

Biosystematics and evolution of the Triatominae

Biosistemática e evolução de triatomíneos

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Abstract *In this paper we summarize the systematics of the 130 currently recognized species of Triatominae and the key features of their evolutionary background. There is increasing evidence that the subfamily has polyphyletic origins, with the various tribes and species groups probably arising from different reduviid lineages in relatively recent times.*

Key words *Triatominae; Classification; Evolution; Insect Vectors*

Resumo *Neste trabalho resume-se a sistemática das 130 espécies de triatomíneos atualmente reconhecidas, com os elementos principais de sua evolução. Existem evidências crescentes para a origem polifilética da subfamília. As diferentes tribos e grupos de espécies que a compõem teriam surgido recentemente, a partir de diferentes linhagens de reduvídeos.*

Palavras-chave *Triatominae; Classificação; Evolução; Insetos Vetores*

Introduction

The subfamily Triatominae (Hemiptera: Reduviidae) is customarily organized into 5 tribes with 14 genera (Lent & Wygodzinsky, 1979; Schofield, 1994), although three additional genera have recently been proposed (Carcavallo et al., 1998; Lent et al., 1994; Jurberg & Galvão, 1997). At present, 130 species are recognized (Table 1), all characterized by an obligate blood-sucking habit and various associated adaptations including modifications of the mouthparts, saliva, and digestive functions. The subfamily is defined as a collection of hematophagous Reduviidae (Jeannel, 1919), although it is increasingly apparent that this assemblage is rather artificial and is probably unsustainable as a monophyletic grouping (Schofield, 1988). For example, the two main tribes – Triatomini and Rhodniini – seem to have little in common other than a basic reduviid form overlaid with convergent characters associated with a blood-sucking diet. Apart from their differences in morphology (Lent & Wygodzinsky, 1979) these two tribes show consistent differences in sensorial patterns (Catalá, 1997; Catalá & Schofield, 1994), salivary gland physiology (Ribeiro et al., 1998), and DNA analysis (Garcia et al., 1998; Stothard et al., 1998; Lyman et al., 1999) and have probably originated from quite different predatory forms. The Indian genus *Linshcosteus* seems to have evolved independently from the New World species of Triatominae (Gorla et al., 1997) and so probably merits independent tribal status.

Several lines of evidence support the idea that the Triatominae have evolved relatively recently from various of the predatory reduviids (Schofield, 1988; Schofield & Dolling, 1993). The evolution of these blood-sucking forms can be envisaged through a transitional phase of nest-dwelling forms initially feeding on the guilds of nest-dwelling invertebrates but progressively adapting to exploit the vertebrate nest-building host itself. Such a transition brings several advantages, especially in terms of protection from other predators and from climatic extremes, as well as the more reliable supply of protein-rich food. The improved food supply and protection from climatic extremes mean that reproduction becomes less dependent on seasonal changes, and population density can increase up to the limits of the available nutrition. However, the transition also requires several adaptations. Mouthparts of predators are generally robust and strongly chitinized (often curved), whereas those of blood-sucking forms are slim and slender, reflecting the physical dif-

ferences of the host integument. Salivary function must also be modified. The requirement of predators is for a toxic saliva that can rapidly immobilize the invertebrate prey, whereas blood-suckers need a more benign saliva that will not stimulate adverse reactions from the vertebrate host (Schofield et al., 1986). Thus for humans the bite of a predatory reduviid is generally very painful, and amongst the Triatominae a painful bite – such as that of *Triatoma rubrofasciata*, whose bite can provoke anaphylactic shock – can be considered a primitive character (cf. Ryckman & Bentley 1979; Ribeiro et al., 1998).

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

The process of speciation within the Triatominae is not well understood, but is subject to a major research effort because it encompasses the processes by which Triatominae can adapt from sylvatic to domestic environments – and so assume greater significance as vectors of Chagas disease to humans. By morphological, biochemical, and genetic criteria, the different genera and species of Triatominae seem to form a series of species groups, which generally show a discrete geographical distribution. This is additional evidence for their polyphyletic origins, which is now being supported by physiological comparisons and by genetic analysis based on isoenzymes and RAPD profiles (Garcia et al., 1998), as well as sequence

analysis of ribosomal and mitochondrial DNA (Garcia & Powell, 1998; Stothard et al., 1998; Lyman et al., 1999). We can assume that amongst sylvatic species of Triatominae, natural selection may play an important role in speciation, so that many species and species groups have adapted to highly specific host and habitat associations. Well-known examples include *Cavernicola pilosa* which is invariably found in bat caves, and species of *Psammolestes* which are invariably associated with the woven-stick nests of furnariid weaver birds. In contrast, there are many groups of sylvatic species that remain relative generalists, such as the *Triatoma sordida* group which can be found in a very wide range of habitats. To a certain extent, species can be ranked in accordance with their degree of adaptation to more stable habitats, such as the domestic environment, and it may be that the more generalist species represent those which still have the potential for further adaptation to more specific habitats.

Studies of *Triatoma infestans* and *Rhodnius prolixus*, the two most widespread domestic species, reveal a further adaptive process which seems of major importance. In the case of *T. infestans*, true sylvatic populations are known only from the Cochabamba/Sucre region of central Bolivia, where bugs can be found amongst rock piles associated with wild guinea pigs. Elsewhere, this species is almost exclusively domestic, although peridomestic populations can also be found in regions with a climate similar to that of central Bolivia. Comparison of *T. infestans* populations from many different localities reveals that each has a generally low level of population variability (in fact, they have been likened to pseudo-clones), but there are detectable genetic and phenetic differences between panmictic populations. The overall population structure can be well explained by a process of genetic drift, using a model of "isolation by distance". The genetic differences between populations reflect their geographic distance apart (Dujardin et al., 1998a). It is also interesting to note a general reduction in physical size and in genome size in populations further from the putative source in central Bolivia. For example, populations from Uruguay are noticeably smaller than Bolivian populations, and have only about two-thirds of the total DNA content per cell (Panzera et al., 1998).

A similar pattern is shown by *R. prolixus*. This species is believed to derive from palm tree populations in the llanos of Venezuela and Colombia, but like *T. infestans*, has been spread in association with humans into other areas of these countries and into parts of Central Amer-

Table 1

Tribes and Genera of the Triatominae (Hemiptera: Reduviidae).

Tribe	Genus	No. species
Alberproseniini	<i>Alberprosenia</i>	2
Bolboderini	<i>Belminus</i>	6
	<i>Bolboderia</i>	1
	<i>Microtriatoma</i>	2
	<i>Parabelminus</i>	2
Cavernicolini	<i>Cavernicola</i>	2
	<i>Torrealbaia</i>	1
Rhodniini	<i>Psammolestes</i>	3
	<i>Rhodnius</i>	14
Triatomini	<i>Dipetalogaster</i>	1
	<i>Eratyrus</i>	2
	<i>Linshcosteus</i>	5
	<i>Panstrongylus</i>	13
	<i>Paratriatoma</i>	1
	<i>Triatoma</i>	75*
Total		130

* 1) Note that some authors place *Triatoma spinolai* in a separate genus, *Mepraia*, following Lent et al. (1994). However, acceptance of this taxon would leave unresolved the position of *Triatoma breyeri* and *Triatoma eratyrusiformis*, which have been classed within the *spinolai* group (Lent & Wygodzinsky, 1979; Schofield, 1988). Frias et al. (1998) have denoted northern Chilean populations of *T. spinolai* (approximately from 18°S to 26°S) as *Mepraia gajardoí*.
2) Jurberg & Galvão (1997) place *Triatoma matsunoí* in a separate genus, *Hermanlenticia*.

ica. The Central American populations are also smaller than their South American cousins, and show a highly restricted genetic repertoire as revealed by RAPD profiles (Dujardin et al., 1998b). In this case, the differences seem to reflect a series of genetic bottlenecks and subsequent genetic drift, and lend substantial support to the arguments favoring control of Chagas disease in Central America by eradicating all *R. prolixus* populations (Schofield & Dujardin, 1997). As the processes of speciation and adaptation in Triatominae become better understood, it may be possible to propose future measures to assist in monitoring this process in areas experiencing major land-use change, and also to consider interventions to prevent the eventual domestication of some species.

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