Chapter 13
Hematophagous Bugs (Reduviidae, Triatominae)

José Jurberg, Cleber Galvão, Christiane Weirauch, and Felipe F.F. Moreira

Abstract The members of the subfamily Triatominae (Heteroptera, Reduviidae) are vectors of *Trypanosoma cruzi* (Chagas), 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 chapter, the authors summarize the current knowledge on the systematics, phylogeny, evolution, and biology of these vectors and discuss the implications for human health.

13.1 Introduction

The Triatominae are bloodsucking bugs, which since the discovery of Carlos Chagas (1909) have been recognized as actual or potential vectors of Chagas disease. The first triatomine bug species was described in 1773, by C. De Geer (Fig. 13.1), but according to Lent and Wygodzinsky (1979), the first report on aspects and habits dated back to 1590 by Reginaldo de Lizárraga. While traveling 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 in the H.M.S. Beagle in 1835, when he wrote: "One which I caught at Iquique, (for they

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Fig. 13.1 Male of *Triatoma rubrofasciata* (formerly *Cimex rubrofasciatus*), the first formally described species of Triatominae (From Jurberg and Galvão 2006)

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 1845; Lent and Wygodzinsky 1979).

American trypanosomiasis or Chagas disease was discovered in 1909. Two years before, the Brazilian physician Carlos Chagas (1879–1934) was sent by Oswaldo Cruz to Lassance, a small village in the state of Minas Gerais, Brazil, to conduct an antimalaria campaign in the region where a railway was being built. Chagas stayed in the area for about 1 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. 13.2). 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 as palpitation, and Chagas observed arrhythmia and signs of heart failure among local

Fig. 13.2 *Panstrongylus megistus*, the species of Triatominae in which C. Chagas found *T. cruzi* (From Jurberg and Galvão 2006)

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 in an 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 2 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 set of discoveries unparalleled in international medicine to this day. As a result of his work, in 1912 Chagas received the Schaudinn Award from the Institute of Tropical Diseases in Hamburg, Germany (Chagas Fo 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 Fo 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 to 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 and Lent (1936, 1941), Usinger (1944), Abalos and Wygodzinsky (1951), and Ryckman (1962), culminating in the grand works by Lent and Wygodzinsky (1979) and Carcavallo et al. (1998/1999). Relevant information concerning the triatomines was also compiled by Jurberg and Galvão (2006), which served as a basis for the preparation of the present chapter.

13.1.1 Chagas Disease

Currently there is no vaccine or effective cure for chronic Chagas disease, 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 the World Health Organization, an estimated 28 million people are at risk of the disease, with 15 million currently infected (Guhl and Lazdins-Helds 2007).

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. Infection remains in the insect throughout its lifespan and can occur both in the nymphs and adults. 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.

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. 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 *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.

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 10–15 years after the acute phase, and Chagasic cardiopathy is the most common manifestation, the digestive form producing visceromegalies, especially megaesophagus and megacolon.

13.1.2 Epidemiological Importance and Implications for the Human Health

All triatomine bugs must be regarded as potential vectors of *T. cruzi*, which infects a wide variety of sylvatic and domestic mammals, but so far only a few species have become well adapted to living in human dwellings, thereby acquiring epidemiological importance for humans (Jurberg and Galvão 2006). The most important vector species are *Triatoma infestans* (Klug), *T. brasiliensis* Neiva, *T. dimidiata* (Latreille), *Panstrongylus megistus* (Burmeister), and *Rhodnius prolixus* (Stål). 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). Each year about 500,000 people are infected with the disease, which is still incurable. The existing drugs are only partially effective in the acute phase, which mainly attacks the heart and digestive tract. Approximately 10 % of the 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).

13.1.3 Control

After the successful campaign to control domestic triatomine populations in some South American countries, the new target of studies should be the species invading controlled areas. In recent years, there has been increased reporting of sylvatic species invading human dwellings and peridomiciliary environment in South America (Valente et al. 1998; Coura et al. 1999; Valente 1999; Almeida et al. 2000; Sandoval et al. 2000, 2004; Galvão et al. 2001b; Vivas et al. 2001; Wolff and Castillo 2002; Sousa et al. 2004; Sousa and Galvão 2004). The majority of these findings are adult insects and flight represents an important form of dispersion to previously controlled areas. Studies on triatomine flight capacity can facilitate 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 reinfestation 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 must be applied both on 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 the 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 and packed earthen floors, and have domestic and wild animals living in the same environment, thus facilitating massive infestations by 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 and Research

Despite extensive research on Chagas disease, little information has been generated to teach rural communities about it. The most effective control 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 the 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 nonstop for more than a century. In 1989, the Triatomines Laboratory was transformed into the current *Laboratório Nacional e Internacional de Referência em Taxonomia de Triatomíneos* (LNIRTT; National and International Reference Laboratory for Triatomine Taxonomy) (Jurberg 1999), housing the world's largest collection of triatomines, with about 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 approximately 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.

13.2 General Characteristics and Diagnosis

Most triatomine species can be identified on the basis of their external morphology. Their general appearance is similar to that of other reduviids, and the general external and internal morphologies are shown in Fig. 13.3. Detailed schemata of morphological traits were published by Lent and Wygodzinsky (1979) and several scanning electron microscopy illustrations were provided by Carcavallo et al. (1998/1999). The length of most species varies from 20 to 28 mm, but *Dipetalogaster maxima* (Uhler) can reach 44 mm in length, and the smallest species is *Alberprosenia goyovargasi* (Martínez & Carcavallo), with 5 mm. The color pattern (Figs. 13.4, 13.5, 13.6, 13.7, 13.8, and 13.9) varies, with an overall black or piceous color and spotted patterns of yellow, brown, orange, or red (Jurberg et al. 2004, 2012, 2014).

Adults differ from nymphs by the presence of ocelli and well-developed external genitalia and wings, with the exception of two species of *Mepraia* Mazza, Gajardo & Jörg 1940, which display wing polymorphism (Jurberg et al. 2002). Females are larger than males and have pointed or truncate abdominal apex, whereas in males

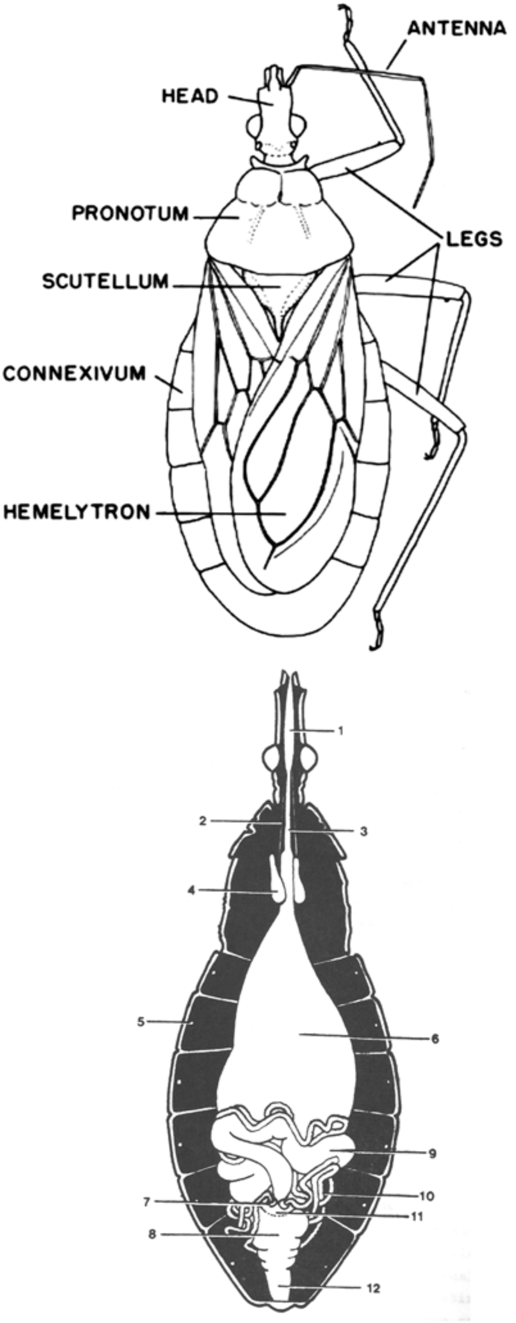


Fig. 13.3 General external and internal morphologies of the Triatominae (1, pharynx; 2, salivary duct; 3, esophagus; 4, salivary gland; 5, third respiratory spiracle; 6, promesenterium; 7, basal ampoule; 8, rectal ampoule; 9, postmesenterium; 10, Malpighian tubules; 11, light zone; 12, rectum) (From Lent and Wygodzinsky 1979 and Ramírez 1985)

Fig. 13.4 Color pattern of triatomine bugs: *Rhodnius brethesi* (From Jurberg and Galvão 2006)

Fig. 13.5 Color pattern of triatomine bugs: *Rhodnius nasutus* (From Jurberg and Galvão 2006)

Fig. 13.6 Color pattern of triatomine bugs: *Triatoma tibiamaculata* (From Jurberg and Galvão 2006)

Fig. 13.7 Color pattern of triatomine bugs: *Triatoma lecticularia* (From Jurberg and Galvão 2006)

Fig. 13.8 Color pattern of triatomine bugs: *Triatoma carcavalloi* (From Jurberg and Galvão 2006)

Fig. 13.9 Color pattern of triatomine bugs: *Triatoma brasiliensis* (From Jurberg and Galvão 2006)

the apex is rounded. The morphology of triatomine eggs and nymphs (Fig. 13.10) has been the focus of several studies, and a summary of these works was provided by Galvão et al. (2005).

Besides the external structure, size, proportions, and coloration, genital features and the internal morphology also provide insights to the taxonomy and systematics of the Triatominae. The morphology of the salivary glands and proportions between the testicular tubes aid on the generic differentiation, and the structure of male genitalia can be used for the specific diagnosis, as demonstrated in Lent and Wygodzinsky (1979), Gonçalves et al. (1987), and Santos et al. (1997). These characters, in association with the study of live specimens when available, and the use of molecular, cytogenetic, morphometric, and histochemical tools provide support for the discovery of cryptic species and for the development of phylogenetic analysis (Jurberg 2003; Galvão 2003).

Fig. 13.10 Eggs, nymphs, and female of *Triatoma brasiliensis* (From Jurberg and Galvão 2006)

13.2.1 Salivary Glands

The salivary complex is an important characteristic for the differentiation of the genera of Triatominae. The structures forming the complex are homogeneous among the genera, but display variable shapes (Figs. 13.11 and 13.12). Del Ponte (1921) was the first to demonstrate the importance of the salivary complex of the triatomines for the understanding of the taxonomy of the group, using *Triatoma infestans* as a model. Other comparative studies have been performed using different species of the genera *Triatoma* Laporte, *Mepraia*, *Panstrongylus* Berg, *Psammolestes* Bergroth, and *Rhodnius* Stål (Barreto 1922; Baptist 1941; Barth 1954).

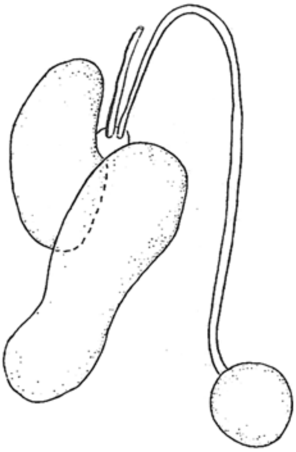


Fig. 13.11 Salivary complex of *Triatoma infestans* (From Santos et al. 1997)

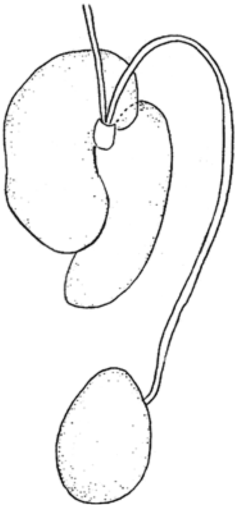


Fig. 13.12 Salivary complex of *Panstrongylus megistus* (From Santos et al. 1997)

13.2.2 Phallic Structure

Opposite to the females, in which the genital plates are simple and extremely homogeneous, the male genital complex of the Triatominae is composed of approximately 15 features, which are highly variable and can be used for generic and specific differentiation (Singh-Pruthi 1925; Dupuis 1955, 1963; Lent and Jurberg 1969, 1975) (Figs. 13.13 and 13.14). This variation was first studied by Lent and Jurberg (1965), who used the comparative analysis of the phallic structures as a tool for the identification of a new species in the genus *Psammolestes* (*P. tertius* Lent & Jurberg), at that time composed by only two species.

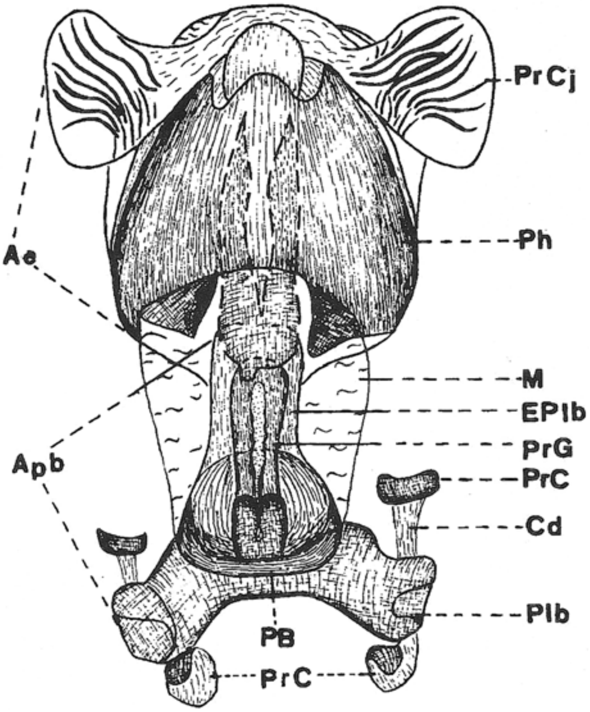


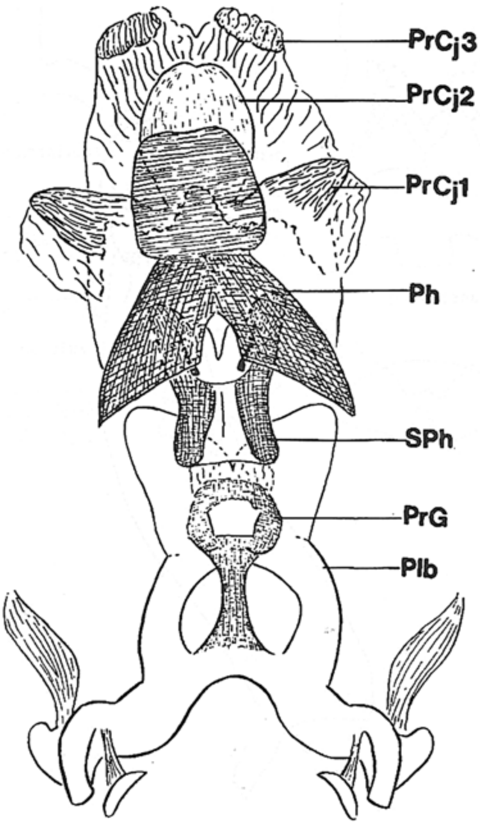
Fig. 13.13 Phallus of *Mepraia spinolai* in ventral view (*Ae* aedeagus, *Apb* articular apparatus, *Cd* dorsal connection, *EPlb* median extension of the basal plate, *M* membrane, *PB* basal bridge, *PrC* capitate process, *PrCj* conjunctive process, *Ph* phallosome, *PrG* process of the gonopore) (From Lent and Jurberg 1967)

Through the continuous use of this technique, phallic structures have been investigated in 16 genera and a great amount of species by the above cited authors, which culminated with the construction of a comparative table of presence/absence (+/−) and shape of the genital structure of the triatomines, which was presented in Carcavallo et al (1998/1999) and herein reproduced on Fig. 13.15. It is important to notice on the board that *Rhodnius stali* Lent, Jurberg & Galvão and *R. pictipes* Stål share some features with species of *Triatoma* that are not present on other species of the genus, which is an issue that needs to be further investigated (Figs. 13.16 and 13.17).

13.2.3 Testicular Tubes

Schreiber et al. (1968) noticed that the triatomines present a fixed number of seven testicular tubes (Fig. 13.18), but with different composition according to the genera, which proportioned taxonomists a new tool for characterizing and confirming

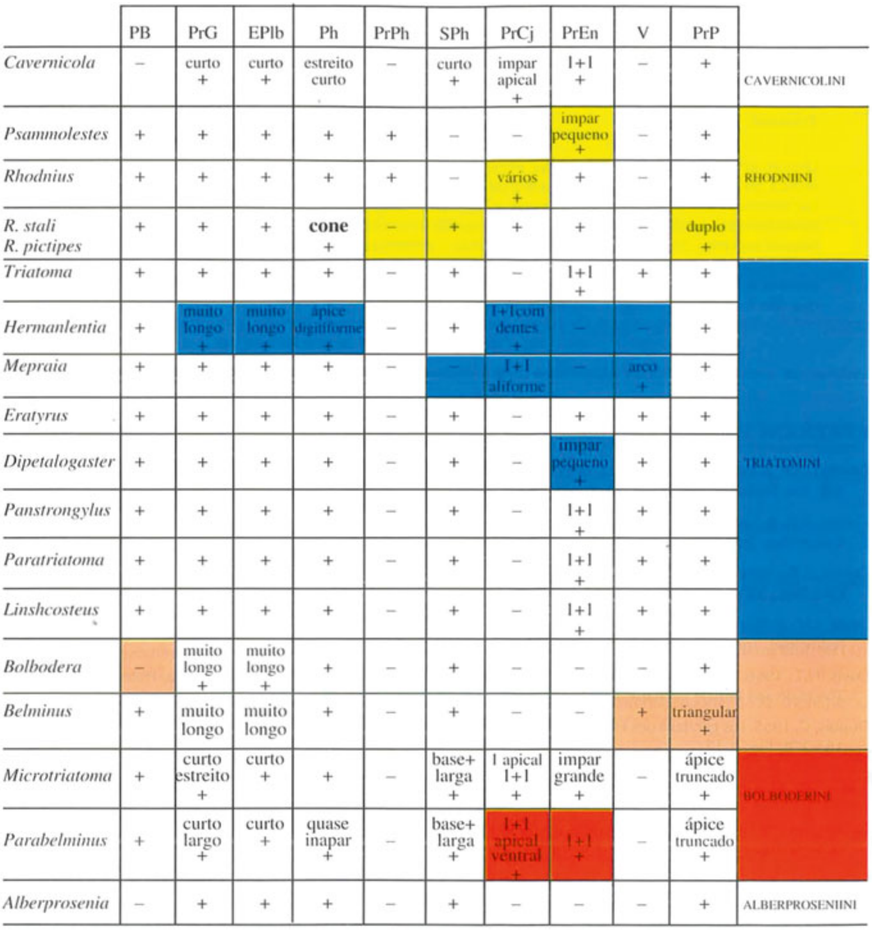
Fig. 13.14 Phallus of *Rhodnius stali* in ventral view (*Ph* phallosome, *PlB* basal plate, *PrCj 1, 2, 3* processes of the conjunctive 1, 2, 3, *SPh* support of the phallosome) (From Lent et al. 1993)



generic statuses. An example is the revalidation by Lent et al. (1994) of the genus *Mepraia*, in which there is a very short tube, two short tubes, two medium tubes, and one long tube. Males of *Rhodnius* present five short and two long; those of *Triatoma* have three short, two medium, and two long; and in *Panstrongylus* there are seven tubes of uniform size.

13.3 General Biology and Ecology

Knowledge of triatomine biology in the natural habitat 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 climatic stability and access to a blood source. Most of them tolerate a range of air humidity between 30 and 80 %, and temperatures of 24–28 °C are satisfactory. Their development is usually slow at temperatures below 16 °C, whereas temperatures above 40 °C are lethal. During the rigorous winters of Patagonia, they undergo lethargy, and on strong summers they increase the number of blood meals in order to compensate the higher loss of water.



	PB	PrG	EPlb	Ph	PrPh	SPh	PrCj	PrEn	V	PrP	
Cavernicola	–	curto +	curto +	estreito curto	–	curto +	impar apical +	1+1 +	–	+	CAVERNICOLINI
Psammolestes	+	+	+	+	+	–	–	impar pequeno +	–	+	
Rhodnius	+	+	+	+	+	–	vários +	+	–	+	RHODNIINI
R. stali *R. pictipes*	+	+	+	**cone** +	–	+	+	+	–	duplo +	
Triatoma	+	+	+	+	–	+	–	1+1 +	+	+	
Hermanlentia	+	muito longo +	muito longo +	ápice digitiforme +	–	+	1+1com dentes +	–	–	+	
Mepraia	+	+	+	+	–	–	1+1 aliforme	–	arco +	+	
Eratyrus	+	+	+	+	–	+	–	+	+	+	
Dipetalogaster	+	+	+	+	–	+	–	impar pequeno +	+	+	TRIATOMINI
Panstrongylus	+	+	+	+	–	+	–	1+1 +	+	+	
Paratriatoma	+	+	+	+	–	+	–	1+1 +	+	+	
Linshcosteus	+	+	+	+	–	+	–	1+1 +	+	+	
Bolbodera	–	muito longo +	muito longo +	+	–	+	–	–	–	+	
Belminus	+	muito longo	muito longo	+	–	+	–	–	+	triangular +	
Microtriatoma	+	curto estreito +	curto +	+	–	base+ larga +	1 apical 1+1 +	impar grande +	–	ápice truncado +	BOLBODERINI
Parabelminus	+	curto largo +	curto +	quase inapar +	–	base+ larga +	1+1 apical ventral +	1+1 +	–	ápice truncado +	
Alberprosenia	–	+	+	+	–	+	–	–	–	+	ALBERPROSENIINI

Fig. 13.15 Comparative scheme of phallic structures on Triatominae genera (*PB* basal bridge, *PrG* process of the gonopore, *EPlb* median extension of the basal plate, *Ph* phallosome, *PrPh* process of the phallosome, *SPh* support of the phallosome, *PrCj* conjunctive process, *PrEn* process of the endosoma, *V* vesica, *PrP* process of the pygophore) (From Carcavallo et al. 1998/1999)

In general, most triatomines 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.

Most species of the subfamily are sylvatic, living in bird nests or animal dens, under tree bark, or in tree hollows, bromeliads, palm trees, and other ecotopes, feeding on various animals. Gaunt and Miles (2000) summarized the habitats of representatives 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, dur-

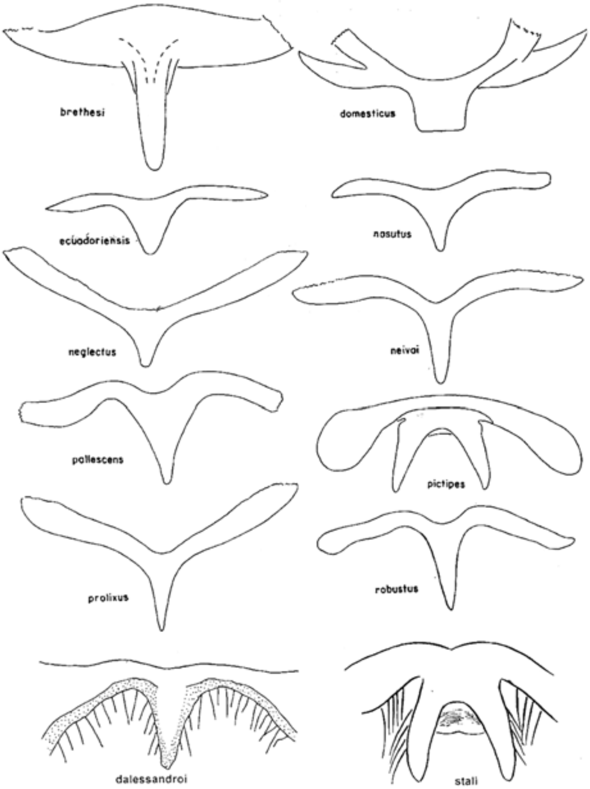


Fig. 13.16 Differences between the median processes of the pygophores of 11 species of the genus *Rhodnius* (From Carcavallo et al. 1998/1999)

ing their evolutionary process some species acquired the capacity to colonize man-made structures near human dwellings, like chicken coops and pigsties, and are thus referred to as peridomiciliated. Others can colonize the interior of human dwellings and are thus called domiciliated. The latter are epidemiologically more important, since they account for transmission of the disease to humans (Carcavallo et al. 1998/1999). Many rural inhabitants live in dwellings with straw roofs and mud walls, and these provide various forms of shelter for the triatomines (Fig. 13.19).

13.3.1 Locomotory Activity

According to Browne (1975), there are two forms of locomotory 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

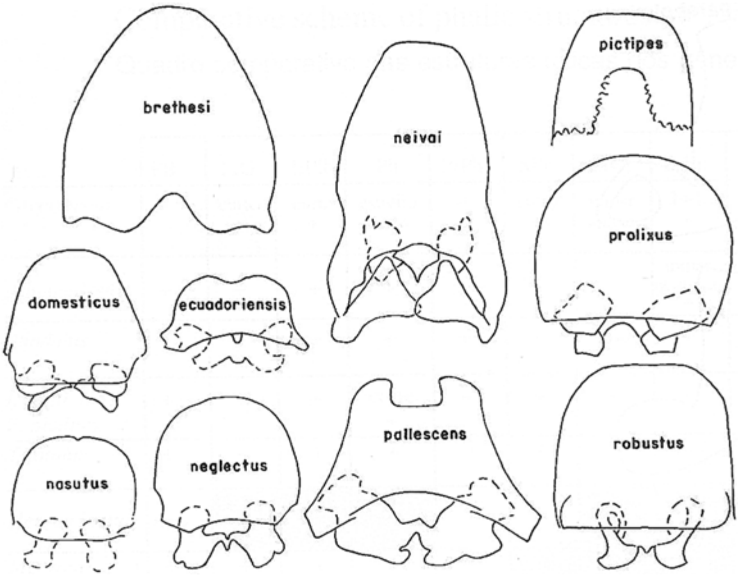


Fig. 13.17 Differences between the phallosomes of ten species of the genus *Rhodnius* (From Carcavallo et al. 1998/1999)

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 and 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.

13.3.2 Aggregation

Aggregative behavior in triatomines is mediated principally by the response to the presence of chemical signals (Velázquez-Antich 1968). Studies performed with *T. infestans* and *Rhodnius prolixus* demonstrated the existence of gregarious behavior as a response to volatile substances found in the feces (Schofield and 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* Corrêa & Espínola.

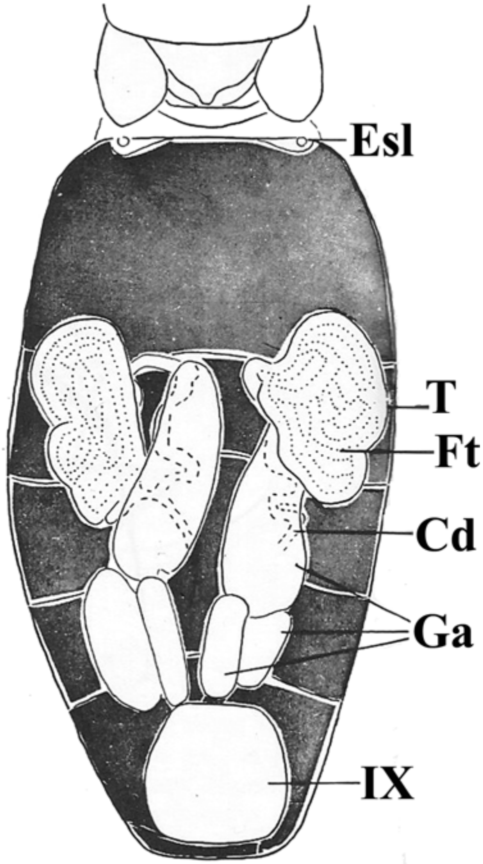


Fig. 13.18 Dissected abdomen of a male *Mepraia spinolai* showing structure of the sexual organs (*Cd* deferent canal, *Esl* spiracle, *Ft* testicular follicles, *Ga* accessory gland, *IX* pygophore or ninth abdominal segment, *T* testicle) (From Gonçalves et al. 1987)

Despite the various attempts of 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, in order to aid the control and monitoring of triatomine populations.

13.3.3 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

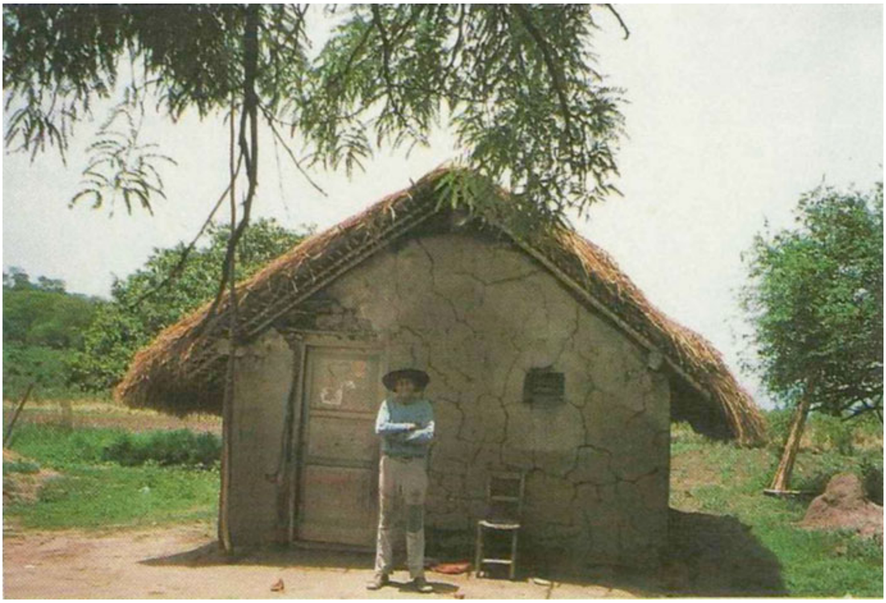


Fig. 13.19 Rural dwelling subject to infestation by triatomine bugs (From Carcavallo et al. 1998/1999)

from the ground) and the presence or absence of this behavior. This behavior's epidemiological implications deserve further investigation, since it 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.

13.3.4 Dispersion

Dispersion in triatomines can occur passively, i.e., 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 about 200 m (Schofield and Matthews 1985), but flights of more than 1 km have been observed in the field (Schweigmann et al. 1988). Triatomine flight capacity has been studied both in the field and the laboratory primarily based on releasing and recapturing the insects and has furnished important information on the most flight-capable species. However, no experiments have been done so far focusing on observations of flight behavior itself (Lehane and Schofield 1981; Schofield et al. 1991, 1992; Galvão et al. 2001b).

Fig. 13.20 Triatomine eggs: agglutinated eggs of *Rhodnius domesticus* (From Jurberg and Galvão 2006)

Fig. 13.21 Triatomine eggs: free eggs of *Triatoma brasiliensis* (From Jurberg and Galvão 2006)

13.3.5 Eggs and Oviposition

In general, the eggs of the majority of triatomine species are deposited free in the environment, although some species have an adhesive substance that makes the eggs stick to the substrate (Figs. 13.20 and 13.21). *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* Neiva and *T. delpontei* Romaña & Abalos, 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* L., a migratory bird, can have its eggs spread when they are adhered to the bird's feathers. *Psammolestes arthuri* (Pinto), on its turn, oviposits in clusters, like members of the reduviid subfamilies Harpactorinae and Apiomerinae (Lent and Wygodzinsky 1979).

Oviposition normally occurs 10–30 days after copulation, which can be repeated several times during the adult's lifespan, although a female fecundated just once remains permanently fertilized. 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 (protonymph).

13.3.6 Feeding and Development

Triatomine bugs are obligatory hematophagous insects in all stages of their development and in both sexes, requiring numerous blood meals to complete their development. The amount of blood ingested varies according to the species as well as in relation to the life stage, and generally the 4th and 5th instar nymphs are the ones that feed the most. 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.

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. 1998/1999). 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 and 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* (Stål) and *T. rubrovaria* (Blanchard) 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 triatomines are considered stenophagic, that is, adapted to feeding only on given hosts, but the vast majority have eclectic feeding habits. Carcavallo et al. (1998/1999) published an extensive list correlating each species to its respective food source, which can be identified through techniques like the precipitin test (Siqueira 1960; Freitas et al. 1960). The results, however, may reflect much more the predominance of a given host or hosts in an area than a true food preference, and it is common to detect the presence of blood from various hosts in a single insect, which 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, and bilateral antennectomy results in the impossibility of locating a heat source. According to Lazzari and 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. Other types of observations, aimed to characterize the species with greatest vector potentials, are to check the number of bites per meals, duration of the meal, and defecation site. These aspects are highly epidemiologically relevant, because with more contacts between vectors and hosts, greater is 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 5 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 and Smith 1977; Mascarenhas 1990; Galvão et al. 2001a; Dias-Lima and Sherlock 2002, Martínez-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 and Costa (1989a, b).

In the domestic environment, these insects generally suck the blood of their victims at night while they are asleep, and the bites generally occur on the uncovered parts of the body. That is why the most popular name for the triatomine bugs in Brazil is *barbeiro* (meaning barber in Portuguese; for a list of vernacular names, see Table 13.1). The sleeping individuals are unaware of the bugs, because the bites are generally painless due to the anesthetic and anticlotting action of the saliva, although rare cases of hypersensitivity can occur. Some species may defecate while feeding, while others defecate soon afterwards or even abandon the food source and defecate far from the sucking site, a fact characterizes them as either good or bad transmitters of the Chagas disease.

The triatomines are parasites with slow development, whose life cycle from egg to adult includes five nymphal stages (Fig. 13.22), ranging from 3 to 4 months in *Rhodnius prolixus* up to 2 years in *Panstrongylus megistus.* This life span can vary considerably according to the temperature to which the bugs are submitted, a fact that was early studied by Neiva (1913), who observed that high temperatures accelerated the embryonic period of *Triatoma infestans*. Carcavallo and 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,

Table 13.1 Examples of vernacular names for Triatominae

Region	Names
USA	Kissing bug, conenose bug, big bedbug (note that "assassin bug" refers to predatory Reduviidae)
	China bug (refers to *T. protracta* on the Pacific coast, once assumed to come from the orient)
	Red-banded conenose (refers to *T. rubrofasciata* and/or *T. sanguisuga*)
Mexico	Chinche besucona (Spanish—"kissing bug")
	Chinche hosicona [Spanish—"trunked bug" (trunked, as in elephant)]
	Chinche picuda (Spanish—"biting bug")
	Chinchona (Spanish—"big bug")
	Pik (Nahuatl, probably refers to the sound made when flying bug strikes wall)
Belize	Bush chinche (implies the absence of domestic Triatominae in Belize)
Central America	Chinche besucona (or just chinche; note that "telepate" more usually refers to cimicid bedbugs)
	Talaje (Spanish—"cutting bug," but mainly applied to cimicid bedbugs)
	Chuluyu (NE Honduras—usually applied specifically to *R. prolixus*, probably derives from *chuzu*, "needle" or "spear," + *uyu*, "alive")
	Polvoso (Spanish—"dusty"; in NE Honduras usually applied specifically to *T. dimidiata*, probably refers to the habit of nymphs to cover themselves with dust)
	Chinche bebe sangre (Costa Rica, Spanish—"blood-drinking bug")
Cuba	Sangrejuela (Spanish—"bloodstealer," also refers to leeches)
Colombia	Pito (Spanish—"whistle" or "horn," but may also refer to the bug's extended mouthparts)
	Chinche picuda
Venezuela	Chipo (colloquial Spanish—"little bug")
	Îipi (Macuxi Indians; refers specifically to *T. maculata*)
Ecuador	Chinchorro (Spanish + Quechua—"large bug")
Peru	Chirimacha (Quechua—"bug that dislikes the cold" or "drunk with the cold")
Paraguay	Chichá guazú (Guarani, probably derived from Spanish *chinche*, "bug," + Guarani *guazú*, "big")
	Itchajuponja (Ayoreo, probably derived from Spanish *chinche*, "bug," + *jupona*, "sucker")
	Sham bui tá (Aché—"insect that does harm by its dejections" mainly used for blister beetles)
	Timbucú (in the Guarani of the Chiriguano and Tapieté groups, signifies "long beak")
Bolivia	Vinchuca (Quechua—"bug that lets itself fall")
	Uluchi (Quechua—"bug without wings"; refers to nymphal stages)
	Timbucú
Chile	Vinchuca
Argentina	Vinchuca
Uruguay	Vinchuca

(continued)

Table 13.1 (continued)

Region	Names
Brazil	Barbeiro (Portuguese—"barber" or "shaver")
	Furão (Portuguese—"big piercing bug")
	Chupão (Portuguese—"big sucking bug")
	Bicudo (Portuguese—"beaked bug")
	Fincão [Portuguese (Brazil-RS)]—"big piercing bug")
	Cascudo [Portuguese (Brazil-MG)—"thick-skinned bug," used mainly for nymphs]
	Chupança [Portuguese (NE Brazil)—"sucking bug"]
	Procotó (or brocotó, borocotó) [Portuguese (NE Brazil)—"bug that hides in cracks"]
	Gigolô [Portuguese (NE Brazil)—"exploiter, esp. of women"]
	Percevejo (or bicho) de parede [Portuguese (NE Brazil)—"wall bedbug"]
	Gaudério (or bicho gaudério) [Portuguese (Brazil-PE)—"indigent thief"] rondão [Portuguese (NE Brazil)—"big bug that observes from hiding"]
	Percevejão (Portuguese—"big bedbug")
	Percevejo do sertão (Portuguese—"bedbug from Sertão," sertão = interior of Brazil)
	Percevejo das pedras (Brazil-RGS) (Portuguese—"bedbug among the stones"; *T. rubrovaria*)
	Piolho de piassava (Brazil-Amazon region) (Portuguese—"louse from the piassaba palm"; *R. brethesi*)
	Vunvum (Portuguese—probably onomatopoeic for the sound of bug flight)
	Josipak [Matacos Indians (Roraima)]
	Îipi [Macuxi Indians (Roraima and Venezuela); refers specifically to *T. maculata*]

From Schofield and Galvão (2009)

1988, 1989a, b, c, 1990a, b, 1992), Silva and Silva (1988a, b, c, d, e, 1989, 1990a, b, 1991, 1993), and Silva et al. (1995) compared the developmental times of several species reared at 25 and 30 °C, showing a reduction of approximately 30 days in three species of *Rhodnius* and from 40 to 60 days in *Triatoma* species. Various other authors have demonstrated acceleration in the developmental period of different species submitted to increased temperature (Galvão et al. 1995, 1999b; Rocha et al. 1994, 2001a, b).

According to most authors, when associated with low relative humidity, the cycle is shortened by metabolic alteration and dehydration, increasing the number of meals to balance the energy budget and water loss. These results support the hypothesis that higher temperatures and lower relative humidity, as possible consequences of global warming, could accelerate the life cycle of triatomines. The result is a change in the population dynamics of some Chagas disease vectors, extending their geographic distribution towards more temperate regions as well increasing the density of some populations.

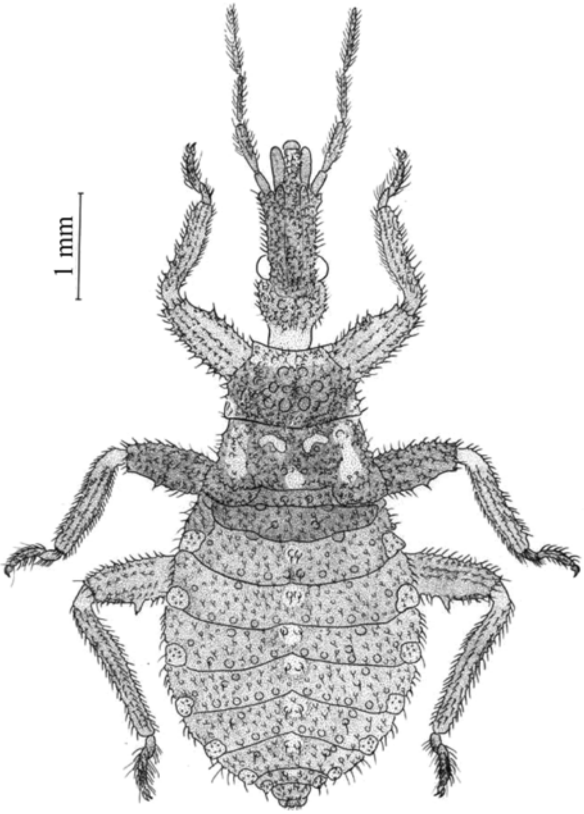


Fig. 13.22 Fourth instar nymph of *Belminus herreri* (From Rocha et al. 2002)

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 h. Of course in nature the insect is influenced by 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 (Carcavallo et al. 1998/1999).

Laboratory Rearing

Important information on triatomine biology has been obtained through rearing and observation in the laboratory and 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 LNIRTT, Oswaldo Cruz Institute, Rio de Janeiro, 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). Strips of filter paper are placed inside the crystallizers to 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 abovementioned 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 crystallizers to allow recently hatched nymphs to have contact with their natural digestive tract symbionts, which aid in digesting blood.

13.3.7 Reproduction

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 lifespan. Courting is not complex in this group of insects, and copulation in some species has been observed in the laboratory. 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 (Fig. 13.23) (Abalos and Wygodzinsky 1951; Hack and Bar 1979; Lent and Wygodzinsky 1979; Lima et al. 1986; Rojas et al. 1990; Manrique and Lazzari 1994). Copulation itself can last 15–30 min, and the male fertilizes the female by depositing spermatophores in her vagina. The spermatophores then burst and release the spermatozoa that migrate to the spermathecae, where they remain protected while awaiting the passage of the successive ova to fertilize.

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 and 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 and Lazzari (1994), studying *Triatoma infestans*. On the other hand, the complete absence of sexual attraction was demonstrated by Schofield and Moreman (1979), Hack and Bar (1979), and Lima and MacCord (1994), which can probably be explained by the differing methodologies applied.

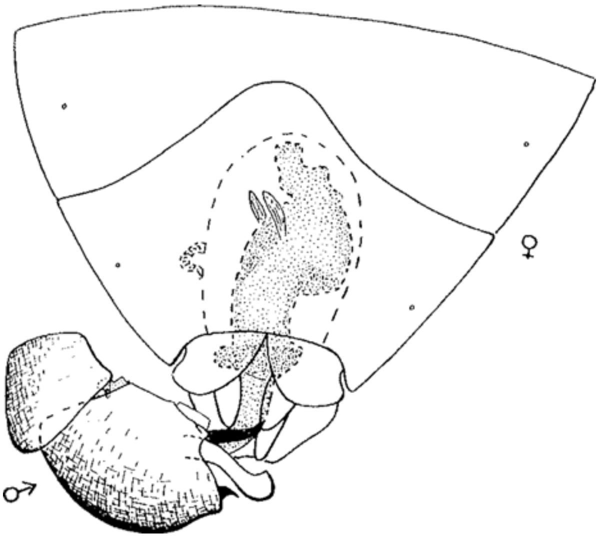


Fig. 13.23 Last abdominal segments of a male and a female of *Rhodnius prolixus* during copulation (From Carcavallo et al. 1998/1999)

13.4 Classification and Diversity

The subfamily Triatominae includes 146 extant species (Galvão et al. 2003; Schofield and Galvão 2009; Rosa et al. 2012; Gonçalves et al. 2013; Jurberg et al. 2013), and its current classification that recognizes five tribes is based mainly on the revision by Lent and Wygodzinsky (1979), the most important systematic study concerning the group. Since that revision, there has been considerable work, including the descriptions of several new taxa. Therefore, a summary of the recent classification and a list of Neotropical species updated from Galvão et al. (2003) and Schofield and Galvão (2009) are herein provided (Tables 13.2 and 13.3). Regarding the identification of the genera and species, extensive dichotomous keys were provided by Lent and Wygodzinsky (1979), Lent et al. (1994), and Carcavallo et al. (1998/1999).

13.4.1 Phylogeny and Evolution

Triatominae has long been classified as a subfamily of the predominantly predatory Reduviidae (Usinger 1943; Maldonado-Capriles 1990; Schuh and Slater 1995). The subfamily is diagnosed, among other features, by the slender and straight labium of its members and their blood-feeding habits (Lent and Wygodzinsky 1979; Clayton 1990; Weirauch 2008). However, phylogenetic relationships of Triatominae are not

Table 13.2 Current systematic classification of the subfamily Triatominae

Subfamily	Tribes	Genera	Number of valid names
Triatominae	Alberproseniini	*Alberprosenia*	2
	Bolboderini	*Belminus*	8
		Bolbodera	1
		Microtriatoma	2
		Parabelminus	2
	Cavernicolini	*Cavernicola*	2
	Rhodniini	*Psammolestes*	3
		Rhodnius	18
	Triatomini	*Dipetalogaster*	1
		Eratyrus	2
		Hermanlentia	1
		Linshcosteus	6
		Meccus	3
		Mepraia	3
		Nesotriatoma	3
		Panstrongylus	14
		Paratriatoma	1
		Triatoma[1]	71

Updated from Galvão et al. (2003) and Schofield and Galvão (2009)

[1] Excluding *T. dominicana*, a fossil species

Table 13.3 Checklist of the Neotropical species of Triatominae, with their geographical distribution

Species and author	Countries or territories
Alberprosenia goyovargasi Martínez & Carcavallo	Venezuela
A. malheiroi Serra, Atzingen & Serra	Brazil
Belminus costaricensis Herrer, Lent & Wygodzinsky	Costa Rica, Mexico
B. herreri Lent & Wygodzinsky	Colombia, Panama
B. laportei Lent, Jurberg & Carcavallo	Brazil
B. peruvianus Herrer, Lent & Wygodzinsky	Peru
B. pittieri Osuna & Ayala	Venezuela
B. rugulosus Stål	Colombia, Venezuela
Bolbodera scabrosa Valdés	Cuba
Microtriatoma borbai Lent & Wygodzinsky	Brazil
M. trinidadensis (Lent)	Brazil, Bolivia, Colombia, Peru, Trinidad and Tobago, Venezuela
Parabelminus carioca Lent	Brazil
P. yurupucu Lent & Wygodzinsky	Brazil
Cavernicola lenti Barrett & Arias	Brazil

(continued)

Table 13.3 (continued)

Species and author	Countries or territories
C. pilosa Barber	Brazil, Colombia, Panama, Peru, Venezuela
Psammolestes arthuri (Pinto)	Colombia, Venezuela
P. coreodes Bergroth	Argentina, Bolivia, Brazil, Paraguay
P. tertius Lent & Jurberg	Brazil
Rhodnius amazonicus Almeida, Santos & Sposina	Brazil, French Guiana
Rhodnius brethesi Matta	Brazil, Colombia, Venezuela
R. colombiensis Mejia, Galvão & Jurberg	Colombia
R. dalessandroi Carcavallo & Barreto	Colombia
R. domesticus Neiva & Pinto	Brazil
R. ecuadoriensis Lent & León	Ecuador, Peru
R. milesi Carcavallo, Rocha, Galvão & Jurberg	Brazil
R. montenegrensis Rosa, Rocha, Gardim, Pinto, Mendonça, Ferreira-Filho, Carvalho, Camargo, Oliveira, Nascimento, Cilense & Almeida	Brazil
R. nasutus Stål	Brazil
R. neglectus Lent	Brazil
R. neivai Lent	Colombia, Venezuela
R. pallescens Barber	Belize, Colombia, Costa Rica, Panama
R. paraensis Sherlock, Guitton & Miles	Brazil
R. pictipes Stål	Belize, Brazil, Colombia, Ecuador, Guyana, French Guiana, Peru, Suriname, Trinidad and Tobago, Venezuela
R. prolixus Stål	Bolivia, Brazil, Colombia, Costa Rica, El Salvador, Ecuador, Guatemala, Guyana, French Guiana, Honduras, Mexico, Nicaragua, Panama, Suriname, Trinidad and Tobago, Venezuela
R. robustus Larrousse	Bolivia, Brazil, Colombia, Ecuador, French Guiana, Peru, Venezuela
R. stali Lent, Jurberg & Galvão	Bolivia, Brazil
R. zeledoni Jurberg, Rocha & Galvão	Brazil
Dipetalogaster maxima (Uhler)	Mexico
Eratyrus cuspidatus Stål	Colombia, Ecuador, Guatemala, Mexico, Panama, Peru, Venezuela
E. mucronatus Stål	Bolivia, Brazil, Colombia, Ecuador, Guatemala, Guyana, French Guiana, Panama, Peru, Suriname, Trinidad and Tobago, Venezuela

(continued)

Table 13.3 (continued)

Species and author	Countries or territories
Hermanlentia matsunoi (Fernández-Loayza)	Peru
Meccus bassolsae (Alejandre Aguilar, Nogueda Torres, Cortéz Jimenez, Jurberg, Galvão & Carcavallo)	Mexico
M. longipennis (Usinger)	Mexico
M. mazzottii (Usinger)	Mexico
M. pallidipennis (Stål)	Mexico
M. phyllosomus (Burmeister)	Mexico
M. picturatus (Usinger)	Mexico
Mepraia gajardoi Frias, Henry & Gonzalez	Chile
M. spinolai (Porter)	Chile
Nesotriatoma bruneri Usinger	Cuba
N. flavida (Neiva)	Cuba
N. obscura Maldonado & Farr	Jamaica
Paratriatoma hirsuta Barber	Mexico, USA
Panstrongylus chinai (Del Ponte)	Ecuador, Peru, Venezuela
P. diasi Pinto & Lent	Bolivia, Brazil
P. geniculatus (Latreille)	Argentina, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, Guatemala, Guyana, French Guiana, Mexico, Nicaragua, Panama, Paraguay, Peru, Suriname, Uruguay, Trinidad and Tobago, Venezuela
P. guentheri Berg	Argentina, Bolivia, Paraguay, Uruguay
P. howardi (Neiva)	Ecuador
P. humeralis (Usinger)	Panama
P. lenti Galvão & Palma	Brazil
P. lignarius (Walker)	Brazil, Peru, Guyana, Suriname, Venezuela
P. lutzi (Neiva & Pinto)	Brazil
P. megistus (Burmeister)	Argentina, Bolivia, Brazil, Paraguay, Uruguay
P. mitarakaensis Bérenger & Blanchet	French Guiana
P. rufotuberculatus (Champion)	Argentina, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, Mexico, Panama, Peru, Venezuela
P. tupynambai Lent	Brazil, Uruguay
T. arthurneivai Lent & Martins	Brazil
T. baratai Carcavallo & Jurberg	Brazil
T. barberi Usinger	Mexico
T. bolivari Carcavallo, Martínez & Pelaez	Mexico
T. boliviana Martínez, Chávez, Sossa, Aranda, Vargas & Vidaurre	Bolivia
T. brailovskyi Martínez, Carcavallo & Pelaez	Mexico

(continued)

Table 13.3 (continued)

Species and author	Countries or territories
T. brasiliensis Neiva	Brazil
T. breyeri Del Ponte	Argentina
T. carcavalloi Jurberg, Rocha & Lent	Brazil
T. carrioni Larrousse	Ecuador, Peru
T. circummaculata (Stål)	Brazil, Uruguay
T. costalimai Verano & Galvão	Brazil
T. deaneorum Galvão, Souza & Lima	Brazil
T. delpontei Romaña & Abalos	Argentina, Bolivia, Brazil, Uruguay, Paraguay
T. dimidiata (Latreille)	Belize, Colombia, Costa Rica, El Salvador, Ecuador, Guatemala, Honduras, Mexico, Nicaragua, Panama, Peru, Venezuela
T. dispar Lent	Colombia, Costa Rica, Ecuador, Panama
T. eratyrusiformis Del Ponte	Argentina
T. garciabesi Carcavallo, Cichero, Martínez, Prosen & Ronderos	Argentina, Bolivia
T. gerstaeckeri (Stål)	USA, Mexico
T. gomeznunezi Martínez, Carcavallo & Jurberg	Mexico
T. guasayana Wygodzinsky & Abalos	Argentina, Bolivia, Paraguay
T. guazu Lent & Wygodzinsky	Brazil
T. hegneri Mazzotti	Mexico
T. incrassata Usinger	USA, Mexico
T. indictiva Neiva	USA, Mexico
T. infestans (Klug)	Argentina, Bolivia, Brazil, Chile, Ecuador, Paraguay, Peru, Uruguay
T. jatai Gonçalves, Teves-Neves, Santos-Mallet, Carbajal-de-la-Fuente & Lopes	Brazil
T. jurbergi Carcavallo, Galvão & Lent	Brazil
T. klugi Carcavallo, Jurberg, Lent & Galvão	Brazil
T. lecticularia (Stål)	USA, Mexico
T. lenti Sherlock & Serafim	Brazil
T. limai Del Ponte	Argentina
T. maculata (Erichson)	Aruba, Brazil, Bonaire, Curaçao, Colombia, Guyana, French Guiana, Suriname, Venezuela
T. matogrossensis Leite & Barbosa	Brazil
T. melanocephala Neiva & Pinto	Brazil
T. mexicana (Herrich-Schaeffer)	Mexico
T. neotomae Neiva	USA, Mexico

(continued)

Table 13.3 (continued)

Species and author	Countries or territories
T. nigromaculata (Stål)	Colombia, Peru, Venezuela
T. nitida Usinger	Costa Rica, Guatemala, Honduras, Mexico
T. oliveirai (Neiva, Pinto & Lent)	Brazil
T. patagonica Del Ponte	Argentina, Uruguay
T. peninsularis Usinger	Mexico
T. petrochiae Pinto & Barreto	Brazil
T. pintodiasi Jurberg, Cunha & Rocha	Brazil
T. platensis Neiva	Argentina, Paraguay, Uruguay
T. protracta (Uhler)	USA, Mexico
T. pseudomaculata Corrêa & Espínola	Brazil
T. recurva (Stål)	USA, Mexico
T. rubida (Uhler)	USA, Mexico
T. rubrofasciata (De Geer)	Andaman Islands, Angola, Argentina, Azores, Bahamas, Brazil, Burma, Cambodia, Caroline Islands, China, Comoros, Congo, Cuba, Dominican Republic, Formosa, French Guiana, Goa, Grenada, Guadeloupe, Haiti, Hawaii, Hong Kong, India, Indonesia (Borneo, Java, Sumatra), Jamaica, Madagascar, Malaysia, Martinica, Mauritius Islands, New Guinea, Okinawa, Philippines, Saint Croix, Saint Vincent, Saudi Arabia, Seychelles, Sierra Leone, Singapore, South Africa, Sri Lanka, Thailand, USA, Venezuela, Vietnam, Zanzibar
T. rubrovaria (Blanchard)	Argentina, Brazil, Uruguay
T. ryckmani Zeledón & Ponce	Costa Rica, Guatemala, Honduras
T. sanguisuga (Leconte)	USA, Mexico
T. sherlocki Papa, Jurberg, Carcavallo, Cerqueira & Barata	Brazil
T. sinaloensis Ryckman	Mexico
T. sordida (Stål)	Argentina, Bolivia, Brazil, Paraguay, Uruguay
T. tibiamaculata (Pinto)	Brazil
T. vandae Carcavallo, Jurberg, Rocha, Galvão, Noireau & Lent	Brazil
T. venosa (Stål)	Bolivia, Colombia, Costa Rica, Ecuador, Peru
T. vitticeps (Stål)	Brazil
T. williami Galvão, Souza & Lima	Brazil
T. wygodzinskyi Lent	Brazil

Updated from Galvão et al. (2003)

resolved, with problems persisting in three areas. First, it is unclear if Triatominae are actually monophyletic, i.e., derived from a single ancestor that gave rise to the entire clade of blood-feeding assassin bugs (Hypsa et al. 2002; Schofield and Galvão 2009; Weirauch and Munro 2009; Patterson and Gaunt 2010; Hwang and Weirauch 2012). Second, different groups of predatory Reduviidae have been proposed to be the closest relatives of the Triatominae. Third, relationships and evolutionary history of clades within the Triatominae are not well understood.

Alternative phylogenetic hypotheses show Triatominae to be monophyletic (Hypsa et al. 2002; Weirauch and Munro 2009; Patterson and Gaunt 2010), paraphyletic (Hwang and Weirauch 2012), or polyphyletic (de Paula et al. 2005; Schofield and Galvão 2009). This directly impacts our understanding of the number of times blood feeding evolved within the Reduviidae, as well as the ecological circumstances under which this transition occurred. Triatominae were considered a natural group or clade until Schofield (1994) suggested that they may in fact represent a polyphyletic assemblage of multiple blood-feeding lineages derived independently from predatory ancestors. This hypothesis stimulated a number of phylogenetic studies that attempted to clarify origin and relationships of Triatominae. Several analyses were hampered by poor sampling of in-group (Triatominae) and/or out-group (remaining Reduviidae) taxa or were based on insufficient character data, e.g., Weirauch (2008; 162 morphological characters; only four spp. of Triatominae), Weirauch and Munro (2009; 3,300 bp of 16S, 28S, and 18S rDNA; only five spp. of Triatominae), Hypsa et al. (2002; 57 spp. of Triatominae, but mostly based on ~500 bp of 16S rDNA), or de Paula et al. (2005; 57 of Triatominae and 15 out-group spp.; 16S rDNA only).

Two recent analyses are derived from more substantial datasets: Patterson and Gaunt (2010) analyzed one ribosomal nuclear gene (D2 region of 28S rDNA) and four protein-coding mitochondrial loci (~2,700 bp), 45 out-group taxa, and 13 species of Triatominae representing the tribes Bolboderini, Triatomini, and Rhodniini. Despite a substantial amount of missing data, their analyses showed strong support for the monophyly of Triatominae. The dataset of Hwang and Weirauch (2012) comprised 178 spp. of Reduviidae and out-groups and included 13 spp. of Triatominae (Cavernicolini, Rhodniini, and Triatomini) and five molecular markers (rDNA: 16S, 18S, 28S D2, 28S D3–5; nuclear protein coding: wingless; ~3,700 bp). Triatominae were rendered paraphyletic by the reduviine genus *Opisthacidius* Berg that formed the sister group to the *Rhodnius* + *Cavernicola* clade. These current conflicting hypotheses ask for further testing using comprehensive molecular and morphological datasets and should aim on including representatives of all five triatomine tribes.

Even with the question of triatomine monophyly unresolved, recent analyses converge on placing kissing bugs in close relationship with a small number of predatory Reduviidae. Earlier authors proposed either an assemblage comprising Salyavatinae, Sphaeridopinae, and Reduviinae (Usinger 1943), Physoderinae (Lent and Wygodzinsky 1979), Stenopodainae (Clayton 1990; some trees only), Harpactorinae or Reduviinae (Hypsa et al. 2002), or Harpactorinae, Ectrichodiinae, Reduviinae, and Salyavatinae (de Paula et al. 2005) as closest relatives of the Triatominae. Subsequent analyses, based on molecular and morphological data sets,

Fig. 13.24 Lateral view of *Linshcosteus karupus*

found a sister group relationship of large-bodied Reduviinae (different combinations of the genera *Zelurus* Hahn, *Centrogonus* Bergroth, and *Opisthacidius*) with the Triatominae, with the Stenopodainae forming the sister group to that clade (Weirauch 2008; Weirauch and Munro 2009; Patterson and Gaunt 2010; Hwang and Weirauch 2012).

Given that the larger picture of triatomine relationships is only beginning to emerge, it is not surprising that lower-level relationships among kissing bugs are largely obscure. It is unclear if the five tribes are monophyletic and even the monophyly of the genera *Triatoma* and *Rhodnius* is not well established (e.g., Lent and Wygodzinsky 1979; Garcia and Powell 1998; Sainz et al. 2004; de Paula et al. 2005). The Oriental distribution of the *T. rubrofasciata* complex and the morphologically distinctive, genus *Linshcosteus* Distant that is classified within the Triatomini (Hypsa et al. 2002) has long puzzled researchers. Patterson and Gaunt (2010) found (based on a fixed molecular clock model) that Triatominae originated around 107 million years ago, before the Gondwanan breakup. Under this scenario, the disjunct distribution of Triatominae could be attributed to vicariance. Based on a (generally thought to be more reliable) relaxed clock model using fossil calibration points, Hwang and Weirauch (2012) showed Triatominae to be much younger (~32 million years), making dispersal from South America the currently better supported hypothesis.

13.4.2 Geographical Distribution

The vast majority of the triatomines is found only in the New World, although a few species occur in East Asia and the coast of Australia. In the Neotropical and Nearctic regions, species are found between 42°N and 46°S. One species, *Triatoma rubrofasciata*, is tropicopolitan, and additional seven species of *Triatoma* occur in Southern and Southeastern Asia and Northern Australia. *Linshcosteus* (Fig. 13.24) is the only genus restricted to the Old World, specifically to the Indian subcontinent (Galvão et al. 2003). Carcavallo et al. (1998/1999) provided several maps showing the geographical distribution and altitudinal/latitudinal dispersion of all American species of Triatominae.

13.5 Concluding Remarks

More than a century after the discovery of the medical importance of the triatomines, there are still millions of people infected or living at risk of contracting Chagas disease, of which they are vectors. In addition to the classical vectorial transmission of the disease by the direct contact with the contaminated feces of these insects due to their hematophagous habits, alternative ways of transmission emerge as serious public health issues. In some regions of northern Brazil, for example, the ingestion of food contaminated by infected triatomines, especially the locally appreciated *açaí* pulp, is responsible for outbreaks of acute Chagas disease (Nóbrega et al. 2009). Also, due to massive human migration, the disease has been more often reported from non-endemic areas, mainly due to blood transfusions or organ transplants from infected, but not symptomatic, immigrants from Latin America (Kirchhoff 1993). Considering these facts, it becomes clear that studies concerning the taxonomy, evolution, biology, and ecology of triatomine bugs are extremely urgent in order to support the control of a highly neglected disease.

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