



Classification, evolution, and species groups within the Triatominae

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ABSTRACT

Classification of the Triatominae has become a complex balance between traditional approaches and a wide variety of evolutionary interpretations. On the one hand is the need for a stable classification of practical use for those involved in vector surveillance and control. On the other is the desire to adequately reflect evolutionary theory derived from a range of molecular, cytogenetic and morphometric comparisons, with additional complications raised by current interpretations of the subfamily as a recently derived polyphyletic assemblage. Here we review key aspects of triatomine systematics and evolution, to derive a pragmatic classification that seeks to build on traditional morphological concepts within the context of current evolutionary theories.

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The Triatominae are classified as a subfamily of the Reduviidae (Hemiptera, Heteroptera) defined by their blood-sucking habit and morphological adaptations associated with host-finding and blood feeding. At present, 140 extant species are formally recognised (Table 1) although some may be no more than minor variants. On the other hand, with increasing field research, it is likely that new variants will be encountered, some of which may merit formal description as new species. All are probably capable of transmitting *Trypanosoma cruzi* – causative agent of Chagas disease – although relatively few are of epidemiological significance as vectors of *T. cruzi* to humans. Those of greatest importance are populations that have adapted to live in close contact with humans, for example by colonising rural dwellings, although these are currently subject to a series of large-scale control interventions (cf. Dias et al., 2002; Schofield et al., 2006) which are expected to change radically the distribution and relative importance of these species.

Although the Reduviidae are of world-wide distribution, roughly from 55°N to 55°S, the Triatominae are primarily found in the Americas, roughly from 46°N to 46°S. One species, *Triatoma rubrofasciata*, is recorded from port areas throughout the tropics and subtropics, and a small group of seven related species of *Triatoma* are recorded from eastern Asia (from China to northern Australia). In addition, the atypical genus *Linshcosteus*, with six described species, is known only from the Indian subcontinent. However, except for some infected immigrants from Latin America, the causative agent of Chagas disease is not yet found naturally in the Old World. Apart from *T. rubrofasciata* in some port areas, no triatomine species has yet been reported from Africa, Europe or the Middle East, and it has

been suggested that Triatominae may not have evolved in these regions if the available ecological niches for this type of blood-sucking bug were already occupied by a diversity of Cimicidae (cf. Schofield, 2000).

Current evidence suggests that the Triatominae represent a polyphyletic assemblage, with the different tribes and species groups derived from different lineages within the predatory Reduviidae. However, precise relationships between the predaceous and haematophagous forms are by no means clear, and there is considerable epidemiological convenience in maintaining the current classification of Triatominae as a single subfamily. Nevertheless, as evidence accrues for their polyphyletic origins, the implication is that features of one group of Triatominae may not necessarily be shared with other groupings derived from different ancestral lineages (cf. Schaefer, 2003, 2005). The aim of this review is to summarise what is currently known and theorised about the evolution of the Triatominae, as well as to recapitulate relevant aspects of their systematics and taxonomy.

1. Nomenclature

T. rubrofasciata was the first species of Triatominae to be described, as *Cimex rubro-fasciatus* De Geer 1773, and remains the type species of the genus *Triatoma*. The genus *Triatoma* was erected by Laporte (1832–1833) in a redescription of the same species (as *Triatoma gigas*) based on specimens with broken antennae showing only three of the four antennal segments (Tri-atoma = three-segments). On examination of fresh specimens, and realising his mistake, he changed the generic name to *Conorhinus* (lit: con-nose) (Laporte, 1832–1833) but the generic name *Triatoma* has priority (cf. ICZN, 1999). As further species were described, Jeannel (1919) formally differentiated the group at suprageneric level as

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Table 1
Classification of Triatominae used in this review.

Tribe	Genus	Number of species
Alberproseniini	<i>Alberprosenia</i>	2
Bolboderini	<i>Belminus</i>	8
	<i>Bolboderia</i>	1
	<i>Microtriatoma</i>	2
	<i>Parabelminus</i>	2
Cavernicolini	<i>Cavernicola</i>	2
Rhodniini	<i>Psammolestes</i>	3
	<i>Rhodnius</i>	16
Triatomini	<i>Dipetalogaster</i>	1
	<i>Eratyrus</i>	2
	<i>Hermanlenticia</i>	1
	<i>Linshcosteus</i>	6
	<i>Panstrongylus</i>	13
	<i>Paratriatoma</i>	1
	<i>Triatoma</i>	80

the tribe Triatomini, while the subfamilial designation of Triatominae (to include Triatomini and other tribes) is generally attributed to Usinger (1939). Regrettably, the familial denomination 'Triatomidae' reached the literature from Pinto (1926) although no characters were offered then (or since) to merit such a ranking; but some parasitologists continue to refer incorrectly to 'triatomid bugs' rather than to 'triatomine bugs'.

In the vernacular, species of Triatominae have accrued a wide range of common names (Table 2) that have possible significance in relation to their adaptations to human dwellings and consequent human awareness of them. Where precolombian cultures were prominent, the vernacular names tend to derive from precolombian languages such as Quechua (Ecuador, Peru, Chile, Argentina), Aymara (Bolivia) or Nahuatl (Mexico), or from the indigenous Amazonian cultures such as Ticuna and Huitota (Rodríguez, 2004), whereas elsewhere the common names tend to derive from the corresponding European language. The implication is that the bugs were well-known to settled precolombian and Amazonian cultures, but perhaps not to the more nomadic cultures, for example of Brazil and Paraguay. This idea is reinforced in one sense by archaeological studies showing signs of chronic Chagas disease – and in some cases evidence of *T. cruzi* DNA – in precolombian mummies from Peru and Chile (Aufderheide et al., 2004; Rothhammer et al., 1985) and also in the converse sense from epidemiological studies in Paraguay showing an initial absence of Chagas disease in nomadic groups, compared with a rise in seropositivity associated with triatomine colonisation of homes when these groups were first settled during the 1950s (Canese, 1973; Canese and Brice, 1977).

Many of the vernacular names also offer insight to local behaviour of the bugs. The term 'vinchuca' widely used in Chile, Argentina and Uruguay, is derived from Quechua and typically translated as "he that lets himself fall", perhaps referring to bugs falling from the house roof to reach their hosts below. In Peru, the widely used term is 'chirimacha', again from Quechua, usually translated as "drunk with the cold" and assumed to refer to the bugs' dislike of very cold conditions (and absence from the high Andes). Both examples seem to refer to bugs colonising human dwellings, as is the case in those regions with *Triatoma infestans*; but in Mexico, vernacular names for Triatominae such as 'pik' in Nahuatl, are more usually translated as referring to the noise made by adult bugs flying into houses and striking the internal walls, reflecting perhaps the more usual silvatic habitats of Mexican and Central American bug populations. In Venezuela, Triatominae are generally referred to as 'chupos' which seems a diminutive of 'chinche' perhaps reflecting the smaller size of the predominant local vectors, *Rhodnius prolixus*; although in Colombia the same bugs are

known as 'pitos' which seems unlikely to derive from the common term for a whistle and may more likely derive from the way the bugs extend their mouthparts prior to feeding. In Brazil, amongst the various local names are 'furão' (big piercing bug), 'chupão' (big sucking bug), although the most widely used is 'barbeiro' (lit. barber or shaver) assumed to refer either to the bugs biting the face, which is usually the part uncovered when asleep, or to the blood-letting traditionally carried out by barbers (Rezende and Rassi, 2008). A similar concept lies behind the US term 'kissing bug', although this term seems to have been originally coined by US newspapers such as the *New York Times* to describe attacks by *Reduvius personatus*.¹ In Paraguay, the most widely used term is 'chichá guazu' derived from the Spanish 'chinche' (=bug) and Guaraní adjective 'guazu' (=big). Other terms used by different ethnic groups tend to be derived from similar concepts such as the Ayoreo 'itchájuponja' derived from Spanish 'chinche' (bug) and 'jupona' (sucker). However, the Aché hunters of NE Paraguay use the expression 'Sham bui tá' which is literally translated as "insect that does harm by its dejections", a term equally applied to blister beetles (family Meloidae) and apparently adapted by the Aché when they were first settled during the 1970s and received instruction about Triatominae and Chagas disease from local health workers.

2. Classification

As a subfamily of the Reduviidae, the Triatominae are customarily classified into 5 tribes and 15 genera (Lent and Wygodzinsky, 1979) (Table 1) although several other arrangements have been proposed (e.g. Carcavallo et al., 2000; Galvão et al., 2003). Most of these classifications have been based on morphological characteristics, although comparisons of cytogenetic characters and genomic DNA sequences have sometimes challenged this approach. There are several difficulties in reaching a stable classification of the group, which we have summarised below.

Diagnosis of the subfamily: Although generally defined as haematophagous Reduviidae, the Triatominae are by no means the only reduviids that suck vertebrate blood, and nor are all Triatominae obligate blood-suckers. Amongst other reduviid subfamilies for example, facultative blood-sucking is found in species of Emeisiinae, Harpactorinae, Peiratinae, Physoderinae, and Reduviinae (Schofield and Dolling, 1993), while amongst the Triatominae, predatory behaviour (ie. feeding on invertebrate haemolymph) has been reported in species of *Belminus* (Sandoval et al., 2000, 2004, 2009), *Eratyrus* (Miles et al., 1981), and in several species of *Triatoma* (eg. Abalos and Wygodzinsky, 1951; Kalshoven, 1970; Lorosa et al., 2000; Ruas-Neto et al., 2001). Intermediate forms of haematophagy are also seen, such as cleptohaematophagy—the taking of vertebrate blood by piercing the intestine of another blood-sucking insect (eg. Sandoval et al., 2000; Ryckman, 1951). From studies of several species of *Belminus*, Sandoval et al. (2009) suggest that these species of Triatominae are primarily predaceous, but adapted to take haemolymph or blood (stomach contents) without undue damage to their prey—unlike most other reduviid predators which tend to kill their prey.

Similarly, stringent morphological differences between Triatominae and other Reduviidae are not apparent. Morphological features most usually used to distinguish Triatominae from other reduviid subfamilies such as the straight rostrum addressed to the gula, the ability of the third rostral segment to flex upwards, and the presence of smooth pointed stylets, are believed to have

¹ In July 1899, there were numerous reports of people in the Eastern States of the USA being bitten by insects, most of which were identified as *Reduvius personatus* (Howard, 1899) although some may have been *T. sanguisuga*.

Table 2
Examples of vernacular names for Triatominae.

Region	Names
USA	kissing bug, cone-nose bug, big bedbug (note that 'assassin bug' refers to predatory Reduviidae) China bug (refers to <i>T. protracta</i> on Pacific coast, once assumed to come from the orient) red-banded cone-nose (refers to <i>T. rubrofasciata</i> and/or <i>T. sanguisuga</i>)
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 sound made when flying bug strikes wall)
Belize	bush chinche (implies 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 <i>R. prolixus</i> , probably derives from <i>chuzu</i> 'needle' or 'spear' + <i>uyu</i> 'alive') polvoso (spanish—'dusty'; in NE Honduras usually applied specifically to <i>T. dimidiata</i> , probably refers to 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 <i>T. maculata</i>)
Equador	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 <i>chinche</i> 'bug' + guarani <i>guazú</i> 'big') itchajuponja (ayoreo, probably derived from spanish <i>chinche</i> 'bug' + <i>jupona</i> '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
Brazil	barbeiro (portuguese—'barber' or 'shaver') furão (portuguese—'big piercing bug') chupão (portuguese—'big sucking bug') bicudo (portuguese—'beaked bug') fincão (portuguese [Brazil-RGS])—'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') perceveão (portuguese—'big bedbug') percevejo do sertão (portuguese—'bedbug from the sertão, sertão = interior of Brazil) percevejo das pedras [Brazil-RGS] (portuguese—'bedbug amongst the stones'; <i>T. rubrovaria</i>) piolho de piassava [Brazil-Amazon region] (portuguese—'louse from the piassava palm'; <i>R. brethesi</i>) vunvum (portuguese—probably onomatopoeic for the sound of bug flight) josipak (Matacos indians [Roraima]) îipi (Macuxi Indians [Roraima and Venezuela]; refers specifically to <i>T. maculata</i>)

derived in association with the ability to feed on vertebrates (e.g. Cobben, 1978), but are by no means exclusive to the Triatominae. In particular, a straight rostrum is common to many Apiomerinae, Physoderinae, and some Reduviinae and Harpactorinae (cf. Schuh and Slater, 1995; Carcavallo et al., 1999). In some cases, the morphological similarities are so pronounced that predaceous taxa have been erroneously described as species of Triatominae—e.g. '*Mictrotriatoma pratai*' = *Aradomorpha championi* (Reduviinae) (Lent, 1982), and '*Torrealbaia martinezi*' = *Amphibolus venator* (Harpactorinae) (Forero et al., 2004).

Biogeography: Although most species of Triatominae occur exclusively in the Americas, there is one widespread species – *T. rubrofasciata* – reported from port areas throughout the New and Old World tropics and subtropics, together with a group of 6 other species of *Triatoma* in parts of east Asia which are collectively denoted as the rubrofasciata complex. In addition, a group of 6

species of the genus *Linshcosteus* are found in various localities of India, usually occupying rockpiles and generally associated with small rodents and bats (Galvão et al., 2002; Patterson et al., 2001). These *Linshcosteus* were suggested to possibly merit independent tribal status, not only for their distribution but also because of morphological characteristics not shared with the majority of other Triatominae such as their unusually broad abdomen and relatively short rostrum that does not reach the prosternal sulcus. This idea was formalised by Carcavallo et al. (2000) as the tribe 'Linshcosteusini' although comparisons of 16S and 28S DNA sequences (Hypsa et al., 2002; Patterson, 2007) now suggest that *Linshcosteus* species are genetically close to *T. rubrofasciata* and may be local derivatives from a *rubrofasciata*-like ancestor.

Further confusion has arisen for the North American and Caribbean species of *Triatoma*, which seem biogeographically and genetically separate from the South American species. Some of

these, normally assigned to the phyllosoma complex, have been redesignated as the genus *Meccus*, while the Caribbean species of the flavida complex have been redesignated as the genus *Nesotriatoma* (Galvão et al., 2003). Again however, genetic comparisons fail to support such designations, although the North American species as a whole do seem to form a subgeneric grouping distinct from the South American species (see below).

Polyphyletic origins: There is now substantial evidence that the Triatominae represent a polyphyletic group—especially with respect to the tribes Rhodniini and Triatomini. This idea was initially based on the marked morphological disparity between species of the two tribes (Catalá, 1997; Schofield, 1988, 1996) together with fundamental physiological differences, especially at the level of salivary gland physiology (Ribeiro et al., 1998; Soares et al., 2000). Morphometric comparisons based on head and wing shape also supported the idea of polyphyly, since the grouping of the two tribes could be consistently disrupted by including well-characterised predatory Reduviinae in the comparison (J. Rodriguez and JP unpublished—see Fig. 1). Extensive genetic comparisons including representatives of several other reduviid subfamilies have since endorsed the concept, and suggest that the Triatomini and Rhodniini are derived from quite different reduviid subfamilies (Paula et al., 2005; Patterson, 2007). The sister group of the Triatomini seems most likely to be the Reduviinae, while the sister group for the Rhodniini may possibly be the Stenopodainae or Salyavatinae (Paula et al., 2005; Patterson, 2007) (Fig. 2). From morphological studies, Ambrose (1999) concluded that the Salyavatinae are the most primitive of the predatory reduviids, and possibly ancestral to the subfamilies Triatominae and Ectrichodiinae. However, precise derivative lineages remain unclear, and are further complicated by increasing evidence that several of the predatory subfamilies may also be polyphyletic—especially the Reduviinae and Harpactorinae.

Phenetic variability: The morphological species concept is also challenged by the phenetic variability seen in many triatomine populations, affecting features such as size, head and wing shape, sensorial arrays, genital morphology, and colour patterns. This variability has led to a number of specific and subspecific names based on relatively minor morphological differences, many of which are now being progressively synonymised (Lent and Wygodzinsky, 1979; Galvão et al., 2003; Gumiel et al., 2003; Marcilla et al., 2002; Garcia et al., 2005). In some cases, the variants may have a genetic basis such as the red-eye forms of *T. infestans* (*T. i. erythrophthalmus*) which is due to a single recessive autosomal gene (Pires et al., 2002). However, morphological variants can also arise through a phenomenon known as ‘morphological plasticity’ (Dujardin et al., 1999) whereby populations of the same parentage, but reared in isolation, can display a form of ‘phenetic drift’ leading to overtly different phenotypes within a very few generations.² Experimentally, such divergence has been shown – both in metric and chromatic characters – within no more than five generations (eg. Dujardin et al., 2000, 2007; Catalá et al., 2004; Rodríguez Rodríguez et al., 2007).

Phenotypic variation can also arise through presentation of different phenotypes in response to different environments. This may be a form of selection from a genetic basis, although the low genetic variability shown by most triatomine populations would suggest this may not always be the case, and phenetic variants often show no genetic variance with currently available genetic markers. Different environments may also trigger epigenetic mechanisms (e.g. heterochromatin formation, histone acetylation, methylation) pro-

ducing heritable changes of the phenotype without affecting DNA sequence (see Dujardin et al., this issue).

Genetic and cytogenetic variability: In terms of haplotype, most Triatominae show a complement of 20 autosomes plus XY, although multiple sex chromosomes occur in the spinolai complex (*Mepraia*), *Eratyus mucronatus*, *T. tibiamaculata*, *T. vitticeps*, and in all the North American species of *Triatoma* so far examined except for *T. lecticularia* (Panzera et al., 1998). However, chromosome behaviour and morphology (in terms of heterochromatin blocks) can show important variation within morphologically defined species, giving rise to the concept of ‘cryptic species’ or chromosomally defined ‘forms’ (e.g. Panzera et al., 2004, 2006). The idea of cryptic species has also been encouraged by genetic differences within morphologically defined taxa, again giving rise to the concept of genetically defined ‘forms’ (Panzera et al., 2000; Monteiro et al., 1999, 2000; Pavan and Monteiro, 2007; Noireau et al., 1997, 1998). Where such differences have been associated with phenetic and biogeographical differences, this had led to subspecific and specific designations – as with forms of *T. brasiliensis* (Costa, 1999; Monteiro et al., 2004; Costa and Felix, 2007) – and as additional genetic information accrues, there seems an inevitable tendency to assign specific status to genetically defined forms.

Demographic effects on population differentiation: Triatominae are often described as *K*-strategists (*sensu* MacArthur and Wilson, 1967) in the sense that they are typically adapted to the relatively stable habitat offered by a house or other vertebrate nest. In such habitats, when the bug population is at or near the carrying capacity of that environment, then the rate of population increase (R_0) approaches unity, implying that most offspring will not reach reproductive age (Schofield et al., 1999). This imposes selection favouring energetic efficiency, resulting in a trend to population monomorphy (cf. Schofield, 1996). At the other extreme however, if dispersing individuals encounter a resource-rich habitat, then, during the subsequent growth phase of the newly founded population, a much wider range of genotypes and phenotypes can be presented—some of which may randomly predominate. At this stage, there is no genetic barrier between the original and the dispersed populations, and yet they may show clearly discernible genetic or phenotypic differences (e.g. Noireau et al., 1998) which can tempt new taxonomic designations. As the new population increases again towards the carrying capacity of the new habitat, it will tend again to monomorphy, but not necessarily of the same form as the original (e.g. Gumiel et al., 2003). This demographic process may be behind much of the variation between neighbouring populations of Triatominae – for example amongst members of the phyllosoma and protracta complexes of Mexico and North America – and may be a precursor to subsequent speciation where the newly differentiated populations remain isolated.

Species concept: Although rarely stated, it is clear from recent literature that the species concept for Triatominae tends to differ between authors, although this is far from unique to this group. The biological species concept (e.g. Mayr et al., 1953) is difficult to sustain for Triatominae, partly because of the practical difficulties in demonstrating reproductive isolation but also because of the ease with which many species will form hybrids in artificial situations (e.g. Pérez et al., 2005). At the other extreme however, it seems unwise to adopt a concept based on small differences between populations – whether morphological or molecular – even if the difference appears consistent over one or more generations. But the morphological species concept, on which most of triatomine classification is based, is challenged both by the phenetic variability of many populations, and also by the phenomenon of morphological plasticity (see above). Similarly, the idea of a genetic species concept, based for example on a defined genetic distance between groups, is challenged both by practicability and by a lack of distance consistency between currently accepted taxa

² Morphological plasticity and phenetic drift represent the same concept. Both refer to phenotypic plasticity, measured by the range of phenotypes that a single genotype can express in response to different conditions.

Table 3
Probable species groups and complexes within the genus *Triatoma*.

Group	Complex	Subcomplex	Species
Rubrofasciata (mainly North American and Old World)	Phyllosoma	Dimidiata	<i>dimidiata</i> , <i>hegneri</i> , <i>brailovskyi</i> , <i>gomeznunezi</i> ,
		Phyllosoma (=Meccus)	<i>bassolsae</i> , <i>bolivari</i> , <i>longipennis</i> , <i>mazzottii</i> , <i>mexicana</i> , <i>pallidipennis</i> , <i>phyllosoma</i> , <i>picturata</i> , <i>ryckmani</i> , <i>flavida</i> , <i>bruneri</i> , <i>obscura</i>
	Flavida (=Nesotriatoma) Rubrofasciata		<i>amicitiae</i> , <i>bouvieri</i> , <i>cavernicola</i> , <i>leopoldi</i> , <i>migrans</i> , <i>pugasi</i> , <i>rubrofasciata</i> , <i>sinica</i>
Dispar (Andean)	Dispar	Protracta	<i>barberi</i> , <i>incrassata</i> , <i>neotomae</i> , <i>nitida</i> , <i>peninsularis</i> , <i>protracta</i> , <i>sinaloensis</i>
		Lecticularia	<i>gerstaeckeri</i> , <i>indictiva</i> , <i>lecticularia</i> , <i>recurva</i> , <i>rubida</i> , <i>sanguisuga</i>
Infestans (South American)	Infestans	Brasiliensis	<i>brasiliensis</i> , <i>juazeirensis</i> , <i>melanica</i> , <i>melanocephala</i> , <i>petrochiae</i> , <i>lenti</i> , <i>sherlocki</i> (<i>tibiamaculata?</i>) (<i>vitticeps?</i>)
		Infestans	<i>delpontei</i> , <i>infestans</i> , <i>platensis</i>
		Maculata	<i>arthurneivai</i> , <i>maculata</i> , <i>pseudomaculata</i> <i>wygodzinskyi</i>
		Matogrossensis	<i>baratai</i> , <i>costalimai</i> , <i>deaneorum</i> , <i>guazu</i> , <i>jurbergi</i> , <i>matogrossensis</i> , <i>vandae</i> , <i>williami</i>
		Rubrovaria	<i>carcavalloi</i> , <i>circummaculata</i> , <i>klugi</i> , <i>limai</i> , <i>oliveirai</i> , <i>rubrovaria</i> , <i>garciahesi</i> , <i>guasayana</i> , <i>patagonica</i> , <i>sordida</i>
	Spinolai (=Mepraia)	Sordida	<i>breyeri</i> , <i>eratyrusiformis</i> , <i>spinolai</i> , <i>gajardo</i>

Relationships of *T. tibiamaculata* and *T. vitticeps* are very uncertain. Both occur in eastern Brazil and show some morphological similarities with species of the brasiliensis complex. But unlike most other South American *Triatoma* they show multiple sex chromosomes and usually cluster with North American *Triatoma* in phylogenetic comparisons of DNA sequences.

and between methods of distance estimate. We have no clear solution to this problem, and prefer to retain the morphological species concept as far as possible, both for consistency with previous work, and for practical reasons in terms of ease of use by field workers. Species are thus defined in morphological terms with reference to the name-bearing type (ICZN, 1999).

But as molecular genetic data become more illustrative of relationships within and between morphologically defined taxa, it may be that this species concept will need consensual revision. Interpreting currently available studies of phenetic variation and plasticity, reinforced in many cases with genetic data, seems to suggest much closer – and more dynamic – relationships between many morphologically defined taxa than might have previously been expected. This gives rise to the ‘mountain range metaphor’ whereby populations are likened to mountain ranges, with specific names given – for practical purposes – to the peaks, but without necessarily defining where one mountain ends and another starts. This was presaged in the idea of species complexes within the genus *Triatoma* (Usinger, 1944; Lent and Wygodzinsky, 1979) and *Rhodnius* (Barrett, 1991; Schofield and Dujardin, 1999) although the reticence of Lent and Wygodzinsky (1979) to adopt subspecific designations may merit revision.

Emotional aspects of names: Almost half of all species names given to Triatominae are given in honour of particular people, most in recognition of their work on Triatominae and/or Chagas disease—many of whom are still active. This seems an appropriate way to recognise and honour the contributions made, but can lead to difficulties if the eponymous taxon is subsequently deemed to be a junior synonym. Reticence in relegating such names stems not just from a desire not to offend, but also from the fact that the synonymised names remain occupied and so unavailable for other taxa in the same genus (ICZN, 1999).

Clinal variation and sampling effects: Species of Triatominae tend to occupy substantial geographical ranges, sometimes displaying a degree of clinal variation along a major latitudinal axis. In the past, when it was more difficult to compare collections from different countries, the geographical variants tended to be given different names, such that a large number of synonymies are now attributed to some of the most widespread species—*T. infestans* for example, distributed over seven countries of South America, has 13 specific and 3 subspecific synonymies (Galvão et al., 2003). The same may be true of *Panstrongylus lignarius*, widely distributed over the Ama-

zonian countries, whose variants in Peru designated as *P. herreri* have been synonymised on the basis of genetic similarity (Marcilla et al., 2002; Galvão et al., 2003).

For species of epidemiological significance, populations now tend to be sampled over a wide area so that continuous or clinal variation can be assessed. In the case of *Panstrongylus megistus* for example, clinal variation from southern to northeastern Brazil is revealed by genetic differences, size differences, and biological differences relating to fecundity, egg-size, and degree of domestic adaptation (Barbosa et al., 2003, 2004). Similarly with *T. dimidiata*, variation in metric and genetic characters has been described as clinal along a NW-SE axis from Mexico to Panama (Schofield, 2002) although this also appears to include at least three morphologically defined subspecies (Usinger, 1944) that can be genetically discriminated (Bargues et al., 2008; Panzera et al., 2006). For silvatic species however, where populations may be sampled much more focally, the sampled subsets may be considered in isolation – and receive specific designation – when they may in fact represent components of an unknown continuous population. In the case of the Bolboderini for example, the eight species of *Belminus* are described from a similar number of sample sites spanning an area from Mexico to Peru (Sandoval et al., 2007), while the two species of *Microtriatoma* represent no more than a dozen samples spanning the area from Panama to Bolivia and southern Brazil (De la Riva et al., 2001). As pointed out by Lent and Wygodzinsky (1979) more extensive sampling may well change this taxonomic concept, although the sampling difficulty is compounded by current institutional reticence to maintain extensive collections.

Systematic difficulties can also be raised by the need to rationalise a biologically relevant classification with the practical requirements of those involved with Chagas disease surveillance and control. The importance of the Triatominae rests primarily with their epidemiological significance as vectors of *T. cruzi* – causative agent of Chagas disease (American trypanosomiasis) – so that it would make little sense to develop a classification and nomenclature that confuses, rather than assists, those involved in Chagas disease control. At the tribal and generic levels for example, although current interpretations indicate the subfamily to be polyphyletic, there would be no practical sense in attempting to relegate the tribes and genera of the Triatominae to the various reduviid subfamilies from which they may have evolved (see below). Similarly,

there is little to be gained from changing well-established generic names to reflect biological divergence within a genus such as *Triatoma*, nor in erecting new taxa based on characters that cannot be readily perceived by field personnel involved in vector surveillance, especially if the putative new taxa show no relevant biological or epidemiological differences.

With these difficulties in mind, we have here proposed a pragmatic classification that seeks to maintain as much as possible of customary practice, while still reflecting evolutionary aspects as currently deduced for the subfamily (Tables 1 and 3). This classification retains the tribes and genera of Lent and Wygodzinsky (1979) together with *Hermanlenticia* (Jurberg and Galvão, 1997), but excluding *Mepraia* until further work can establish the status of other members of the spinolai complex (*T. breyeri* and *T. eratyrisiformis*).³ Specific names and synonymies follow Galvão et al. (2003) with the addition of *B. ferroae* (Sandoval et al., 2007), *B. corredori* (Galvão and Angulo, 2006), *P. mitakaraensis* (Bérenger and Blanchet, 2007), and *T. boliviana* (Martinez et al., 2007), but with the exclusion of *P. sherlocki* (Jurberg et al., 2001) which now seems to be a chromatic variant of *P. lutzi* (Garcia et al., 2005). We have included the specific designations of *melanica* and *juazeirensis* as they are well characterised (Costa et al., 2006; Costa and Felix, 2007) even though their original designations as subspecies of *T. brasiliensis* probably reflects better their affinities (Lent and Wygodzinsky, 1979; Costa et al., 1997). Our assessment of species groups and complexes within the genus *Triatoma* follows from Dujardin and Schofield (2004), with modifications based on current genetic comparisons. These suggest that the genus is composed of three principal groups representing South American species (infestans group—all south of the Amazon, except *T. maculata*), North American species (rubrofasciata group—all north of the Amazon, except *T. rubrofasciata* and associated species of the Old World rubrofasciata complex), and the small dispar complex of five species that seem to form a discrete grouping along the Andean mountains, and with genetic characteristics that strongly differentiate them from others of the genus (Table 3). The rationale underlying these groupings is further discussed below.

3. Evolution of the Triatominae

The systematics of insect classification substantially predate evolutionary theory, and can give the impression that a well-established classification in some way reflects or predicts evolutionary relationships. In essence however, the two concepts are quite different. Traditional classifications seek to be useful, either as pragmatic operational groupings, or by offering possible inferences about particular attributes—we infer, for example, that all Triatominae can be vectors of *T. cruzi*, not because this has been exhaustively demonstrated, but because it is an implied characteristic of the group. We may also use a robust classification to predict aspects of evolutionary theory, or even to disclose possible sampling discrepancies in apparently discontinuous groupings. Moreover, cladistical analyses always need an *a priori* monophyletic hypothesis to be tested, which is usually based on the traditional classification (Galvão, 2003; Stevens and Schofield, 2003). But it seems wise not to confuse the two concepts. As far as possible, nomenclature and classification should be stable (ICZN, 1999) whereas evolutionary theory, by its nature, is dynamic and liable to change as new data become available. This is particularly so of

the Triatominae, where there is a need to balance pragmatic classification with evolutionary theory concerning what seems to be a recently developed group that is prone to genetic and phenetic drift and still in the process of adaptation to different situations. And there is a further complication implicit in these concepts, because of the need to rationalise morphological with molecular approaches, and also to rationalise the results from different molecular markers which tend to reveal different levels of divergence depending on their relative rates of evolutionary change (Stevens and Schofield, 2003) and also seem to evolve at different rates in different taxa (eg. Monteiro et al., 2004). Here we consider the origin and evolutionary age of the Triatominae, and possible geographic centres of species radiation.

4. Origins of Triatominae

There is consensus that the Triatominae are derived from predatory reduviids, and they are classically defined as “haematophagous Reduviidae” (Lent and Wygodzinsky, 1979) although some of the Bolboderini are now known to be primarily predaceous (Sandoval et al., 2009). From their classification as a single subfamily, the default assumption is that they represent a monophyletic group—i.e. all derived from a single ancestral form, with the defining synapomorphic trait being the blood-sucking habit and associated morphological and physiological adaptations. Nevertheless, several arguments have been advanced to suggest that these blood-sucking forms may have different origins within the predatory reduviid subfamilies, thus representing a polyphyletic or paraphyletic group (Schaefer, 2003). In a sense, the question hinges on which came first—adaptation of predators to different habitats followed by independent evolution of haematophagy in several of these, or development of haematophagy followed by adaptation of the specialised blood-sucking form to a range of different habitats (Schofield, 1988). As emphasised by Schaefer (2005) the question – single or multiple origins of haematophagy in the Triatominae – has some importance, because it affects the level of confidence with which we might infer attributes of different species.

Almost all Hemiptera have piercing-and-sucking mouthparts, adapted to pierce or lacerate tissues and engorge on the underlying fluids (Cobben, 1978). All Coleorrhyncha, Auchenorrhyncha and Sternorrhyncha (formerly Homoptera) and many Heteroptera are phytophagous, although it is argued that the predatory habit is the basal state of the Heteroptera, giving rise both to phytophagous and haematophagous forms in several of the Heteropteran families (Schuh and Slater, 1995). Many of the predaceous Heteroptera will occasionally take vertebrate blood, either indirectly via a blood-sucking prey – as in some Emesinae preying on blood-engorged sandflies (Wygodzinsky, 1966) or mosquitoes (White et al., 1972) – or by biting vertebrates directly, and it would appear that a degree of vertebrate blood-sucking is a relatively simple adaptation for many of the predatory Heteroptera. Facultative haematophagy occurs in the Lygaeidae (Cleradini), Anthocoridae (Dufouriellini, Xylocorini), and Reduviidae (Emesinae, Harpactorinae, Peiratinae, Physoderinae, Reduviinae, Triatominae), while obligate haematophagy is well-known in the Cimicidae and Polycetenidae (both probably derived from the Anthocoridae) and in most of the Triatominae (Schofield and Dolling, 1993). It is likely that haematophagy in these groups developed first through adaptation of predators to feed on the guilds of other invertebrates occupying vertebrate nests, followed by progressive adaptation to exploit also the vertebrate hosts themselves (Schofield, 1988). The simplicity of this assumed adaptive route, from free-living predator to nest-dwelling predator to facultative and then obligate blood-sucker, suggests that it probably occurred in several lineages—implying possible polyphyly in those groups currently defined by their blood-sucking

³ Note however, that evidence is accruing – morphological, molecular and cytogenetic – to suggest that *eratyrisiformis* and *breyeri* should be included with *spinolai* and *gajardoi* within the genus *Mepraia*. For example, *eratyrisiformis* typically clusters with *spinolai* in phylogenetic analyses (e.g. Hyppa et al., 2002) and also has multiple sex chromosomes like *spinolai* and *gajardoi*, but unlike most other South American *Triatoma* (Panzeria et al., 1998).

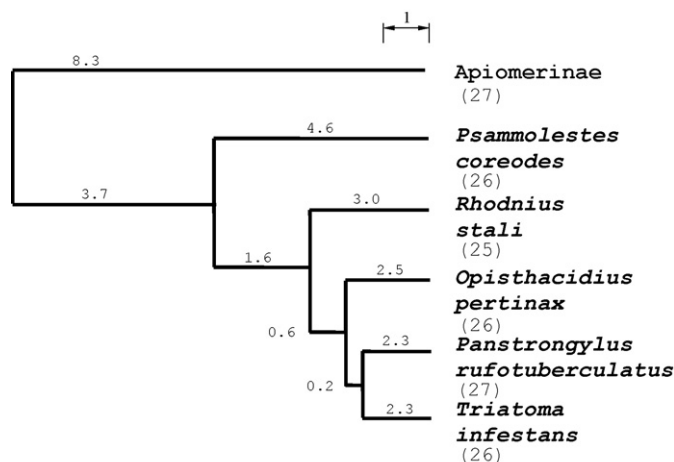


Fig. 1. Morphometric comparison of selected Triatominae with a predatory Reduviinae (*Opisthacidius pertinax*) based on Mahalanobis distances between wing-shape (from J. Rodriguez and J.P. Dujardin, unpublished 1999). Numbers in parenthesis indicate number of wings analysed. Input data were partial warps derived from 6 wing landmarks, i.e. 8 variables including the uniform component of shape. The analysis is included for historical interest (by permission of the authors) since it seems to be the first analytical demonstration of possible polyphyly in the Triatominae.

habit. The idea of a monophyletic origin for a haematophagous group such as the Triatominae implies that the blood-sucking habit arose only once in the group, and that all current blood-sucking forms in the group are derived from that single ancestral form. For the Triatominae, this is difficult to reconcile with their wide geographical distribution and 'nest-dwelling' habit, because it implies that a specialised ancestral nest-dweller would subsequently adapt to range of different habitats associated with a range of different hosts (Schofield, 1988). By contrast, the frequency of facultative haematophagy in different Heteropteran lineages, together with independent progression to obligate haematophagy in at least two separate lineages – Reduviidae and Anthocoridae – is perhaps the first indication that the blood-sucking habit might not necessarily imply a monophyletic origin for any of the haematophagous Heteropteran groups. The alternative, that obligate blood-sucking forms might sometimes revert to a predaceous habit, is generally discounted because of the degree of physiological and behavioural specialisation involved in haematophagy (cf. Schofield et al., 1999).

Further evidence for polyphyly in the Triatominae – at least at the tribal level – is adduced from comparative differences in form. Except for the mouthparts, the Triatomini have a body form that matches that of the Reduviinae (or Ectrichodinae in the case of *Panstrongylus*), while the body form of the Rhodniini more closely resembles that of some Salyvatinae or Stenopodainae, and that of the Cavernicolini shares some morphological features with the Apioemerinae. Marked differences are also shown at the level of salivary gland physiology, with the Rhodniini possessing nitrophenols that give the characteristic red colour to their salivary glands compared to the translucence of the glands of Triatomini (Pereira et al., 1998; Soares et al., 2000) and the saliva of Rhodniini consistently shows different ionic dependence to that of the Triatomini (Ribeiro et al., 1998)—both suggestive of origins from different predatory ancestors. Parasite susceptibility also differs markedly between the two tribes, with only the Rhodniini acting as competent vectors for *Trypanosoma rangeli*, and only the Triatomini showing susceptibility to infection with *Blastocrithidia triatomae* (see Vallejo et al., this issue). The two tribes also show marked differences in DNA fragment length (Tartarotti and Ceron, 2005) and in haploid DNA content (Panzeria et al., 2007).

Comparisons based on morphometric characters (Rodriguez, 2003; J. Rodriguez and J.P. Dujardin, unpublished; see Fig. 1) or on nuclear or mitochondrial DNA sequences also support the idea of polyphyletic origins, since the grouping of Rhodniini with Triatomini can be disrupted by addition of sequences from predatory reduviid families (Schofield, 2004; Paula et al., 2005; Patterson, 2007, see also Fig. 2). Opposing arguments, that the Triatominae are a monophyletic group, were given by Hyspa et al. (2002) based primarily on a phylogenetic analysis of sequences of 16S mt-DNA fragments from 57 triatomine taxa with two predatory reduviid taxa (*Ariulus cristatus* and *Reduvius personatus*), but using as outgroup taxa from the Fulgoroidea and Gerromorpha which are probably too distant to allow polyphyletic resolution. Re-analysis of the same 16S data set (taken from GeneBank) together with a range of different reduviids, generally shows disruption of the Rhodniini + Triatomini clade by Reduviinae (*R. personatus*), Ectrichodinae (*Echtrychotes*) and some Harpactorinae (*Sphedanolestes*, *Isyndus*, *Blasticus*) associated with the Triatomini, and other Harpactorinae (*Sycanus*) and Salyvatinae (*Lisarda*) associated with the Rhodniini (M. Gaunt and C.J. Schofield, unpublished; Paula et al., 2005; see also Fig. 2). Similar results can be obtained with available 28S, 12S, cyt-b, and CO1 sequences (Schofield, 2004; Patterson, 2007) in the sense that the supposed Triatomini + Rhodniini clade is disrupted by one or more of the predatory taxa. However, although the general concept of polyphyly within the Triatominae now seems well-supported, precise relationships with the other reduviid subfamilies remain unclear, partly because other tribes of Triatominae have yet to be included in the analyses, and also because the same analyses indicate probable polyphyly in the two largest Reduviid subfamilies – Reduviinae and Harpactorinae – which will complicate the assessment of relationships (cf. Weirauch, 2008).

As pointed out by Carcavallo et al. (1999) the hypothesis of polyphyly helps explain many features of the Triatominae, both biological and morphological. The idea that predatory forms adapted to different habitats and then developed haematophagy, helps explain the remarkably close habitat and host associations shown by many triatomine taxa such as the relationship between *Psammolestes* species and nests of Dendrocolaptid birds (irrespective of the host currently occupying the nest), Cavernicolini with bats, or between species of *Panstrongylus* and the subterranean edentates, or members of the *T. protracta* complex so closely associated with the nests of *Neotoma* rodents. In morphological terms, the idea of polyphyly also helps explain the major anatomical differences between some of the tribes of Triatominae, contrasted with their noteworthy similarities to taxa from other subfamilies such as the similarities between the Alberproseniini and some Cetherinae, and between Cavernicolini and some Apioemerinae, suggesting possible sister groups for these tribes. It also helps explain the broadly discrete geographical distribution of major triatomine groups, with the Triatomini forming three principal groupings, in the sub-arid biome of the caatinga-cerrado-chaco corridor of South America (infestans group), the Andean cordillera (dispar complex), and the drier regions of Central and North America (rubrofasciata group), broadly separated by the Rhodniini of the Amazonian forest region (Schofield, 1988).

5. Evolutionary age

The question of polyphyly also affects consideration of the evolutionary age of Triatominae. Some authors have assumed that the group is evolutionarily 'old' (e.g. Gaunt and Miles, 2000; Barges et al., 2000), largely basing this on the estimated age of sequence divergence between Rhodniini and Triatomini. But the sequences used for such 'molecular clocks' appear to have no relation to a haematophagous habit, so that assessment of evolutionary age by

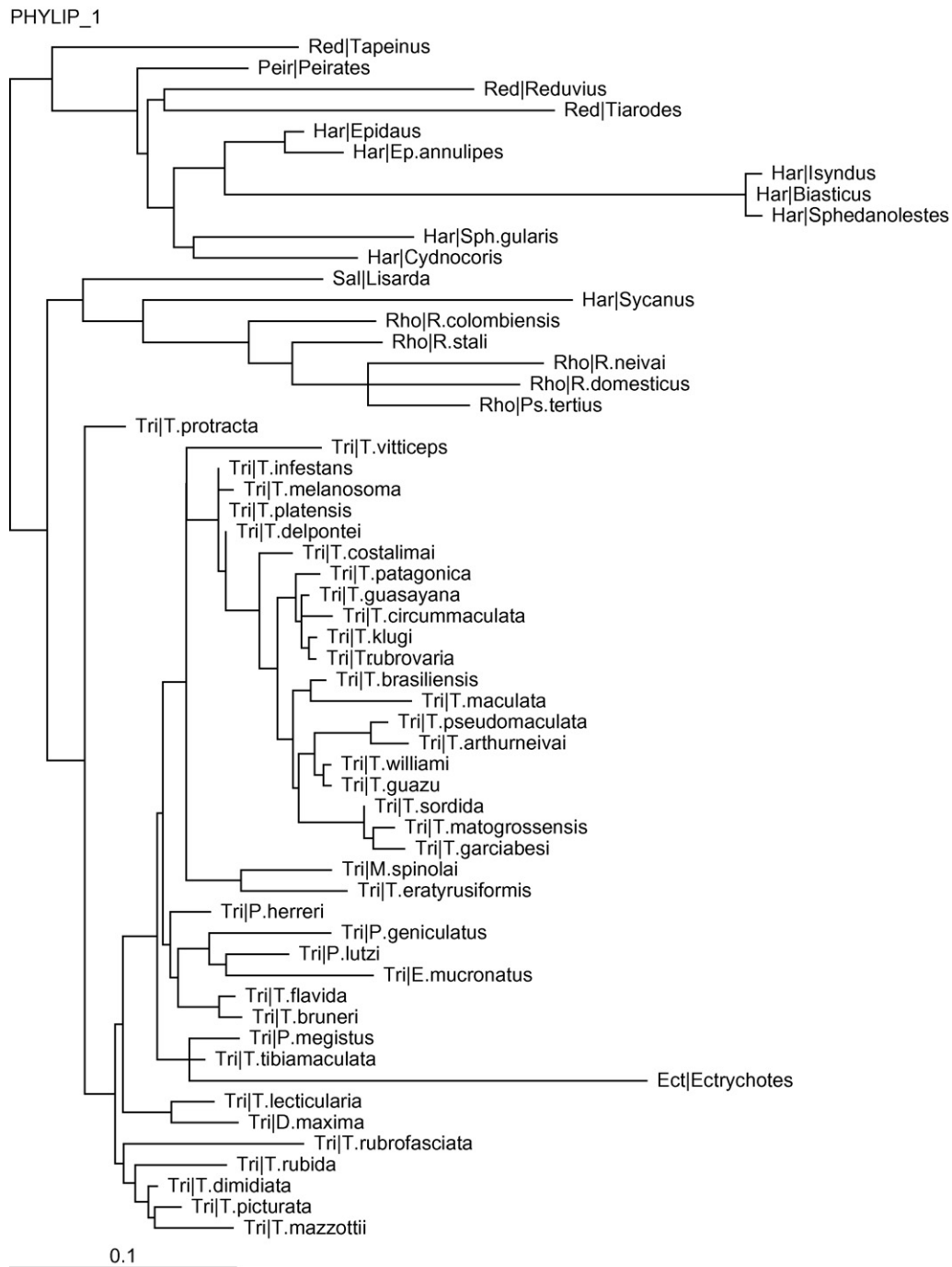


Fig. 2. Re-analysis of sequences of 16S fragments from *Hypsa et al. (2002)* with additional predatory Reduviidae sequences (GeneBank) using the General Time Reversible model of *Waddell and Steel (1997)* (from M. Gaunt and C.J. Schofield, unpublished 2002). The model incorporated four discrete rates of the gamma distribution to model mutation rate heterogeneity between nucleotide sites. The phylogeny was produced using PAUP4 and constitutes a 7-parameter model with five rates of nucleotide substitution, the proportion of invariant sites, and the gamma distribution. Parameters were estimated heuristically using maximum likelihood. Again included for historical interest, this seems to have been the first phylogenetic demonstration of probable polyphyly in the Triatominae [note clustering of *Lisarda* (Salyavatinae) and *Sycanus* (Harpactorinae) with the Rhodniini, and disruption of the 'north american' clade of Triatomini by *Echtrychotes* (Echtrichodinae)]. Key: Red-Reduviinae; Peir-Peiratinae; Har-Harpactorinae; Sal-Salyavatinae; Ect-Echtrichodinae; Tri-Triatomini; Rho-Rhodniini.

this approach could only be valid if the group were monophyletic (i.e. already haematophagous at the time of tribal divergence). If not, the estimates are suggesting divergence between ancestral forms that may or may not have been haematophagous, and seem most likely to represent early forms of the predatory ancestors.

The idea that haematophagy – as shown by the Triatominae – is a relatively recent phenomenon, has been discussed in detail by *Schofield (2000)*. The main arguments can be summarised as

follows:

- (1) Biogeography: Since Triatominae seem not to have evolved in Africa (possibly due to competition with Cimicidae) they presumably developed after continental separation.
- (2) Host associations: Suggesting that haematophagy could not have developed until after the establishment of suitable hosts in the Americas.

- (3) Morphological similarity between Triatominae and predatory Reduviidae, suggesting limited evolutionary divergence.
- (4) Persistence of predatory behaviour in many triatomine species, with some displaying only facultative haematophagy or intermediate feeding patterns such as cleptohaematophagy.
- (5) Lack of a mycetome (all other haematophagous insects have developed a system for storing essential symbionts).
- (6) Apparent capacity for rapid adaptation—adduced from speciation of the Old World rubrofasciata complex, which, if derived from forms transported from the Americas on sailing ships (e.g. Gorla et al., 1997) has occurred within a period of not more than 300 years (Patterson et al., 2001).

This discussion was originally put forward in the context of the estimated time of divergence between the main evolutionary lineages of *T. cruzi* – now known as *T. cruzi* I and *T. cruzi* II – since it was suggested that the parasitological divergence was most likely due to Triatominae vectoring the original form of the parasite (*cruzi* I) to new host species. Estimates of the probable timing of this parasitological divergence have since been revised downwards (Machado and Ayala, 2001), and are currently at around 10 mya for the first divergence to *cruzi* IIb (South American, mainly human and rodent isolates), and 4 mya for divergence of the other *cruzi* II lineages (Brisse et al., 2003) adding support to the idea of Triatominae as a relatively recent group. However, given the evidence for polyphyly and the apparent ease of development of haematophagy within the Reduviidae, it seems possible that other haematophagous lines may have developed which are no longer currently represented. This may be the case of '*T. dominicana*' (Poinar, 2005) named on the basis of an exuvium in dominican amber dated at 15–20 mya (Iturralde-Vinent and MacPhee, 1996), because other than *T. rubrofasciata* reported from ports, there are no currently known species of Triatominae in either the Dominican Republic or Haiti. Alternatively, it may be that the exuvium – which shows no mouthparts – in fact represents a predatory form morphologically similar to extant Triatominae.

6. Possible centres of species radiation

The idea of recent polyphyletic evolution of the Triatominae implies several possible centres of species radiation, in the sense that monophyletic groups within the subfamily need not have all developed at the same time, nor in the same place—an idea presaged by the insightful work of Forattini (1980). Given that the majority of species are found only in the Americas we can infer New World origins for most, although the presence of eight species of *Triatoma* and six of *Linshcosteus* in the Old World has led to suggestions of an Old World origin for these groups (e.g. Patterson, 2007). Such a concept would imply extensive levels of population extinction both in Asia and northern North America, and dates the evolution of haematophagy prior to a substantial number of vicariant events since some 30 mya. The alternative (e.g. Gorla et al., 1997; Schofield, 1988; Hyspa et al., 2002; Patterson et al., 2001) suggests that all Triatominae are of New World origin, and that the Old World species of *Triatoma* and *Linshcosteus* are derived from *T. rubrofasciata* transported from the southern USA associated with rats on sailing ships. It is suggested that Reduviidae did not develop obligate haematophagy in Africa, possibly due to competition with Cimicidae which appear to be evolutionarily 'older' and of African-Middle Eastern origin (Schofield, 2000).

For the Americas, it is inferred from biogeographical aspects that the Rhodniini (*Rhodnius* and *Psammolestes*) developed in the humid Amazon region (Paula et al., 2007) with subsequent radia-

tion eastwards to neighbouring areas of the caatinga-cerrado-chaco corridor, northwards to the llanos of Venezuela and Colombia, and also through the Andes-Sierra Nevada pass of Colombia into southern Central America and regions east of the Andes (Schofield and Dujardin, 1999). This idea is broadly consistent with genetic and phenetic comparisons that reveal two lineages (*pictipes* and *robustus* groups, *sensu* Abad-Franch and Monteiro, 2005, 2007) with the *prolixus* group east of the Andes (*R. prolixus*, *R. robustus*, *R. neivai*, *R. nasutus*, *R. neglectus*, *R. milesi*, *R. dalessandroi*, *R. domesticus* and the three species of *Psammolestes*), and the *pictipes* group comprising one subgroup west of the Andes (*R. pallidus*, *R. colombiensis*, *R. ecuadoriensis*) and one east of the Andes in the Amazon region (*R. pictipes*, *R. brethesi*, *R. paraensis*, *R. stali*, *R. amazonicus*) (see Abad-Franch et al., this issue). The tribe is considered to be monophyletic or paraphyletic (Lyman et al., 1999; Monteiro et al., 2000; Hyspa et al., 2002; Paula et al., 2007) possibly derived from a form represented today by *R. pictipes*, which is widespread and tends to be more generalist in habit than the other species, and also shares genital characteristics with other Triatominae that are not shared with other Rhodniini except for *R. stali* (Jurberg, 1996). Species of *Rhodnius* tend to be associated with palm-tree habitats, and a degree of specialist association with particular palms is apparent in some species. Original divergence between the two lineages – i.e. between *pictipes* and *robustus* – is suggested to relate to spatial habitat divergence, in the sense that *pictipes* tends to occupy a range of habitats from forest floor to sub-canopy, while *robustus* tends to occupy canopy-level habitats (TV Barrett, personal communication). Alternatively, there is also evidence to suggest that the *pictipes* group originated in northern parts of the Amazon region, and spread southwards, while the *robustus* group developed in southern parts and spread northwards (F. Abad-Franch, personal communication).

Regions to the south, west, and north of the Amazon basin are occupied by species of Triatomini—a diverse tribe that seems to form three main lineages, probably of polyphyletic or paraphyletic origin. The *dispar* complex seems the most genetically divergent (Schofield, 2004; J.S. Patterson unpublished; Bargues et al., 2008) with five species recorded from the region of the Andean cordillera, from *nigromaculata* in Venezuela and Colombia, through *venosa*, *dispar* and *carrioni* in Colombia, Ecuador and northern Peru, to the recently described *boliviana* in the Bolivian Andes (Martinez et al., 2007). Except for *boliviana* in the south, the other species seem to form a relatively discrete geographical continuum, implying that there may be similar populations – intermediate between *carrioni* and *boliviana* – occupying regions of the central and southern cordillera of Peru.

Other Triatomini south of the Amazon are grouped together as the *infestans* group, assumed to be monophyletic or paraphyletic but with no clear suggestion about either original form or origin – other than the broad concept of being from the caatinga-cerrado-chaco region. 38 species are recognised and grouped into 8 species complexes – mainly on the basis of morphological similarity and biogeographical cohesion, but with increasing evidence (and adjustments) based on genetic comparisons. The one species that does not readily fit this pattern is *T. maculata*, which occurs in regions of the northern fringes of the Amazon basin in Venezuela and Colombia. It is morphologically similar to *T. pseudomaculata* of NE Brazil, and the two species will interbreed in the laboratory, although with reduced fertility (Belisario et al., 2007). Abad-Franch and Monteiro (2007) – assuming an older origin for the tribe than indicated here – suggest that contemporary *maculata* populations represent relicts from the times when tropical dry forest corridors traversed the Amazon region from north to south in the early pleiocene, with putative intermediate forms thus becoming extinct. An alternative idea, based on the arboreal habits of the two species, is that *maculata* is an isolated derivative from *pseudomaculata*,

carried to the north Amazon regions by migrating birds (Schofield, 1988). There is no direct observational evidence to support this latter suggestion, and the genetic divergence between the two species is currently considered too great to be explained by such a mechanism (Abad-Franch and Monteiro, 2007; Carbajal de la Fuente et al., 2008).⁴

In genetic terms however, the concept of a South American clade of *Triatoma* is also questioned by the position of *T. tibiamaculata* and *T. vitticeps*. Both are South American with some morphological similarities to members of the brasiliensis complex, but phylogenetic analyses based on 16S sequences generally group them with North American species (e.g. Hypsa et al., 2002; see also Fig. 2). They also display multiple sex chromosomes like the majority of North American *Triatoma* (Panzer et al., 1998). *T. vitticeps* has epidemiological significance as vector of Chagas disease in parts of central Brazil, and we hope that further studies using different genetic markers will help to clarify its affinities (Souza et al., 2008).

The remaining Triatomini to the north of the Amazon seem to fit more easily into a monophyletic pattern radiating from a putative origin in southern Mexico (Yucatan region). The basal form may be represented by the generalist and highly variable *T. dimidiata* (although a similar but larger undescribed species from the Peten of Guatemala might be more primitive, D. Bustamente and C. Monroy, unpublished). *T. dimidiata* displays three main morphological forms previously given subspecific status characterised mainly by differences in head length (Usinger, 1944)—the shortest head being found in some Mexican specimens (*T.d. maculipennis*) and the longest in Colombian specimens (*T.d. capitata*) with intermediate forms in between (*T.d. dimidiata*). These three forms, together with a predominantly silvatic form in the Yucatan peninsula, can also be differentiated genetically (Bargues et al., 2008) and broadly correspond to different cytotypes distinguishable by marked differences in autosomal heterochromatin patterns (Panzer et al., 2006). These forms of *dimidiata* are distributed from southern Mexico to northern Colombia. However, the *dimidiata* populations of Ecuador and northern Peru correspond morphologically and genetically to the *T.d. dimidiata* form in southern Mexico, Guatemala and Honduras, and are thought to have been accidentally transported there along precolombian maritime trade routes (Abad-Franch et al., 2001).

The morphological variability of *T. dimidiata* is exemplified by populations on the island of Cozumel described as *T. hegneri*; these can freely interbreed with *dimidiata* (R.E. Ryckman, unpublished) and are genetically sufficiently similar to be considered as a further subspecies (Bargues et al., 2008) with the morphological differences presumably resulting from relative isolation of this 'island race'. The same idea may also apply to the morphologically similar species of the flavida complex (= *Nesotriatoma*) on the islands of Cuba (*T. flavida*, *T. bruneri*) and Jamaica (*T. obscura*) which seem derived from a basal clade that includes *T. dimidiata* and representatives of the phyllosoma and lecticularia complexes (M. Gaunt and C.J. Schofield, unpublished, see Fig. 2). Similarly, from their morphology, biogeography, and genetic relationships, it seems reasonable to assume that the phyllosoma and lecticularia complexes could have derived from a *dimidiata* lineage, although links with the protracta complex currently appear less obvious (see Ibarra-Cerdeña et al., this issue). As suggested by Guhl and Schofield (2005) the possible links between the *dimidiata*-phyllosoma lineage may be represented by *T. gerstaeckeri* to the lecticularia complex, and

T. nitida to the protracta complex, since they both show some intermediate characteristics. However, this idea merits further examination, both genetically and cytogenetically—especially in the case of *T. nitida* which is the only species of *Triatoma* to display chromosomal reduction, with only 18 autosomes.

Derivation of *T. rubrofasciata*, and other members of the rubrofasciata complex, from the lecticularia complex seems less problematic—indeed, the original description of *lecticularius* was based on two specimens of which one was subsequently synonymised with *variegatus* which is a junior synonym of *rubrofasciata* (Lent and Wygodzinsky, 1979). Genetically there seems little to distinguish the two complexes, which remain clustered in phylogenetic analyses based on various mitochondrial and nuclear gene sequences (Schofield, 2004; Patterson et al., 2001; Patterson, 2007) although precise clarification of their relationships will probably require analysis of a large number of specimens to cover the wide geographic range and morphological variability of many of the species. In the case of *T. sanguisuga* for example, widely distributed throughout the continental USA, some forms are morphologically more similar to *rubrofasciata* than the latter is to other members of the rubrofasciata complex. And *T. rubrofasciata* itself, distributed throughout the tropics and subtropics, is one of the most variable species of all, ranging from melanic forms in Hawaii⁵ to bright orange-marked specimens in south India (Schofield, 1988).

A characteristic of *lecticularia* and several other North American species of *Triatoma*, is the relatively short head with antennal insertions closer to the eyes than in most South American species of the genus—characters that are often used to define the genus *Panstrongylus*. Genetically also, species of *Panstrongylus* are often seen to cluster with the North American *Triatoma*, although since all species of *Panstrongylus* occur in South America this has been assumed to reflect a lack of resolution in the phylogenetic analyses (e.g. Hypsa et al., 2002; Marcilla et al., 2002). In further analyses however, *Panstrongylus* is persistently grouped with North American *Triatoma* (Schofield, 2004), and seems likely to have derived from a similar root (see Patterson et al., this issue). The basal species may be represented by *P. rufotuberculatus* or *P. geniculatus*, both of which are widespread generalist species that have also been reported from Central America and southern Mexico. It may be that the ancestral meso-American forms of this genus spread southwards after the joining of the isthmus of Panama, reaching a geographical bifurcation due to the northern part of the Andean Cordillera, and giving rise to the current South American groupings of *lignarius/herrerri*, *humeralis*, *howardi* and *chinai* mainly west of the Andes, and *geniculatus*, *mitakaraensis*, *lutzi*, *diasi*, *lenti*, *tupynambai*, *guentheri*, and *megistus* east of the Andes. Except for *megistus*, these groupings are also supported by the morphological cladogram of Lent and Wygodzinsky (1979) and by cytogenetic comparisons (Crossa et al., 2002). The apparent relationship between *Panstrongylus* and the North American *Triatoma* is perhaps also indicated by the remarkable chromatic convergence between *P. howardi* and *T. dimidiata* (Abad-Franch et al., 2001).

7. Conclusions

Evidence that the Triatominae do not represent a monophyletic group poses a number of challenges for their classification, which we have largely abnegated in the interests of preserving a pragmatic approach of use to those involved in Chagas disease surveillance and control. And we use the same justification to advise caution in taxonomic adjustments at the level of genus and species. In addition, evidence that these haematophagous reduviids are of relatively

⁴ There is some disparity in published mt-DNA sequences for *maculata*; the 16S sequence of Hypsa et al. (2002) (AY035465) is well separated from that of *pseudomaculata* (AY035461), but that of Garcia et al. (2001) (AF324524) is virtually indistinguishable. Note however, that the origin of the latter sequence (AF324524) is given as Sergipe, Brazil (Sainz et al., 2003) where *pseudomaculata* is widespread but *maculata* has not been recorded.

⁵ A melanic form of *rubrofasciata* has also been recently found in Thailand (J.P. Dujardin, personal communication).

recent evolution is based partly on their relative lack of divergence from predatory forms. This, coupled with their morphological plasticity and capacity for genetic and phenetic drift, gives a picture of a dynamic system in which final specialisation may not yet be apparent in many of the currently described taxa. The implication is that some of these taxa may not be stable, again advising caution in taxonomic adjustments.

The idea of Triatominae as a polyphyletic assemblage implies that the monophyletic groupings within the subfamily may not have arisen at the same place, nor at the same time, and there is no obvious reason not to suppose that other haematophagous lineages may have arisen that are no longer represented by extant forms. However, since this also implies that different groupings may have less in common with each other than previously supposed, we believe it important to establish which are the monophyletic groupings within the Triatominae – irrespective of their taxonomic status – in order to infer possible common attributes related to their biology, epidemiological significance, and response to control interventions.

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References

- Abad-Franch, F., Monteiro, F.A., 2005. Molecular research and the control of Chagas disease vectors. *Anais Acad. Bras. Ciênc.* 77, 437–454.
- Abad-Franch, F., Monteiro, F.A., 2007. Biogeography and evolution of Amazonian triatomines (Heteroptera: Reduviidae): implications for Chagas disease surveillance in humid forest ecoregions. *Mem. Inst. Oswaldo Cruz* 102 (Suppl. 1), 57–70.
- Abad-Franch, F., Paucar, A., Carpio, C., Cuba, C.A., Aguilar, H.M., Miles, M.A., 2001. Biogeography of Triatominae (Hemiptera: Reduviidae) in Ecuador: implications for the design of control strategies. *Mem. Inst. Oswaldo Cruz* 96, 611–620.
- Abalos, J.W., Wygodzinsky, P., 1951. Las Triatominae Argentinas (Reduviidae, Hemiptera). Universidad Nacional de Tucumán/Instituto de Medicina Regional, Publication 601, Monograph, vol. 2, pp. 1–179.
- Ambrose, D.P., 1999. Assassin bugs. Science publishers New Hampshire, USA and Oxford and IBH Publ.Co. Pvt. Ltd., New Delhi, India, p. 337.
- Aufderheide, A.C., Salo, W., Madden, M., Streitz, J., Buikstra, J., Guhl, F., Arriaza, B., Renier, C., Wittmers Jr, L.E., Fornaciari, G., Allison, M., 2004. A 9,000-year record of Chagas disease. *PNAS* 101, 2034–2039.
- Barbosa, S.E., Dujardin, J.P., Soares, R.P., Pires, H.H., Margonari, C., Romanha, A.J., Panzera, F., Linardi, P.M., Duque-De-Melo, M., Pimenta, P.F., Pereira, M.H., Diotaiuti, L., 2003. Interpopulation variability among *Panstrongylus megistus* (Hemiptera: Reduviidae) from Brazil. *J. Med. Entomol.* 40, 411–420.
- Barbosa, S.E., Diotaiuti, L., Braga, E.M., Pereira, M.H., 2004. Variability of the salivary proteins of 20 Brazilian populations of *Panstrongylus megistus* (Hemiptera: Reduviidae: Triatominae). *Acta Trop.* 92, 25–33.
- Bargues, M.D., Marcilla, A., Ramsey, J.M., Dujardin, J.P., Schofield, C.J., Mas-Coma, S., 2000. Nuclear rDNA-based molecular clock of the evolution of Triatominae (Hemiptera: Reduviidae), vectors of Chagas disease. *Mem. Inst. Oswaldo Cruz* 95, 567–573.
- Bargues, M.D., Kłisiowicz, D.R., Gonzalez-Candelas, F., Ramsey, J.M., Monroy, C., Ponce, C., Salazar-Schettino, P.M., Panzera, F., Abad-Franch, F., Sousa, O.E., Schofield, C.J., Dujardin, J.P., Guhl, F., Mas-Coma, S., 2008. Phylogeography and genetic variation of *Triatoma dimidiata*, the main Chagas disease vector in Central America, and its position within the genus *Triatoma*. *PLoS Neglect. Trop. Dis.* 7, 2 (5), e233.
- Barrett, T.V., 1991. Advances in triatomine bug ecology in relation to Chagas Disease. *Adv. Disease Vector Res.* 8, 143–176.
- Belisario, C.J., Pessoa, G.C.D., Diotaiuti, L., 2007. Biological aspects of crosses between *Triatoma maculata* (Erichson, 1848) and *Triatoma pseudomaculata* Correa and Espinola 1964 (Hemiptera: Reduviidae). *Mem. Inst. Oswaldo Cruz* 102, 517–521.
- Bérenger, J.-M., Blanchet, D., 2007. A new species of the genus *Panstrongylus* from French Guiana (Heteroptera: Reduviidae: Triatominae). *Mem. Inst. Oswaldo Cruz* 102, 733–736.
- Brisse, S., Henriksson, J., Barnabé, C., Douzery, E.J.P., Berkvens, D., Serrano, M., De Carvalho, M.R.C., Buck, G.A., Dujardin, J.-C., Tibayrenc, M., 2003. Evidence for genetic exchange and hybridization in *Trypanosoma cruzi* based on nucleotide sequences and molecular karyotype. *Inf. Gen. Evol.* 2, 173–183.
- Canese, A., 1973. Epidemiología de la enfermedad de Chagas en el Paraguay. *Rev. Parag. Microbiol.* 8, 13–18.
- Canese, J., Brice, E., 1977. Diagnóstico de la enfermedad de Chagas en aborígenes del Chaco paraguayo. *Rev. Parag. Microbiol.* 11, 9–10.
- Carbajal de la Fuente, A.L., Noireau, F., Catalá, S.S., 2008. Inferences about antennal phenotype: the “*Triatoma maculata* complex” (Hemiptera: Triatominae) is valid? *Acta Trop.* 106, 16–21.
- Carcavallo, R.U., Jurberg, J., Lent, H., 1999. Phylogeny of the Triatominae. In: Atlas of Chagas Disease Vectors in the Americas, vol. III. Editora FIOCRUZ, Rio de Janeiro, pp. 925–969.
- Carcavallo, R.U., Jurberg, J., Lent, H., Noireau, F., Galvão, C., 2000. Phylogeny of the Triatominae (Hemiptera Reduviidae). Proposals for taxonomic arrangements. *Entomol. Vectores* 7 (Suppl. 1), 1–99.
- Catalá, S., 1997. Antennal sensilla of Triatominae Hemiptera Reduviidae. A comparative study of five genera. *Int. J. Insect Morphol. Embriol.* 26, 67–73.
- Catalá, S.S., Maida, D.M., Caro-Riño, H., Jaramillo, N., Moreno, J., 2004. Changes associated with laboratory rearing in antennal sensilla patterns of *Triatoma infestans*, *Rhodnius prolixus*, and *Rhodnius pallescens* (Hemiptera, Reduviidae Triatominae). *Mem. Inst. Oswaldo Cruz* 99, 25–30.
- Cobben, R.H., 1978. Evolutionary trends in Heteroptera. Part 2. Mouthpart-Structures and Feeding Strategies. *Med. Landbouww. Wageningen* vol. 78, no. 5, pp. 1–407.
- Costa, J., 1999. The synanthropic process of Chagas disease vectors in Brazil, with special attention to *Triatoma brasiliensis* Neiva, 1911 (Hemiptera, Reduviidae, Triatominae) population, genetical, ecological, and epidemiological aspects. *Mem. Inst. Oswaldo Cruz* 94 (Suppl. 1), 239–241.
- Costa, J., Felix, M., 2007. *Triatoma juazeirensis* sp. nov. from the state of Bahia Northeastern Brazil (Hemiptera: Reduviidae: Triatominae). *Mem. Inst. Oswaldo Cruz* 102, 87–90.
- Costa, J., Barth, O.M., Marchon-Silva, V., Almeida, C.E., Freitas-Sibajev, M.G., Panzera, F., 1997. Morphological studies on the *Triatoma brasiliensis* Neiva, 1911 (Hemiptera, Reduviidae Triatominae)—genital structures and eggs of different chromatic forms. *Mem. Inst. Oswaldo Cruz* 92, 493–498.
- Costa, J., Argolo, A.M., Felix, M., 2006. Redescription of *Triatoma melanica* Neiva and Lent 1941 new status (Hemiptera: Reduviidae: Triatominae). *Zootaxa* 1385, 47–52.
- Crossa, R.P., Hernández, M., Caraccio, M.N., Rose, V., Valente, S.A., da Costa Valente, V., Mejía, J.M., Angulo, V.M., Ramírez, C.M., Roldán, J., Vargas, F., Wolff, M., Panzera, F., 2002. Chromosomal evolution trends of the genus *Panstrongylus* (Hemiptera, Reduviidae), vectors of Chagas disease. *Inf. Gen. Evol.* 2, 47–56.
- De la Riva, J., Matias, A., Torrez, M., Martínez, E., Dujardin, J.P., 2001. Adults and nymphs of *Microtriatoma trinidadensis* (Lent 1951) (Hemiptera: Reduviidae) caught from peridomestic environment in Bolivia. *Mem. Inst. Oswaldo Cruz* 96, 889–894.
- Dias, J.C.P., Silveira, A.C., Schofield, C.J., 2002. The impact of Chagas disease control in Latin America. *Mem. Inst. Oswaldo Cruz* 97, 603–612.
- Dujardin, J.P., Schofield, C.J., 2004. In: Maudlin, I., Holmes, P.H., Miles, M.A. (Eds.), *Triatominae: Systematics Morphology and Population Biology*, The Trypanosomiasis, CAB International, pp. 181–201.
- Dujardin, J.P., Panzera, P., Schofield, C.J., 1999. Triatominae as a model of morphological plasticity under ecological pressure. *Mem. Inst. Oswaldo Cruz* 94 (Suppl. 1), 223–228.
- Dujardin, J.P., Schofield, C.J., Panzera, F., 2000. Les Vecteurs de la Maladie de Chagas. *Recherches Taxonomiques, Biologiques et Génétiques. Academie Royale des Sciences d'Outre Mer, Brussels*, 162 pp.
- Dujardin, J.P., Beard, C.B., Ryckman, R., 2007. The relevance of wing geometry in entomological surveillance of Triatominae vectors of Chagas disease. *Inf. Gen. Evol.* 7, 161–167.
- Forattini, O.P., 1980. Biogeografia, origem e distribuição da domiciliação de triatomíneos no Brasil. *Rev. Saúde Púb.* 14, 265–299.
- Forero, D., Weirauch, C., Baena, M., 2004. Synonymy of the reduviid (Hemiptera: Heteroptera) genus *Torrebaia* (Triatominae) with *Amphibolus* (Harpactorinae), with notes on *Amphibolus venator* (Klug 1830). *Zootaxa* 670, 1–12.
- Galvão, C., 2003. A sistemática dos triatomíneos (Hemiptera, Reduviidae), de De Geer ao DNA. *Entomol. Vectores* 10, 511–530.
- Galvão, C., Angulo, V.M., 2006. *Belminus corredori*, a new species of Bolboderini (Hemiptera: Reduviidae: Triatominae) from Santander (Colombia). *Zootaxa* 1241, 61–68.
- Galvão, C., Patterson, J.S., Rocha, D.S., Jurberg, J., Carcavallo, R.U., Rajen, K., Ambrose, D.P., Miles, M.A., 2002. A new species of Triatominae from Tamil Nadu, India. *Med. Vet. Entomol.* 16, 75–82.
- Galvão, C., Carcavallo, R.U., Rocha, D.S., Jurberg, J., 2003. A checklist of the current valid species of the subfamily Triatominae Jeannel, 1919 (Hemiptera, Reduviidae) and their geographical distribution, with nomenclatural and taxonomic notes. *Zootaxa* 202, 1–36.
- García, B.A., Moriyama, E.N., Powell, J.R., 2001. Mitochondrial DNA sequences of triatomines (Hemiptera: Reduviidae): phylogenetic relationships. *J. Med. Entomol.* 38, 675–683.
- García, B.A., Moriyama, E.N., Souza, L., Souza, R.C.M., Paula, A.S., Borges, E.C., Barbosa, S.E., Schofield, C.J., Diotaiuti, L., 2005. Occurrence and variability of *Panstrongylus lutzii* in the State of Ceará, Brazil. *Rev. Soc. Bras. Med. Trop.* 38, 410–415.
- Gaunt, M., Miles, M., 2000. The ecotopes and evolution of triatomine bugs (Triatominae) and their associated trypanosomes. *Mem. Inst. Oswaldo Cruz* 95, 557–565.
- Gorla, D.E., Dujardin, J.P., Schofield, C.J., 1997. Biosystematics of old world Triatominae. *Acta Trop.* 63, 127–140.
- Guhl, F., Schofield, C.J., 2005. Prioridades para el control vectorial en los países Andinos: *Rhodnius prolixus* en Colombia y Venezuela, *Triatoma dimidiata* en Colombia y Ecuador, *Rhodnius ecuadoriensis* en Ecuador y Perú. VI Reunión de la Iniciativa

- Andina para el Control de la Enfermedad de Chagas. Un. de Los Andes, Bogota, pp. 245–252.
- Gumiel, M., Catalá, S., Noireau, F., Rojas de Arias, A., Garcia, A., Dujardin, J.P., 2003. Wing geometry in *Triatoma infestans* (Klug) and *T.melanosoma* Martinez Olmedo and Carcavallo (Hemiptera: Reduviidae). Syst. Entomol. 28, 173–179.
- Howard, L.O., 1899. The Insects to which the Name “kissing bug” Became Applied During the Summer of 1899. USDA Division of Entomology, Bulletin 22.
- Hypsa, V., Tietz, D., Zrzavy, J., Rego, R.O., Galvão, C., Jurberg, J., 2002. Phylogeny and biogeography of Triatominae (Hemiptera Reduviidae): molecular evidence of a New World origin of the asiatic clade. Mol. Phylog. Evol. 23, 447–457.
- ICZN, 1999. International Code of Zoological Nomenclature, fourth ed. ITZN London, 306 pp.
- Iturralde-Vinent, M.A., MacPhee, R.D.E., 1996. Age and paleogeographic origin of Dominican amber. Science 273, 1850–1852.
- Jeannel, R., 1919. Hemicopterales et Reduviidae. In: Voyage de Ch.Alluaud et R.Jeannel en Afrique orientale (1911–1912). Resultats scientifiques—Hemiptera 3, 131–314.
- Jurberg, J., 1996. Uma abordagem filogenética entre os Triatomíneos baseada nas estruturas fálicas. In: Schofield, C.J., Dujardin, J.P., Jurberg, J. (Eds.), Proceedings of the International Workshop on Population Genetics and Control of Triatominae, Santo Domingo de los Colorados, Ecuador. INDRE Mexico City, pp. 51–52.
- Jurberg, J., Carcavallo, R.U., Lent, H., 2001. *Panstrongylus sherlocki* sp.n. do Estado da Bahia (Hemiptera, Reduviidae Triatominae). Entomologia y Vectores 8, 261–274.
- Jurberg, J., Galvão, C., 1997. *Hermanlenticia* n.gen. da tribo Triatomini, com um rol de espécies de Triatominae (Hemiptera Reduviidae). Mem. Inst. Oswaldo Cruz 92, 181–185.
- Kalshoven, L.G.E., 1970. Observations on the blood-sucking reduviid *Triatoma rubrofasciata* (De Geer) in Java. Entomol. Bericht. 30, 41–47.
- Laporte, F.L., 1832–1833. Essai d'une classification systématique de l'ordre des Hémiptères (Hémiptères Hétéroptères, Latr.). Magazine de Zoologie (Guérin) vol. 2, 88 pp.
- Lent, H., 1982. *Microtriatoma pratai* Sherlock and Guitton, 1982 é sinonimo do hemiptero predador *Aradomorpha championi* Lent and Wygodzinsky, 1944 (Reduviidae Reduviinae). Mem. Inst. Oswaldo Cruz 77, 449–451.
- Lent, H., Wygodzinsky, P., 1979. Revision of the Triatominae (Hemiptera, Reduviidae), and their significance as vectors of Chagas disease. Bull. Am. Mus. Nat. Hist. 163, 123–520.
- Lorosa, E.S., Jurberg, J., Souza, A.L., Vinhaes, M.C., Nunes, I.M., 2000. Hemolinfa de Dictyoptera na manutenção do ciclo biológico silvestre de *Triatoma rubrovaria* (Blanchard, 1843) e *Triatoma circummaculata* (Stal, 1859) (Hemiptera, Reduviidae Triatominae). Entomol. Vectores 7, 287–296.
- Lyman, D.F., Monteiro, F.A., Escalante, A.A., Cordón-Rosales, C., Wesson, D.M., Dujardin, J.P., Beard, C.B., 1999. Mitochondrial DNA sequence variation among Triatominae vectors of Chagas disease. Am. J. Trop. Med. Hyg. 60, 377–386.
- MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, 203 pp.
- Machado, C.A., Ayala, F.J., 2001. Nucleotide sequences provide evidence of genetic exchange among distantly related lineages of *Trypanosoma cruzi*. PNAS 98, 7396–7401.
- Marcilla, A., Barges, M.D., Abad-Franch, F., Panzera, F., Carcavallo, R.U., Noireau, F., Galvão, C., Jurberg, J., Miles, M.A., Dujardin, J.P., Mas-Coma, S., 2002. Nuclear rDNA ITS-2 sequences reveal polyphyly of *Panstrongylus* species (Hemiptera: Reduviidae: Triatominae), vectors of *Trypanosoma cruzi*. Inf. Gen. Evol. 1, 225–235.
- Martinez, E., Chavez, T., Sossa, D., Aranda, R., Vargas, B., Vidaurre, P., 2007. *Triatoma boliviana* sp.n. de los valles subandinos de La Paz, Bolivia (Hemiptera: Reduviidae: Triatominae), similar a *Triatoma nigromaculata* Stal 1859. Bol. Inst. Invest. Salud Des. 3, 1–11.
- Mayr, E., Linsley, E.G., Usinger, R.L., 1953. Methods and Principles of Systematic Zoology. McGraw-Hill, New York, p. 328.
- Miles, M.A., Arias, J.R., de Souza, A., Póvoa, M., 1981. Chagas disease in the Amazon basin III. Ecotopes of ten triatomine bug species (Hemiptera: Reduviidae) from the vicinity of Belém, Para state, Brazil. J. Med. Entomol. 18, 266–278.
- Monteiro, F.A., Pérez, R., Panzera, F., Dujardin, J.P., Galvão, C., Rocha, D., Noireau, F., Schofield, C.J., Beard, C.B., 1999. Mitochondrial DNA variation of *Triatoma infestans* populations and its implication for the specific status of *T.melanosoma*. Mem. Inst. Oswaldo Cruz 94 (Suppl. 1), 229–238.
- Monteiro, F.A., Wesson, D.M., Dotson, E.M., Schofield, C.J., Beard, C.B., 2000. Phylogeny and molecular taxonomy of the Rhodniini derived from mitochondrial and nuclear DNA sequences. Am. J. Trop. Med. Hyg. 62, 460–465.
- Monteiro, F.A., Donnelly, M.J., Beard, C.B., Costa, J., 2004. Nested clade and phylogeographic analyses of the Chagas disease vector *Triatoma brasiliensis* in Northeast Brazil. Mol. Phylog. Evol. 32, 46–56.
- Noireau, F., Flores, R., Gutierrez, T., Dujardin, J.P., 1997. Detection of silvatic dark morphs of *Triatoma infestans* in the Bolivian chaco. Mem. Inst. Oswaldo Cruz 92, 583–584.
- Noireau, F., Gutierrez, T., Zegarra, M., Flores, R., Brenière, F., Dujardin, J.P., 1998. Cryptic speciation in *Triatoma sordida* (Hemiptera: Reduviidae) from the Bolivian chaco. Trop. Med. Int. Health 3, 364–372.
- Panzera, F., Scvortzoff, E., Perez, R., Panzera, Y., Hornos, S., Cestau, R., Nicolini, P., Delgado, V., Alvarez, F., Mazzella, M.C., Cossio, G., Martinez, M., Salvatella, R., 1998. Cytogenetics of Triatomines. In: Atlas of Chagas disease vectors in the Americas, vol. II. Editora FIOCRUZ, Rio de Janeiro, pp. 621–664.
- Panzera, F., Pérez, R., Nicolini, P., Hornos, S., Costa, J., Borges, E., Diotaiuti, L., Schofield, C.J., 2000. Chromosome homogeneity in populations of *Triatoma brasiliensis* Neiva 1911 (Hemiptera - Reduviidae - Triatominae). Cad. Saúde Públ. 16 (Suppl. 2), 83–88.
- Panzera, F., Dujardin, J.P., Nicolini, P., Caraccio, M.N., Rose, V., Tellez, T., Bermúdez, H., Barges, M.D., Mas-Coma, S., O'Connor, J.E., Pérez, R., 2004. Genomic changes of Chagas disease vector, South America. Emerg. Infect. Dis. 10, 438–446.
- Panzera, F., Ferrandis, I., Ramsey, J., Ordóñez, R., Salazar-Schettino, P.M., Cabrera, M., Monroy, M.C., Barges, M.D., Mas-Coma, S., O'Connor, J.E., Angulo, V.M., Jaramillo, N., Córdón-Rosales, C., Gómez, D., Pérez, R., 2006. Chromosomal variation and genome size support existence of cryptic species of *Triatoma dimidiata* with different epidemiological importance as Chagas disease vectors. Trop. Med. Int. Health 11, 1092–1103.
- Panzera, F., Ferrandis, I., Ramsey, J., Salazar-Schettino, P.M., Cabrera, M., Monroy, C., Barges, M.D., Mas-Coma, S., O'Connor, J.E., Angulo, V.M., Jaramillo, N., Pérez, R., 2007. Genome size determination in Chagas disease transmitting bugs (Hemiptera-Triatominae) by flow cytometry. Am. J. Trop. Med. Hyg. 76, 516–521.
- Patterson, J.S., 2007. Comparative morphometric and molecular genetic analyses of Triatominae (Hemiptera: Reduviidae). Ph.D. thesis. University of London, 253 pp.
- Patterson, J.S., Schofield, C.J., Dujardin, J.P., Miles, M.A., 2001. Population morphometric analysis of the tropicopolitan bug *Triatoma rubrofasciata* and relationships with Old World species of *Triatoma*: evidence of New World ancestry. Med. Vet. Entomol. 15, 443–451.
- Paula, A.S., Diotaiuti, L., Schofield, C.J., 2005. Testing the sister-group relationship of the Rhodniini and Triatomini (Insecta: Hemiptera: Reduviidae: Triatominae). Mol. Phylog. Evol. 35, 712–718.
- Paula, A.S., Diotaiuti, L., Galvão, C., 2007. Systematics and biogeography of Rhodniini (Heteroptera: Reduviidae: Triatominae) based on 16S mitochondrial rDNA sequences. J. Biogeogr. 34, 699–712.
- Pavan, M.G., Monteiro, F.A., 2007. A multiplex PCR assay that separates *Rhodnius prolixus* from members of the *Rhodnius robustus* cryptic species complex (Hemiptera: Reduviidae). Trop. Med. Int. Health 12, 751–758.
- Pereira, H., Penido, C.M., Martins, M.S., Diotaiuti, L., 1998. Comparative kinetics of bloodmeal intake by *Triatoma infestans* and *Rhodnius prolixus*, the two principal vectors of Chagas disease. Med. Vet. Entomol. 12, 84–88.
- Pérez, R., Hernández, M., Quintero, O., Scvortzoff, E., Canale, D., Méndez, L., Cohanoff, C., Martino, M., Panzera, F., 2005. Cytogenetic analysis of experimental hybrids in species of Triatominae (Hemiptera-Reduviidae). Genetica 125, 261–270.
- Pinto, C., 1926. Classificação dos Triatomídeos (Hemipteros-Heteropteros hematofagos). Sciencia Med. 4, 485–490.
- Pires, H.H.R., Abrão, D.O., Machado, E.M.M., Schofield, C.J., Diotaiuti, L., 2002. Eye colour as a genetic marker for fertility and fecundity of *Triatoma infestans* (Klug, 1834) Hemiptera, Reduviidae, Triatominae. Mem. Inst. Oswaldo Cruz 97, 675–678.
- Poinar Jr., G., 2005. *Triatoma dominicana* sp.n. (Hemiptera: Reduviidae: Triatominae), and *Trypanosoma antiquus* sp.n. (Stercoraria: Trypanosomatidae), the first fossil evidence of a triatomine-trypanosomatid vector association. Vector-borne Zoon. Dis. 5, 72–81.
- Rezende, J.M., Rassi, A., 2008. Por que os Triatomíneos são chamados de “barbeiros”? Rev. Pat. Trop. 37, 75–83.
- Ribeiro, J.M., Schneider, M., Isaias, T., Jurberg, J., Galvão, C., Guimaraes, J.A., 1998. Role of salivary antihemostatic components in blood feeding by triatomine bugs (Heteroptera). J. Med. Entomol. 35, 599–610.
- Rodriguez, J.R., 2003. Morfometria geométrica dos hemielitros de reduviídeos predadores e hematofagos: convergência ou parentesco evolutivo? Thesis. FIOCRUZ, Rio de Janeiro, 41 pp.
- Rodriguez, M.H., 2004. Etnoconocimiento de los vectores de la enfermedad de Chagas de las comunidades indígenas Ticuna y Huitoto del trapezio amazonico, departamento del Amazonas Colombia. In: Proceedings of the ECLAT-AMCHA International Workshop on Chagas disease surveillance in the Amazon Region, Palmari, Brazil. Universidad de Los Andes, Bogota, pp. 75–82.
- Rodriguez Rodríguez, J., Fuentes González, O., Nodarse, J.F., Monzote Fidalgo, L., Dujardin, J.P., 2007. Morphometric changes of *Triatoma flavida* Neiva 1911 (Hemiptera:Triatominae) in the transition from sylvatic to laboratory conditions. Rev. Inst. Med. Trop. São Paulo 49, 127–130.
- Rothhammer, F., Allison, M.J., Núñez, L., Standen, V., Arriaza, B., 1985. Chagas disease in pre-Columbian South America. Am. J. Phys. Anthropol. 68, 495–498.
- Ruas-Neto, A.L., Corseuil, E., Cavalleri, A., 2001. Development of reuprestrian triatomines (Hemiptera: Reduviidae: Triatominae) following haemolymphagy on blaberids (Blattodea: Blaberidae) in Rio Grande do Sul State, Brazil. Entomol. Vectores 8, 205–216.
- Ryckman, R.E., 1951. Recent observations of cannibalism in *Triatoma* (Hemiptera: Reduviidae). J. Parasitol. 37, 433–434.
- Sainz, A.C., Maura, L.V., Moriyama, E.N., Garcia, B.A., 2003. Phylogeny of triatomine vectors of *Trypanosoma cruzi* suggested by mitochondrial DNA sequences. Genetica 121, 229–240.
- Sandoval, C.M., Joya, M., Gutiérrez, M., Angulo, V.M., 2000. Cleptohaematophagy in *Belminus herrei*. Med. Vet. Entomol. 14, 100–101.
- Sandoval, C.M., Duarte, R., Gutiérrez, R., Rocha, D.S., Angulo, V.M., Esteban, L., Reyes, M., Jurberg, J., Galvão, C., 2004. Feeding sources and natural infection of *Belminus herrei* (Hemiptera, Reduviidae, Triatominae) from dwellings in Cesar, Colombia. Mem. Inst. Oswaldo Cruz 99, 137–140.
- Sandoval, C.M., Pabon, E., Jurberg, J., Galvão, C., 2007. *Belminus ferroae* n.sp. from the Colombian north-east, with a key to the species of the genus (Hemiptera: Reduviidae: Triatominae). Zootaxa 1443, 55–64.

- Sandoval, C.M., Ortiz, N., Lorosa, E., Galvão, C., Rodríguez, O., Scorza, J.V., Gutiérrez, R., 2009. *Belminus ferroae*, a predaceous Triatominae colonizing rural houses in the Department of Norte de Santander, Colombia. *J. Med. Entomol.*, submitted.
- Schaefer, C.W., 2003. Triatominae (Hemiptera: Reduviidae): systematic questions and some others. *Neotrop. Entomol.* 32, 1–10.
- Schaefer, C.W., 2005. Why are the subfamily relationships of Triatominae (Hemiptera: Reduviidae) important? *Entomol. Vectores* 12, 19–35.
- Schofield, C.J., 1988. The biosystematics of Triatominae. In: Service, M.W. (Ed.), *Biosystematics of Haematophagous Insects*, Systematics Association special volume 37. Clarendon press, Oxford, UK, pp. 284–312.
- Schofield, C.J., 1996. Biosystematics and adaptive trends in Triatominae. In: Schofield, C.J., Dujardin, J.P., Jurberg, J. (Eds.), *Proceedings of the International Workshop on Population Genetics and Control of Triatominae*. Santo Domingo de los Colorados, Ecuador. INDRE Mexico City, pp. 45–50.
- Schofield, C.J., 2000. *Trypanosoma cruzi*—the vector-parasite paradox. *Mem. Inst. Oswaldo Cruz* 95, 535–544.
- Schofield, C.J., 2002. Evolución y control del *Triatoma dimidiata*. Taller para el establecimiento de pautas técnicas en el control de *Triatoma dimidiata*. San Salvador, 11–13 March 2002. PAHO document OPS/HCP/HCT/214/02, pp. 12–18.
- Schofield, C.J., 2004. Evolution and dispersal of *Triatoma* and *Rhodnius* in the Americas. In: IX European Multicollloquium of Parasitology, Valencia, Spain, pp. 179–180.
- Schofield, C.J., Dolling, W.R., 1993. Bedbugs and kissing-bugs (bloodsucking Hemiptera). In: Lane, R.P., Crosskey, R.W. (Eds.), *Medical Insects and Arachnids*. Chapman and Hall, London, UK, pp. 483–516.
- Schofield, C.J., Dujardin, J.P., 1999. Theories on the evolution of *Rhodnius*. *Actual. Biol. (Medellin)* 70, 183–197.
- Schofield, C.J., Diotaiuti, L., Dujardin, J.P., 1999. The process of domestication in Triatominae. *Mem. Inst. Oswaldo Cruz* 94 (Suppl. 1), 375–378.
- Schofield, C.J., Jannin, J., Salvatella, R., 2006. The future of Chagas disease control. *Trends Parasitol.* 21, 583–588.
- Schuh, R.T., Slater, J.A., 1995. *True bugs of the World (Hemiptera: Heteroptera) Classification and Natural History*. Cornell University Press, 336 pp.
- Soares, R.P., Sant'Anna, M.R., Gontijo, N.F., Romanha, A.J., Diotaiuti, L., Pereira, M.H., 2000. Identification of morphologically similar *Rhodnius* species (Hemiptera: Reduviidae: Triatominae) by electrophoresis of salivary heme proteins. *Am. J. Trop. Med. Hyg.* 62, 157–161.
- Souza, R., de, C.d., Barbosa, S.E., Sonoda, I.V., Azeredo, B.V., Romanha, A.J., Diotaiuti, L., 2008. Population dynamics of *Triatoma vitticeps* (Stål, 1859) in Itanhomi, Minas Gerais, Brazil. *Mem. Inst. Oswaldo Cruz* 103, 14–20.
- Stevens, J., Schofield, C.J., 2003. Phylogenetics and sequence analysis—some problems for the unwary. *Trends Parasitol.* 19, 582–588.
- Tartarotti, E., Ceron, C.R., 2005. Ribosomal DNA ITS-1 intergenic spacer polymorphism in triatomines (Triatominae Heteroptera). *Biochem. Genetics* 43, 365–373.
- Usinger, R.L., 1939. Descriptions of new Triatominae with a key to genera (Hemiptera Reduviidae). *Univ. Calif. Publ.* 7, 33–56.
- Usinger, R.L., 1944. The Triatominae of North and Central America and the West Indies, and their public health significance. *US Publ. Hlth. Bull.* 288, 1–83.
- Waddell, P., Steel, M., 1997. General time-reversible distances with unequal rates across sites, mixing gamma and inverse Gaussian distributions with invariant sites. *Mol. Phylog. Evol.* 8, 398–414.
- Weirauch, C., 2008. Cladistic analysis of Reduviidae (Heteroptera: Cimicomorpha) based on morphological characters. *System. Entomol.* 33, 229–274.
- White, G.B., Boreham, P.F.L., Dolling, W.R., 1972. Synanthropic emesine bugs (Reduviidae Emesinae) as predators of endophilic mosquitoes. *Trans. R. Soc. Trop. Med. Hyg.* 66, 535–536.
- Wygodzinsky, P.W., 1966. A monograph of the Emesinae (Reduviidae Hemiptera). *Bull. Am. Mus. Nat. Hist.* 133, 1–614.