detailed schemata of morphological traits were published by LENT & WYGODZINSKY (1979) and several scanning electron microscopy illustrations were provided by CARCAVALLO et al. (1998/99). Adults differ from nymphs by the presence of ocelli, and well-developed external genitalia and wings (with the exception of two species of *Mepraia*, which display wing polymorphism – see JURBERG et al. 2002). Females have a appointed or truncate abdominal apex, while in males the apex is rounded. Females are larger than males, and the largest triatomine is *Dipetalogaster maxima* (UHLER), which can reach 44 mm in length. The smallest species is *Alberprosenia goyovargasi* MARTÍNEZ & CARCAVALLO, 5 mm long. The length of most species usually varies from 20 to 28 mm. The color pattern (Figs 5-10) varies, with an overall black or piceous color and spotted patterns of yellow, brown, orange, or red (JURBERG et al. 2004). The morphology of triatomine eggs and nymphs (Fig. 11) has been the target of several studies, and a summary of these works was provided by GALVÃO et al. (2005).

Systematics and current classification

Current classification of this subfamily is based mainly on the revision by LENT & WYGODZINSKY (1979), the most important systematic work on this subfamily. Since that revision there has been considerable work, including the descriptions of several new taxa, and therefore in the present paper the authors provide a summary of the recent classification updated from GALVÃO (2003), GALVÃO et al. (2003) and FORERO et al. (2004) (see Table 1). Although generally recognized as a monophyletic subfamily of the Reduviidae adapted to a blood-feeding strategy (USINGER 1944; LENT & WYGODZINSKY 1979; CLAYTON 1990; SCHUH & SLATER 1995), the subfamily Triatominae still has several serious phylogenetic questions in regard to its origin and evolution (SCHAEFER 1998, 2003, 2005). SCHOFIELD (1988) proposed a concept of polyphyletic origin of the triatomines, and according to his view the Asiatic fauna consists of at least two independent lineages derived from different reduviid stocks. The first Asiatic lineage consists of several species of *Triatoma*, which had evolved from what was originally the New World species *Triatoma rubrofasciata* (DE GEER) after its introduction into the Old World. The other lineage is represented by the genus *Linshcosteus*, a supposedly autochthonous Asiatic lineage of blood-feeding reduviids. This view was supported by GORLA et al. (1997) through morphometric analysis, where all species of *Linshcosteus* were shown to be unrelated to the species of *Triatoma* recorded from the Old World. On

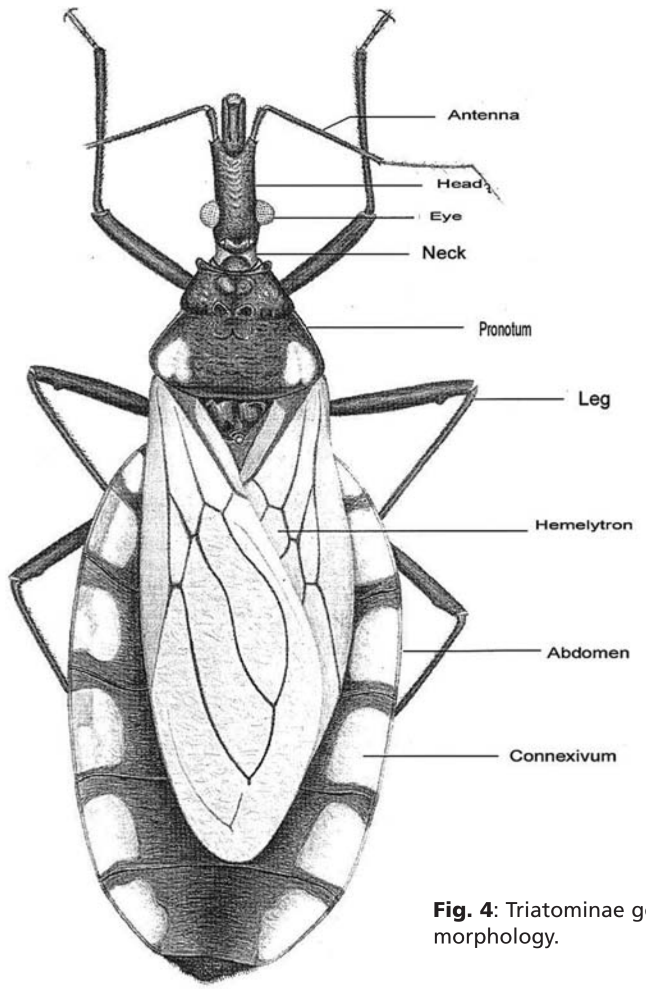

Fig. 4: Triatominae general external morphology.

Fig. 5: Color pattern of triatomine bugs: *Rhodnius stali* LENT, JURBERG & GALVÃO 1993.

Fig. 6: Color pattern of triatomine bugs: *Triatoma rubrovaria* (BLANCHARD 1843).

Fig. 7: Color pattern of triatomine bugs: *Triatoma sherlocki* PAPA, JURBERG, CARCAVALLO, CERQUEIRA & BARATA 2002.

Fig. 8: Color pattern of triatomine bugs: *Triatoma dimidiata* (LATREILLE 1811).

Fig. 9: Color pattern of triatomine bugs: *Triatoma infestans* (KLUG 1834).

the other hand, molecular cladistic analysis of 57 species (HYPSA et al. 2002) showed the genus *Linshcosteus* and *Triatoma rubrofasciata* as sister groups. The *Linshcosteus-T. rubrofasciata* clade nests firmly within Triatomini, supporting a monophyletic origin of Triatominae. According to SCHAEFER (2005) the most important question about phylogenetic relationships of the Triatominae can be divided in two parts: Is Triatominae actually a truly independent subfamily at all? And, if Triatominae is a separate subfamily, to which other reduviid subfamilies is Triatominae closely related? Attempting to solve this puzzle, several scientists have used molecular data to infer phylogenetic relationships (GARCIA & POWELL 1998; STOTHARD et al. 1998; LYMAN et al. 1999; GARCIA 1999; MARCILLA et al. 2002; SAINZ et al. 2004). Unfortunately, most of these papers are based on limited taxa sampling and are hence unable to solve the questions of the (entire) Triatomine subfamily phylogeny. A recently published paper (PAULA et al. 2005) analyzes mitochondrial rDNA sequences of several triatomine genera and some representatives of other reduviid subfamilies. This analysis suggests that the Triatominae itself and *Rhodnius* and *Triatoma* genera are polyphyletic. Although this paper is an important contribution, it must be supported by additional analyses including morphological characters. In conclusion, all these studies indicate that we still have insufficient knowledge to answer these questions and that much additional research is needed.

Extensive dichotomous keys for the identification of Triatominae species were provided by LENT & WYGODZINSKY (1979), LENT et al. (1994) and CARCAVALLO et al. (1998/99).

Geographical distribution

The vast majority of Triatominae species are found only in the New World; a few species are found in East Asia and on the coast of Australia. In the Neotropical and Nearctic regions the species are found between 42°N and 46°S. One species, *Triatoma rubrofasciata* is tropicopolitan, and an additional seven species of *Triatoma* occur in southern and southeastern Asia and north-

Fig. 10: Color pattern of triatomine bugs: *Triatoma nitida* USINGER 1939.

Tab. 1: Current systematic classification of the Triatominae subfamily (updated from GALVÃO 2003; GALVÃO et al. 2003; FORERO et al. 2004).

Subfamily	Tribes	Genera	Number of valid names
Triatominae	Alberproseniini	*Alberprosenia*	2
	Bolboderini	*Belminus*	6
		Bolbodera	1
		Microtriatoma	2
		Parabelminus	2
	Cavernicolini	*Cavernicola*	2
	Linshcosteini	*Linshcosteus*	6
	Rhodniini	*Psammolestes*	3
		Rhodnius	16
	Triatomini	*Dipetalogaster*	1
		Eratyrus	2
		Hermanlentia	1
		Meccus	6
		Mepraia	2
		Nesotriatoma	3
		Panstrongylus	13
		Paratriatoma	1
		Triatoma	67
Total		**18**	**136**

Tab. 2: Geographical distribution of triatomine species (updated from GALVÃO et al. 2003).

Species and author	Countries
Alberprosenia goyovargasi MARTÍNEZ & CARCAVALLO 1977	Venezuela
A. malheiroi SERRA, ATZINGEN & SERRA 1980	Brazil
Belminus costaricencis HERRER, LENT & WYGODZINSKY 1954	Costa Rica, Mexico
B. herreri LENT & WYGODZINSKY 1979	Colombia, Panama
B. laportei LENT, JURBERG & CARCAVALLO 1995	Brazil
B. peruvianus HERRER, LENT & WYGODZINSKY 1954	Peru
B. pittieri OSUNA & AYALA 1993	Venezuela
B. rugulosus STÅL 1859	Colombia, Venezuela
Bolbodera scabrosa VALDÉS 1910	Cuba
Microtriatoma borbai LENT & WYGODZINSKY 1979	Brazil
M. trinidadensis (LENT 1951)	Brazil, Bolivia, Colombia, Peru,Trinidad, Venezuela
Parabelminus carioca LENT 1943	Brazil
P. yurupucu LENT & WYGODZINSKY 1979	Brazil
Cavernicola lenti BARRETT & ARIAS 1985	Brazil
C. pilosa BARBER 1937	Brazil, Colombia, Panama, Peru, Venezuela
Linshcosteus carnifex DISTANT 1904	India
L. chota LENT & WYGODZINSKY 1979	India
L. confumus GHAURI 1976	India
L. costalis GHAURI 1976	India
L. kali LENT & WYGODZINSKY 1979	India
L. karupus GALVÃO, PATTERSON, ROCHA & JURBERG 2002	India
Psammolestes arthuri (PINTO1926)	Colombia, Venezuela
P. coreodes BERGROTH 1911	Argentina, Bolivia, Brazil, Paraguay
P. tertius LENT & JURBERG 1965	Brazil
Rhodnius amazonicus ALMEIDA, SANTOS & SPOSINA 1973	Brazil, French Guyana
Rhodnius brethesi MATTA 1919	Brazil, Colombia, Venezuela
R. colombiensis MEJIA, GALVÃO & JURBERG 1999	Colombia
R. dalessandroi CARCAVALLO & BARRETO 1976	Colombia
R. domesticus NEIVA & PINTO 1923	Brazil
R. ecuadoriensis LENT & LEÓN 1958	Ecuador, Peru
R. milesi CARCAVALLO, ROCHA, GALVÃO & JURBERG 2001	Brazil
R. nasutus STÅL 1859	Brazil
R. neglectus LENT 1954	Brazil
R. neivai LENT 1953	Colombia, Venezuela
R. pallescens BARBER 1932	Belize, Colombia, Costa Rica, Panama
R. paraensis SHERLOCK, GUITTON & MILES 1977	Brazil
R. pictipes STÅL 1872	Belize, Brazil, Colombia, Ecuador, Guyana, French Guyana, Peru, Suriname, Trinidad, Venezuela
R. prolixus STÅL 1859	Bolivia, Brazil, Colombia, Costa Rica, El Salvador, Ecuador, Guatemala, Guyana, French Guyana, Honduras, Mexico, Nicaragua, Panama, Suriname, Trinidad, Venezuela
R. robustus LARROUSSE 1927	Bolivia, Brazil, Colombia, Ecuador, French Guyana, Peru, Venezuela
R. stali LENT, JURBERG & GALVÃO 1993	Bolivia, Brazil
Dipetalogaster maxima (UHLER 1894)	Mexico
Eratyrus cuspidatus STÅL 1859	Colombia, Ecuador, Guatemala, Mexico, Panama, Peru, Venezuela
E. mucronatus STÅL 1859	Bolivia, Brazil, Colombia, Ecuador, Guatemala, Guyana, French Guyana, Panama, Peru, Suriname, Trinidad, Venezuela

ern Australia. *Linshcosteus* (Fig. 12) is the only genus restricted to the Old World, specifically, to the Indian subcontinent (GALVÃO et al. 2003). CARCAVALLO et al. (1999) provided several maps showing the geographical distribution and altitudinal/latitudinal dispersion of all American Triatominae species.

Habitats

Knowledge of triatomine species biology in their natural habitats is scarce, and for several species the natural ecotopes have not been described. Triatominae species are found in almost any habitat offering a degree of permanence, climatic shelter, and access to a blood source. Most species tolerate a range of air humidity between 30-80 %, and temperatures of 24-28 °C are satisfactory to them. Their development is usually slow at temperatures below 16 °C, whereas temperatures above 40 °C are lethal. Several species have specific habitats. For example, *Triatoma infestans* is found almost exclusively in human dwellings, *Cavernicola lenti*, a sylvatic species, is closely related to tree hollows inhabited by bats, and species from of the genus *Psammolestes* occur only in the nests of certain birds. Most triatomine species are sylvatic, living in bird nests, animal dens, under tree bark or in tree hollows, bromeliads, palm trees, and other ecotopes, feeding on various animals. GAUNT & MILES (2000) summarize the habitats of the triatomine genera *Rhodnius* and *Triatoma*, showing that most species in the former genus live in or associated with palm trees, while most species in the latter genus live in or associated with rocky/terrestrial habitats. However, during their evolutionary process some species acquired the capacity to colonize manmade structures near human dwellings, like chicken coops, pigsties and such species are thus referred to as peridomiciliated. Others can colonize the interior of human dwellings and are thus called domiciliated. The latter are more important, since they account for transmission of the disease to humans (CARCAVALLO et al. 1998/99). Many rural inhabitants live in dwellings with straw roofs and mud walls, and these provide various forms of shelter for the triatomines (Fig. 13).

Behaviour and biological aspects

Egg laying and life cycle. In general the eggs of the majority of triatomine species are deposited free in the environment, although some species have an adhesive substance which makes the eggs stick to the substrate (Fig. 14, 15). *Triatoma infestans*, a domiciliated species that originally inhabited rodent nests, is still found in the Bolivian altiplano and lays its eggs loose in the sites it inhabits. *Triatoma platensis* and *Triatoma delpontei*, ornithophilous species, stick their eggs to the substrate of the bird nests in which they live. Species of *Rhodnius* also stick their eggs to the substrate. *Rhodnius prolixus*, which inhabits the nest of *Mycteria americana*, a migratory bird, can have its eggs spread when they are adhered to the bird's feathers. *Psammolestes arthuri* oviposits in clusters, like members of such reduviid subfamilies as Harpactorinae and Apiomerinae (LENT & WYGODZINSKY 1979).

Oviposition normally occurs 10 to 30 days after copulation, which can be repeated several times during the adult's lifespan, although a female fecundated just once remains permanently fertilized. Copulation can last 15 to 30 minutes, and the male fertilizes the female by depositing spermatophores in the female vagina; these burst and release the spermatozoa which migrate to the spermathecae, where they remain protected while awaiting the passage of the successive ova to fertilize them. The number of eggs varies by species and principally as a function the female's degree of feeding. Recently laid eggs are whitish or pearly in color and change color over time until they become pinkish or brownish, near the day of hatching. During this phase, with the eggs transparent, one can see the black ocular spots, as the 1st stage nymphs emerge from the egg leaving the exuviae appearing (proto-nymph).

The longevity of nymphs and adults varies by species and ambient conditions. Laboratory experiments generally use what are considered ideal conditions for most species, with a mean temperature close to 28 °C and relative humidity around 70 %, blood feeding on adequate sources for each species, and a photoperiod of 12 hours. Of course in nature the insect is influenced by

Species and author	Countries
Hermanlentia matsunoi (FERNÁNDEZ-LOAYZA 1989)	Peru
Meccus bassolsae (AGUILAR, TORRES, JIMENEZ, JURBERG, GALVÃO & CARCAVALLO 1999)	Mexico
M. longipennis (USINGER 1939)	Mexico
M. mazzottii (USINGER 1941)	Mexico
M. pallidipennis (STÅL 1872)	Mexico
M. phyllosomus (BURMEISTER 1835)	Mexico
M. picturatus (USINGER 1939)	Mexico
Mepraia gajardoi FRIAS, HENRY & GONZALEZ 1998	Chile
M. spinolai (PORTER 1934)	Chile
Nesotriatoma bruneri USINGER 1944	Cuba
N. flavida (NEIVA 1911)	Cuba
N. obscura MALDONADO & FARR 1962	Jamaica
Paratriatoma hirsuta BARBER 1938	Mexico, USA
Panstrongylus chinai (DEL PONTE 1929)	Ecuador, Peru, Venezuela
P. diasi PINTO & LENT 1946	Bolivia, Brazil
P. geniculatus (LATREILLE 1811)	Argentina, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, Guatemala, Guyana, French Guyana, Mexico, Nicaragua, Panama, Paraguay, Peru, Suriname, Uruguay, Trinidad, Venezuela
P. guentheri BERG 1879	Argentina, Bolivia, Paraguay, Uruguay
P. howardi (NEIVA 1911)	Ecuador
P. humeralis (USINGER 1939)	Panama
P. lenti GALVÃO & PALMA 1968	Brazil
P. lignarius (WALKER 1873)	Brazil, Peru, Guyana, Suriname, Venezuela
P. lutzi (NEIVA & PINTO 1923)	Brazil
P. megistus (BURMEISTER 1835)	Argentina, Bolivia, Brazil, Paraguay, Uruguay
P. rufotuberculatus (CHAMPION 1899)	Argentina, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, Mexico, Panama, Peru, Venezuela
P. sherlocki JURBERG, CARCAVALLO & LENT 2001	Brazil
P. tupynambai LENT 1942	Brazil, Uruguay
Triatoma amicitiae LENT 1951	Sri Lanka
T. arthurneivai LENT & MARTINS 1940	Brazil
T. baratai CARCAVALLO & JURBERG 2000	Brazil
T. barberi USINGER 1939	Mexico
T. bolivari CARCAVALLO, MARTÍNEZ & PELAEZ 1987	Mexico
T. bouvieri LARROUSSE 1924	Nicobar Islands, Philippine, Vietnam
T. brailovskyi MARTÍNEZ, CARCAVALLO & PELAEZ 1984	Mexico
T. brasiliensis NEIVA 1911	Brazil
T. breyeri DEL PONTE 1929	Argentina
T. carcavalloi JURBERG, ROCHA & LENT 1998	Brazil
T. carrioni LARROUSSE 1926	Ecuador, Peru
T. cavernicola ELSE & CHEONG 1977	Malaysia
T. circummaculata (STÅL 1859)	Brazil, Uruguay
T. costalimai VERANO & GALVÃO 1958	Brazil
T. deaneorum GALVÃO, SOUZA & LIMA 1967	Brazil
T. delpontei ROMAÑA & ABALOS 1947	Argentina, Bolivia, Brazil, Uruguay, Paraguay
T. dimidiata (LATREILLE 1811)	Belice, Colombia, Costa Rica, El Salvador, Ecuador, Guatemala, Honduras, Mexico, Nicaragua, Panama, Peru, Venezuela
T. dispar LENT 1950	Colombia, Costa Rica, Ecuador, Panama
T. eratyrusiformis DEL PONTE 1929	Argentina
T. garciabesi CARCAVALLO, CICHERO, MARTÍNEZ, PROSEN & RONDEROS 1967	Argentina, Bolivia
T. gerstaeckeri (STÅL 1859)	USA, Mexico
T. gomeznunezi MARTÍNEZ, CARCAVALLO & JURBERG 1994	Mexico
T. guasayana WYGODZINSKY & ABALOS 1949	Argentina, Bolivia, Paraguay

Species and author	Countries
T. guazu Lent & Wygodzinsky 1979	Brazil
T. hegneri Mazzotti 1940	Mexico
T. incrassata Usinger 1939	USA, Mexico
T. indictiva Neiva 1912	USA, Mexico
T. infestans infestans (Klug 1834)	Argentina, Bolivia, Brazil, Chile, Ecuador, Paraguay, Peru, Uruguay
T. infestans melanosoma Martínez, Olmedo & Carcavallo 1987	Argentina
T. jurbergi Carcavallo, Galvão & Lent 1998	Brazil
T. klugi Carcavallo, Jurberg, Lent & Galvão 2001	Brazil
T. lecticularia (Stål 1859)	USA, Mexico
T. lenti Sherlock & Serafim 1967	Brazil
T. leopoldi (Schoudeten 1933)	Australia, Indonesia
T. limai Del Ponte 1929	Argentina
T. maculata (Erichson 1848)	Aruba, Brazil, Bonaire, Curacao, Colombia, Guyana, French Guyana, Suriname, Venezuela
T. matogrossensis Leite & Barbosa 1953	Brazil
T. melanocephala Neiva & Pinto1923	Brazil
T. mexicana (Herrich-Schaeffer 1848)	Mexico
T. migrans Breddin 1903	India, Indonesia, (Borneo, Java, Sumatra), Malaysia, Philippine, Thailand
T. neotomae Neiva 1911	USA, Mexico
T. nigromaculata (Stål 1872)	Colombia, Peru, Venezuela
T. nitida Usinger 1939	Costa Rica, Guatemala, Honduras, Mexico
T. oliveirai (Neiva, Pinto & Lent 1939)	Brazil
T. patagonica Del Ponte 1929	Argentina, Uruguay
T. peninsularis Usinger 1940	Mexico
T. petrochiae Pinto & Barreto 1925	Brazil
T. platensis Neiva 1913	Argentina, Paraguay, Uruguay
T. protracta (Uhler 1894)	USA, Mexico
T. pseudomaculata Corrêa & Espínola 1964	Brazil
T. pugasi Lent 1953	Indonesia (Java)
T. recurva (Stål 1868)	USA, Mexico
T. rubida (Uhler 1894)	USA, Mexico
T. rubrofasciata (De Geer 1773)	Andaman Islands, Angola, Argentina, Azores, Bahamas, Brazil, Burma, Cambodia, Caroline Islands, China, Comores, Congo, Cuba, Dominican Republic, Formosa, French Guyana, Goa, Grenada, Guadaloupe, Haiti, Hawaii, Hong Kong, India, Indonesia (Borneo, Java, Sumatra) Jamaica, Madagascar, Malaysia, Martinica, Mauritius Islands, New Guinea, Okinawa, Philippine, Saint Croix, Saint Vincent, Saudi Arabia, Seychelles, Serra Leone, Singapure, South Africa, Sri Lanka, Thailand, USA,Venezuela, Vietnam, Zanzibar
T. rubrovaria (Blanchard 1843)	Argentina, Brazil, Uruguay
T. ryckmani Zeledón & Ponce 1972	Costa Rica, Guatemala, Honduras
T. sanguisuga (Leconte 1855)	USA, Mexico
T. sherlocki Papa, Jurberg, Carcavallo, Cerqueira & Barata 2002	Brazil
T. sinaloensis Ryckman 1962	Mexico
T. sinica Hsiao 1965	China
T. sordida (Stål 1859)	Argentina, Bolivia, Brazil, Paraguay, Uruguay
T. tibiamaculata (Pinto 1926)	Brazil
T. vandae Carcavallo, Jurberg, Rocha, Galvão, Noireau & Lent 2002	Brazil
T. venosa (Stål 1872)	Bolivia, Colombia, Costa Rica, Ecuador, Peru
T. vitticeps (Stål 1859)	Brazil
T. williami Galvão, Souza & Lima 1965	Brazil
T. wygodzinskyi Lent 1951	Brazil

various factors that are difficult to control in the laboratory. Results obtained in the laboratory are thus merely an approximation of what occurs in nature, but knowledge of the biological cycles and population dynamics allows an estimation of the species' growth and colonization capacity, principally for anthropophilic species, but also for so-called secondary species with a tendency towards domiciliation (Canale et al. 1999).

Temperature. The importance of temperature and humidity for triatomine biology was studied early by Neiva (1913) who observed that high temperatures accelerated the embryonic period of *Triatoma infestans*. Carcavallo & Martínez (1972) obtained shorter cycles in specimens of three species of *Triatoma* reared at high temperatures as compared to those reared at variable temperatures. Silva (1985, 1988, 1989a, 1989b, 1989c, 1990a, 1990b, 1992), Silva & Silva (1988a, 1988b, 1988c, 1988d, 1988e, 1989, 1990a, 1990b, 1991, 1993) and Silva et al. (1995) compared the developmental times of several species reared at 25 °C and 30 °C showing a reduction of approximately 30 days in three species of *Rhodnius* and from 40 to 60 days in *Triatoma* species. According to most authors, when associated with low relative humidity the cycle is shortened by metabolic alteration and dehydration, increasing the number of blood meals to balance the energy budget and water loss. Various authors have demonstrated acceleration in the developmental period of several species submitted to increased temperature (Galvão et al. 1995, 1999b; Rocha et al. 1994, 2001a, 2001b). These results support the hypothesis that higher temperatures and lower relative humidity, as possible consequences of global warming, could accelerate the life cycle. The result is a change in the population dynamics of some Chagas disease vectors, extending the geographic distribution towards more temperate regions as well increasing the density of some populations. The literature shows the results of dozens of observations on the life cycles of these insects in the laboratory, a summary of the principal studies was published by Canale et al. (1999).

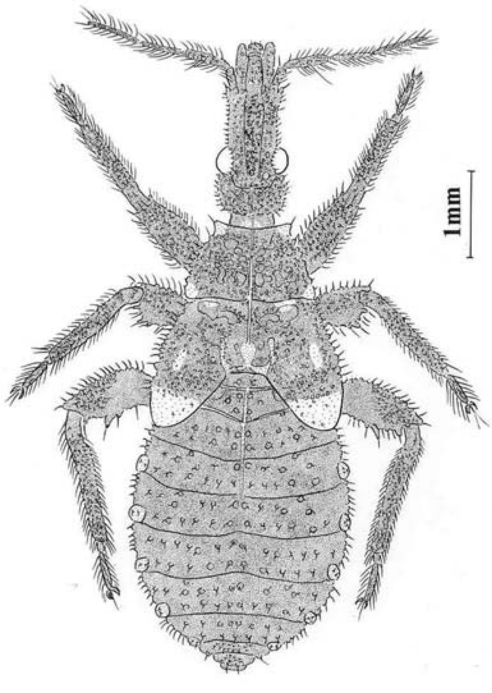

Fig. 11: *Belminus herreri* LENT & WYGODZINSKY 1979, fifth instar nymph.

Fig. 12: Lateral view, head of fifth instar nymph of *Linshcosteus karupus* GALVÃO, PATTERSON, ROCHA, & JURBERG 2002.

Fig. 13: Rural dwelling infested by triatomine bugs.

Fig. 14: Triatominae eggs: agglutinated eggs (*Rhodnius brethesi* MATTA 1919).

Fig. 15: Triatominae eggs: right-free eggs (*Triatoma brasiliensis* NEIVA 1911).

Feeding habits. As obligatory hematophages in all stages of their development and in both sexes, triatomines require numerous blood meals to complete their development. The vast majority of species feed on the blood of mammals or birds, but some can feed on reptile or amphibian blood (CARCAVALLO et al. 1998b). Coprophagy (ingestion of feces), kleptohematophagy (sucking blood already ingested by another triatomine), and hemolymphagy (sucking hemolymph from other arthropods) have also been reported by various authors (LAFONT 1912; BRUMPT 1914; LENT & MARTINS 1940; WOOD 1941; RYCKMAN 1951; SANDOVAL et al. 2000). LOROSA et al. (2000) and RUAS-NETO et al. (2001) showed that hemolymphagy can be an important survival strategy in nature, observing *T. circummaculata* and *T. rubrovaria* sucking blattids (cockroaches) in natural rock piles. Laboratory experiments by these authors demonstrated that the biological cycle of both species can be completed exclusively with hemolymph from these insects; however, after the imaginal molt, the males and females of both species could not survive on hemolymph. According to some authors, this aspect could be correlated with studies on the evolution of these two species, which still show this ancestral predatory characteristic.

Some species are considered stenophagic, that is, adapted to feeding only on given hosts, but the vast majority have eclectic feeding habits. CARCAVALLO et al. (1998b) published an extensive list correlating each species to its respective food source. Food sources can be identified through techniques like precipitin (SIQUEIRA 1960; FREITAS et al. 1960), but the results may reflect much more the predominance of a given host or hosts in an area than a true food "preference". It is common to detect the presence of blood from various hosts in a single insect. This result can lead to different interpretations. Could it mean great species mobility? host mobility? absence of preference? opportunism? These questions can only be answered safely by associating these results with those obtained through ethological studies. Feeding behavior depends on various types of stimuli in order to induce hematophagy. Various studies have demonstrated that heat and carbon dioxide are the principal stimuli involved in the search for and biting of the host (BOTTO-MAHAN et al. 2002), but heat appears to act only on the search for food and does not interfere in the feeding itself. The thermoreceptors are concentrated mainly in the antennae, which perform characteristic movements in the presence of a heat source. Bilateral antennectomy results in the impossibility of locating a heat source. According to LAZZARI & NÚÑEZ (1989), it is possible to make *Triatoma infestans* nymphs suck cold blood, as long as the bite is induced by thermal stimulation of the antennae. Another type of observation, aimed at characterizing the species with greatest vector potential, is to check the number of bites/meals, duration of the meal, and defecation site. These aspects are highly relevant epidemiologically, because the more contacts that occur between vectors and hosts, the greater the probability of infection or transmission of *Trypanosoma cruzi* (ROCHA et al. 1997).

Resistance to long periods of fasting and the fact that many species are generalists favor their survival in nature. This capacity of the triatomines has been known for decades. In 1926 Uribe reported the survival of a 3rd instar nymph of *Rhodnius prolixus* for five months. The literature shows discrepancies in the survival periods of various species studied according to the methodology employed, which can show variation in the feeding sources, relative humidity, and temperature, as well as the stress the insect suffers during handling (WOOD 1951; FRIEND & SMITH 1977; MASCARENHAS 1990; GALVÃO et al. 2001a; DIAS-LIMA & SHERLOCK 2002; MARTINEZ-IBARRA et al. 2003). Resistance to fasting can vary between and within species. Among the different stages, the 4th and 5th are normally most resistant, because of their higher capacity to ingest blood. Various authors have focused their laboratory studies on the resistance period to fasting among the various species, including GALVÃO et al. (1996, 1999a) and JURBERG & COSTA (1989a, 1989b).

Locomotor activity. According to BROWNE (1975) there are two forms of locomotor activity, one spontaneous (circadian), apparently without interference from external stimuli, and another oriented by external stimuli. Triatomines display various processes with temporal modulation, and spontaneous locomotor activity is one of these processes that can be observed individually and can be considered a true circadian rhythm. Various authors used actographic records to demonstrate that locomotor activity in both adults and nymphs is intensified during the early hours of the nocturnal period (SCHOFIELD 1976, NÚÑEZ 1982, SETTEMBRINI 1984, LAZZARI 1992). According to LAZZARI (1992), the circadian rhythm of spontaneous locomotor activity is divided into two well demarcated moments: the search for food occurs in late afternoon/dusk and the search for shelter occurs at dawn. This hypothesis was tested subsequently by LORENZO & LAZZARI (1998), who filmed the locomotor activity of insects in an arena containing refuges and concluded that *Triatoma infestans* demonstrated greater activity and motivation to feed in the early hours of the evening than at the end of this period.

Aggregation. Aggregative behavior in triatomines is mediated principally by the response to the presence of chemical signals (VELÁZQUEZ ANTICH 1968). Studies performed with *Triatoma infestans* and *Rhodnius prolixus* demonstrated the existence of gregarious behavior as a response to volatile substances found in feces (SCHOFIELD & PATTERSON 1977; ONDARZA et al. 1986). Aggregation mediated by chemical substances contained in feces was recently demonstrated by PIRES et al. (2002) in *Panstrongylus megistus* and by VITTA et al. (2002) in *Triatoma pseudomaculata*. Despite the various attempts at analysis, the nature of the chemical signal present in feces is still not well known, but it is known that feces act as signalers for the insects' refuges. These results show the need for future research aimed at the characterization of an interspecific gregarious chemical compound, aimed at aiding the control and monitoring of triatomine populations.

Camouflage. The ability of *Triatoma dimidiata* nymphs to camouflage themselves with particles of dust from the soil was described in detail by HASE (1940). ZELEDÓN et al. (1969) observed the same species in both the field and the laboratory and called attention to this behavior's epidemiological importance. According to ZELEDÓN et al. (1973), this behavior is present in various triatomine species, but to variable degrees, and it appears to be completely absent in others. One can clearly establish a correlation between the habitats where some species live (in contact with as opposed to distant from the ground) and the presence or absence of this behavior. This behavior's epidemiological implications deserve further investigation, since the behavior interferes directly with the efficiency of control measures, and prior knowledge of the species presenting this behavior is necessary in order to develop entomological surveillance methodologies.

Dispersion. Dispersion can occur passively, done involuntarily by humans, or actively, through the adult insects' flight (GALVÃO et al. 2001b). Knowledge is still limited concerning the mechanisms involved in dispersion by flight. The insects apparently respond directly to external conditions, but not to an internal clock. This is an extremely relevant aspect, because areas that have been chemically treated and are free of triatomine foci can be recolonized by flying specimens. In *Triatoma infestans*, the mean flight distance is some 200 meters (SCHOFIELD & MATTHEWS 1985), but flights of more than 1 kilometer have been observed in the field (SCHWEIGMANN et al. 1988). Triatomine flight capacity has been studied both in the field and the laboratory; nearly all these studies were based on releasing and recapturing the insects, and have furnished important information on the most flight-worthy species. However, no experiments have been done so far focusing on observations of flight behavior itself (LEHANE & SCHOFIELD 1981; SCHOFIELD et al. 1991, 1992; GALVÃO et al. 2001b).

Sexual behavior. The first information on copulation in triatomines was published by NEIVA (1914), who noted that *Panstrongylus megistus* females appeared to copulate only once, maintaining the eggs fertile throughout their own lifespan. Courting is not complex in this group of insects, and copulation in some species has been observed in the laboratory by some authors.

Tab. 3: Summarized information on experimental interspecific crossing in Triatominae (based on CARCAVALLO et al. 1998a).

Inter-crossing	interfertile progenies
T. hegneri x *T. dimidiata*	unfertile
T. picturata x *T. pallidipennis*	(F_2)
T. mazzottii x *T. picturata*	(F_2)
T. phyllosoma x *T. picturata*	(F_2)
T. phyllosoma x *T. pallidipennis*	(F_2)
T. mazzotti x *T. longipennis*	(F_2)
T. platensis x *T. delpontei*	(F_2)
T. platensis x *T. delpontei*	(F_2)
T. infestans x *T. platensis*	(F_2)
T. infestans x *T. rubrovaria*	(F_1)
T. sinaloensis x *T. peninsularis*	(not)
T. protracta x *T. sinaloensis*	(F_1)
T. barberi x *T. protracta*	(F_1)
T. barberi x *T. rubida*	(F_1: nymph V)
T. maculata x *T. sordida*	(F_1)
T. maculata x *T. sordida*	(F_1)
T. maculata x *T. infestans*	(F_1)
T. maculata x *T. infestans*	(not)
T. maculata x *T. brasiliensis*	(F_1)
T. maculata x *T. brasiliensis*	(not)
T. maculata x *T. pseudomaculata*	(F_1, partial)
T. pseudomaculata x *T. sordida*	(F_1)
T. pseudomaculata x *T. infestans*	(F_1)
T. petrocchiae x *T. brasiliensis*	(one nymph)
R. prolixus x *R. neglectus*	(F_1)
R. prolixus x *R. neglectus*	(not)
R. prolixus x *R. robustus*	(F_2)
R. pictipes x *R. prolixus*	(Nymph III) (unpublished)
T. matogrossensis x *T. vandae*	(unpublished)

Prior to copulation the male approaches the female, attempting to immobilize her with the three legs on one side of the body in a dorsolateral position (ABALOS & WYGODZINSKY 1951; HACK & BAR 1979; LENT & WYGODZINSKY 1979; LIMA et al. 1986; ROJAS et al. 1990; MANRIQUE & LAZZARI 1994). The presence of sexual pheromones in triatomines has been the target of research for many years, and evidence of chemical attraction between males and females was found in *Rhodnius prolixus* by VELAZQUEZ ANTICH (1968) and in *Triatoma infestans* and *Panstrongylus megistus* by NEVES & PAULINI (1981). According to BALDWIN et al. (1971), sexual pheromones are released during copulation, leading to an aggregation of males around the couple. Similar conclusions were obtained by MANRIQUE & LAZZARI (1994), studying *Triatoma infestans*. On the other hand, the complete absence of sexual attraction was demonstrated by SCHOFIELD & MOREMAN (1979), HACK & BAR (1979), and LIMA & MACCORD (1994). Differing methodologies probably explain what are often contrasting results.

Hybridization. An interesting aspect is the hybridization capacity of these insects under natural conditions. Many species live in sympatry in nature and can produce interfertile progenies up to F_2, while those that do not extend beyond F_1 are partially interfertile. Ecological barriers act as an important obstacle against the meeting of different populations that are superimposed in geographic areas. However, this possibility has led various researchers to conduct hybridizations in the laboratory. Table 3 shows the results obtained by various authors in the laboratory (MAZZOTTI & OSÓRIO 1941; MAZZOTTI 1943; USINGER 1944; ABALOS 1948; RYCKMAN 1962; USINGER et al. 1966; ESPÍNOLA 1971; ZÁRATE & ZÁRATE 1985; GALÍNDEZ-GIRÓN et al. 1994; CARCAVALLO et al. 1998a).

Laboratory rearing

Important information on triatomine biology has been obtained through rearing and observation in the laboratory, it is not difficult to establish and maintain colonies of these insects. Some appropriate requirements include the control of air temperature and relative humidity. In the "Laboratório Nacional e Internacional de Referência em Taxonomia de Triatomíneos" (National and International Reference Laboratory for Triatomine Taxonomy) at the Oswaldo Cruz Institute in Rio de Janeiro, the colonies are maintained in glass crystallizers (20 cm high by 20 cm in diameter), covered with a reduced-mesh nylon screen to avoid the escape of 1st instar nymphs and the entry of predators (microhymenoptera, ants, and spiders). Placed inside the crystallizers are strips of filter paper that help absorb the humidity and increase the circulating area. A wooden stand placed inside each crystallizer serves as a support for the hosts (pigeons and mice), which are anesthetized and immobilized before being offered as the food source. Black paper strips are placed outside each crystallizer to limit the amount of light striking the recipient.

Success in maintaining the colonies depends on adherence to the above-mentioned items, taking into consideration that offering the same food source repeatedly for long periods of time leads to deficiencies in the insect's development. When cleaning the recipients, the strips of filter paper, which become soiled with the insects' feces, are changed so the environment does not become overloaded, but some strips impregnated with feces are left in the environment to allow recently hatched nymphs to have contact with their natural digestive tract symbionts, which aid in digestion of the blood.

Epidemiological importance and implications for human health

The main importance of the subfamily Triatominae is its capacity to transmit *Trypanosoma cruzi*, the causative agent of Chagas disease or American trypanosomiasis. All species of triatomine bugs must be regarded as potential vectors of *T. cruzi*, which infect a wide variety of sylvatic and domestic mammals, but thus far only a few triatomine species have become well-adapted to living in human dwellings, thereby acquiring epidemiological importance for humans. The most important vector species are *Triatoma infestans*, *T. brasiliensis*, *T. dimidiata*, *Panstrongylus megistus*, and *Rhodnius prolixus*. Heavy domestic infestations of triatomines can be highly stressful, because these populations can reach several hundred individuals of different stages, representing a high daily blood loss.

According to the World Health Organization, Chagas disease is the third most important parasitic disease (next to malaria and schistosomiasis), based on the resulting disability and work limitations. In Latin America it is the fourth most important disease, following respiratory diseases, diarrhea, and AIDS (SCHOFIELD 1994). According to sero-epidemiological estimates, there are ten to twenty million infected individuals in Latin America, and ninety million people live in risk areas. Each year some five hundred thousand people are infected with the disease, for which there is still no cure. The existing drugs are only partially effective in the acute phase, which mainly attacks the heart and digestive tract. Some 10 % of infected individuals develop clinical signs and symptoms of chronic Chagas disease.

Occurrence of the classic form of the disease in a given area depends on three basic factors: presence of *T. cruzi* (the etiological agent), domiciliated triatomine bugs (vectors), and humans and other mammals (hosts) inhabiting the domiciliary environment. In addition to the classic infection model through contaminated triatomine feces, accounting for 80 % of the infections, other mechanisms contribute to cases of Chagas disease, such as transfusion of contaminated blood and blood products (16 %), congenital transmission from infected mothers (2 %), and the rest from organ transplants, infection by the oral route through ingestion of contaminated food, and laboratory accidents (SCHOFIELD 1994).

Control

After the successful campaign to control domestic triatomine populations in some South America countries, the new target of studies should be the species invading controlled areas. In recent years has been increased reporting of sylvatic species invading human dwellings and peridomiciliary environment in South American countries (COURA et al. 1999; VALENTE et al. 1998; VALENTE 1999; ALMEIDA et al. 2000; SANDOVAL et al. 2000, 2004; GALVÃO et al. 2001b; VIVAS et al. 2001; WOLFF & CASTILLO 2002; SOUSA et al. 2004; SOUSA & GALVÃO 2004). The majority of these finds are adult insects; and, as mentioned previously, triatomine flight represents an important form of dispersion to previously controlled areas. Studies on triatomine flight capacity can also facilitate early identification of species with the tendency to invade dwellings and to allow the application of adequate vector surveillance. Effective surveillance is obviously important to avoid re-infestation after control, or resurgence of any vector population. Chagas disease control should be based on various independent but complementary work fronts, and has become a public health priority in the affected countries, due to epidemiological relevance and the high financial costs for the economy.

Use of insecticides. Vector control uses residual-action insecticides, which should be applied to both the inside and outside parts of houses and outbuildings. One problem is that the insecticides do not affect eggs laid in inaccessible places like cracks and crevices in buildings. The vector species that are subject to control should be considered, since the biological cycle should be the basis for systematizing the intervals and number of insecticide applications over the course of the year.

Housing improvement. This should be a primary goal, because typical poor rural dwellings are made of mud and wattle, with thatched palm roofs, packed earthen floors, and have domestic and wild animals living in the same environment, thus facilitating massive infestations of triatomines. Anti-triatomine measures include construction of simple housing with measures like smooth walls without cracks, ceramic tile roofs protected below with ceilings, and well organized furniture and utensils to avoid the formation of refuges for insects.

Health education. Despite extensive research on Chagas disease, little information has been generated to teach rural communities about the disease. The most effective measure is a health education project targeting rural communities and health professionals. A population that is well-informed about the disease is better prepared to prevent the entry and persistence of vectors, and to notify health authorities about existing problems. Information about the disease and vectors and the means to control them should be provided to the entire population, in the school system, on radio and television, and in community centers through leaflets, posters, and films. Unfortunately this is still a distant reality in Latin American countries.

When Carlos Chagas discovered the medical importance of triatomine bugs in 1909 only 33 species were known, and it was up to Arthur Neiva (through the Oswaldo Cruz Institute) to launch taxonomical studies on this group by creating the embryo for the Triatomines Laboratory that has been operating non-stop for 96 years. In 1989 the Triatomines Laboratory was transformed into the current "Laboratório Nacional e Internacional de Referência em Taxonomia de Triatomíneos" (National and International Reference Laboratory for Triatomine Taxonomy) (JURBERG 1999), housing the world's largest collection of triatomines, with some 24,000 dry specimens, consisting of the Herman Lent Collection with 9,000 specimens and the Rodolfo Carcavallo Collection with 15,000 specimens. The Laboratory has a large-scale insectary and is currently rearing 43 species in some 150 crystallizers, in addition to a collection kept in alcohol, with 45 species. The collections remain open and continue to receive material and make donations, and the Laboratory is open to new scientific collaboration.

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Zusammenfassung

Die Arten der Unterfamilie Triatominae (Heteroptera, Reduviidae) sind Vektoren von *Trypanosoma cruzi* (CHAGAS 1909), dem Erreger der "Chagas disease" oder Amerikanische Trypanosomiasis. Als wichtige Vektoren sind Triatominae schon seit Jahrzehnten Gegenstand der Forschung verschiedener Aspekte ihrer Systematik, Biologie, Ökologie, Biogeographie und Evolution. In der vorliegenden Arbeit geben die Autoren einen Überblick zum aktuellen Kenntnisstand zur Biologie, Ökologie und Systematik dieser Vektoren und diskutieren deren Bedeutung für die menschliche Gesundheit.

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