Speciation Processes in Triatominae

Marcio G. Pavan, Cristiano Lazoski, and Fernando A. Monteiro

Abstract This chapter intends to familiarize the reader with the basic concepts regarding speciation in insects, through the description and exemplification of the three most common speciation modes described in the specialized literature on the subject: the allopatric, parapatric, and sympatric speciation modes.

We also argue that nowadays there is, perhaps, an excess of species concepts to choose from. Two of those have been used more often by the Triatominae research community: the biological species concept and the phylogenetic species concept. The idea first advanced by De Queiroz (Syst Biol 56(6):879–886, 2007) that the proposition of a single species concept that would unify all concepts available is not only desirable but also essential at this point. The issue of overconservative systematics is considered with emphasis on the paraphyly of *Triatoma.* The implications of phenotypic plasticity in traditional triatomine taxonomy are also addressed.

How long does it take for a new species of triatomine to be formed? Early proposals envisioned very short time intervals say, a few hundred years, for the process to be completed. Two well-studied examples are presented.

How do triatomines speciate? Vicariance and allopatric speciation seem to be the norm in Triatominae speciation. Three examples are discussed. Nonetheless, sympatric speciation has also been evoked to account for the generation of particular species within cryptic species complexes. Two examples are given.

Finally, a discussion toward the benefits of relying on integrative and evolutionarily sound taxonomy approaches is offered.

M. G. Pavan
Laboratório de Mosquitos Transmissores de Hematozoários, Instituto Oswaldo Cruz, Fiocruz, Rio de Janeiro, Brazil

C. Lazoski
Laboratório de Biodiversidade Genômica, Departamento de Genética, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil
e-mail: lazoski@acd.ufrj.br

F. A. Monteiro (✉)
Laboratório de Epidemiologia e Sistemática Molecular, Instituto Oswaldo Cruz, Fiocruz, Rio de Janeiro, Brazil
e-mail: fam@ioc.fiocruz.br

A. Guarneri, M. Lorenzo (eds.), *Triatominae - The Biology of Chagas Disease Vectors*, Entomology in Focus 5, https://doi.org/10.1007/978-3-030-64548-9_3

Keywords Speciation · Sympatry · Allopatry · Species concepts · Systematics · Phenotypic plasticity

1 Toward a Unified Species Concept

The diversity of life is measured essentially in terms of number of species, even though there is an ongoing debate focusing on what a species is and how organisms speciate. The last three decades have seen prominent challenges to the current views of species concepts and species delimitation due to the advances in molecular biology and genetics (Mallet 1995). The definition of a species will depend on which species concept you choose among the 27 available definitions (Mayden 1997; Wilkins 2011). By far, the most used and widespread definition is the biological species concept (BSC), which considers species as groups of interbreeding individuals, with boundaries defined by intrinsic barriers to gene flow that have a genetic basis (Mayr 1963). The main limitation of the BSC is that populations of the same species found at a distance from each other (allopatric populations) that could not be suitably treated, because they are not in contact to randomly mate. Not even the successful crossing of allopatric populations under laboratory conditions will prove conspecificity since all ecological/geographical barriers are being removed (Claridge et al. 1985; Mallet 1995). Moreover, different cases of bona fide species hybridizing at secondary contact zones [i.e., lineages that occur at least partially in a same geographical area (sympatry) after the speciation process] are well-known. For example, although the malaria vectors *Anopheles gambiae*, *A. coluzzii*, and *A. fontenillei* (Diptera: Culicidae) are valid species, introgressed genomic regions are found that encompass genes associated with detoxification, desiccation tolerance, and olfactory perception, which are the characteristics that can alter their ability as malaria vectors (Barron et al. 2018).

Beyond the practical use of the BSC, the debate over what a species is and how it should be defined has been a matter of a long theoretical dispute among biologists. Personal expertise with respect to a particular research model or taxonomic group of interest has contributed to a “divergent radiation” in the proposal of species concepts. It is now clear that this “species definition competition” has generated more heat than knowledge. Recent countercurrent attempts have been made toward the proposal of a “unified species concept” (Table 1). Most species concepts agree in treating *existence as separately evolving metapopulation lineage* (i.e., “an inclusive population made up of connected subpopulations extended through time”) as the primary defining property of the species category, but they disagree in adopting different properties acquired by lineages during the course of divergence (e.g., intrinsic reproductive isolation, diagnosability, and monophyly) as secondary defining properties (secondary species criteria). In other words, lineages do not have to be morphologically distinguishable, diagnosable, monophyletic, intrinsically reproductively isolated, ecologically divergent, or anything else to be considered species, but only

Table 1 Often-used contemporary species concepts and the properties upon which they are based (modified from de Queiroz 2007). de Queiroz's (2007) proposal is an attempt toward the unification of all species concepts presented here. Properties marked with an asterisk should be viewed as operational criteria (lines of evidence) relevant to assessing lineage separation of a single general concept that defines species as separately evolving metapopulation lineages

Species concept	Property(ies)	Advocates/References
Biological	Interbreeding (natural reproduction resulting in viable and fertile offspring)	Mayr (1942) and Dobzhansky (1950)
(reproductive) isolation	*Intrinsic reproductive isolation (absence of interbreeding between heterospecific organisms based on intrinsic properties, as opposed to extrinsic [geographic] barriers)	Mayr (1942) and Dobzhansky (1970)
Recognition	Shared specific mate recognition or fertilization system (mechanisms by which conspecific organisms, or their gametes, recognize one another for mating and fertilization)	Paterson (1985) and Masters et al. (1987)
Ecological	*Same niche or adaptive zone (all components of the environment with which conspecific organisms interact)	Van Valen (1976) and Andersson (1990)
Evolutionary	Unique evolutionary role, tendencies, and historical fate	Simpson (1951), Wiley (1978) and Mayden (1997)
Cohesion	Phenotypic cohesion (genetic or demographic exchangeability)	Grismer (1999, 2001), Templeton (1989, 1998)
Phylogenetic	Heterogeneous (see next three entries)	See next three entries
Hennigian	Ancestor becomes extinct when lineage splits	Hennig (1966), Ridley (1989) and Meier and Willmann (2000)
Monophyletic	*Monophyly (consisting of an ancestor and all of its descendants; commonly inferred from possession of shared derived character states)	Rosen (1979), Donoghue (1985) and Mishler (1985)
Diagnosable	*Diagnosability (qualitative, fixed difference)	Nelson and Platnick (1981), Cracraft (1983) and Nixon and Wheeler (1990)

to be evolving separately from other lineages (for more information, see de Queiroz 2007). It is time to put aside disagreements about species definition and focus on empirical data that can be used as evidence of lineage separation and species boundaries. Taxonomists have to agree that the definition of robust species concepts depends upon several lines of evidence, including morphological traits and ecological and molecular data.

2 Insect Diversity and Speciation

Insects are one of the most diverse group of multicellular organisms, being represented by at least 10–30 million species (Erwin 1982), which accounts for 60–65% of all living eukaryotic biodiversity (Hammond 1992). The high diversity of insect taxa is partially explained by their compact size, which allows for the occupation of small and different portions of habitats and the specialization on the use of resources that larger animals are unable to exploit (Bush and Butlin 2004). Insects are often used as model organisms in evolution research due to their relatively short generation time and the practical advantages of laboratory rearing, enabling to test speciation hypotheses with proper sample sizes (Mullen and Shaw 2014).

Speciation is a subject that has intrigued investigators for centuries. The term was coined by the American biologist Orator F. Cook in 1906, as the process by which new species arise from existing ones (Cook 1906). However, knowledge advancement on this issue has been hampered by two main limiting factors: (1) the impossibility of witnessing the phenomenon unravels in real-time (with the exception of fast-evolving viruses; Meyer et al. 2016) and (2) the difficulty in reaching a consensus regarding the understanding of what a species is and how it should be delimited.

Although alternative methods to categorize the speciation process have been proposed (cf. Butlin et al. 2008), the most used concepts rely on the geographical context of speciation, which can be assigned to three broad categories: allopatric, parapatric, and sympatric speciation methods.

Allopatric speciation occurs when an ancestral population is divided into at least two daughter populations geographically isolated; in this context, gene flow between populations is absent or, if present, largely irrelevant. Thus, these populations accumulate mutations independently, develop some degree of genetic divergence, and might become genetically isolated. A complete allopatric speciation can occur if populations of incipient species develop pre- or postzygotic barriers for reproduction. In the case of a possible secondary contact zone, selection against hybrids (reinforcement) can occur and bimodal populations (admixed local populations with a deficit of hybrid genotypes) are observed. If sexual barriers are not complete and a secondary contact zone exists between species, hybridization events occur and thus the allopatric speciation is considered incomplete, with unimodal populations (intermediate hybrid genotypes predominating).

The grasshoppers *Chorthippus brunneus* and *C. jacobsi* (Orthoptera: Acrididae) are found in Spain at a narrow band along the north coast and south of the Cantabrian Mountain, respectively. These species possibly speciated in allopatry, but have been in contact since the Pleistocenic post-glacial range expansion (Bridle et al. 2002). They can be distinguished by the number of stridulatory pegs (although there is a small degree of overlap) and different male-calling songs (Bailey et al. 2004). In the contact zone, populations with bimodal distribution are observed, with strong assortative mating, based on spatial (probably associated with habitat specialization), seasonal, and behavioral isolation (Bailey et al. 2004). Other examples on insects illustrate hybrid zones with binomial distribution, such as observed in *Heliconius* butterflies (Lepidoptera: Nymphalidae), and ground crickets of the *Allonemobius* (Orthoptera: Gryllidae), which show strong prezygotic isolation due to assortative mating and homogamic fertilization (gamete recognition evolves faster than mate recognition), respectively (Howard et al. 1998). On the other hand, populations with unimodal distributions were observed in pine and larch budmoth host races of *Zeiraphera diniana* (Lepidoptera: Tortricidae), defined by Bush and Diehl (1982) as "populations of a species that are partially reproductively isolated from other conspecific populations as a direct consequence of adaptation to a specific host." Behavioral and molecular studies indicate that the probability of hybridization between sympatric host races is around 2–3.5% (Emelianov et al. 2003, 2004). When in sympatry, a strong genomic heterogeneity between host races in areas where hybridization occurs was observed, but no genomic heterogeneity in divergent geographical populations of the same host race. These results suggested that the divergence with gene flow is driven by selection in sympatric regions and also that low hybridization rates are sufficient to homogenize much of the genetic variation in neutral genomic regions in terms of host adaptation.

Parapatric and sympatric modes of speciation are much more controversial among molecular biologists, since considerable interspecific gene flow hampers population divergence (cf. Jiggins 2006). Because there are no clear geographical barriers, levels of assortative mating, habitat preferences, local adaptation, and hybrid fitness reduction must overcome genetic homogenization mechanisms in order to achieve speciation. Simulation models and theoretical studies proposed that high population divergence indeed requires little or no gene flow (Orr 1995; Tang and Presgraves 2009; Nosil and Flaxman 2010). In a low gene flow scenario, it is possible for populations to diverge through the fixation of adaptive mutations via positive selection (Barrett et al. 2008; Nosil and Flaxman 2010), or simply through genetic drift in small populations. In those cases, natural selection can overcome genome homogenization (through gene flow and recombination) by maintaining isolated gene pools without the intervention of geographic barriers (Turelli et al. 2001).

Parapatric speciation can be explained as an ancestral population that becomes two daughter species occupying contiguous ranges (while sympatric speciation occurs when the geographical ranges of the daughter species overlap). In both cases, speciation seems to be shaped by disruptive selection, as a consequence of favoring the evolution of specialist over generalist species through niche-partitioning or microhabitat preference. The stick insects *Timema cristinae* (Phasmatodea: Timematidae) is a great example of parapatric speciation on its course. This species inhabits southwestern North America, feeding and mating on two different host plant species that differ in foliage and general morphology. Host-specific populations have differences in morphology and can live in parapatry (Nosil 2007). Surprisingly, significantly stronger sexual isolation mechanisms seem to occur in parapatry, which means that there is a sign of ecological reinforcement (Nosil 2007). Next-generation sequencing (NGS) analysis based on thousands of Single-nucleotide polymorphism (SNPs) revealed that host adaptation leaves subtle differentiation patterns across the genome. Moreover, divergent selection on traits not related to host use (i.e., genes not related to reproductive isolation) seems to be more relevant for generating genomic divergence between the populations. Under greater geographical separation, gradual reductions in gene flow facilitate speciation (Nosil et al. 2012).

Probably the most recognized example of sympatric speciation was observed in the apple maggot, the tephritid fruit flies sibling species complex *Rhagoletis pomonella* (Diptera: Tephritidae). Many researchers believed that the colonization of a new host in a sympatric environment and the further host preferences had started the reproductive isolation between host races based on different diapause and eclosion periods (Bush 1969; Filchak et al. 2000; Dambroski et al. 2005). From DNA sequence data of three nuclear loci and mtDNA, Feder et al. (2003) concluded that the host races became geographically isolated ~1.5 million years ago (Ma), and rare episodes of gene flow with inversion polymorphisms (restricting recombination) might have affected key diapause traits and formed adaptive clines. Therefore, these populations must have experienced a past allopatry in order to accumulate molecular changes (Xie et al. 2007) before became sympatric species. Nowadays, it is known that the barrier for gene flow remains incomplete (4–6% gene flow/generation), but most genome regions show significant geographic and host-associated variation that can account for by initial diapause intensity and eclosion time, which cause a temporal isolation between populations (Doellman et al. 2019). It is worth mentioning that sympatric populations of different host races are genetically more divergent in comparison to geographic populations within the races, which suggest that host races are being recognized as different genotypic entities in this region (Doellman et al. 2019).

The advances of molecular biology and mathematical models unveil that the geographical contextualized categories of speciation (allopatric, parapatric, and sympatric) are actually interconnected and depend on the time-frame in which they have been analyzed. As stated by Butlin et al. (2008), "At each stage of speciation, there is a spatial context on the sympatry to allopatry continuum which determines the extent of the extrinsic isolation between diverging populations." Geographical isolation reduces homogenizing gene flow and facilitates speciation events, but the evolutionary forces that shape variability are also tightly linked to the ecological factors and the mating interactions in speciation events (Fitzpatrick et al. 2009; Nosil et al. 2009).

3 Overconservative Systematics and the Paraphyly of *Triatoma*

The subfamily Triatominae is composed exclusively by hematophagous insects and seems to have evolved from predaceous Reduviidae bugs ~40 Ma (Hwang and Weirauch 2012; Ibarra-Cerdeña et al. 2014; Justi et al. 2016), which coincides with the invasion and diversification of caviomorph rodents and small marsupials (Flynn and Wyss 1998; Poux et al. 2006; Antoine et al. 2012), and birds (Burns 1997) in South America.

This subfamily includes 150 extant and two extinct recognized species, which are classified in 16 genera and five tribes (Monteiro et al. 2018). These species occur mainly in the Americas including the Caribbean, but can also be found in southeast Australasia (Lent and Wygodzinsky 1979).

Triatoma is the most species-rich genus in the subfamily Triatominae and includes 73 species within the tribe Triatomini (Galvão and Paula 2014). Most of this diversification could be associated with cladogenetic events caused by climatic and geological changes occurred during the formation of the Americas (Hwang and Weirauch 2012; Justi et al. 2016; Monteiro et al. 2018) and can be well explained by vicariance.

Species of *Triatoma* have been clustered by several authors in different groups and complexes based on their external morphology and geographical distributions (Usinger 1944; Ryckman 1962; Usinger et al. 1966; Lent and Wygodzinsky 1979; Carcavallo et al. 2000). Since the beginning of the use of molecular markers to test evolutionary hypotheses in Triatominae, some authors have proposed rearrangements for this original classification (Schofield and Galvão 2009; de la Rúa et al. 2014; Pita et al. 2016). Some of these studies also included morphometry (de la Rúa et al. 2014) and chromosomal analysis by Fluorescence in situ hybridization (FISH) (Pita et al. 2016).

Based on new cytogenetic and morphometric data and phylogenetic results of the very important work by Hypša et al. (2002) (see below), Schofield and Galvão (2009) proposed the currently most accepted Triatomini assemblage, which subdivides species in three groups, eight complexes, and eight subcomplexes.

Historically, the use of molecular markers to study the phylogeny of *Triatoma* (Table 2) started with one or few mitochondrial genes and few representatives of these species groups and complexes (Lyman et al. 1999; García et al. 2001; Monteiro et al. 2001), advancing over time to analyze with more markers, including nuclear markers (Marcilla et al. 2001, 2002), and a growing addition of more Triatomini species (Hypša et al. 2002; de Paula et al. 2005; Hwang and Weirauch 2012; de la Rúa et al. 2014; Ibarra-Cerdeña et al. 2014; Justi et al. 2014, 2016; Pita et al. 2016). Those first studies with limited species representing the groups and complexes (Lyman et al. 1999; García et al. 2001; Monteiro et al. 2001); however, either showed weak support for the original classification based on morphological characters (Lent and Wygodzinsky 1979; Carcavallo et al. 2000) or were inconclusive (Table 2).

It was only with the analysis of a larger and taxonomically more comprehensive set of triatomine specimens that it became clearly demonstrated that the proposed species groups and complexes did not comprise reciprocally monophyletic assemblages (Hypša et al. 2002). Phylogenetic analyses based on 12S and 16S mtDNA sequencing rejected the monophyly of Triatomini rearrangements and indicated the paraphyly of *Triatoma* with respect to *Linshcosteus*, *Dipetalogaster*, *Eratyrus*, and *Panstrongylus* (Hypša et al. 2002). Table 2 shows that the number of species used in phylogenetic studies (more than the chosen markers) was decisive to establish that

Table 2 Molecular studies presenting results that can be used to reject or not the arrangements of "species groups and complexes" in Triatomini tribe. Studies were based on different markers and are showed in a progressive order of number of species (*N*) representing those Triatomini groupings plus markers (with a few exceptions)

Species groups and complexes[a]	*N*	Molecular marker	Reference
Inconclusive or weak support	9	16S, cytb	Lyman et al. (1999)
	9	16S, cytb	Monteiro et al. (2001)
	17	12S, 16S	García et al. (2001)
	12	ITS-2	Marcilla et al. (2001)
	15	ITS-2	Marcilla et al. (2002)
	10	16S, 18S, 28S, wingless	Hwang and Weirauch (2012)
Rejection[b]	43	16S	Hypša et al. (2002)
	43	16S	de Paula et al. (2005)
	18	ITS-2	de la Rúa et al. (2014)
	40	12S, 16S, COI, cytb, 18S, 28S	Ibarra-Cerdeña et al. (2014)
	27	COI, COII, cytb, 18S, 28S	Justi et al. (2014)
	52	16S	Justi et al. (2014)
	21	FISH	Pita et al. (2016)
	56	16S, 18S, 28S, wingless	Justi et al. (2016)

[a] Species groups and complexes within the genus *Triatoma* in accordance with Lent and Wygodzinsky (1979), and Schofield and Galvão (2009)

[b] Occasional support for some groups does not validate the overall arrangement

the morphological classification of groups and complexes of Triatomini was not correct ("weak support/inconclusive": 9–17 species; "rejection": 18–56 species; Table 2). In fact, it is known that the addition of molecular markers and taxa in phylogenetic analyzes should increase its accuracy (Wiens and Tiu 2012).

What followed after the important work of Hypša et al. (2002) were phylogenetic studies continuing to demonstrate the fragility of the initial morphological grouping hypotheses, but with discussions still considering at least their partial validity (de Paula et al. 2005; Hwang and Weirauch 2012; de la Rúa et al. 2014; Ibarra-Cerdeña et al. 2014; Justi et al. 2014). Further research aimed at revealing new lines of evidence to help understand relationships within Triatomini.

The addition of biogeography analyzes brought a new light to an already promising integrative taxonomic scenario (Justi et al. 2016; Monteiro et al. 2018). In a recent review, Monteiro et al. (2018) presented a new taxonomic arrangement hypothesis to represent the relationships between species groups and complexes of *Triatoma*. The hypothesis aimed to incorporate current evolutionary theories into the traditional classification scheme based on morphology (e.g., Schofield and Galvão 2009), by including new molecular, cytogenetic, morphometric, and biogeographical data published ever since (Monteiro et al. 2018).

In addition to the presentation of a rigorous and updated classification based on literature data, the authors proposed a new nomenclature consistent with the evolutionary scenario that relied on two main observations: (1) studies that reinforced the paraphyly of *Triatoma* also clearly supported the existence of three lineages in Triatomini (Justi et al. 2014, 2016; Monteiro et al. 2018) and (2) the meaning of the term "species complex" in triatomine systematic studies varies depending on the context from "subgeneric assemblages defined by morphological similarity" (e.g., Lent and Wygodzinsky 1979; Schofield and Galvão 2009) to "cryptic species" (i.e., morphologically indistinguishable species; e.g., Monteiro et al. 2003).

Therefore, Monteiro et al. (2018) proposed an arrangement for the Triatomini that followed an hierarchy of: (1) three major evolutionary "lineages" composed by *Triatoma dispar*, "North American," and South American; (2) 11 "clades" within lineages defined by common ancestry and broad biogeographic correspondences; and (3) 19 "species groups" within clades, with some of these groups matching "species complexes" defined as closely related, morphologically similar or even indistinguishable species usually disclosed as a result of molecular investigations (Table 3 and Fig. 3 of Monteiro et al. 2018). The meaning of the term "species complex" in triatomine systematic studies varies depending on the context from "subgeneric assemblages defined by morphological similarity" (e.g., Lent and Wygodzinsky 1979; Schofield and Galvão 2009) to "cryptic species" (i.e., morphologically indistinguishable species; e.g., Monteiro et al. 2003).

Of the three lineages designation proposed by Monteiro et al. (2018), the "North American" lineage has the greatest morphological diversity and comprises most nominal genera (nine). In comparison, the South American lineage has only two genera: *Triatoma* and *Eratyrus*. The high morphological plasticity of Triatominae (Dujardin et al. 1999, 2009) can lead to misidentification and taxonomic uncertainties (Pita et al. 2016). However, most of the diversification seen in the "North American" lineage seems consistent with phylogenetic evidences (Galvão et al. 2003).

Although there are still many issues within Triatomini to be clarified, the accumulation of data in the literature has already shown that *Triatoma* is not monophyletic. Is it time to discuss the suitability of a taxonomic revision? Should the "North American" lineage retain the generic epithet "*Triatoma*" as it includes the type species of the genus, *Triatoma rubrofasciata*?

4 Phenotypic Plasticity and Classical Taxonomy

Phenotypic variability affects traits often used in classical taxonomy including color patterns (Abad-Franch et al. 2009; Pavan et al. 2015) or the size and shape of bodies, heads, wings (Schachter-Broide et al. 2004; Hernández et al. 2011; Nattero et al. 2013; Sandoval et al. 2015), and genital structures (Schofield and Galvão 2009). Chromatic variations of single or near-sibling species can result from adaptive plasticity, which may confound taxonomic classification. Indeed, the discovery of cryptic lineages with different vector capacity(ies) and also chromatic variants of single species from different micro-environments were some of the greatest achievements on the taxonomy of triatomines in the early 2000s.

Rhodnius neglectus is the most abundant *Rhodnius* species in the Cerrado biome. It inhabits various palm tree species, including those of the genera *Attalea*, *Acrocomia*, *Mauritia*, *Oenocarpus*, and *Syagrus* (Gurgel-Gonçalves et al. 2004; Abad-Franch et al. 2009). This species can be misidentified as *R. nasutus*, particularly in the nearby Caatinga biome and in Caatinga-Cerrado transitional areas (Dias et al. 2008; Lima and Sarquis 2008). *Rhinacanthus nasutus* is found predominantly in the Caatinga inhabiting *Copernicia prunifera* palms (Sarquis et al. 2004), but may also be found in other palms and trees in this region (Dias et al. 2008; Lima et al. 2012). The high similarity between those two vector species and the lack of reliable diagnostic characters leads naturally to an uncertainty regarding proper taxonomic identification and determination of their geographical boundaries.

The identification of these species is based on morphological characters as chromatic patterns of body and antennae, overall body size, and male genitalia (Lent and Wygodzinsky 1979). However, Harry (1993b) detected no clear-cut differences in the male genitalia structures; in addition, important chromatic variation has been described in both species (Barrett 1995).

Abad-Franch et al. (2009) applied a geometric morphometrics aiming to differentiate *R. neglectus* from *R. nasutus* and found wing and head shape differences between these species. Some specimens from Curaçá, Bahia (Brazil) collected in *C. prunifera* palms, although phenotypically similar to *R. nasutus*, were clustered within the *R. neglectus* group, while others from the same location were clustered within *R. nasutus*. If morphometry is able to correctly assign both species, these results showed that *R. neglectus* and *R. nasutus* are sympatric in the Cerrado-Caatinga transitional area and the former species may have chromatic forms similar to those observed in the latter.

Recent observations of *Rhodnius* insects at Caatinga and Caatinga-Cerrado revealed specimens with dubious chromatic patterns. Individuals collected in *M. flexuosa* palms had a dark phenotype, a similar color to the palm fibers and base of fronds, and with coloration and diagnostic traits of *R. neglectus*. However, those collected in *C. prunifera* palms displayed a lighter chromatic pattern more similar to that of *R. nasutus* (Pavan et al. 2015). Since *R. neglectus* and *R. nasutus* may occur in sympatry (Abad-Franch et al. 2009), it raises the possibility of natural hybridization.

An alternative explanation for this observation is that *R. neglectus* would exhibit one chromatic phenotype similar to *R. nasutus* and different from the pattern described by Lent and Wygodzinsky (1979). If correct, the lighter coloration of *R. neglectus* from *C. prunifera* may be naturally selected. This coloration might have improved its chances of survival and reproduction, since they would be camouflaged with the light substrate of *C. prunifera* fibers. Therefore, populations with light phenotype increased in frequency in these palm trees, as they would be less conspicuous and thus less predated than the typical phenotypes.

Phenotypic variation was also observed for *R. nasutus*, and it seems to be governed by the microhabitat it lives in. In Ceará, Brazil, this species was collected in five different palm tree species (Dias et al. 2008). The holotype of *R. nasutus* has a pale brownish-yellow coloring, with a red-like appearance and dark brown dots in certain regions of the body and appendices (Lent and Wygodzinsky 1979). Although populations inhabiting *C. prunifera* palms presented a reddish color, according to the original species description, other populations from *A. intumescens*, *A. speciosa*, *M. flexuosa*, and *S. oleracea* palms were chestnut-colored (Dias et al. 2008). As observed for *R. neglectus*, body coloration of *R. nasutus* specimens corresponded exactly to the fibers and base of fronds, strengthening the hypothesis that *Rhodnius* species have genes, which provide a menu of different phenotype possibilities, and the environment determines the phenotypic outcome by natural selection.

5 Tempo and Mode of Triatomine Speciation

As summarized in a recent review paper on the evolution and biogeography of the Triatominae (Monteiro et al. 2018), most studies focusing on the existence of cryptic triatomine taxa using molecular markers have often relied on two species concepts: the Biological Species Concept (BSC, Mayr 1963) and the Phylogenetic Species Concept (PSC, Cracraft 1989). We have learned that allopatric speciation seems to be the rule for most Reduviids (Monteiro et al. 2018). Here, we present three examples of triatomine speciation that probably involved vicariance and diversification with low/no gene flow among ancestral lineages. It is widely accepted that speciation is a process that requires very long time intervals to take place, usually hundreds of thousands of years (Butlin et al. 2008). With regard to the time needed for triatomines to speciate, two hypotheses were put forth that clearly challenged the *tempo* required for traditional insect speciation to occur (see below).

5.1 Fast or Slow Diversification?

***Triatoma rubrofasciata* and Old World Triatominae**

The first hypothesis was advanced in an attempt to account for the occurrence of the six *Linshcosteus* and seven *Triatoma* species found in the Old World. It was suggested that they all descend from *T. rubrofasciata*, as a result of merchant shipping between the Americas and Asia during the sixteenth to seventeenth centuries, perhaps as a consequence of very fast (300 years) adaptive radiation processes (Schofield 1988; Gorla et al. 1997; Patterson et al. 2001; Schofield and Galvão 2009; Dujardin et al. 2015a, b). It is now well established that all Old World Triatominae are monophyletic and likely derive from a successful founding event that occurred approximately 20 Ma, with ancestral triatomine populations crossing the Bering land bridge, likely benefiting from the association with rodents, ultimately reaching Eurasia (Hypša et al. (2002); Patterson and Gaunt 2010; Justi et al. 2016).

The Origin of *Rhodnius prolixus*

The second hypothesis suggested that *R. prolixus*, the most important Chagas vector in Venezuela, Colombia and parts of Central America, is a domestically adapted "derivative" of a sylvatic *R. robustus* lineage, and that speciation was the consequence of a "discrete event in Venezuela at some time after the establishment of European settlements in the 16th century" (Schofield and Dujardin 1999). This hypothesis was proposed based on morphometric (Dujardin et al. 1998, 1999) and genetic evidence (allozymes and mtDNA; Harry et al. 1992, Stothard et al. 1998, respectively), available at the time, which pointed to a lack of phenotypic and genetic variability in *R. prolixus* populations. Further research relying on better sampling of both wild and domestic *R. prolixus* populations collected from six Venezuelan states and analyzed for mtDNA and microsatellites have challenged this view by revealing high levels of genetic variation (Fitzpatrick et al. 2008).

5.2 *Vicariance and Allopatric Speciation of Triatomines*

Rhodnius robustus and the *Refugium* Theory

For many years, the taxonomic status of *R. robustus* was questioned due to a combination of three factors: morphological similarity, loose diagnosis, and poor sampling (cf. Monteiro et al. 2003; Pavan and Monteiro 2007). Although indistinguishable according to morphological and isozymic analyses (Harry 1993a, 1994), these species play very different epidemiological roles—*R. prolixus* is an efficient domestic vector, whereas *R. robustus* populations are entirely sylvatic. Monteiro et al. (2003) put an end to the controversy of the validity of *R. robustus* as a bona fide species through the analysis of DNA sequences of mitochondrial and nuclear markers (663-bp fragment of cytochrome b (cytb) and the D2 variable region of the 28S nuclear RNA), revealing that *R. robustus* is not only a valid species separated from *R. prolixus*, but also represents a paraphyletic complex of at least four cryptic lineages (*R. robustus* I, II, III, IV). Pavan et al. (2013) further confirmed the paraphyletic assemblage of *R. robustus* with respect to *R. prolixus* through the analysis of another nuclear marker, the fourth intron of the transmembrane protein 165 (TP165) gene. The separation of *R. prolixus* and *R. robustus* was further corroborated by a behavior study showing that nymphs of *R. prolixus* and *R. robustus* II display different locomotor activity patterns on an automated recording system (Pavan et al. 2016).

The first attempt to associate triatomine phylogeographic patterns with possible vicariant events based on molecular clock time-estimates was published in 2003 by Monteiro and collaborators. A particular and notorious example of vicariant speciation is that of the *refugium* theory, advanced to account for the pattern of diversification seen in the Amazon region. The view that diversification of the Amazonian biota was caused by glaciation cycles during the Pleistocene was first introduced by Haffer (1969). The theory attempts to explain the latest of the series of differentiation events beginning in the Cenozoic that contributed to the development of the modern biota of the Amazon basin. In short, it is based on the premise that climatic changes during the Pleistocene caused rain forests to contract into isolated pockets separated by savannah. This would have confined small populations and favored their divergence by genetic drift, which would have facilitated allopatric speciation (Monteiro et al. 2003). The authors used in their phylogeographic inferences the value of 2.3% of sequence divergence per million years estimated for recently diverged arthropod taxa (Brower 1994). They concluded that all estimates between the clades within both Amazon and Orinoco regions are compatible with a Pleistocene origin and are consisted with the *refugium* theory (Monteiro et al. 2003).

Triatoma rubida and the Baja California Peninsula

Triatoma rubida was initially described as five morphologically distinguishably allopatric subspecies based mainly on chromatic differences in markings along the conexivum, distributed in Mexico and the USA: *T. rubida rubida* from the Cape region, Baja California Sur, *T. rubida cochimiensis* from Central Baja California peninsula, *T. rubida jaegeri* from Pond Island, Gulf of California, and *T. rubida sonoriana* from Sonora (all strictly Mexican subspecies); and *T. rubida uhleri* from Veracruz, Mexico, and Southwestern USA (Usinger 1944; Ryckman 1967). The "five subspecies" proposition was, however, later challenged in the 1979 revision of Lent and Wygodzinsky, who stated: "Although specimens seem to cluster around the phenotypes mentioned, not all fall easily into the categories listed above; there does seem to be a prevalence of comparatively light-colored, large-sized forms in the north and of smaller, more intensely pigmented forms in the southern part of the total range of the species. Much more abundant material than that examined by us, especially from Mexico, combined with rearing experiments, is needed for an understanding of the biosystematics of *Triatoma rubida*."

The separation of the Baja California Peninsula from mainland Mexico during the formation of the Gulf of California 5–8 Ma is believed to be the vicariant event that caused the geographic isolation of ancestral *T. rubida* populations and gave rise to *T. rubida cochimiensis* (Baja peninsula) and *T. rubida sonoriana* (Sonora). Pfeiler et al. (2006) used this geological event to calibrate the first mtDNA molecular clock for triatomines: 1.1–1.8% pairwise sequence divergence per million years (lower than the 2.3% divergence for mtDNA generally applied to insects; Brower 1994).

Triatoma dimidiata and the Isthmus of Tehuantepec

The *T. dimidiata* cryptic species complex was first recognized by Marcilla et al. (2001) based on ITS-2 sequence divergence between bugs from Yucatan and specimens from elsewhere in Mexico and from Central and South America. Following studies based on cytogenetics and genome size (Panzera et al. 2006) and mtDNA (Dorn et al. 2009; Monteiro et al. 2013) corroborated these observations. Relying on mtDNA markers (cytb and ND4), Monteiro et al. (2013) described five genetically well-differentiated, monophyletic groups (named groups I–IV plus *T. hegneri*). Their results revealed that mtDNA groups I, II, and III match, respectively, ITS-2 groups 1, 2, and 3. Group IV represented cave-dwelling Belize specimens. As pointed out by Bargues et al. (2008) and Monteiro et al. (2013), some of these genetically divergent groups clearly deserved specific status. In accordance with these orientations, the two genetically most divergent groups III and IV were recently raised to the specific level and formally described as *T. mopan* and *T. huehuetenanguensis*, respectively (Dorn et al. 2018; Lima-Cordón et al. 2019).

With regard to Groups I and II (and based on their present distribution), as the Isthmus of Tehuantepec is known to represent an important recent geological barrier for a number of sister taxa of birds, mammals, and butterflies, Monteiro et al. (2013) have suggested that the Isthmus of Tehuantepec orogeny (15–5 Ma) might have been the vicariant event responsible for the splitting of the ancestral population that led to their origin. Although groups I and II still have a subspecies status, we argue that they merit specific status.

5.3 *Parapatric/Sympatric Triatomine Speciation*

Triatoma brasiliensis Complex and the Homoploid Hybridization Hypothesis

Organisms may also speciate quite rapidly via polyploidy (Lukhtanov et al. 2015). Polyploidy (or hybrid speciation) is the term given to a set of processes whereby two species hybridize and instantly generate a third new species. They can be classified as allopolyploidy (i.e., involving a genome-doubling event that provides reproductively isolation); or homoploid hybrid speciation that occurs without an increase in ploidy (Coyne and Orr 2004).

The northeastern Brazil Chagas species complex *Triatoma brasiliensis* was comprised of three subspecies—*T. b. brasiliensis*, *T. b. macromelasoma*, and *T. b. melanica*—defined based on chromatic differences of the pronotum, legs, and hemelytra (Galvão 1956). These subspecies were, however, synonymized by Lent and Wygodzinsky (1979), who argued that intermediate forms could be found in nature. Further allozyme-based analyses showed the three subspecies were real evolutionary lineages, and yet another form was later discovered (*juazeiro* form; Costa et al. 1997). Monteiro et al. (2004) confirmed the existence of the four forms based on mtDNA cytb phylogenetic analysis of specimens collected from the whole distribution area of the species. *Juazeiro* and *melanica* forms were raised to the specific level and formally described as *T. melanica* (Costa et al. 2006) and *T. juazeirensis* (Costa and Felix 2007). Kimura-2-parameter distances based on mtDNA evidence that bona fide sister *Triatoma* species diverge in more than 7.5% (K2P > 0.075) (cf. Monteiro et al. 2004), while intraspecific variation does not exceed 2%. Genetically less divergent sister forms *brasiliensis* and *macromelasoma* diverged in more than 2% (K2P = 0.027), and thus, were given subspecific ranks (Costa et al. 2013).

Costa et al. (2009) have analyzed morphometric, morphological, ecological, and geographic distribution data to advance the hypothesis that *T. brasiliensis macromelasoma* is a product of hybridization between the subspecies *T. b. brasiliensis* and *T. juazeirensis*. Authors acknowledge, however, that the evidence presented is not yet conclusive and that further studies are required to strengthen their claim (Costa et al. 2009). The subject has been recently revisited in a study based on chromosomal analysis, and band sizes of an ITS-1 PCR-amplified fragment (Guerra et al. 2019). Those authors also sequenced DNA from the three taxa for a fragment of the ND1 mitochondrial gene, which gave unexpectedly low pairwise genetic distances (Tamura-Nei < 0.006), pointing to a possible problem with the taxonomic identification of the specimens themselves (Guerra et al. 2019). It is well established that this magnitude of differentiation characterizes within-population or, at most, within-species levels of variation (Monteiro et al. 2004). Not surprisingly, all species showed the same cytogenetic characteristics (Guerra et al. 2019).

The speciation process of the *T. brasiliensis* complex probably involves ecological and/or temporal barriers (sympatric areas in the present may represent secondary contact zones of parapatric/allopatric populations), since they still have not evolved either pre- or post-mating barriers, as revealed by successful hybridizations in laboratory conditions (Almeida et al. 2012). New studies on ecology and genomics focusing on possible ecological selection (which would prevent backcrossing), behavioral changes (e.g., different periods of activity), or even chromosomal arrangements are still needed to clarify this issue.

The *Rhodnius pallescens—R. colombiensis*: A Case of Sympatric Speciation?

The *Rhodnius pallescens* complex is composed by three recognized species that occur in the trans-Andean region (Pacific area of South and Central America)—*R. pallescens*, *R. colombiensis,* and *R. ecuadoriensis*. *Rhodnius. ecuadoriensis* is restricted to southern Ecuador and northern Peru, occupying *Phytelephas aequatorialis* palms (Abad-Franch et al. 2009). This species is isolated from the others of this complex by geographical barriers, the Andean mountains, and probably speciated through allopatry (Galvão et al. 2003; Abad-Franch et al. 2009). *Rhodnius. pallescens* is widely distributed across Central America and Colombia in different ecological zones, inhabiting *Attalea butyracea* and *Cocos nucifera* palm trees (Díaz et al. 2014). *Rhodnius. colombiensis* seems to be restricted to the Andean Valley of Magdalena River in central Colombia (Moreno et al. 1999). Although this species inhabits the same ecoregion and same palm tree species as *R. pallescens*, natural hybrids had not been reported (Díaz et al. 2014).

Laboratory crosses reveals the existence of both pre-zygotic and post-zygotic reproductive barriers. Female *R. pallescens* I and male *R. colombiensis* do not produce progeny, while female *R. colombiensis* and male *R. pallescens* I produce infertile F1 hybrids (Gómez-Palacio et al. 2012). Cytogenetics analyses reveal that *R. colombiensis* structural chromosomes suffered rearrangements and DNA loss in comparison to the other species of the complex (Panzera et al. 2007; Gómez-Palacio et al. 2012; Díaz et al. 2014). A clear demarcation of the biogeographical distribution of the four lineages of the complex and additional analyses within and between *R. pallescens* lineages using different molecular markers are still needed for a better knowledge on the evolutionary trends, geographical dispersion, and signs of possible adaptive radiation.

6 Toward an Integrative and Evolutionarily Sound Taxonomy

We emphasize the importance of integrating morphological, ecological, behavioral, and molecular tools to elucidate epidemiological and taxonomic unresolved questions in triatomines. Abad-Franch et al. (2013) performed an integrative taxonomic analysis to describe *Rhodnius barretti* as a new species of triatomine. They evaluated traditional morphological traits, morphometric data, and molecular phylogenetics using a fragment of cytb. This species is difficult to distinguish phenotypically from those of the *R. robustus* lineage, with the exception of the sympatric *R. robustus* II that presents chromatic (lighter coloration) and size (larger individuals) differences. However, *R. barretti* differs from *R. robustus s.l.* in the shape of both head and wings, and also in length ratios of certain anatomical structures. Moreover, phylogenetic reconstructions showed that this species is a basal member of the "*R. robustus* lineage," which encompasses *R. nasutus*, *R. neglectus*, *R. prolixus,* and the other five members of the *R. robustus* complex (Abad-Franch et al. 2013).

Besides the *R. prolixus* genome (Mesquita et al. 2015), the mitochondrial genomes of *T. dimidiata* and *T. infestans* are already available (Dotson and Beard 2001; Pita et al. 2017). As genome-sequencing is increasingly employed for non-model organisms, the ability to evaluate the taxonomic identity or status of a particular triatomine species via transcriptomes, proteomes, or metabolomes is now possible. These approaches have recently begun to be applied to triatomines, including *T. brasiliensis* (Marchant et al. 2015), *T. dimidiata* (Kato et al. 2010), *R. prolixus* (Ribeiro et al. 2014), and *T. infestans* (Traverso et al. 2016; Gonçalves et al. 2017). Genomic data were also useful for the identification of parasite, vector, and the microbiota present in *T. dimidiata* (Orantes et al. 2018). In the context of near-sibling species and varieties of single species, Brito et al. (2019) recently synonymized *Rhodnius montenegrensis* as *R. robustus*. Most likely, the upcoming years of triatomine research will present us with the gathering of increasingly large datasets that contain separate lines of evidence from independent loci.

An alternative approach for generating genomic data at a lower cost for population genetics studies and phylogenetic analyses of closely related species is the double-digested restriction-site-associated DNA sequencing (ddRAD-seq) method. This technique was first employed as a population genomics study to infer the structuring of *R. ecuadoriensis* populations in Ecuador (Hernandez-Castro et al. 2017). This method increases the coverage of different regions of the genome and recovers reliable microsatellite and SNP data (Davey and Blaxter 2011; Kai et al. 2014).

An overlooked issue in population studies of triatomines is the difficulty of infestation foci detection, especially when colonies are small and occupy structurally complex ecotopes (Abad-Franch et al. 2010, 2014; Valença-Barbosa et al. 2014; Pavan et al. 2015). A comprehensive approach must include genetic and ecological data of triatomine species to better understand the adaptive nature of plasticity (whether is heritable and ontogenetic), and detailed frequencies of different chromatic variations in the environment (Murren et al. 2015).

New genomic tools can help explore adaptive plasticity and the following approaches deserve further attention: (1) the "omic" basis behind it, (2) comparative genomics of near-sibling species to understand its evolution, and (3) epigenetic components of inheritance that may influence plastic responses (Richards et al. 2010; Glastad et al. 2011; Zhang et al. 2013; Murren et al. 2015).

References

Abad-Franch F, Monteiro FA, Jaramillo ON, Gurgel-Gonçalves R, Dias FBS, Diotaiuti L (2009) Ecology, evolution, and the long-term surveillance of vector-borne Chagas disease: a multi-scale appraisal of the tribe Rhodniini (Triatominae). Acta Trop 110:159–177

Abad-Franch F, Ferraz G, Campos C, Palomeque FS, Grijalva MJ et al (2010) Modeling disease vector occurrence when detection is imperfect: infestation of Amazonian palm trees by triatomine bugs at three spatial scales. PLoS Negl Trop Dis 4(3):e620

Abad-Franch F, Pavan MG, Jaramillo ON, Palomeque FS, Dale C, Chaverra D, Monteiro FA (2013) *Rhodnius barretti*, a new species of Triatominae (Hemiptera: Reduviidae) from western Amazonia. Mem Inst Oswaldo Cruz 108:92–99

Abad-Franch F, Diotaiuti L, Gurgel-Gonçalves R, Gürtler RE (2014) On bugs and bias: improving Chagas disease control assessment. Mem Inst Oswaldo Cruz 109(1):125–130

Almeida CE, Oliveira HL, Correia N, Dornak LL, Gumiel M, Neiva VL, Harry M, Mendonça VJ, Costa J, Galvão C (2012) Dispersion capacity of *Triatoma sherlocki*, *Triatoma juazeirensis* and laboratory-bred hybrids. Acta Trop 122:71–79

Andersson L (1990) The driving force: species concepts and ecology. Taxon 39:375–382

Antoine P-O, Marivaux L, Croft DA, Billet G, Ganerød M, Jaramillo C, Martin T, Orliac MJ, Tejada J, Altamirano AJ, Duranthon F, Fanjat G, Rousse S, Gismondi RS (2012) Middle Eocene rodents from Peruvian Amazonia reveal the pattern and timing of caviomorph origins and biogeography. Proc R Soc London B 279:1319–1326

Bailey RI, Thomas CD, Butlin RK (2004) Premating barriers to gene exchange and their implications for the structure of a mosaic hybrid zone between *Chorthippus brunneus* and *C. jacobsi* (Orthoptera: Acrididae). J Evol Biol 17:108–119

Bargues MD, Klisiowicz DR, González-Candelas F, Ramsey JM, Monroy C, Ponce C, Salazar-Schettino PM, Panzera F, Abad-Franch F, Sousa OE, Schofield CJ, Dujardin JP, 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 Negl Trop Dis 2:e233

Barrett TV (1995) Species interfertility and crossing experiments in Triatomine systematics. In: Schofield CJ, Dujardin JP, Jurberg J (eds) Proceedings of the international workshop on population genetics and control of Triatominae. INDRE Press, Mexico, pp 72–77

Barrett RDH, Rogers SM, Schluter D (2008) Natural selection on a major armor gene in threespine stickleback. Science 322:255–257. https://doi.org/10.1126/science.1159978

Barron MG, Paupy C, Rahola N, Akone-Ella O, Ngangue MF, Theodel A, Wilson-Bahun TA, Pombi M, Kengne P, Costantini C, Simard F, Gonzalez J, Ayala D (2018) A new species in the *Anopheles gambiae* complex reveals new evolutionary relationships between vector and non-vector species. bioRxiv:460667. https://doi.org/10.1101/460667

Bridle JR, de la Torre J, Bella JL, Butlin RK, Gosalvez J (2002) Low levels of chromosomal differentiation between the grasshoppers *Chorthippus brunneus* and *Chorthippus jacobsi* (Orthoptera; Acrididae) in northern Spain. Genetica 114:121–127

Brito RN, Geraldo JA, Monteiro FA, Lazoski C, Souza RCM, Abad-Franch F (2019) Transcriptome-based molecular systematics: *Rhodnius montenegrensis* (Triatominae) and its position within the *Rhodnius prolixus-Rhodnius robustus* cryptic-species complex. Parasit Vectors 12(1):305. https://doi.org/10.1186/s13071-019-3558-9

Brower AVZ (1994) Rapid morphological radiation and convergence in the butterfly, *Heliconius erato*, inferred from patterns of mitochondrial DNA evolution. PNAS USA 91:6491–6495

Burns KJ (1997) Molecular systematics of tanagers (Thraupinae): evolution and biogeography of a diverse radiation of Neotropical birds. Mol Phylogenet Evol 72:334–348

Bush GL (1969) Sympatric host race formation and speciation in frugivorous flies of the genus *Rhagoletis* (Diptera: Tephritidae). Evolution 23:237–251

Bush GL, Diehl SR (1982) Host shifts, genetic models of sympatric speciation and the origin of parasitic insect species. In: Visser JH, Minks AK (eds) Insect and host plant. Pudoc, Wageningen, pp 297–305

Bush GL, Butlin RK (2004) Sympatric speciation in insects. In: Dieckmann U, Doebeli M, Metz JAJ, Tautz D (eds) Adaptive speciation. Cambridge University Press, Cambridge, pp 229–248

Butlin RK, Galindo J, Grahame JW (2008) Sympatric, parapatric or allopatric: the most important way to classify speciation? Phil Trans R Soc London B 363:2997–3007. https://doi.org/10.1098/rstb.2008.0076

Carcavallo RU, Jurberg J, Lent H, Noireau F, Galvão C (2000) Phylogeny of the Triatominae (Hemiptera: Reduviidae). Proposals for taxonomic arrangements. Entomol Vectores 7:1–99

Claridge MF, den Hollander J, Morgan JC (1985) Variation in courtship signals and hybridization between geographically definable populations of the rice brown planthopper, *Nilaparvata lugens* (Stål). Biol J Linn Soc 24:35–49

Cook OF (1906) Factors of species-formation. Science 23:506–507

Costa J, Freitas Sibajev MGR, Marcon Silva V, Pires MQ, Pacheco RS (1997) Isoenzymes detect variation in populations of *Triatoma brasiliensis* (Hemiptera: Reduviidae: Triatominae). Mem Inst Oswaldo Cruz 92:459–464

Costa J, Argolo AM, Felix M (2006) Redescription of *Triatoma melanica* Neiva & Lent, 1941, new status (Hemiptera: Reduviidae: Triatominae). Zootaxa 1385:47–52

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, Peterson AT, Dujardin JP (2009) Morphological evidence suggests homoploid hybridization as a possible mode of speciation in the Triatominae (Hemiptera, Heteroptera, Reduviidae). Infect Genet Evol 9(2):263–270

Costa J, Correia NC, Neiva VL, Goncalves TCM, Felix M (2013) Revalidation and redescription of *Triatoma brasiliensis macromelasoma* Galvão, 1956 and an identification key for the *Triatoma brasiliensis* complex (Hemiptera: Reduviidae: Triatominae). Mem Inst Oswaldo Cruz 108:785–789

Coyne JA, Orr HA (2004) Speciation. Sinauer Associates, Sunderland

Cracraft J (1983) Species concepts and speciation analysis. Curr Ornithol 1:159–187

Cracraft J (1989) Speciation and its ontology: the empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. In: Otte D, Endler JA (eds) Speciation and its consequences. Sinauer Associates, Sunderland, MA, pp 28–59

Dambroski HR, Linn C Jr, Berlocher SH, Forbes AA, Roelofs W, Feder JL (2005) The genetic basis for fruit odor discrimination in *Rhagoletis* flies and its significance for sympatric host shifts. Evolution 59:1953–1964

Davey J, Blaxter M (2011) RADSeq: next-generation population genetics. Briefs Funct Genomics 10(2):108

de la Rúa NM, Bustamante DM, Menes M, Stevens L, Monroy C, Kilpatrick CW, Rizzo D, Klotz SA, Schmidt J, Axen HJ, Dorn PL (2014) Towards a phylogenetic approach to the composition of species complexes in the North and Central American *Triatoma*, vectors of Chagas disease. Infect Genet Evol 24:157–166

de Paula AS, Diotaiuti L, Schofield CJ (2005) Testing the sister-group relationship of the Rhodniini and Triatomini (Insecta: Hemiptera: Reduviidae: Triatominae). Mol Phylogenet Evol 35:712–718

de Queiroz K (2007) Species concepts and species delimitation. Syst Biol 56(6):879–886

Dias FBS, Bezerra CM, Machado EM, Casanova C, Diotaiuti L (2008) Ecological aspects of *Rhodnius nasutus* Stål, 1859 (Hemiptera: Reduviidae: Triatominae) in palms of the Chapada do Araripe in Ceará, Brazil. Mem Inst Oswaldo Cruz 103(8):824–830

Díaz S, Panzera F, Jaramillo-O N, Perez R, Fernandez R, Vallejo G, Saldana A, Calzada JE, Triana O, Gómez-Palacio A (2014) Genetic, cytogenetic and morphological trends in the evolution of the *Rhodnius* (Triatominae: Rhodniini) trans-Andean group. PLoS One 9(2):e87493. https://doi.org/10.1371/journal.pone.0087493

Dobzhansky T (1950) Mendelian populations and their evolution. Am Nat 84:401–418

Dobzhansky T (1970) Genetics of the evolutionary process. Columbia University Press, New York

Doellman MM, Egan SP, Ragland GJ, Meyers PJ, Hood GR, Powell THQ, Lazorchak P, Hahn DA, Berlocher SH, Nosil P, Feder JL (2019) Standing geographic variation in eclosion time and the genomics of host race formation in *Rhagoletis pomonella* fruit flies. Ecol Evol 9:393–409. https://doi.org/10.1002/ece3.4758

Donoghue MJ (1985) A critique of the biological species concept and recommendations for a phylogenetic alternative. Bryologist 88:172–181

Dorn PL, Calderón C, Melgar S, Moguel B, Solórzano E, Dumonteil E, Rodas A, de la Rúa N, Garnica R, Monroy C (2009) Two distinct *Triatoma dimidiata* (Latreille, 1811) taxa are found in sympatry in Guatemala and Mexico. PLoS Negl Trop Dis 3:e393

Dorn PL, Justi SA, Dale C, Stevens L, Galvão C, Lima-Cordón R, Monroy C (2018) Description of *Triatoma mopan* sp. n. from a cave in Belize (Hemiptera, Reduviidae, Triatominae). ZooKeys 775:69–95. https://doi.org/10.3897/zookeys.775.22553

Dotson EM, Beard CB (2001) Sequence and organization of the mitochondrial genome of the Chagas disease vector, *Triatoma dimidiata*. Insect Mol Biol 10:205–225

Dujardin JP, Muñoz M, Chavez T, Ponce C, Moreno J, Schofield CJ (1998) The origin of *Rhodnius prolixus* in Central America. Med Vet Entomol 12:113–115

Dujardin JP, Chávez T, Moreno JM, Machane M, Noireau F, Schofield CJ (1999) Comparison of isoenzyme electrophoresis and morphometric analysis for phylogenetic reconstruction of the Rhodniini (Hemiptera: Reduviidae: Triatominae). J Med Entomol 36:653–659

Dujardin JP, Costa J, Bustamante D, Jaramillo N, Catalá S (2009) Deciphering morphology in Triatominae: the evolutionary signals. Acta Trop 110(2–3):101–111

Dujardin JP, Lam TX, Khoa PT, Schofield CJ (2015a) The rising importance of *Triatoma rubrofasciata*. Mem Inst Oswaldo Cruz 110:319–323

Dujardin JP, Pham Thi K, Truong Xuan L, Panzera F, Pita S, Schofield CJ (2015b) Epidemiological status of kissing-bugs in South East Asia: a preliminary assessment. Acta Trop 151:142–149

Emelianov I, Simpson F, Narang P, Mallet J (2003) Host choice promotes reproductive isolation between host races of the larch budmoth *Zeiraphera diniana*. J Evol Biol 16:208–218

Emelianov I, Marec F, Mallet J (2004) Genomic evidence for divergence with gene flow in host races of the larch budmoth. Proc Biol Sci 271(1534):97–105. https://doi.org/10.1098/rspb.2003.2574

Erwin TL (1982) Tropical forests: their richness in Coleoptera and other arthropod species. Coleopt Bull 36:74–75

Feder JF, Berlocher SH, Roethele JB, Dambroski H, Smith JJ, Perry WL, Gavrilovic V, Filchak KE, Rull J, Aluja M (2003) Allopatric genetic origins for sympatric host-plant shifts and race formation in *Rhagoletis*. PNAS USA 100:10314–10319. https://doi.org/10.1073/pnas.1730757100

Filchak KE, Roethele JB, Feder JL (2000) Natural selection and sympatric divergence in the apple maggot *Rhagoletis pomonella*. Nature 407:739–742

Fitzpatrick BM, Fordyce JA, Gavrilets S (2009) Pattern, process and geographic modes of speciation. J Evol Biol 22:2342–2347

Fitzpatrick S, Feliciangeli MD, Sánchez-Martín MJ, Monteiro FA, Miles MA (2008) Molecular genetics reveal that silvatic *Rhodnius prolixus* do colonise rural houses. PLoS Negl Trop Dis 2:e210

Flynn JJ, Wyss AR (1998) Recent advances in South American mammalian paleontology. Trends Ecol Evol 13(11):449–454

Galvão AB (1956) *Triatoma brasiliensis macromelasoma* n. subsp. (Reduviidae: Hemiptera). Rev Bras Mal D Trop 7:455–457

Galvão C, Paula AS (2014) Sistemática e evolução dos vetores. In: Galvão C (ed) Vetores da doença de Chagas no Brasil. Sociedade Brasileira de Zoologia, Curitiba, pp 25–32

Galvão C, Carcavallo RU, Rocha DS, 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 BA, Moriyama EN, Powell JR (2001) Mitochondrial DNA sequences of triatomines (Hemiptera: Reduviidae): phylogenetic relationships. J Med Entomol 38:675–683

Glastad KM, Hunt BG, Yi SV, Goodisman MAD (2011) DNA methylation in insects: on the brink of the epigenomic era. Insect Mol Biol 20:553–565

Gómez-Palacio A, Jaramillo-O N, Caro-Riaño H, Díaz S, Monteiro FA, Pérez R, Panzera F, Triana O (2012) Morphometric and molecular evidence of intraspecific biogeographical differentiation of *Rhodnius pallescens* (Hemiptera: Reduviidae: Rhodniini) from Colombia and Panama. Infect Genet Evol 12:1975–1983

Gonçalves LO, Oliveira LM, D'Ávila Pessoa GC, Rosa ACL, Bustamante MG, Belisário CJ, Resende DM, Diotaiuti LG, Ruiz JC (2017) Insights from tissue-specific transcriptome sequencing analysis of *Triatoma infestans*. Mem Inst Oswaldo Cruz 112:456–457

Gorla DE, Dujardin JP, Schofield CJ (1997) Biosystematics of old World Triatominae. Acta Trop 63:127–140

Grismer LL (1999) An evolutionary classification of reptiles on islands in the Gulf of California, Mexico. Herpetologica 55:446–469

Grismer LL (2001) An evolutionary classification and checklist of amphibians and reptiles on the Pacific islands of Baja California, Mexico. Bull South Calif Acad Sci 100:12–23

Guerra AL, Borsatto KC, Teixeira NPD, Madeira FF, de Oliveira J, da Rosa JA, Azeredo-Oliveira MTV, Alevi KCC (2019) Revisiting the homoploid hybrid speciation process of the *Triatoma brasiliensis macromelasoma* Galvão, 1956 (Hemiptera, Triatominae) using cytogenetic and molecular markers. Am J Trop Med Hyg 100(4):911–913. https://doi.org/10.4269/ajtmh.17-0813

Gurgel-Gonçalves R, Duarte MA, Ramalho ED, Palma ART, Romaña ED, Cuba CA (2004) Spatial distribution of Triatominae populations (Hemiptera: Reduviidae) in *Mauritia flexuosa* palm trees in Federal District of Brazil. Rev Soc Bras Med Trop 37(3):241–247

Haffer J (1969) Speciation in Amazonian forest birds. Science 165:131–137

Hammond PM (1992) Species inventory. In: Groombridge B (ed) Global biodiversity, status of the earth's living resources. WCMC/Chapman and Hall, London, pp 17–39

Harry M (1993a) Isozymic data question the specific status of some blood-sucking bugs of the genus *Rhodnius*, vectors of Chagas disease. Trans R Soc Trop Med Hyg 87:492–493

Harry M (1993b) Use of the median process of the pygophore in the identification of *Rhodnius nasutus*, *R. neglectus*, *R. prolixus* and *R. robustus* (Hemiptera: Reduviidae). Ann Trop Med Parasitol 87:277–282

Harry M (1994) Morphometric variability in the Chagas disease vector *Rhodnius prolixus*. Jpn J Genet 69:233–250

Harry M, Galíndez I, Cariou ML (1992) Isozyme variability and differentiation between *Rhodnius prolixus*, *R. robustus* and *R. pictipes*, vectors of Chagas disease in Venezuela. Med Vet Entomol 6:37–43

Hennig W (1966) Phylogenetic systematics. University of Illinois Press, Urbana

Hernández ML, Abrahan LB, Dujardin JP, Gorla DE, Catalá SS (2011) Phenotypic variability and population structure of peridomestic *Triatoma infestans* in rural areas of the arid Chaco (Western Argentina): spatial influence of macro- and microhabitats. Vector-Borne Zoonotic Dis 11(5):503–513. https://doi.org/10.1089/vbz.2009.0253

Hernandez-Castro LE, Paterno M, Villacís AG, Andersson B, Costales JA, De Noia M, Ocaña-Mayorga S, Yumiseva CA, Grijalva MJ, Llewellyn MS (2017) 2b-RAD genotyping for population genomic studies of Chagas disease vectors: *Rhodnius ecuadoriensis* in Ecuador. PLoS Negl Trop Dis 11(7):e0005710. https://doi.org/10.1371/journal.pntd.0005710

Howard DJ, Gregory PG, Chu J, Cain ML (1998) Conspecific sperm precedence is an effective barrier to hybridization between closely related species. Evolution 52:511–516

Hwang WS, Weirauch C (2012) Evolutionary history of assassin bugs (Insecta: Hemiptera: Reduviidae): insights from divergence dating and ancestral state reconstruction. PLoS One 7:e45523

Hypša V, Tietz DF, Zrzavý J, Rego RO, Galvão C, Jurberg J (2002) Phylogeny and biogeography of Triatominae (Hemiptera: Reduviidae): molecular evidence of a New World origin of the Asiatic clade. Mol Phylogenet Evol 23:447–457

Ibarra-Cerdeña CN, Zaldívar-Riverón A, Peterson AT, Sánchez-Cordero V, Ramsey JM (2014) Phylogeny and niche conservatism in North and Central American triatomine bugs (Hemiptera: Reduviidae: Triatominae), vectors of Chagas' disease. PLoS Negl Trop Dis 8:e3266

Jiggins CD (2006) Sympatric speciation: why the controversy? Curr Biol 16:333–334. https://doi.org/10.1016/j.cub.2006.03.077

Justi SA, Galvão C, Schrago CG (2016) Geological changes of the Americas and their influence on the diversification of the Neotropical kissing bugs (Hemiptera: Reduviidae: Triatominae). PLoS Negl Trop Dis 10:e0004527

Justi SA, Russo CA, Mallet JR, Obara MT, Galvão C (2014) Molecular phylogeny of Triatomini (Hemiptera: Reduviidae: Triatominae). Parasit Vectors 7:149

Kai W, Nomura K, Fujiwara A, Nakamura Y, Yasuike M, Ojima N, Masaoka T, Ozaki A, Kazeto Y, Gen K, Nagao J, Tanaka H, Kobayashi T, Ototake M (2014) A ddRAD-based genetic map and its integration with the genome assembly of Japanese eel (*Anguilla japonica*) provides insights into genome evolution after the teleost-specific genome duplication. BMC Genomics 15:233. https://doi.org/10.1186/1471-2164-15-233

Kato H, Jochim RC, Gómez EA, Sakoda R, Iwata H, Valenzuela JG, Hashiguchi Y (2010) A repertoire of the dominant transcripts from the salivary glands of the blood-sucking bug, *Triatoma dimidiata*, a vector of Chagas disease. Infect Genet Evol 10:184–191

Lent H, Wygodzinsky P (1979) Revision of the Triatominae (Hemiptera, Reduviidae) and their significance as vectors of Chagas disease. Bull Am Mus Nat Hist 163:125–520

Lima AF, Jeraldo VL, Silveira MS, Madi RR, Santana TB et al (2012) Triatomines in dwellings and outbuildings in an endemic area of Chagas disease in northeastern Brazil. Rev Soc Bras Med Trop 45(6):701–706

Lima MM, Sarquis O (2008) Is *Rhodnius nasutus* (Hemiptera; Reduviidae) changing its habitat as a consequence of human activity? Parasitol Res 102(4):797–800

Lima-Cordón RA, Monroy MC, Stevens L, Rodas A, Rodas GA, Dorn PL, Justi SA (2019) Description of *Triatoma huehuetenanguensis* sp. n., a potential Chagas disease vector (Hemiptera, Reduviidae, Triatominae). ZooKeys 820:51–70. https://doi.org/10.3897/zookeys.820.27258

Lukhtanov VA, Shapoval NA, Anokhin BA, Saifitdinova AF, Kuznetsova VG (2015) Homoploid hybrid speciation and genome evolution via chromosome sorting. Proc R Soc B 282:20150157. https://doi.org/10.1098/rspb.2015.0157

Lyman DF, Monteiro FA, Escalante AA, Cordón-Rosales C, Wesson DM, Dujardin JP, Beard CB (1999) Mitochondrial DNA sequence variation among Triatomine vectors of Chagas disease. Am J Trop Med Hyg 60:377–386

Mallet J (1995) A species definition for the modern synthesis. Trend Ecol Evol 10:294–304

Marchant A, Mougel F, Almeida C, Jacquin-Joly E, Costa J, Harry M (2015) De novo transcriptome assembly for a non-model species, the blood-sucking bug *Triatoma brasiliensis*, a vector of Chagas disease. Genetica 143:225–239

Marcilla A, Bargues MD, Abad-Franch F, Panzera F, Noireau F, Galvão C, Jurberg J, Miles MA, Dujardin JP, Mas-Coma S (2002) Nuclear rDNA ITS-2 sequences reveal polyphyly of *Panstrongylus* species (Hemiptera: Reduviidae: Triatominae), vectors of *Trypanosoma cruzi*. Infect Genet Evol 1:225–235

Marcilla A, Bargues MD, Ramsey JM, Magallón-Gastélum E, Salazar-Schettino PM, Abad-Franch F, Dujardin JP, Schofield CJ, Mas-Coma S (2001) The ITS-2 of the nuclear rDNA as a molecular marker for populations, species, and phylogenetic relationships in Triatominae (Hemiptera: Reduviidae), vectors of Chagas disease. Mol Phylogenet Evol 18:136–142

Masters JC, Rayner RJ, McKay IJ, Potts AD, Nails D, Ferguson JW, Weissenbacher BK, Allsopp M, Anderson ML (1987) The concept of species: recognition versus isolation. S Afr J Sci 83:534–537

Mayden RL (1997) A hierarchy of species concepts: the denouement in the saga of the species problem. In: Claridge MF, Dawah HA, Wilson MR (eds) Species: the units of diversity. Chapman and Hall, London, pp 381–423

Mayr E (1942) Systematics and the origin of species. Columbia University Press, New York

Mayr E (1963) Animal species and evolution. The Belknap Press of Harvard University Press, Cambridge

Meier R, Willmann R (2000) The Hennigian species concept. In: Wheeler QD, Meier R (eds) Species concepts and phylogenetic theory. Columbia University Press, New York, pp 30–43

Mesquita RD, Vionette-Amaral RJ, Lowenbergerd C, Rivera-Pomar R, Monteiro FA, Minx P, Spieth J, Carvalho AB, Panzera F, Lawson D, Torres AQ, Ribeiro JMC, Sorgine MHF, Waterhouse RM, Montague A-FF, Alves-Bezerra M, Amaral LR, Araujo HM, Araujo RN, Aravindu LMJ, Atella GC, Azambuja P, Berni M, Bittencourt-Cunha PR, Braz GRC, Calderón-Fernández G, Carareto CMA, Christensen MB, Costa IR, Costa SG, Dansa M, Daumas-Filho CRO, De-Paula IF, Dias FA, Dimopoulos G, Emrich SJ, Esponda-Behrens N, Fampa P, Fernandez-Medina RD, Fonseca RN, Fontenele M, Fronick C, Fulton LA, Gandara AC, Garcia ES, Genta FA, Giraldo-Calderón GI, Gomes B, Gondim KC, Granzotto A, Guarneri AA, Guigóf R, Harry M, Hughes DST, Jablonka W, Jacquin-Joly E, Juárez MP, Koerich LB, Langek AB, Latorre-Estivalis JM, Lavore A, Lawrence GG, Lazoski C, Lazzari CR, Lopes RR, Lorenzo MG, Lugon MD, Majerowicz D, Marcet PL, Mariotti M, Masuda H, Megy K, Melo ACA, Missirlis F, Mota T, Noriega FG, Nouzova M, Nunes RD, Oliveira RLL, Oliveira-Silveira G, Ons S, Orchard I, Pagola L, Paiva-Silva GO, Pascual A, Pavan MG, Pedrini N, Peixoto AA, Pereira MH, Pike

A, Polycarpo C, Prosdocimi F, Ribeiro-Rodrigues R, Robertson HM, Salerno AP, Salmon D, Santesmasses D, Schama R, Seabra-Junior ES, Silva-Cardoso L, Silva-Neto MAC, Souza-Gomes M, Sterkel M, Taracena ML, Tojo M, Tu ZJ, Tubio JMC, Ursic-Bedoya R, Venancio TM, Walter-Nuno AB, Wilson D, Warren WC, Wilson RK, Huebner E, Dotson EM, Oliveira PL (2015) Genome of *Rhodnius prolixus*, an insect vector of Chagas disease, reveals unique adaptations to hematophagy and parasite infection. PNAS USA 112:14936–14941

Meyer JR, Dobias DT, Medina SJ, Servilio L, Gupta A, Lenski RE (2016) Ecological speciation of bacteriophage lambda in allopatry and sympatry. Science 354(6317):1301–1304

Mishler BD (1985) The morphological, developmental, and phylogenetic basis of species concepts in bryophytes. Bryologist 88:207–214

Monteiro FA, Escalante AA, Beard CB (2001) Molecular tools and triatomine systematics: a public health perspective. Trends Parasitol 17:344–347

Monteiro FA, Barrett TV, Fitzpatrick S, Cordón-Rosales C, Feliciangeli D, Beard CB (2003) Molecular phylogeography of the Amazonian Chagas disease vectors *Rhodnius prolixus* and *R. robustus*. Mol Ecol 12:997–1006

Monteiro FA, Donnelly MJ, Beard CB, Costa J (2004) Nested clade and phylogeographic analyses of the Chagas disease vector *Triatoma brasiliensis* in Northeast Brazil. Mol Phylogenet Evol 32:46–56

Monteiro FA, Peretolchina T, Lazoski C, Harris K, Dotson EM, Abad-Franch F, Tamayo E, Pennington PM, Monroy C, Cordón-Rosales C, Salazar-Schettino PM, Gómez-Palacio AM, Grijalva MJ, Beard CB, Marcet PL (2013) Phylogeographic pattern and extensive mitochondrial DNA divergence disclose a species complex within the Chagas disease vector *Triatoma dimidiata*. PLoS One 8:e70974

Monteiro FA, Weirauch C, Felix M, Lazoski C, Abad-Franch F (2018) Evolution, systematics, and biogeography of the Triatominae, vectors of Chagas disease. Adv Parasitol 99:265–344. https://doi.org/10.1016/bs.apar.2017.12.002

Moreno J, Galvão C, Jurberg J (1999) *Rhodnius colombiensis* sp. n da Colômbia, com quadros comparativos entre estruturas fálicas do gênero *Rhodnius* Stal, 1859 (Hemiptera, Reduviidae, Triatominae). Entomol Vectores 6:601–617

Mullen SP, Shaw KL (2014) Insect speciation rules: unifying concepts in speciation research. Annu Rev Entomol 59:339–361

Murren CJ, Auld JR, Callahan H, Ghalambor CK, Handelsman CA, Heskel MA, Kingsolver JG, Maclean HJ, Masel J, Maughan H, Pfennig DW, Relyea RA, Seiter S, Snell-Rood E, Steiner UK, Schlichting CD (2015) Constraints on the evolution of phenotypic plasticity: limits and costs of phenotype and plasticity. Heredity 115(4):293–301. https://doi.org/10.1038/hdy.2015.8

Nattero J, Malerba R, Rodríguez CS, Crocco L (2013) Phenotypic plasticity in response to food source in *Triatoma infestans* (Klug, 1834) (Hemiptera, Reduviidae: Triatominae). Infect Genet Evol 19:38–44

Nelson G, Platnick NI (1981) Systematics and biogeography. Columbia University Press, New York

Nixon KC, Wheeler QD (1990) An amplification of the phylogenetic species concept. Cladistics 6:211–223

Nosil P (2007) Divergent host-plant adaptation and reproductive isolation between ecotypes of *Timema cristinae*. Am Nat 169:151–162

Nosil P, Flaxman SM (2010) Conditions for mutation-order speciation. Proc R Soc B 278:399–407. https://doi.org/10.1098/rspb.2010.1215

Nosil P, Harmon LJ, Seehausen O (2009) Ecological explanations for (incomplete) speciation. Trends Ecol Evol 24:145–156

Nosil P, Parchman TL, Feder JL, Gompert Z (2012) Do highly divergent loci reside in gene regions affecting reproductive isolation? A test using next-generation sequence data in *Timema* stick insects. BMC Evol Biol 12:164

Orantes LC, Monroy C, Dorn PL, Stevens L, Rizzo DM, Morrissey L, Hanley JP, Rodas AG, Richards B, Wallin KF, Cahan SH (2018) Uncovering vector, parasite, blood meal and microbiome patterns from mixed-DNA specimens of the Chagas disease vector *Triatoma dimidiata*. PLoS Negl Trop Dis 12(10):e0006730. https://doi.org/10.1371/journal.pntd.0006730

Orr HA (1995) The population genetics of speciation: the evolution of hybrid incompatibilities. Genetics 139:1805–1813

Panzera F, Ferrandis I, Ramsey JM, Ordóñez R, Salazar-Schettino PM, Cabrera M, Monroy MC, Bargues MD, Mas-Coma S, O'Connor JE, Angulo VM, Jaramillo N, Cordón-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. Tropical Med Int Health 11:1092–1103

Panzera F, Ferrandis I, Ramsey J, Salazar-Schettino PM, Cabrera M, Monroy C, Bargues MD, Mas-Coma S, O'Connor JE, Angulo VM, 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

Paterson HEH (1985) The recognition concept of species. In: Vrba ES (ed) Species and speciation. Transvaal Museum, Pretoria, pp 21–29

Patterson JS, Gaunt MW (2010) Phylogenetic multi-locus codon models and molecular clocks reveal the monophyly of haematophagous reduviid bugs and their evolution at the formation of South America. Mol Phylogenet Evol 56:608–621

Patterson JS, Schofield CJ, Dujardin JP, Miles MA (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

Pavan MG, Monteiro FA (2007) A multiplex PCR assay that separates *Rhodnius prolixus* from members of the *Rhodnius robustus* cryptic species complex (Hemiptera: Reduviidae). Tropical Med Int Health 12:751–758

Pavan MG, Mesquita RD, Lawrence GG, Lazoski C, Dotson EM, Abubucker S, Mitreva M, Randall-Maher J, Monteiro FA (2013) A nuclear single-nucleotide polymorphism (SNP) potentially useful for the separation of *Rhodnius prolixus* from members of the *Rhodnius robustus* cryptic species complex (Hemiptera: Reduviidae). Infect Genet Evol 14:426–433

Pavan MG, Rivas GBS, Dias FBS, Gurgel-Gonçalves R (2015) Looks can be deceiving: cryptic species and phenotypic variation in *Rhodnius* spp., Chagas disease vectors. In: Pontarotti P (ed) Evolutionary biology: biodiversification from genotype to phenotype. Springer, Cham, pp 345–372

Pavan MG, Correa-Antônio J, Peixoto AA, Monteiro FA, Rivas GBS (2016) *Rhodnius prolixus* and *R. robustus* (Hemiptera: Reduviidae) nymphs show different locomotor patterns on an automated recording system. Parasit Vectors 9:239

Pfeiler E, Bitler BG, Ramsey JM, Palacios-Cardiel C, Markow TA (2006) Genetic variation, population structure, and phylogenetic relationships of *Triatoma rubida* and *T. recurva* (Hemiptera: Reduviidae: Triatominae) from the Sonoran Desert, insect vectors of the Chagas' disease parasite *Trypanosoma cruzi*. Mol Phylogenet Evol 41:209–221

Pita S, Lorite P, Nattero J, Galvão C, Alevi KC, Teves SC, Azeredo-Oliveira MT, Panzera F (2016) New arrangements on several species subcomplexes of *Triatoma* genus based on the chromosomal position of ribosomal genes (Hemiptera - Triatominae). Infect Genet Evol 43:225–231

Pita S, Panzera F, Vela J, Mora P, Palomeque T, Lorite P (2017) Complete mitochondrial genome of *Triatoma infestans* (Hemiptera, Reduviidae, Triatominae), main vector of Chagas disease. Infect Genet Evol 54:158–163

Poux C, Chevret P, Huchon D, de Jong WW, Douzery EJ (2006) Arrival and diversification of caviomorph rodents and platyrrhine primates in South America. Syst Biol 55(2):228–244

Ribeiro JM, Genta FA, Sorgine MH, Logullo R, Mesquita RD, Paiva-Silva GO, Majerowicz D, Medeiros M, Koerich L, Terra WR, Ferreira C, Pimentel AC, Bisch PM, Leite DC, Diniz MM, Junior JL, Silva ML, Araujo RN, Gandara AC, Brosson S, Salmon D, Bousbata S, González-Caballero N, Silber AM, Alves-Bezerra M, Gondim KC, Silva-Neto MA, Atella GC, Araujo H, Dias FA, Polycarpo C, Vionette-Amaral RJ, Fampa P, Melo AC, Tanaka AS, Balczun C, Oliveira JH, Gonçalves RL, Lazoski C, Rivera-Pomar R, Diambra L, Schaub GA, Garcia ES, Azambuja P, Braz GR, Oliveira PL (2014) An insight into the transcriptome of the digestive tract of the bloodsucking bug, *Rhodnius prolixus*. PLoS Negl Trop Dis 8:e2594

Richards CL, Bossdorf O, Pigliucci M (2010) What role does heritable epigenetic variation play in phenotypic evolution? Bioscience 60:232–237

Ridley M (1989) The cladistic solution to the species problem. Biol Philos 4:1–16

Rosen DE (1979) Fishes from the uplands and intermontane basins of Guatemala: revisionary studies and comparative geography. Bull Am Mus Nat Hist 162:267–376

Ryckman RE (1962) Biosystematics and hosts of the *Triatoma protracta* complex in North America (Hemiptera: Reduviidae) (Rodentia: Cricetidae). Univ Calif Publ Entomol 27:93–240

Ryckman RE (1967) Six new populations of Triatominae from Western North America (Hemiptera: Reduviidae). Bull Pan-American Res Inst 1:1–3

Sandoval CM, Blanco EEN, Marin RG, Mendez DAJ, Rodríguez NO, Otálora-Luna F, Aldana EJ (2015) Morphometric analysis of the host effect on phenotypical variation of *Belminus ferroae* (Hemiptera: Triatominae). Psyche 2015:613614. https://doi.org/10.1155/2015/613614

Sarquis O, Borges-Pereira J, Mac Cord JR, Gomes TF, Cabello PH, Lima MM (2004) Epidemiology of Chagas disease in Jaguaruana, Ceará, Brazil I: presence of triatomines and index of *Trypanosoma cruzi* infection in four localities of a rural area. Mem Inst Oswaldo Cruz 99(3):263–270

Schachter-Broide J, Dujardin JP, Kitron U, Gürtler RE (2004) Spatial structuring of *Triatoma infestans* (Hemiptera, Reduviidae) populations from northwestern Argentina using wing geometric morphometry. J Med Entomol 41:643–649

Schofield CJ (1988) Biosystematics of the Triatominae. In: Sevice MW (ed) Biosystematics of haematophagous insects, systematics association, special volume 37. Clarendon Press, Oxford, pp 284–312

Schofield CJ, Dujardin JP (1999) Theories on the evolution of *Rhodnius*. Actual Biol 21:183–197

Schofield CJ, Galvão C (2009) Classification, evolution and species groups within the Triatominae. Acta Trop 110:88–100

Simpson GG (1951) The species concept. Evolution 5:285–298

Stothard JR, Yamamoto Y, Cherchi A, García AL, Valente SAS, Schofield CJ, Miles MA (1998) A preliminary survey of mitochondrial sequence variation within triatomine bugs (Hemiptera: Reduviidae) using polymerase chain reaction-based single strand conformational polymorphism (SSCP) analysis and direct sequencing. Bull Entomol Res 88:553–560

Tang SW, Presgraves DC (2009) Evolution of the *Drosophila* nuclear pore complex results in multiple hybrid incompatibilities. Science 323:779–782

Templeton AR (1989) The meaning of species and speciation: a genetic perspective. In: Otte D, Endler JA (eds) Speciation and its consequences. Sinauer Associates, Sunderland, pp 3–27

Templeton AR (1998) Species and speciation: geography, population structure, ecology, and gene trees. In: Howard DJ, Berlocher SH (eds) Endless forms: species and speciation. Oxford University Press, New York, pp 32–43

Traverso L, Sierra I, Sterkel M, Francini F, Ons S (2016) Neuropeptidomics in *Triatoma infestans.* Comparative transcriptomic analysis among triatomines. J Physiol Paris 3:83–98

Turelli M, Barton NH, Coyne JA (2001) Theory and speciation. Trends Ecol Evol 16:330–343

Usinger RL (1944) The Triatominae of North and Central America and the West Indies and their public health significance. US Publ Health Bull 288:1–83

Usinger RL, Wygodzinsky P, Ryckman RE (1966) The biosystematics of Triatominae. Annu Rev Entomol 11:309–330

Valença-Barbosa C, Lima MM, Sarquis O, Bezerra CM, Abad-Franch F (2014) A common Caatinga cactus, *Pilosocereus gounellei*, is an important ecotope of wild *Triatoma brasiliensis* populations in the Jaguaribe valley of northeastern Brazil. Am J Trop Med Hyg 90(6):1059–1062

Van Valen L (1976) Ecological species, multispecies, and oaks. Taxon 25:233–239

Wiens JJ, Tiu J (2012) Highly incomplete taxa can rescue phylogenetic analyses from the negative impacts of limited taxon sampling. PLoS One 7:e42925

Wiley EO (1978) The evolutionary species concept reconsidered. Syst Zool 27:17–26

Wilkins JS (2011) Philosophically speaking, how many species concepts are there? Zootaxa 2765:58–60

Xie X, Rull J, Michel AP, Velez S, Forbes AA, Lobo NF, Aluja M, Feder JL (2007) Hawthorn-infesting populations of *Rhagoletis pomonella* in Mexico and speciation mode plurality. Evolution 61:1091–1105

Zhang Y-Y, Fisher M, Colot V, Bossdorf O (2013) Epigenetic variation creates potential for evolution of plant phenotypic plasticity. New Phytol 197:314–332