

# Biogeography and evolution of Amazonian triatomines (Heteroptera: Reduviidae): implications for Chagas disease surveillance in humid forest ecoregions

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*An ecological-evolutionary classification of Amazonian triatomines is proposed based on a revision of their main contemporary biogeographical patterns. Truly Amazonian triatomines include the Rhodniini, the Cavernicolini, and perhaps Eratyrus and some Bolboderini. The tribe Rhodniini comprises two major lineages (pictipes and robustus). The former gave rise to trans-Andean (pallescens) and Amazonian (pictipes) species groups, while the latter diversified within Amazonia (robustus group) and radiated to neighbouring ecoregions (Orinoco, Cerrado-Caatinga-Chaco, and Atlantic Forest). Three widely distributed Panstrongylus species probably occupied Amazonia secondarily, while a few Triatoma species include Amazonian populations that occur only in the fringes of the region. T. maculata probably represents a vicariant subset isolated from its parental lineage in the Caatinga-Cerrado system when moist forests closed a dry trans-Amazonian corridor. These diverse Amazonian triatomines display different degrees of synanthropism, defining a behavioural gradient from household invasion by adult triatomines to the stable colonisation of artificial structures. Anthropogenic ecological disturbance (driven by deforestation) is probably crucial in the onset of the process, but the fact that only a small fraction of species effectively colonises artificial environments suggests a role for evolution at the end of the gradient. Domestic infestation foci are restricted to drier subregions within Amazonia; thus, populations adapted to extremely humid rainforest microclimates may have limited chances of successfully colonising the slightly drier artificial microenvironments. These observations suggest several research avenues, from the use of climate data to map risk areas to the assessment of the synanthropic potential of individual vector species.*

Key words: Triatominae - ecology - evolution - biogeography - Chagas disease - Amazonia

## AMAZONIA

The Amazon is the largest subregion within the Neotropical biogeographical region. It encompasses 13 biogeographical provinces and over 40 ecoregions (cf. Olson et al. 2001, WWF 2001, Morrone 2006) (Tables I-III, Fig. 1). The greater Amazon biome (~ 6.5 million km<sup>2</sup>) is comprised of many diverse biotic communities. The Amazon River fluvial network, with over 10 thousand tributaries, irrigates > 5 million km<sup>2</sup> of tropical forests (moist and dry, *terra firme* and seasonally flooded, lowland and montane) and the open formations, *Campinas*, *Campinaranas*, and anthropic landscapes that constitute the ecological mosaic of Amazonia. Considered as a whole, the Amazon is the most biologically diverse biome on Earth – as measured by the absolute number of species recorded in each region (Mittermeier et al. 2003).

From a wider (biogeographical, ecological, and evolutionary) perspective, the Amazon complex may be considered to include certain physically contiguous systems and ecoregions with which it shares key aspects of its historical biogeography. The most important among these regions are the Orinoco and Tocantins/Araguaia basins, the Guyanan Shield highlands, and the eastern slopes of the northern-central Andes (including the Peruvian *Selva Alta*, the Yungas, and the inter-Andean valleys draining towards the Amazon-Orinoco system). In Brazil, both the drier ecoregions of the Cerrado and the Caatinga (particularly the relatively humid forests along riverbanks and mountain ranges) and the moist Atlantic Forests harbour animal and plant communities that reveal their ancient biogeographical-evolutionary relationship with Amazonia.

Many factors and processes have been invoked to explain the regional patterns of biological diversification. Whatever the weight of their relative contributions, geological substrate heterogeneity, climatic fluctuations and habitat fragmentation, hydro- and oro-graphical vicariant events, dispersal and adaptive radiation, local extinction, genetic drift or coevolution all have probably played a role. It seems safe enough to admit that the historical evolution of this huge biogeographical complex offered a vast number of ecological-adaptive opportunities (and constraints) for organic diversification by natural selection of variants, thus shaping the systematic relationships among contemporary lineages (cf. Rossetti et al. 2005). It is therefore obvious that a sound understanding of the biology of Amazonian organisms

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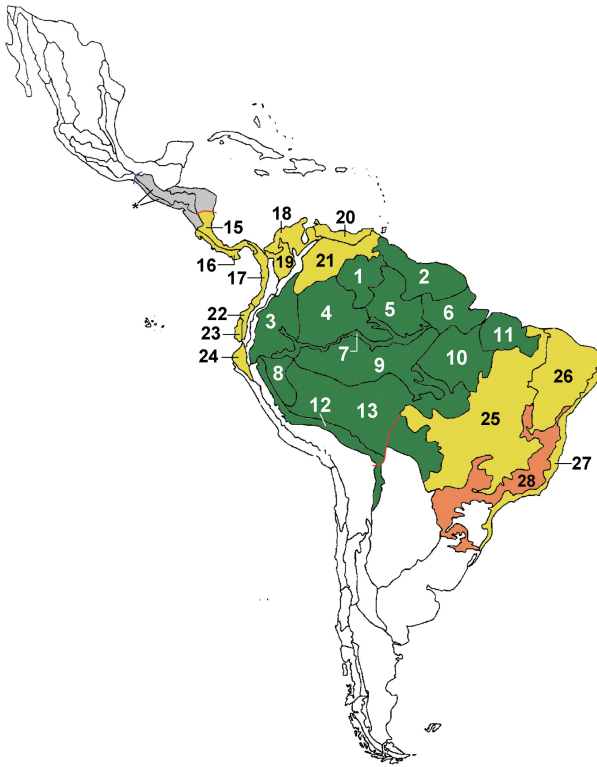


Fig. 1: province biogeography of the Neotropical region and the distribution of *Rhodnius* spp. Numbers indicate biogeographical provinces (after Morrone 2006) specified in Table I. Green areas correspond to the Amazon province. The red line in Central America suggests the northern limit of natural (sylvatic) *R. pallescens* populations. The red line across province number 13 suggests the southern limit of Amazonian *Rhodnius* populations. Grey areas in Mesoamerica indicate the distribution of introduced *R. prolixus* populations (\* = Chiapas province). The orange area corresponds to the Paraná Forest province, where *R. domesticus* likely occurs.

must take into account not only their systematic structuring and current ecological associations, but also the historical (evolutionary) aspects of the different lineages and of the environments where they originated and diversified.

#### THE TRIATOMINAE OF AMAZONIA

The true number of Amazonian triatomine species remains probably unknown. Records from the Amazon-Orinoco-Tocantins/Araguaia systems, the Guyana Shield, and the eastern Andean foothills include no less than 27 recognised species (with a few further taxa probably present in some subregions) grouped into nine genera and five tribes: Rhodniini (ten *Rhodnius* and at least one *Psammolestes* species), Triatomini (four *Triatoma*, three *Panstrongylus*, and two *Eratyrus* species) Cavernicolini (two *Cavernicola* species), Alberproseniini (two *Alberprosenia* species), and Bolboderini (at least two *Belminus* and one *Microtriatoma* species) (see Tables II, III). It is however very likely that many further taxa

occur in the Amazon that have not yet been formally described. Lineages composed of small, dull-coloured, canopy-living organisms (like those within the last three tribes we have just mentioned) are the most obvious candidates to encompass undescribed species. Other likely candidates are those 'species' considered to be either biologically very variable and/or extensively distributed, which might conceal species complexes. The recent finding of moderately divergent mitochondrial haplotypes in phenotypically indistinguishable populations of the widespread *R. robustus* (Monteiro et al. 2003) indicates that the biological diversity of well-known triatomine taxa is also higher than previously thought. The growing use of DNA barcoding techniques in arthropod taxonomy is revealing how underestimated is species richness in biodiversity inventories based on classical phenotypic approaches (see for instance Miller 2007).

Even a superficial biogeographical appraisal suggests that the many triatomine species reported to occur in Amazonia fall into distinct categories. Some must be considered as truly Amazonian, while others evolved elsewhere and occupied the region secondarily. Among the former, some radiated to neighbouring ecoregions and diversified (speciating in some cases), while others remained endemic to their areas of origin. Among the latter, some are populations of widely distributed species, others are found in the ecotones along the fringes of the region, and a few represent isolated populations derived from currently allopatric stem lineages.

In an attempt to put forward a coherent account of the systematic, ecological, and behavioural diversity of Amazonian triatomines, we underscore in this paper the importance of adopting a biogeographical and evolutionary stance – which might be broadly interpreted as phylogeographical. Following this rationale, we present an approximation to the historical biogeography and evolution of the main triatomine lineages known to occur in the greater Amazon, classifying them accordingly, and discuss how this view may foster a biologically sound understanding of synanthropic behavioural trends among these vectors.

#### A PHYLOGEOGRAPHICAL CLASSIFICATION OF AMAZONIAN TRIATOMINES

The draft classification we propose here is based on an approximation to the evolutionary origins and diversification patterns of the Amazonian lineages within the Rhodniini, *Panstrongylus* and *Triatoma*, but we will also consider other groups. The judgments underlying our proposal are biogeographical, ecological, and evolutionary; we made an effort to avoid excess speculation by trying to focus on taxon groups that can be safely considered to be monophyletic, even if they are not recognised as formal systematic units in some cases.

*Truly Amazonian Triatominae* - This group includes all the lineages whose centre of origin, diversification, and dispersal (giving rise to currently sympatric, parapatric or allopatric derived taxa) was probably the core region of moist tropical forests corresponding to contemporary Amazonia.

TABLE I  
Biogeography of the Neotropical region and the distribution of *Rhodnius* spp.

Region	Subregion	Dominion	Province	Number <sup>a</sup>	
Neotropical	Caribbean	Mesoamerican	Mexican Pacific Coast		
			Mexican Gulf		
			Chiapas		
			Eastern Central America	15	
			Western Panamanian Isthmus	16	
			Antillean	Yucatán Peninsula	
				Bahama	
				Cuba	
				Cayman Islands	
				Jamaica	
		Hispaniola			
		Puerto Rico			
		Lesser Antilles			
		Northwestern South American		Chocó	17
				Maracaibo	18
			Magdalena	19	
			Trinidad and Tobago		
			Venezuelan Coast <sup>c</sup>	20	
			Venezuelan Llanos <sup>c</sup>	21	
			Cauca		
			Galápagos Islands		
			Western Ecuador	22	
			Arid Ecuador	23	
		Tumbes-Piura	24		
		Amazonian	Guyana	1	
			Humid Guyana	2	
			Napo	3	
			Imeri	4	
			Roraima	5	
			Amapá	6	
			Várzea	7	
			Ucayali	8	
Madeira	9				
Tapajós-Xingu	10				
Pará	11				
Yungas	12				
Pantanal	13				
Chacoan	Cerrado <sup>c</sup>		25		
	Caatinga <sup>c</sup>	26			
Paraná	Chaco <sup>c</sup>				
	Pampa				
	Brazilian Atlantic Forest	27			
	Paraná Forest <sup>b</sup>	28			
	<i>Araucaria</i> Forest				

Grey cells correspond to provinces with records of naturally occurring *Rhodnius* species and populations; a: numbers as in Fig. 1; b: likely occurrence of natural *Rhodnius* populations; c: recorded occurrence of *Psammolestes* spp.

The paradigmatic example of this group is the tribe Rhodniini, an assemblage of arboricolous triatomines (most of them associated with palm trees) grouped into two genera – *Psammolestes* and *Rhodnius* (Lent & Wygodzinsky 1979, Galvão et al. 2003). While the phylogenetic relationships of many triatomine tribes and genera remain problematic, the Rhodniini are consid-

ered monophyletic beyond controversy (Hypša et al. 2002, De Paula et al. 2005). The two genera within the tribe are however paraphyletic, with *Psammolestes* species sharing a common ancestor with *R. robustus* and its closest relatives (Monteiro et al. 2000, 2002).

The 19 species within the tribe Rhodniini have been classified into two main groups (Schofield & Dujardin

TABLE II

Biogeography of the triatomines from the greater Orinoco (Northwestern South American biogeographical dominion)

Biogeographic province <sup>a</sup>	Hydrographic basin(s)	Ecoregion <sup>b</sup>	Species of Triatominae
Maracaibo	Lake Maracaibo	Maracaibo dry forests	<i>Rhodnius prolixus</i> , <i>R. robustus</i> (I), <i>R. pictipes</i> , <i>R. neivai</i> , <i>Triatoma dimidiata</i> ?, <i>T. maculata</i> , <i>T. nigromaculata</i> , <i>Panstrongylus geniculatus</i> , <i>P. rufotuberculatus</i> , <i>Eratyrus mucronatus</i> , <i>E. cuspidatus</i> , <i>Alberprosenia goyovargasi</i>
		Catatumbo moist forests	<i>R. prolixus</i> , <i>R. robustus</i> (I)?, <i>R. pictipes</i> , <i>T. dimidiata</i> ?, <i>T. maculata</i> ?, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> , <i>E. mucronatus</i> , <i>E. cuspidatus</i> , <i>Cavernicola pilosa</i> ?
		Guajira/Barranquilla xeric scrub	<i>R. prolixus</i> , <i>R. neivai</i> , <i>T. dimidiata</i> ?, <i>T. maculata</i> , <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ?, <i>E. mucronatus</i> ?, <i>E. cuspidatus</i> ?
		Paraguana xeric scrub	<i>R. prolixus</i> , <i>R. robustus</i> (I)?, <i>R. pictipes</i> ?, <i>R. neivai</i> , <i>Psammolestes arthuri</i> , <i>T. dimidiata</i> , <i>T. maculata</i> , <i>T. nigromaculata</i> , <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> , <i>E. mucronatus</i> ?, <i>E. cuspidatus</i>
	Orinoco/Magdalena (Northern Colombia)	Cordillera Oriental montane forests	<i>R. prolixus</i> , <i>R. robustus</i> (I), <i>R. pictipes</i> , <i>R. dalessandroi</i> ?, <i>T. dimidiata</i> (Colombia), <i>T. maculata</i> ?, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ?, <i>E. mucronatus</i> , <i>E. cuspidatus</i> , <i>C. pilosa</i> , <i>Belminus rugulosus</i> ?
Venezuelan Coast	Venezuelan coastal basins	La Costa xeric shrublands	<i>R. prolixus</i> , <i>R. robustus</i> (I)?, <i>R. pictipes</i> ?, <i>P. arthuri</i> , <i>T. dimidiata</i> , <i>T. maculata</i> , <i>T. nigromaculata</i> , <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> , <i>E. mucronatus</i> , <i>E. cuspidatus</i> , <i>B. pittieri</i> , <i>B. rugulosus</i>
		Cordillera La Costa montane forests	<i>R. prolixus</i> , <i>R. robustus</i> (I)?, <i>R. pictipes</i> , <i>T. dimidiata</i> ?, <i>T. maculata</i> ?, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ?, <i>E. mucronatus</i> ?, <i>Microtriatoma trinidadensis</i> , <i>B. pittieri</i> ?, <i>B. rugulosus</i> ?
		Lara/Falcón dry forests	<i>R. prolixus</i> , <i>R. robustus</i> (I), <i>R. neivai</i> , <i>T. dimidiata</i> ?, <i>T. maculata</i> , <i>T. nigromaculata</i> ?, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> , <i>E. mucronatus</i> , <i>E. cuspidatus</i>
	Trinidad basins	Trinidad and Tobago moist forests	<i>E. mucronatus</i> , <i>M. trinidadensis</i>
		Paraguana xeric scrub	<i>R. prolixus</i> , <i>R. robustus</i> (I)?, <i>R. pictipes</i> ?, <i>R. neivai</i> , <i>P. arthuri</i> , <i>T. dimidiata</i> , <i>T. maculata</i> , <i>T. nigromaculata</i> , <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> , <i>E. mucronatus</i> ?, <i>E. cuspidatus</i>
		Araya and Paria xeric scrub	<i>R. prolixus</i> , <i>R. robustus</i> (I)?, <i>T. dimidiata</i> ?, <i>T. maculata</i> ?, <i>P. geniculatus</i> ?, <i>P. rufotuberculatus</i> ?, <i>E. mucronatus</i> ?, <i>E. cuspidatus</i> ?
Venezuelan Llanos	Orinoco	Llanos	<i>R. prolixus</i> , <i>R. robustus</i> (I), <i>R. pictipes</i> , <i>R. dalessandroi</i> , <i>P. arthuri</i> , <i>T. dimidiata</i> , <i>T. maculata</i> , <i>T. nigromaculata</i> , <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> , <i>E. mucronatus</i> , <i>E. cuspidatus</i> , <i>C. pilosa</i> , <i>B. rugulosus</i> ?, <i>M. trinidadensis</i> ?
		Apure/Villavicencio dry forests	<i>R. prolixus</i> , <i>R. robustus</i> (I), <i>R. pictipes</i> ?, <i>P. arthuri</i> , <i>T. dimidiata</i> , <i>T. maculata</i> , <i>T. nigromaculata</i> , <i>P. geniculatus</i> , <i>P. lignarius</i> ??, <i>P. rufotuberculatus</i> , <i>E. mucronatus</i> , <i>E. cuspidatus</i> , <i>C. pilosa</i> , <i>B. rugulosus</i> ?
		Orinoco Delta swamp forests	<i>R. prolixus</i> ?, <i>R. robustus</i> (I, IV)?, <i>R. pictipes</i> , <i>T. dimidiata</i> ?, <i>T. maculata</i> ?, <i>T. nigromaculata</i> ??, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ?, <i>P. lignarius</i> ?, <i>E. mucronatus</i> ?, <i>M. trinidadensis</i>
		Orinoco wetlands	<i>R. prolixus</i> ?, <i>R. robustus</i> (I, IV)?, <i>R. pictipes</i> ?, <i>P. geniculatus</i> ?, <i>P. lignarius</i> ?, <i>P. rufotuberculatus</i> ?, <i>E. mucronatus</i> ?, <i>M. trinidadensis</i> ?

a: after Morrone (2006); b: after WWF (2001); ? indicates the species is probably present in the ecoregion; ?? indicates the species is possibly present in the ecoregion; roman numerals refer to *R. robustus* genotypic groups defined after Monteiro et al. (2003); triatomine records follow Carcavallo et al. (1999) and Galvão et al. (2003).

TABLE III  
Biogeography of the triatomines from the Amazonian subregion

Biogeographic province <sup>d</sup>	Hydrographic basin(s)	Ecoregion <sup>f</sup>	Species of Triatominae	
Napó	Amazonas	Caquetá moist forests	<i>Rhodnius robustus</i> (II), <i>R. pictipes</i> , <i>R. brethesi</i> , <i>Panstrongylus geniculatus</i> , <i>P.s. rufotuberculatus</i> , <i>P. lignarius</i> ?, <i>Eratyus mucronatus</i> , <i>Cavernicola pilosa</i> , <i>Microtriatoma trinidadensis</i>	
		Napo moist forests	<i>R. robustus</i> (II), <i>R. sp.</i> (robustus lineage), <i>R. pictipes</i> , <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ?, <i>P. lignarius</i> (and <i>lignarius-herrerii</i> intermediate forms), <i>E. mucronatus</i> , <i>C. pilosa</i>	
	Solimões/Japurá moist forests		<i>R. robustus</i> (II), <i>R. pictipes</i> , <i>R. brethesi</i> ?, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> , <i>P. lignarius</i> , <i>E. mucronatus</i> , <i>C. pilosa</i> , <i>M. trinidadensis</i> ?, <i>Belminus peruvianus</i> ?	
		Cordillera Oriental montane forests (southern third)	<i>R. prolixus</i> , <i>R. robustus</i> (I, IV)?, <i>R. pictipes</i> , <i>R. dalessandroi</i> ?, <i>T. dimidiata</i> ?, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ?, <i>E. mucronatus</i> , <i>E. cuspidatus</i> , <i>C. pilosa</i> , <i>B. rugulosus</i> ??	
	Amazonas/Orinoco	Eastern Cordillera Real montane forests	<i>R. robustus</i> (II), <i>Rhodnius sp.</i> (robustus lineage)?, <i>R. pictipes</i> , <i>T. carrioni</i> , <i>T. venosa</i> , <i>P. geniculatus</i> ?, <i>P. rufotuberculatus</i> ?, <i>P. lignarius</i> ?, <i>B. peruvianus</i> ?	
		Negro/Branco moist forests	<i>R. prolixus</i> ?, <i>R. robustus</i> (I), <i>R. pictipes</i> , <i>R. brethesi</i> , <i>T. maculata</i> ?, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ?, <i>P. lignarius</i> ?, <i>E. mucronatus</i> , <i>C. pilosa</i> , <i>M. trinidadensis</i>	
	Orinoco	Apuré/Villavicencio dry forests (southern limit)	<i>R. prolixus</i> ?, <i>R. robustus</i> (I), <i>R. pictipes</i> ?, <i>Psammolestes arthuri</i> , <i>T. dimidiata</i> ?, <i>T. maculata</i> , <i>T. nigromaculata</i> ?, <i>P. geniculatus</i> , <i>P. lignarius</i> ?, <i>P. rufotuberculatus</i> , <i>E. mucronatus</i> , <i>E. cuspidatus</i> , <i>C. pilosa</i> , <i>B. rugulosus</i> ??	
		Japurá/Solimões-Negro moist forests	<i>R. robustus</i> (II, IV, *), <i>R. pictipes</i> , <i>R. brethesi</i> , <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> , <i>P. lignarius</i> , <i>Eratyus mucronatus</i> , <i>C. pilosa</i> , <i>M. trinidadensis</i>	
	Imeri	Amazonas	Negro/Branco moist forests	<i>R. prolixus</i> ?, <i>R. robustus</i> (I), <i>R. pictipes</i> , <i>R. brethesi</i> , <i>T. maculata</i> ?, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ?, <i>P. lignarius</i> ?, <i>E. mucronatus</i> , <i>C. pilosa</i> , <i>M. trinidadensis</i>
			Caquetá moist forests	<i>R. robustus</i> (II), <i>R. pictipes</i> , <i>R. brethesi</i> , <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> , <i>P. lignarius</i> , <i>E. mucronatus</i> , <i>C. pilosa</i> , <i>M. trinidadensis</i>
Guyana	Amazonas/Orinoco	Solimões/Japurá moist forests	<i>R. robustus</i> (II), <i>R. pictipes</i> , <i>R. brethesi</i> ?, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> , <i>P. lignarius</i> , <i>E. mucronatus</i> , <i>C. pilosa</i> , <i>M. trinidadensis</i> ?, <i>B. peruvianus</i> ?	
		Rio Negro Campinaranas	<i>R. robustus</i> (I, II)?, <i>R.s pictipes</i> , <i>R. brethesi</i> , <i>P. geniculatus</i> ?, <i>P. rufotuberculatus</i> ?, <i>P. lignarius</i> ?, <i>E. mucronatus</i> ?, <i>C. pilosa</i> ?, <i>M. trinidadensis</i> ?	
	Orinoco	Guyan Highlands moist forests	<i>R. prolixus</i> ?, <i>R. robustus</i> (I), <i>R. pictipes</i> , <i>T. maculata</i> , <i>T. nigromaculata</i> ?, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> , <i>P. lignarius</i> , <i>E. mucronatus</i> , <i>C. pilosa</i> , <i>M. trinidadensis</i> ?	
		Guyan Highlands moist forests	<i>R. prolixus</i> ?, <i>R. robustus</i> (I), <i>R. pictipes</i> , <i>T. maculata</i> , <i>T. nigromaculata</i> ?, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> , <i>P. lignarius</i> , <i>E. mucronatus</i> , <i>C. pilosa</i> , <i>M. trinidadensis</i> ?	
Humid Guyana	Guyanan coastal basins	Llanos	<i>R. prolixus</i> , <i>R. robustus</i> (I), <i>R. pictipes</i> , <i>R. dalessandroi</i> , <i>Psammolestes arthuri</i> , <i>T. dimidiata</i> , <i>T. maculata</i> , <i>T. nigromaculata</i> , <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> , <i>E. mucronatus</i> , <i>E. cuspidatus</i> , <i>C. pilosa</i> , <i>B. rugulosus</i> ?, <i>M. trinidadensis</i> ?	
		Tepuis	<i>T. maculata</i> ?, <i>P. geniculatus</i> ?, <i>E. mucronatus</i> ?, <i>C. pilosa</i> ??	
Humid Guyana	Guyanan coastal basins	Guyan moist forests	<i>R. prolixus</i> ?, <i>R. robustus</i> (IV), <i>R. pictipes</i> , <i>R. amazonicus</i> , <i>R. paraensis</i> , <i>T. dimidiata</i> ?, <i>T. maculata</i> , <i>T. nigromaculata</i> ?, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> , <i>P. lignarius</i> ,	

Biogeographic province <sup>a</sup>	Hydrographic basin(s)	Ecoregion <sup>b</sup>	Species of Triatominae
Roraima	Orinoco	Paramaribo swamp forests	<i>E. mucronatus</i> , <i>C. pilosa</i> ?, <i>M. trinidadensis</i> <i>R. robustus</i> (IV)?, <i>R. pictipes</i> ?, <i>R. amazonicus</i> ??, <i>R. paraensis</i> ??, <i>P. geniculatus</i> ?, <i>P. rufotuberculatus</i> ?, <i>P. lignarius</i> ?, <i>E. mucronatus</i> ?, <i>C. pilosa</i> ?, <i>M. trinidadensis</i> ?
		Orinoco Delta swamp forests	<i>R. prolixus</i> ?, <i>R. robustus</i> (IV, V), <i>R. pictipes</i> , <i>T. dimidiata</i> ?, <i>T. maculata</i> ?, <i>T. nigromaculata</i> ??, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ?, <i>P. lignarius</i> ?, <i>E. mucronatus</i> ?, <i>M. trinidadensis</i>
Amapá	Amazonas	Uatumã-Trombetas moist forests	<i>R. robustus</i> (I, IV), <i>R. pictipes</i> , <i>R. amazonicus</i> , <i>R. brethesi</i> ??, <i>R. paraensis</i> , <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> , <i>P. lignarius</i> , <i>E. mucronatus</i> , <i>C. pilosa</i> , <i>C. lenti</i> , <i>M. trinidadensis</i> ?
		Guyanana savannas	<i>R. prolixus</i> ??, <i>R. robustus</i> (I)?, <i>R. pictipes</i> ?, <i>T. maculata</i> , <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ??, <i>E. mucronatus</i> ?, <i>C. pilosa</i> ?
Ucayali	Amazonas	Uatumã-Trombetas moist forests	<i>R. robustus</i> (I, IV), <i>R. pictipes</i> , <i>R. amazonicus</i> , <i>R. brethesi</i> ??, <i>R. paraensis</i> , <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> , <i>P. lignarius</i> , <i>E. mucronatus</i> , <i>C. pilosa</i> , <i>C. lenti</i> , <i>M. trinidadensis</i> ?
		Marajó várzea forests	<i>R. robustus</i> (IV), <i>R. pictipes</i> , <i>R. amazonicus</i> ?, <i>R. paraensis</i> ?, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ?, <i>P. lignarius</i> , <i>E. mucronatus</i> ?, <i>C. pilosa</i> , <i>M. trinidadensis</i> ?, <i>Alberprosenia malheiroi</i> , <i>B. laportei</i>
Madeira	Amazonas	Gurupa várzea	<i>R. robustus</i> (IV)?, <i>R. pictipes</i> ?, <i>R. amazonicus</i> ?, <i>R. paraensis</i> ?, <i>P. geniculatus</i> ?, <i>P. rufotuberculatus</i> ?, <i>P. lignarius</i> ?, <i>E. mucronatus</i> ?, <i>C. pilosa</i> ?, <i>M. trinidadensis</i> ?
		Guyanana savannas	<i>R. prolixus</i> ??, <i>R. robustus</i> (IV)?, <i>R. pictipes</i> ?, <i>T. maculata</i> ??, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ?, <i>E. mucronatus</i> ?, <i>C. pilosa</i> ?
Ucayali	Amazonas	Ucayali moist forests	<i>R. robustus</i> (II), <i>R. pictipes</i> , <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ?, <i>P. lignarius</i> , <i>E. mucronatus</i> , <i>C. pilosa</i> , <i>M. trinidadensis</i> ?, <i>B. peruvianus</i> ?
		Iquitos várzea	<i>R. robustus</i> (II), <i>R. pictipes</i> , <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ?, <i>P. lignarius</i> ?, <i>E. mucronatus</i> ?, <i>C. pilosa</i> ?, <i>M. trinidadensis</i> ?, <i>B. peruvianus</i> ?
Várzea	Amazonas	Madeira/Tapajós moist forests	<i>R. robustus</i> (II, III, IV), <i>R. pictipes</i> , <i>R. stali</i> , <i>R. brethesi</i> ?, <i>P. tertius</i> ?, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> , <i>P. lignarius</i> , <i>E. mucronatus</i> , <i>C. pilosa</i> , <i>M. trinidadensis</i> ?
		Purus/Madeira moist forests	<i>R. robustus</i> (II, IV, III)?, <i>R. pictipes</i> , <i>R. stali</i> ?, <i>R. brethesi</i> ?, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ?, <i>P. lignarius</i> , <i>E. mucronatus</i> , <i>C. pilosa</i> , <i>M. trinidadensis</i> ?
Várzea	Amazonas	Juruá/Purus moist forests	<i>R. robustus</i> (II), <i>R. pictipes</i> , <i>R. brethesi</i> ??, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> , <i>P. lignarius</i> , <i>E. mucronatus</i> , <i>C. pilosa</i> , <i>M. trinidadensis</i> ?
		Purus várzea	<i>R. robustus</i> (II), <i>R. pictipes</i> , <i>R. brethesi</i> ?, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ?, <i>P. lignarius</i> ?, <i>E. mucronatus</i> ?, <i>C. pilosa</i> ?, <i>M. trinidadensis</i> ?
Várzea	Amazonas	Monte Alegre várzea	<i>R. robustus</i> (II, IV), <i>R. pictipes</i> , <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ?, <i>P. lignarius</i> ?, <i>E. mucronatus</i> ?, <i>C. pilosa</i> ?, <i>M. trinidadensis</i> ?
		Purus várzea	<i>R. robustus</i> (II), <i>R. pictipes</i> , <i>R. brethesi</i> ?, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ?, <i>P. lignarius</i> ?, <i>E. mucronatus</i> ?, <i>C. pilosa</i> ?, <i>M. trinidadensis</i> ?
Várzea	Amazonas	Monte Alegre várzea	<i>R. robustus</i> (II, IV), <i>R. pictipes</i> , <i>R. amazonicus</i> ?, <i>R. paraensis</i> ?, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ?, <i>P. lignarius</i> ?, <i>E. mucronatus</i> ?, <i>C. pilosa</i> ?, <i>M. trinidadensis</i> ?
		Iquitos várzea	<i>R. robustus</i> (II), <i>R. pictipes</i> , <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ?, <i>P. lignarius</i> ?, <i>E. mucronatus</i> ?, <i>C. pilosa</i> ?, <i>M. trinidadensis</i> ?

Biogeographic province <sup>a</sup>	Hydrographic basin(s)	Ecoregion <sup>b</sup>	Species of Triatominae
Tapajós-Xingu	Amazonas	Tapajós/Xingu moist forests	<i>E. mucronatus</i> ?, <i>C. pilosa</i> ?, <i>M. trinidadensis</i> ?, <i>B. peruvianus</i> ? <i>R. robustus</i> (III), <i>R. pictipes</i> , <i>R. brethesi</i> , <i>P. tertius</i> ?, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ?, <i>P. lignarius</i> , <i>E. mucronatus</i> ?, <i>C. pilosa</i> ?, <i>M. trinidadensis</i> ?
Pará	Tocantins-Araguaia/ coastal basins	Xingu/Tocantins-Araguaia moist forests	<i>R. robustus</i> (III), <i>R. pictipes</i> , <i>R. brethesi</i> ?, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> , <i>P. lignarius</i> , <i>E. mucronatus</i> , <i>C. pilosa</i> , <i>M. trinidadensis</i> , <i>Alberprosenia malheiroi</i> ?, <i>B. laportei</i> ?
		Gurupa várzea	<i>R. robustus</i> (IV)?, <i>R. pictipes</i> ?, <i>R. amazonicus</i> ?, <i>R. paraensis</i> ?, <i>P. geniculatus</i> ?, <i>P. rufotuberculatus</i> ?, <i>P. lignarius</i> ?, <i>E. mucronatus</i> ?, <i>C. pilosa</i> ?, <i>M. trinidadensis</i> ?
	coastal basins	Mato Grosso tropical dry forests	<i>R. robustus</i> (III, II)?, <i>R. pictipes</i> ?, <i>R. neglectus</i> ?, <i>P.s tertius</i> , <i>P. geniculatus</i> ?, <i>P. rufotuberculatus</i> ?, <i>P. lignarius</i> ?, <i>C.a pilosa</i> , <i>M. trinidadensis</i>
		Tocantins-Araguaia/Maranhão moist forests	<i>R. robustus</i> (III, IV), <i>R. pictipes</i> , <i>R. milesi</i> , <i>R. neglectus</i> , <i>R. paraensis</i> , <i>P. tertius</i> ?, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ?, <i>P. lignarius</i> , <i>E. mucronatus</i> , <i>C. pilosa</i> ?, <i>A. malheiroi</i> ?, <i>B. laportei</i> ?
Yungas	Pindaré-Paraná	Maranhão Babaçu forests	<i>R. robustus</i> (IV), <i>R. pictipes</i> , <i>R. milesi</i> ?, <i>R. neglectus</i> , <i>R. nasutus</i> , <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ?, <i>P. lignarius</i> , <i>E. mucronatus</i> ?, <i>C. pilosa</i> ?
	Maranhão coastal basins	Northeastern restingas	No data
		Peruvian Yungas	<i>R. robustus</i> (II), <i>R. pictipes</i> , <i>R. ecuadoriensis</i> ?? (primarily trans-Andean), <i>T. carrioni</i> , <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> , <i>P. lignarius herreri</i> , <i>P. chinai</i> ?? (primarily trans- Andean), <i>E. mucronatus</i> ?, <i>E. cuspidatus</i> ?, <i>C. pilosa</i> ?, <i>B. peruvianus</i>
	Amazonas	Bolivian Yungas	<i>R. robustus</i> (II), <i>R. stali</i> , <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ?, <i>P. lignarius</i> ?, <i>E. mucronatus</i> ?, <i>C. pilosa</i> ?, <i>M. trinidadensis</i>
Pantanal	Amazonas-Marañón	Andean Yungas	<i>P. coreodes</i> , <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ?
		Marañón dry forests	<i>R. robustus</i> (II)?, <i>R. ecuadoriensis</i> (primarily trans-Andean), <i>T. carrioni</i> , <i>P. geniculatus</i> ?, <i>P. rufotuberculatus</i> , <i>P. lignarius herreri</i> , <i>P. chinai</i> (primarily trans-Andean), <i>E. mucronatus</i> ?, <i>E. cuspidatus</i> ?, <i>B. peruvianus</i>
	Amazonas	Madeira/Tapajós moist forests	<i>R. robustus</i> (II, III, IV), <i>R. pictipes</i> , <i>R. stali</i> , <i>R. brethesi</i> ?, <i>P. tertius</i> ?, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> , <i>P. lignarius</i> , <i>E. mucronatus</i> , <i>C. pilosa</i> , <i>M. trinidadensis</i> ?
		Purus/Madeira moist forests	<i>R. robustus</i> (II, IV, III)?, <i>R. pictipes</i> , <i>R. stali</i> ?, <i>R. brethesi</i> ?, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ?, <i>P. lignarius</i> , <i>E. mucronatus</i> , <i>C. pilosa</i> , <i>M. trinidadensis</i> ?
Pantanal	Amazonas	Southwestern Amazonian moist forests	<i>R. robustus</i> (II), <i>R. pictipes</i> , <i>R. stali</i> , <i>P. coreodes</i> ?, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> , <i>P. lignarius</i> , <i>E. mucronatus</i> , <i>C. pilosa</i> , <i>M. trinidadensis</i> ?, <i>B. peruvianus</i> ?
		Monte Alegre várzea	<i>R. robustus</i> (II), <i>R. pictipes</i> , <i>R. stali</i> ??, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ?, <i>P. lignarius</i> ?, <i>E. mucronatus</i> ?, <i>C. pilosa</i> ?, <i>M. trinidadensis</i> ?, <i>B. peruvianus</i> ??
	coastal basins	Iquitos várzea	<i>R. robustus</i> (II), <i>R. pictipes</i> , <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ?, <i>P. lignarius</i> ?, <i>E. mucronatus</i> ?, <i>C. pilosa</i> ?, <i>M. trinidadensis</i> ?, <i>B. peruvianus</i> ?
		Mato Grosso tropical dry forests	<i>R.s robustus</i> (III, II)?, <i>R. pictipes</i> ?, <i>R. neglectus</i> ?, <i>P. tertius</i> , <i>P. geniculatus</i> ?, <i>P. rufotuberculatus</i> ?, <i>P. lignarius</i> ?, <i>C. pilosa</i> , <i>M. trinidadensis</i>
Beni savannas		<i>R. robustus</i> (II)?, <i>R. pictipes</i> ?, <i>R. stali</i> , <i>P. tertius</i> ?, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> , <i>E. mucronatus</i> ?, <i>M. trinidadensis</i> ?	

Biogeographic province <sup>a</sup>	Hydrographic basin(s)	Ecoregion <sup>b</sup>	Species of Triatominae
Amazonas/Paraná	Chiquitania dry forests	<i>R. robustus</i> (II?), <i>R. stali</i> , <i>P. coreodes</i> , <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> , <i>E. mucronatus</i> ?, <i>M. trinidadensis</i> ?	
	Paraná/Amazonas	Pantanal	<i>R. robustus</i> (II?), <i>R. stali</i> , <i>P. tertius</i> ?, <i>P. coreodes</i> ?, <i>P. geniculatus</i> , <i>P. rufotuberculatus</i> ?, <i>E. mucronatus</i>
	Paraná/Amazonas/ Araguaia-Tocantins	Cerrado	<i>R. robustus</i> (II, III?)?, <i>R. stali</i> ?, <i>R. neglectus</i> , <i>P. tertius</i> , <i>P. coreodes</i> , <i>P. geniculatus</i> , <i>P.s. rufotuberculatus</i> ?

*a*: after Morrone (2006); *b*: after WWF (2001); ? indicates the species is probably present in the ecoregion; ?? indicates the species is possibly present in the ecoregion; roman numerals refer to *R. robustus* genotypic groups defined after Monteiro et al. (2003); \* indicates the presence of a recently discovered mt *cytb* genotype in this ecoregion (see text). Triatomine records follow Carcavallo et al. (1999) and Galvão et al. (2003).

1999). The ‘pictipes group’ includes species from both the eastern (*pictipes*, *stali*, *brethesi*, *paraensis*, and *amazonicus*) and western (*pallescens*, *colombiensis*, and *ecuadoriensis*) sides of the Andes. The members of the ‘robustus group’ (*robustus*, *prolixus*, *nasutus*, *neglectus*, *milesi*, *dalessandroi*, *domesticus*, and the *Psammolestes*) are all cis-Andean [only *R. neivai*, endemic to the dry forests of the eastern Maracaibo biogeographical province, includes geographically restricted trans-Andean populations]. However, the very presence of two biogeographically well-defined groups of species (cis- and trans-Andean) has also been interpreted as signalling a basal evolutionary split within the tribe. Mitochondrial rDNA sequence analyses failed to provide convincing evidence to uphold any of these two competing hypotheses (Hypša et al. 2001, De Paula et al. 2007), but mt cytochrome *b* gene (*cytb*) genealogies tend to support the existence of two major, monophyletic groups: the ‘pictipes’ and the ‘robustus’ lineages (Abad-Franch & Monteiro 2005 and unpublished data).

Several lines of evidence suggest a palaeo-Amazonian origin of the Rhodniini. First, only three of the known extant species are entirely trans-Andean (see above). Eleven of the 16 cis-Andean species have been recorded in the greater Amazon (including the Orinoco and Tocantins/Araguaia systems); the best studied among these (particularly *R. robustus*) are genetically very diverse entities probably encompassing several, recently diversified cryptic taxa (Monteiro et al. 2003). These data suggest that the core biogeographical region of the tribe would correspond to contemporary Amazonia. The close ecological association between most *Rhodnius* species and palm trees may reflect a long (perhaps up to > 90 million years) process of parallel evolution of both lineages (Gaunt & Miles 2002). Palm trees first evolved in moist tropical forests of the Gondwana floral province during the warm late Cretaceous, and occupied drier life zones secondarily (cf. Cox & Moore 2000). Assuming that the Rhodniini followed their palm ecotopes along this evolutionary pathway, it may be concluded that they also appeared for the first time in humid tropical forests. The exclusively Neotropical range of extant lineages suggests that they probably evolved in the moist Equatorial forests of western Gondwana. The average *cytb* sequence divergences between the more widely distributed representatives of the tribe (*R. pictipes* and *R. robustus*) exceeds 20% (FA-F & FAM, unpublished data), suggesting that their most recent common ancestor lived in the Miocene [10-12 million years ago (Mya); assuming a rate of 2.3% pairwise sequence divergence per million years (Brower 1994)], when flooded moist forests (similar to contemporary *várzea*) prevailed in the Amazon (cf. Hoorn 1994).

The diversification of these palaeo-Amazonian ancestors followed diverse patterns. Mt *cytb* sequence data suggest that *R. pictipes* and *R. pallescens-colombiensis* share a common ancestor that lived in the late Miocene (~ 6 Mya), just before the Andes increased their maximum altitude to over 4000m (Cox & Moore 2000, Abad-Franch et al. 2003). The time since divergence of *R. ecuadoriensis* from its Colombian relatives (*R. pal-*



*lescens* and *R. colombiensis*) (~ 5 Mya) roughly coincides with the uplift of the Andes in the Pliocene. A plausible explanation to the current distribution of the members of the Pacific *Rhodnius* lineage would therefore combine the effects of adaptive radiation and vicariance. An ancestral population perhaps reached the western side of the (then low) Andes range during the late Miocene by migrating from the eastern Orinoco plains; subsequently, the rise of the Andes during the Pliocene split that population into two main clades: the northern (now Colombian) cluster, comprising the ancestral forms of *R. pallescens* and *R. colombiensis*, and an isolated pocket in the south, which adapted to new ecotopes and eventually gave rise to *R. ecuadoriensis* (Abad-Franch et al. 2003).

The bulk of the diversification of the Amazonian *Rhodnius* lineages (the cis-Andean group derived from the ‘pictipes lineage’ and all the known representatives of the ‘robustus lineage’) probably took place in synchrony with the orographic-hydrographic changes and the climatic fluctuations (with profound local and regional ecological impact) that took place in the late Pliocene and the Pleistocene (cf. Rossetti et al. 2005). During interglacial periods for instance, moist forests expanded beyond their current limits, allowing for the colonisation of new regions by representatives of the tribe. Some of them dispersed towards presently arid or semi-arid ecoregions, particularly the Colombian-Venezuelan Llanos to the north and the Brazilian Cerrado and Caatinga to the south. In some cases, these ancestral dispersing populations established ecological associations with dry forest palm species (*Copernicia tectorum*-*R. prolixus*, *C. prunifera*-*R. nasutus*, *Acrocomia* spp.-*R. neglectus*), while in others they reached new territories following *Mauritia flexuosa* gallery forests or adapting to protected microenvironments (*Psammolestes*-bird nests). The genetic consequences of Amazonian moist forest fragmentation during the Pleistocene can be traced in the relationships between *R. robustus* mt *cytb* haplotypes, with at least four moderately distinct variants (~ 2.3-4% sequence divergence) occurring across the greater Amazon (Monteiro et al. 2003, Abad-Franch & Monteiro 2005; see Fig. 2). The phylogeographic hypothesis proposed by Monteiro et al. (2003) to explain the diversification of these Amazonian *R. robustus* clades would receive further support if *R. pictipes* populations (with similar overall geographic distribution) were shown to present comparable patterns of genetic structuring. The question has not been thoroughly examined so far.

*R. domesticus* is probably the living representative of an ancient coastal lineage that remained isolated from its Amazon ancestors when the humid forest corridors linking Amazonia with the Brazilian Atlantic Forest disappeared. A similar process of early isolation might have given rise to *R. neivai* in the northern xeric forests and shrublands of the Maracaibo biogeographical province.

The apparent ecological specialisation of some *Rhodnius* and *Psammolestes* species may have also played a role in the diversification of the tribe. Thus, *R. brethesi* seems to be tightly associated with *Leopoldinia piassaba* palms, and it has been suggested that the distribution of *R. stali* closely matches that of *Attalea*



Fig. 2: approximate province biogeography of *Rhodnius robustus* genotypes [defined after Monteiro et al. (2003) and Pavan & Monteiro (2007)]. A red dot in the central Amazon indicates the collection site of the new *R. robustus* genotype (a member of the *R. robustus* I - *R. prolixus* clade) cited in the text. Biogeographical provinces as in Fig. 1 and Table I.

*phalerata* palms in the southwestern fringe of the Amazon biome (Matías et al. 2003). *R. paraensis* is thought to be associated with an arboreal rodent of the genus *Chrysurus*, and a similar process of host specialisation, in this case involving birds (mainly Furnariidae), may have resulted in the diversification of the *Psammolestes* from an ancestral form belonging to the ‘robustus lineage’.

Some less well-studied triatomine taxa also appear to have evolved in the Amazon moist forests. These include the Cavernicolini, the genus *Eratyrus*, *Microtriatoma trinidadensis*, and perhaps the *Belminus-Parabelminus* lineage. The phylogenetic affinities and evolutionary origins of these groups have not been thoroughly investigated; our statements about them, based on ecological-biogeographic information, are therefore only tentative. The two known *Cavernicola* species live in close association with cave- and hollow tree-dwelling bat colonies (Barrett 1991). *C. pilosa* is a widely distributed species; while records exist from several extra-Amazonian ecoregions, the core of its distribution lies apparently within Amazonia. *C. lenti* has only been reported to occur in a geographically restricted area within the Uatumã-Trombetas moist forests of the Brazilian Amazon. These data suggest an Amazonian origin of the tribe, followed by passive, host-mediated spread

of the *pilosa* lineage. *E. mucronatus* occurs in hollow trees throughout the Amazon-Orinoco basins, whereas cis-Andean *E. cuspidatus* populations seem restricted to Northern Venezuela, also suggesting an Amazonian common ancestor of the genus. The biogeographical pattern of *M. trinidadensis* (which occurs in a ring encompassing the Amazon-Orinoco fringes) could be interpreted as the result of a centrifugal adaptive radiation of populations of Amazonian origin. A prediction of this hypothesis is that the species should be present in central Amazonia, but no records existed from the area (Carcavallo et al. 1999, Galvão et al. 2003) until the recent collection of a male specimen in the Japurá/Solimões-Negro moist forests (Brazilian central Amazon) (FA-F, unpublished). The *Belminus-Parabelminus* lineage has also several representatives in the Amazonas-Orinoco system, but some species are trans-Andean and some (the *Parabelminus*) are endemic to the Brazilian Atlantic Forests; it is therefore difficult to put forward a hypothesis about its origins, and they could well fit also in the second subdivision of our classification.

*Widely distributed lineages* - Several triatomine species reported from the greater Amazon belong to widely distributed lineages whose centre of origin and diversification lies outside the region. They probably occupied Amazonian ecoregions secondarily; while some were awarded formal specific status, others are simply considered geographical populations of their parental species. Representatives of this second major class all belong to the genus *Panstrongylus*, but the *Belminus-Parabelminus* lineage could have followed similar evolutionary pathways.

Amazonian *Panstrongylus* populations belong to three species (*P. geniculatus*, *P. lignarius-herrerii*, and *P. rufotuberculatus*) that seem to be related to the Mesoamerican Triatomini lineage (Marcilla et al. 2002). The ancestors of this lineage evolved several million years before the complete closure of the Panama Isthmus, ~ 3 Mya (Bargues et al. 2000, Cox & Moore 2000), suggesting a secondary occupation of South America by their descendants. *P. geniculatus* is a widely distributed and phenotypically diverse triatomine species. It survives in arid life zones by exploiting highly protected, humid underground microhabitats (particularly armadillo burrows). This strategy probably helped it disperse towards the Amazon across the dry regions of northern South America. Once in the moist Amazon forests, *P. geniculatus* colonised less protected environments such as hollow trees, dead logs, palm tree crowns, and, sporadically, peridomestic pigsties. *P. lignarius* belongs to a small monophyletic group of arboricolous species that occupy moist tropical forests in Central America (*P. humeralis*) and the Amazon (*P. lignarius*). A synanthropic population (*P. herrerii*, recently synonymised with *lignarius*) lives in the dry forests of the Marañón valley in Northeastern Peru. It probably represents a parapatric derivative of lowland Amazonian populations known as *P. lignarius*. Sporadic records suggest that *P. rufotuberculatus* is also present throughout the greater Amazon. Its extensive geographic range, its phylogenetic

affinities with Mesoamerican Triatomini, and its ecological plasticity all suggest a secondary spread of this species across Amazonian ecoregions.

*Relict species: the strange case of T. maculata* - *T. maculata* is the only representative of the genus *Triatoma* with abundant native populations within the greater Amazon. It is probably also the only representative of the biogeographically South American *Triatoma* lineage that occurs north of the parallel 10°S. Its presumed sister species (*T. pseudomaculata*) and its closest relatives (*T. wygodzinskyi* and *T. arthurneivai*) occur in the Caatinga and the Cerrado. The vicariant distribution of these species in dry ecoregions north and south of the moist Amazon forests was interpreted as the result of passive dispersal of nymphs by migratory birds. This hypothesis seems to have been refuted by recent allozyme data showing large genetic distances separating *T. maculata* from *T. pseudomaculata* (as opposed to the very small differences detected between the latter and *T. wygodzinskyi*; dos Santos et al. 2007). These results are compatible with a complex phylogeographic scenario in which an ancestral *Triatoma* population occupied dry corridors linking the arid Brazilian Northeast region with the savannahs of the Orinoco system. The ancestors of extant *T. maculata* populations became isolated from their southern relatives when the moist tropical forest matrix closed those dry corridors, setting out the process of independent evolution we can now trace with genetic markers. The diversification of the southern lineage is reflected in the several species that have been formally described, while the northern clade is still considered monospecific (comprising only *T. maculata*). A thorough assessment of the genetic and phenotypic variability within *T. maculata* may therefore be predicted to reveal much more diversity than would be expected among populations of a recently dispersed species. In summary, contemporary *T. maculata* populations probably represent an old relict from the times when tropical dry forest corridors traversed Amazonia from north to south.

*In the fringes of the Amazon* - A few populations of primarily Andean triatomine species have been recorded in montane foothill forests that belong to the greater Amazon biome. This is the case of *T. carrioni* in Ecuador (where *T. venosa* also occurs) and Northern Peru (Abad-Franch et al. 2001, Cuba Cuba et al. 2002). *T. nigromaculata* also belongs to the *carrioni-venosa-dispar* lineage, and is therefore probably of Andean origin. Its range includes a large portion of the Venezuelan Orinoco and coastal basins and the Guyanan highlands, where it preferentially occurs in dry ecoregions. *P. chinai* and *R. ecuadoriensis*, both primarily trans-Andean, occur in the upper (Andean) stretches of some Peruvian valleys that drain into the Amazon. *R. colombiensis*, occasionally included in checklists of Amazonian triatomines, is endemic to the Magdalena Valley dry forests, and therefore exclusively trans-Andean. Records of *T. sordida* and *T. infestans* in the Bolivian Amazon may be the result of mislabelling or may represent passively dispersed individuals carried beyond their natural biogeographic range. All the species in this class, per-

haps with the exception of *T. nigromaculata*, seem however to have limited tolerance to the general ecological conditions of the core Amazon region, and may therefore be predicted to remain confined to relatively small, peripheral areas.

*Artificial introductions* - *T. rubrofasciata* is a tropicopolitan species that occupies artificial environments in harbour cities, generally in association with rats. Its presence in Belém or São Luís, the main sea harbours of the Brazilian Amazon region, is therefore hardly surprising. The most likely explanation, given the phylogenetic affinities, geographical range, and habits of this species, is that Amazonian populations were introduced by sea trade into the region. Domestic populations of other, more dangerous species are also candidates to artificial introduction.

Particularly worrying is the case of *R. prolixus*, now the main vector of human Chagas disease, which is native to the drier forests of the Orinoco basin system (mainly the Llanos) but may also colonise humid environments. There are sparse records of this species in several Amazonian localities (in Brazil, the Guyanas, and Colombia), and the southern limits of sylvatic *R. prolixus* populations have not been defined so far. Their capacity to adapt to palm tree genera with wide distribution throughout Amazonia (such as *Attalea*) is well documented, and may signal a potential for southward dispersal. In the Venezuelan-Colombian Llanos, sylvatic *R. prolixus* from *Attalea* palms contribute to the infestation and reinfestation of houses and peridomestic structures. Finally, preliminary mt *cytb* data have revealed the existence of a third cryptic taxon within the monophyletic group composed of *R. prolixus* and *R. robustus* I (*sensu* Monteiro et al. 2003). It occurs in *Attalea* palms of the central Brazilian Amazon (FAM & FA-F, unpublished data). The presence of these genotypes in Amazonian moist forests configures a potentially dangerous situation that should be carefully monitored. Introduced *T. infestans* populations reached the southeastern limits of the Brazilian Amazon, but were subsequently eliminated. In northeastern Bolivia, some of the regions where sylvatic populations are common include inter-Andean valleys that drain into the Amazon. Both empirical field data and eco-geographical models (Gorla 2002) suggest however that *T. infestans* has a limited ability to thrive in the warm and humid climate conditions of most Amazonian forest regions. *T. dimidiata* natural populations are on the contrary present in many, extremely diverse ecoregions (from the Yucatán Peninsula to Ecuador), including both dry and moist forest environments, and could perhaps colonise artificial structures in the Amazon.

#### THE ECOLOGICAL AND EVOLUTIONARY CONTEXT OF SYNANTHROPIC TRENDS IN AMAZONIAN TRIATOMINES

Amazonian triatomines are essentially sylvatic. Epidemiological and entomological data suggest however that sporadic contact between *Trypanosoma cruzi*-infected vectors and humans, even if relatively infrequent, occurs throughout the region. Most cases of *T. cruzi* transmission to humans are mediated by adult triatomines

that invade houses, attack forest workers or contaminate food-processing equipment (see Aguilar et al. 2007, this volume). On the other hand, several native triatomine species colonise artificial environments in well-defined micro-regions. These different degrees of synanthropism may be interpreted as a behavioural gradient starting with the mere invasion of a house by an adult adventitious bug and eventually leading to the stable infestation of human dwellings by large breeding vector colonies. Understanding the relative roles of ecological and evolutionary factors in the shaping of this gradient may substantially improve our ability to predict which species are likely to progress along the gradient, and may also help identify weak (and strong) links that could (or could not) be used as the targets of disease prevention strategies. We now present a tentative partition of such ecological and evolutionary components based on our overview of the historical biogeography of Amazonian triatomines.

*Ecological factors* - Random events and ecological pressure linked to anthropic landscape transformation are probably key factors in the initial portion of the behavioural gradient leading to synanthropism. The dynamics of land occupation in the Amazon moist forest ecoregions illustrate particularly well this process. Initially, forest clearance leads to a reduction of wild vertebrate populations; a pattern of selective deforestation in which palm trees are kept in peridomestic environments is commonplace. Palm triatomine populations (mainly *Rhodnius* species) are probably subject to high mortality during this phase, but do not disappear completely. The palms become suitable shelters for opportunistic marsupials and rodents (*Didelphis marsupialis*, *Rattus* spp.) that proliferate in human-modified environments. Residual triatomine populations may take advantage of this situation, using these (now abundant) blood sources to recover and eventually build-up large colonies in some palms (Abad-Franch et al. 2005). When the system nears its carrying capacity, a reduced availability of blood per individual results in adult starved triatomines frequently flying into nearby houses. Humans, palms, adventitious triatomines and opportunistic mammals (often infected by *T. cruzi*) closely coexist in anthropic landscapes throughout the Amazon, increasing disease transmission risk (Aguilar et al. 2007, this volume).

However, it is evident that only a small fraction of the triatomines that reach human dwellings founds viable domestic breeding colonies. Most die off; a few may perhaps lay eggs, but their offspring only reach the reproductive stage on very rare occasions. It is conceivable that the (relatively few) triatomine populations with the capacity of thriving in artificial microenvironments may have acquired (through natural selection) some characteristics that distinguish them from others of the same lineage that cannot establish domestic colonies.

*Evolutionary factors* - Natural selection of any trait that could favour *specifically* the adaptation of a triatomine population to *artificial* ecotopes (built by humans) can only have operated during the last 10 to 12 thousand years, which is the approximate age of the first

known human settlements in the Americas. Such an event seems extremely unlikely in the absence of a very strong and persistent directional selective pressure. We may envisage, however, that a set of traits exists that, having been selected over millions of years for other reasons, confers the ability to exploit domestic habitats to the populations that possess it. Populations of the same lineage lacking those traits would fail to permanently infest households. In such a case, we would expect that only a few populations among all the possible candidates within a given lineage (those that possess the set of traits in question) be able to successfully colonise artificial environments. The biogeographical-evolutionary scenario we have proposed here for the *Rhodnius* suggests that, at least for several lineages within the tribe, natural selection of variants adapted to relatively dry microclimates may be related with the progressing of some species (and not others) along the gradient of synanthropic behaviour.

Thus, all the populations of *Rhodnius* spp. that succeed in colonising artificial environments (mainly of *R. prolixus*, but also of *R. neglectus*, *R. nasutus*, *R. stali*, *R. pallescens*, and *R. ecuadoriensis*) derive from ancestral populations that adapted to arid or semi-arid climates long before human beings reached the Americas. Also within the Amazon, domestication foci (particularly of *R. stali*, but also of *T. maculata* or *P. herreri*) are located in the regions with lowest mean annual rainfall or longest rain-free periods (cf. Sombroek 2001). This pattern may in fact be even more general, affecting other humid forest triatomines; for instance, *T. dimidiata* populations seem to colonise human dwellings only out of the moist forests of the Yucatán-Petén region (Dorn et al. 2007). These observations suggest that species or populations of triatomines that evolved to breed in extremely humid microenvironments (such as Amazonian rainforest palm tree crowns) may have only a limited potential to successfully colonise artificial environments, perhaps as a consequence of low tolerance towards the slightly drier microclimate of human dwellings. A prediction of this hypothesis is that field-collected specimens from moist forest ecotopes would fail to thrive towards the drier end of an artificial humidity gradient in the laboratory. If confirmed, this pattern would signal a truly evolutionary component of the process of infestation and colonisation of human environments by triatomines. It could help us to identify differential risk areas by mapping widely available climate data, and perhaps, in the future, to determine the potential for domiciliation of vector species or populations on an individual basis.

## CONCLUSIONS

The systematic, ecological, and behavioural patterns of any group of organisms are gradually whittled along the evolutionary history of the lineage, from the more or less ancient event at the origin of the clade to the contemporary phenomena that shape the genetic structuring of conspecific populations. One major consequence, as Dobzhansky (1973) observed, is that adopting an evolutionary perspective greatly widens our understanding of those patterns, opening new paths in the search for satisfactory (realistic) answers to old diffi-

cult questions – from infectious disease control and surveillance to the mechanisms involved in the generation, maintenance and loss of biological diversity.

Equipped with ever more sophisticated analytical tools (morphometrics, molecular markers, environmental data obtained by remote sensors onboard artificial satellites, radiocarbon dating) we can face the challenge of adopting this evolutionary stance in our research on Chagas disease vectors, particularly when the questions refer to clearly monophyletic clades. Our review (provisional and incomplete) of the origin and diversification of Amazonian triatomines suggests research avenues that unfold in many directions, from the adequate understanding of the evolution of whole tribes over millions of years to the (probably necessary, and so far widely neglected) demarcation of the truly evolutionary and ‘merely’ ecological processes involved in the synanthropic behavioural gradient of the Triatominae.

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