

REVIEW

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Evolution of hematophagous habit in Triatominae (Heteroptera: Reduviidae)

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Abstract

All members of Triatominae subfamily (Heteroptera: Reduviidae), potential vectors of *Trypanosoma cruzi*, etiologic agent of the Chagas disease, feed on blood. Through evolution, these bugs have fixed special morphological, physiological, and behavioral adaptations (adaptations and exaptations) adequate to feed on blood. Phylogeny suggests that triatomines evolved from predator reduvids which in turn descended from phytophagous hemipterans. Some pleiomorphic traits developed by the reduvid ancestors of the triatomines facilitated and modeled hematophagy in these insects. Among them, mouthparts, saliva composition, enzymes, and digestive symbionts are the most noticeable. However, the decisive step that allowed the shift from predation to hematophagy was a change of behavior. The association of a predator reduvid with nesting vertebrate (≈ 110 to 32 Ma) permitted the shift from an arthropod prey to a vertebrate host. In this work, we review the phylogeny and dispersion of triatomines and the current controversy over the monophyly or polyphyly of this group. We also discuss how these insects were able to overcome, and even have taken advantage of, diverse ancestral and physical barriers to adapt to sucking blood of nidicolous vertebrates. We provide a Spanish version of this work.

Keywords: Latin America; Chagas' disease; Phylogeny; Blood-sucking habit; Triatomines

Introduction

The triatomines are an insect subfamily of the Reduviidae family in the Hemiptera order, known by various names in different regions of America, among which the most common are as follows: vinchuca (from Ecuador to Patagonia), chipo (Venezuela), pito (Colombia), barbeiro (Brazil), chinche (Central America and Mexico), and kissing bug (USA) (Lent and Wygodzinsky 1979; Schofield and Galvão 2009). The members of this subfamily are almost entirely hematophagous, although there are cases of some species that feed on other invertebrates (Sandoval et al. 2004, 2010). It is known that triatomines live together with nidicolous (nesting) vertebrates, whose blood they extract for nourishment, and certain species infest human homes and buildings (Noireau and Dujardin 2010). All triatomines species are considered potential vectors of the *Trypanosoma cruzi* (Chagas) parasite, the etiological agent of the Chagas' disease; nonetheless, only about 20 species are considered of epidemical importance

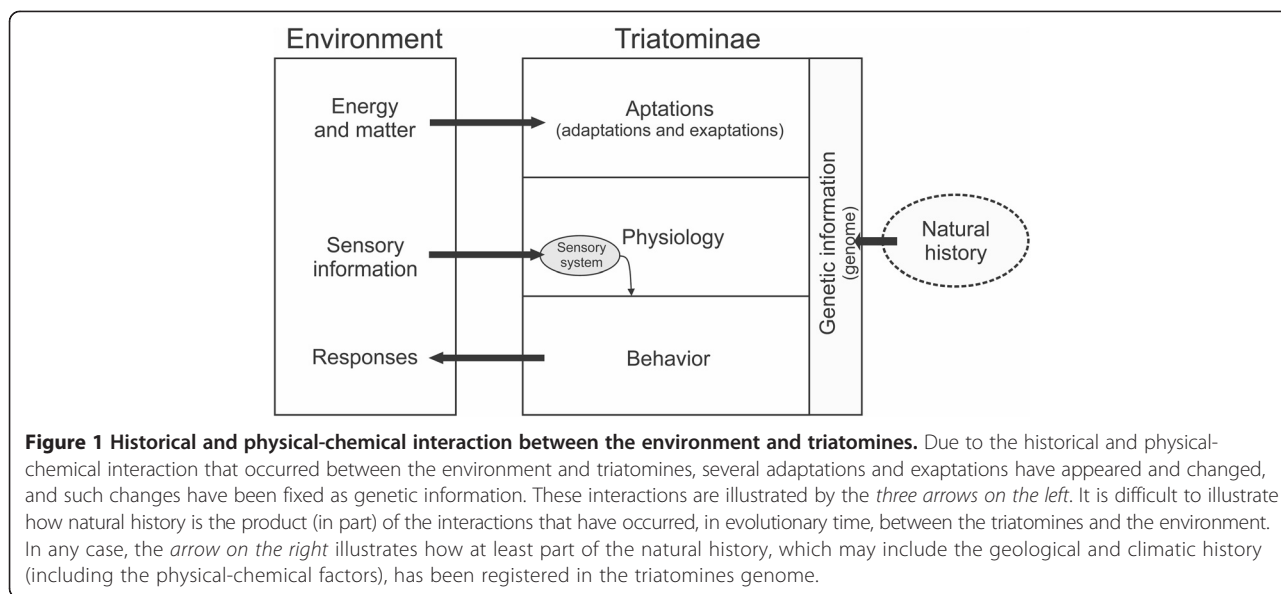
due to their clear involvement in the domestic and peridomestic transmission cycles. The species *Triatoma infestans* (Klug), *Rhodnius prolixus* (Stål), *Triatoma dimidiata* (Latreille), and *Triatoma brasiliensis* (Neiva) are recognized as the principal vectors in Latin America (Lent and Wygodzinsky 1979; Bargues et al. 2010; Rabinovich et al. 2011; Stevens et al. 2011).

The hematophagous habit has marked the natural history of the triatomines. Furthermore, this habit has stamped them with striking anthropological importance, given that this was what included them in the parasite's life cycle and eventually humans as well, as hosts. How the triatomines got to be bloodsuckers depended on the genetic complex these organisms inherited from their non-hematophagous ancestors by means of different evolutionary mechanisms that have been suggested, and the restrictions imposed by their physical surroundings (sensu Dusenbery 2001; Figure 1). In addition to considering the adaptive value of certain morphological, physiological, and behavioral traits associated with this habit, it is necessary to take into consideration how the physical and chemical laws that have governed the universe's functioning made possible its appearance. In

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other words, given that the phenotypical expression is not limited only by restrictions on their functioning but also by the way they were made (physical restraints) and by their past (historical and phylogenetic limits), it must be supposed that the driven force could be as much historical-genetic as environmental (sensu De Renzi 2009; Dusenbery 2001; Figure 1). The theory of functional morphology or biomorphodynamics has advanced considerably towards this neo-evolutionary line of thinking (De Renzi 2009) and has allowed us to understand better the triatomines' evolution (e.g., González et al. 2009). This review will offer a sketch of the phylogeny and radiation of the group and will show how these insects could have overcome, and even taken advantage of, several physical and ancestral barriers to adapt to bloodsucking of a nidicolous host. We discuss how the step from preying to bloodsucking was influenced by, among other things, a change of behavior of the reduvidian ancestors of the triatomines. We provide a Spanish version of this work (Additional file 1).

Review

Triatomines phylogeny

Hemiptera

The beginnings of the Hemiptera order go back to the late Carboniferous, 300 million years ago (Ma), with fossils dated to the Early Permian (Wootton 1981; Burmester 2001; Grimaldi and Engel 2005; Table 1). Nearly 82,000 species have been described within this monophyletic order, and it is by far the largest group of hemimetabolic insects, whose diversity is probably related to the radiation of the angiosperms (Gillot 2005; Grimaldi and Engel 2005; Forero 2008). According to Dolling (1991), the success of hemipterans could be based on the following characteristics: (i) compact flat bodies, a trait which allows them to

find refuge, and in some cases, food; (ii) ability to fly in the adult stage (for the majority of the species), an important characteristic for the exploitation of new and better resources; (iii) a highly concentrated nervous system which permits fast and varied movements; and (iv) the presence

Table 1 Time of emergence of hemipteroid insects and some warm blooded vertebrates

Era	Period	Epoch	Date (Ma)	Originated group (Ma)
Cenozoic	Quaternary	Holocene	0.012	Triatomines domiciliation
		Pleistocene	2.6	
	Neogene	Pliocene	5.3	(Nidicolous vertebrates diversification)
		Miocene	23	
	Paleogene	Oligocene	34	Triatominae (≈32 to 110) ^a
		Eocene	55	
Mesozoic	Cretaceous		144	Birds (≈150)
			206	Mammals (≈200)
			250	Reduviidae (≈230)
Paleozoic	Permian		290	Hemiptera (≈300)
	Carboniferous		354	
	Devonian		417	
	Silurian		443	
	Ordovician		490	
	Cambrian		543	

The geological data correspond to millions of years (Ma). ^aThere is a broad debate about the date of origin of Triatominae; for more information, see the text.

of a piercing-sucking buccal mechanism by means of which they can access various vegetal fluids and animal tissues. In this sense, it is believed that the first Hemiptera were phytophagous and both that entomophagy and hematophagy evolved from these sap and phloem-sucking insects (Grimaldi and Engel 2005).

Heteroptera

Traditionally, the Hemiptera order has been divided in two groups or suborders, Homoptera (Sternorrhyncha and Auchenorrhyncha) and Heteroptera, which includes the triatomines (Dolling 1991; Gillot 2005). With nearly 40,000 known species, Heteroptera is sometimes accepted as a complete order and as a monophyletic taxon (Dolling 1991; Forero 2008; Weirauch and Schuh 2011). This group is recognized principally by its hemelytrous forewings, which present a chitinous area from the anterior part to the middle (corium) and a membranaceous area from the middle to the distal part (Grimaldi and Engel 2005; Weirauch and Schuh 2011). However, the presence of gula, scent glands on the metathorax and abdomen, and a noticeable reduction of the *tentorium* are their principal synapomorphic characteristics (Forero 2008; Weirauch and Schuh 2011). Although the scent glands are quite conspicuous in the group, they are absent in some aquatic forms (Staddon 1979; Weirauch and Schuh 2011). The appearance of a highly versatile sucking mouth, both functional and effective, could have drawn the group's evolution (Vázquez and López 1999) through aptation processes, which means processes of adaptation and exaptation^a (sensu Gould and Vrba 1982; De Renzi 2009). Note that we associate the term *functional* to the concept of adaptations and the term *effective* to that of exaptations; therefore, the adaptations have *functions*, while the exaptations have *effects*^b (Gould and Vrba 1982; De Renzi 2009). Only Heteroptera has a hard conspicuous gula, an area of the cuticle next to the ventral region of the cephalic capsule that separates the mouthparts from the prothorax, which represents a specialized morphologic aptation that permits the suction of liquids (Lent and Wygodzinsky 1979; Grimaldi and Engel 2005). The result has been the ability to move the rostrum forwards and allow them a greater freedom of movement than have members of Sternorrhyncha and Auchenorrhyncha. This versatile proboscis lets the heteroptera to exploit a greater variety of alimentary resources, including animal tissue (Grimaldi and Engel 2005). The absence of predators in Homoptera, and their presence in Heteroptera, suggests that the appearance of predation preceded the appearance of hematophagy, which could signal the divergence of the Reduviidae, and eventually of the Triatominae, within the Heteroptera (Vázquez and López 1999).

Predation is common in heteroptera, and many of the families consist totally of insect predators (entomophages) that occupy a broader range of habitats than the other phytophagous members. The hematophagy appears to have risen more than once stemming from predator heteroptera. Some families, like Cimicidae, Polyctenidae, and Reduviidae, have developed the capacity to feed on vertebrate blood (Lehane 2005). Cimicidae (bedbugs) feed exclusively on vertebrate blood, usually of birds, bats, and human beings; while all the members of the small Polyctenidae family (e.g. *Eoctenes spasmos* Waterhouse) feed on bats in both the Old and the New World (Kim 1985; Lehane 2005). Within the Reduviidae, the members of the Triatominae subfamily feed on the blood of several nidicolous vertebrates. Hence, it seems probable that the hematofagous heteroptera of the Cimicidae, Polyctenidae, and Reduviidae families are all descendents of earlier primitive predator forms, which have not necessarily been intimately related from the phylogenetic point of view, so that hematophagy could have appeared more than once in the history of the evolution of these groups.

The records of hematophagy in other families of Heteroptera have been anecdotic or have only shown a facultative capacity for bloodsucking. The majority of the Lygaeidae family (Cleradini tribe), descendants of earlier plant- and grain-eating forms, are normally seed eaters. But, some of them feed on other insects and can, as in the case of the more developed nymphs and adults of *Clerada apicicornis* (Signoret), steal blood from recently fed triatomines or feed directly on vertebrates in repose under laboratory conditions (Torres et al. 2000). Apparently, some members of the Anthocoridae family or flower bugs, specifically *Anthocoris pilosus* (Jakovlev) and *Lyctocoris campestris* (Fabricius), are facultative blood consumers. Some species of the family Miridae or capsid bugs will feed on vertebrate blood if they are permitted to do so, and at least one member of the Physoderinae (Reduviidae) subfamily, *Cryptophysoderes fairchildi* (Wygodzinsky & Maldonado), can do so also (Carcavallo et al. 2000). Nonetheless, the majority of the bites of these groups are apparently exploratory and do not lead to a prolonged feeding.

Reduviidae

The reduviids comprise 25 subfamilies and nearly 6,800 described species (Maldonado-Capriles 1990; Hwang and Weirauch 2012). They represent a pleisiomorphic family among heteroptera, whose fossil registry suggests the appearance of the first predator forms during the Permian-Triassic, 230 Ma (Maldonado-Capriles 1990; Grimaldi and Engel 2005; Table 1). Nonetheless, there are certain molecular studies that indicate a more recent date, putting the origin at the middle of the Jurassic, 178 Ma (Hwang and Weirauch 2012). These same studies

suggest that the diversification of lineage occurred at the end of the Cretaceous (97 Ma) and continued during the Miocene. Comparatively, the most primitive subfamily would be Peiratinae (originated 97 Ma), while the most developed would be Triatominae (Hwang and Weirauch 2012), whose origin will be discussed later on. Although the Reduviidae family is generally considered to be tropical, the reduviids are distributed throughout all the continents (excepting Antarctica). According to Aldrich (1988), in the reduviids (and the phymatids), the sedentary mode of capturing prey and the use of the proboscis for attack and defense appear to have contributed to the shrinking of the metathoracic and dorsal-abdominal scent glands, along with the evolution of new exocrine glands. Thus, two new pairs of sack-like glands have arisen: the Brindley glands, located on the side of the metathorax (Staddon 1979). The isobutyric acid secretion is always present in the triatomine Brindley glands, except in *Dipetalogaster maximus* (Uhler) that does not bear such glands (Guerenstein and Guerin 2004). The presence of a rostrum (*labium*) mostly short and robust, notably arched and separated from the body that do not extend further than the prosternum, is a unique characteristic of the reduviids. These characteristics of the mouthparts have been lost in a secondary fashion in the triatomines and in some members of the Harpactorinae subfamily, in which we find a longer and more flexible *labium*. As in other families, all the reduviids are able to stridulate, rubbing the peak of the rostrum in a transversally striated groove located on the prosternum (i.e., the stridulitrum or stridulatory sulcus), and have laterally inserted antennae.

With respect to their behavior, the reduviids form an important group of aggressive predators, the majority of the species being hunters that ambush and grab their victims with fore legs frequently modified specifically for that purpose. These morphologic and behavioral characteristics that were developed while the Reduviidae were predators undoubtedly could have eased the way, both on a functional and an effective basis, for the radiation of the Triatominae subfamily.

Triatominae

The Triatominae subfamily is formed by 144 described species, grouped in 15 genera and five tribes (Lent and Wygodzinsky 1979; Galvão et al. 2003; Schofield and Galvão 2009; Bargues et al. 2010; Da Rosa et al. 2012; Gonçalves et al. 2013; Table 2). The majority of the species are concentrated in America, although six species of the *Linschosteus* genus inhabit continental India and eight species of the *Triatoma* genus (*rubrofasciata* complex) are distributed from south-east Asia to New Guinea and the north of Australia (Bargues et al. 2010). No native or endemic species have been found on the African continent. With the exception of some species

Table 2 Tribes, genera, and species in the Triatominae subfamily

Tribes	Genera	Number of species
Alberproseniini	<i>Alberprosenia</i>	2
Bolboderini	<i>Belminus</i>	8
	<i>Bolbodera</i>	1
	<i>Microtriatoma</i>	2
	<i>Parabelminus</i>	2
Cavernicolini ^a	<i>Cavernicola</i>	2
Rhodniini	<i>Psammolestes</i>	3
	<i>Rhodnius</i> ^b	17
Triatomini	<i>Dipetalogaster</i>	1
	<i>Eratyrus</i>	2
	<i>Hermanlenticia</i> ^c	1
	<i>Linschosteus</i> ^d	6
	<i>Panstrongylus</i> ^e	14
	<i>Paratriatoma</i>	1
	<i>Triatoma</i> ^f	81
Total	15	144

Modified from Galvão et al. (2003), Schofield and Galvão (2009), and Bargues et al. (2010). ^aPreviously, Galvão et al. (2003) included *Torrealbaia martinezi* (Carcavallo, Jurberg & Lent) in the Cavernicolini tribe due to strong morphological similarities with that group. Later on, Forero et al. (2004) identified the synonymy existing between *Torrealbaia* (Triatominae) and *Amphibolus* (Harpactorinae) genera and re-describe this species as *Amphibolus venator* (Klug) in Harpactorinae. ^bIncludes *Rhodnius montenegrensis* sp. Described by Da Rosa et al. (2012) for the state of Rondônia in Brazil. ^cFormerly described as *Triatoma matsunoi* (Fernández-Loayza) (Galvão et al. 2003). ^dWas proposed as a new tribe (Linschosteini) due to its geographic distribution and non-shared morphological characteristics (Schaefer and Coscarón 2001; Galvão et al. 2003). Nonetheless, ADN sequence comparisons (16S and 28S) suggest that the species of the *Linschosteus* genus are genetically related to *T. rubrofasciata* and could be local derivations of a common ancestor (Hypša et al. 2002; Schofield and Galvão 2009). ^eIncludes *Panstrongylus martinezorum* described by Ayala (2009) from the vicinity of Puerto Ayacucho - Venezuela, and absent from the lists of Schofield and Galvão (2009), and Bargues et al. (2010). ^fIncludes the *Meccus* (*phyllosoma* complex), *Mepraia* (*spinolai* complex), and *Nesotriatoma* (*flavida* complex) genera previously considered as complete taxa (Galvão et al. 2003), although now they are included in the *rubrofasciata* e *infestans* groups of the *Triatoma* genus (Schofield and Galvão 2009; Bargues et al. 2010). Includes *Triatoma jatai* described by Gonçalves et al. (2013) from Tocantins state, Brazil.

of the *Belminus* genus, all the members of Triatominae are bloodsuckers that live in association with vertebrated hosts, either in sylvan habitats like palm trees, bird nests, rodent burrows, or caves or in domestic and peridomicile dwellings (Lent and Wygodzinsky 1979; Sandoval et al. 2013). Some species live in a variety of ecotopes and feed on different hosts (Carcavallo et al. 1998), while others are more specialized, as occurs with the *Psammolestes* genus whose members are linked to birds of the Furnariidae family or the *Triatoma delpontei* (Romana & Abalos) which is associated with the psittacine parrots *Myiopsitta monachus* (Boddaert) (Salvatella et al. 1993). Other specialized examples are *Triatoma rubrofasciata* (De Geer) and *Cavernicola pilosa* (Barber), species that prefer to feed on rodents and bats respectively

(Lent and Wygodzinsky 1979; Noireau and Dujardin 2010).

Monophyly, polyphyly, or paraphyly

The first phylogenetic hypothesis for the Triatominae subfamily states a monophyletic origin (Usinger 1944). This hypothesis was followed and developed by Lent and Wygodzinsky (1979) on the base of three autoapomorphies: (i) the hematophagous feeding habit; (ii) the presence of a *labium* with flexible membranaceous connections between the second and third segment of the mouthparts, which permits advancing the distal pointed segment of the rostrum upwards when is in feeding position; and (iii) the loss of the dorsal scent glands in nymphs. However, there is a controversy with marked differences of opinion about whether the hematophagous habit appeared just once or more times during the phylogenetic history of the group (Galvão 2003). Schofield (1988) is the principal advocate of the polyphyletic hypothesis for the subfamily and states that not only the members of the Rhodniini tribe but also other genera within the Triatomini tribe (*Dipetalogaster*, *Panstrongylus*, and *Eratyrus*) may represent groups which originated from different phylogenetically unrelated reduviids. This idea was originally based on the morphologic disparity exhibited by members of these tribes, along with the existing differences in the physiology of their salivary glands and population parameters (Schofield 1996; Catalá 1997; Ribeiro et al. 1998). The study of nucleotide diversity among the members of the Rhodniini and Triatomini tribes by Marcilla et al. (2001) is proposed as an argument in favor of this hypothesis. De Paula et al. (2005) present the first molecular evidence of the polyphyletic origin of the subfamily and showed a separation between the Rhodniini and Triatomini tribes by predatory groups. In that work, it is suggested that the Reduviinae subfamily is a brother group of Triatomini, and the subfamilies Salyavatinae and Harpactorinae are brother groups of Rhodniini. According to Schofield and Galvão (2009), there is substantial evidence to support the polyphyletic origin of the triatomines, based mainly on genetic comparisons using the mitochondrial marker 16S and on morphometric comparisons based on the form of head and wings. These authors point out that the previous phylogenetic reconstructions were the result of artifacts in the analysis, products of the exclusion of predatory taxa highly characteristic of Reduviinae. The evolutionary process that this approach visualizes is that the hematophagous habit arose several times within Triatominae, and so the existing subfamily would represent a polyphyletic assembly of species that has been defined on the basis of convergent apomorphic characteristics related to hematology (Schofield 1988; Schofield and Galvão 2009). In the last decade, several phylogenetic reconstructions that

recover the monophyletic or paraphyletic hypotheses of Triatominae have been published. However, it is appropriate to point out that a consensus about the origin of the Triatominae is still far away. Hypša et al. (2002) began the first work on the molecular phylogeny of the subfamily that included 57 taxa of Triatominae with representatives of both the Old and the New World. As external groups, different taxa were included belonging to both Reduviidae and non-Reduviidae. These authors conclude that monophyly of Triatominae is supported by the observations emerged from their work. The paraphyly of *Rhodnius* with respect to *Psammolestes* is proved, such as Lyman et al. (1999) had originally proposed. This finding showed how morphological and ecological changes produce a loss of diagnostic characters which would be expected to be shared by the members of a single monophyletic group. The *Panstrongylus*, *Dipetalogaster*, and *Eratyrus* genera and the species of the Asian clade were grouped with the *Triatoma* genus, which was taken to be the first evidence of the neotropical origin of the subfamily. In conclusion, the authors suggest that at least the hypothesis of separate origins for the genera of the Triatomini tribe appears to be untrue. Later on, Weirauch (2008) lent support to the monophyletic hypothesis in his extensive cladistic study that includes the analysis of 162 morphological characters in 75 species of several subfamilies of Reduviidae and some taxa of the Triatominae. Weirauch and Munro (2009) offered a cladistic analysis of Reduviidae that included 94 taxa (89 of Reduviidae and five external groups), based on molecular data of the mitochondrial marker 16S and the three nuclear markers 18S, 28SD2, and 28SD3-5. This study offered arguments favoring the hypothesis that the hematophagous habit evolved only once in Triatominae, and shed light on the question of the probable brother clades of Triatominae. In the same way, Patterson and Gaunt (2010) gave their support to the monophyletic hypothesis through an analysis of the nuclear marker 28SD2, the mitochondrial markers cytochrome oxidase (cox 1, cox 1 3', and cox 2) and cytochrome b. This work included for the first time a representative of the Bolboderini tribe (*Microtriatoma trinidadensis* Lent) in the analyses of the subfamily.

More recently, Hwang and Weirauch (2012), in a phylogenetic analysis with five molecular markers and 178 taxa representing 18 of the 25 known subfamilies of the Reduviidae, were not able to establish the monophyletic nature of the subfamily but neither could they find support for the polyphyletic hypothesis. On the contrary, their results show that Triatominae is paraphyletic regarding of the Reduviinae genus *Opisthacidius* with a high level of statistical support or that it is part of a polytomy which also includes *Opisthacidius*. The authors point out that additional data are required to clarify the relations among the clades involved and that the disagreement of

their results with previous studies is explained by the inclusion in their study of a greater number of taxa and the form of sampling them. It is appropriate to mention here that previously, authors like Hypša et al. (2002), Schaefer (2003), and Patterson and Gaunt (2010) had admitted the possibility that the origin of this subfamily could include the paraphyletic hypothesis. The controversy is apparently disputing three propositions because at the moment, it is not clear whether the Triatominae subfamily descended from one (monophyletic) ancestor, more than one (polyphyletic) ancestors, or if the group includes the common ancestor but not all the descendants (paraphyletic). However, this last possibility doesn't rule out the monophyly but simply suggests that the descendents available for the study are incomplete (Schaefer 2003, 2005). Studies done by Lent and Wygodzinsky (1979), Hypša et al. (2002), Schaefer (2003, 2005), Schofield and Galvão (2009), Bargues et al. (2010), Stevens et al. (2011), and Hwang and Weirauch (2012) offer critical discussions of the matter.

Origin and radiation of the triatomines

Several doubts are underlying the hypotheses about the origin of any taxon; the most common of which questions the period in which a certain group arose and the geologic and biogeographic events that have conditioned it, needless to mention that those interested in the study of Triatominae are not indifferent to these concerns. As was previously mentioned, the origin and radiation of the Triatominae is at the moment a hotly discussed topic and is related to the monophyly, polyphyly, and paraphyly of the group. Certainly, the idea of a recent polyphyletic evolution in Triatominae implies the possibility that several radiation centers may exist (Schofield and Galvão 2009), and it is therefore not to be expected that the monophyletic groups in the subfamily have necessarily formed at the same time or in the same place. However, the radiation of Triatominae can only be inferred from existing evidence and the group's present distribution. Given the complete absence of triatomines in Europe, the absence of endemic forms in Africa, the existence of very few species in Asia, and the majority in America, their origin is suggested to be in the New World. Nonetheless, the presence of species of the *Triatoma* and *Linshcosteus* genera in the Old World has led some to suggest an origin outside of America for one or both genera (Gorla et al. 1997; Schofield and Galvão 2009). This latest consideration would imply mass extinctions of the populations previously distributed in Asia and the northern part of America and at the same time an evolutionary appearance of hematophagy preceding a considerable number of vicariant events (Patterson et al. 2001; Schaefer and Coscarón 2001; Schofield and Galvão 2009). The most recent opinions based on several

analyses of phylogenetic reconstruction with molecular markers and morphological analyses consider that all the triatomines are of New World origin and that therefore the species of the *Triatoma* and *Linshcosteus* genera in the Old World are derived from a population of *T. rubrofasciata* (Patterson et al. 2001; Hypša et al. 2002; Patterson and Gaunt 2010; Hwang and Weirauch 2012).

In the last few decades, several hypotheses have been suggested referring to the scale of time in which the triatomines arose by means of the use of molecular clocks (see Bargues et al. 2000; Gaunt and Miles 2002; Patterson and Gaunt 2010; Hwang and Weirauch 2012). The first hypothesis following a polyphyletic point of view was offered by Bargues et al. (2000), who propose the appearance of Reduviinae at the time of the isolation of South America and indicate divergence time between the Triatomini and Rhodniini tribes of 48.9 and 64.4 Ma during the separation of South America, Antarctica, and Australia (Table 1). Later on, Gaunt and Miles (2002) predict that the Triatominae's origin lies between 99.8 and 93.5 Ma, coinciding with the formation of what today is South America during the splitting of Gondwana (>95 Ma). This study also emphasizes the correspondence with the megafossils of palms which date from 83.3 to 71.3 Ma, opening the possibility of the coevolution of the palms and the *Rhodnius* genus or the divergence of Rhodniini and Triatomini as a result of the adaptation of a genus' to a specific habitat. Recently, Patterson and Gaunt (2010) have made a more complete analysis to obtain a time scale between the predator reduvids and the triatomines, with the difference that five different markers were included and a greater number of taxa from three of the five accepted tribes in Triatominae. The results showed a high grade of coincidence among the five loci that were used. The time of divergence between Reduviinae (*Zelurus* spp. and *Opisthacidius* spp.) and Triatominae was calculated to be between 109 and 107 Ma. These predator reduvids are limited to the south of the American continent, and therefore, their evolution would have occurred before the splitting of Gondwana, while the evolution of the Triatominae is calculated during the origin of South America (95 Ma).

A third hypothesis proposes that the triatomines are even more recent and evolved in the Oligocene, in other words, when South America was already isolated from Antarctica and the rest of America. In this case, the large-scale related events would be a well-documented period of radiation of neotropical mammals and birds, and a period of wide diversification of ecotypes. According to Hwang and Weirauch (2012), this last hypothesis has a methodological advantage over the others due to the fact that the analysis includes a relaxed molecular clock, not a fixed one, which produces a significant improvement in the estimates because it does not assume a constant

variation rate. These authors propose a relative recent appearance of the Triatominae, which in comparison with the Cimicidae (from approximately 100 Ma) could help to explain the lesser degree of selectivity of the host with respect to this older group.

The information afforded by the fossil record about the Reduviidae subfamilies that can be considered reliable comes from the Eocene and Miocene, which does not shed much light about the period of greatest diversification of the lines of this group (Hwang and Weirauch 2012). Poinar (2005) reported a triatomine (*Triatoma dominicana* Poinar) infected with trypanosomes (*Trypanosoma antiguus* Poinar) and bat hair fossilized in Dominican amber, which indicates the existence of an association between triatomines, trypanosomatids, and nidicolous vertebrates in the Middle Tertiary, specifically in Late Eocene and Early Miocene (Table 1). In this sense, the notably high grade of speciation that was reached by birds and nidicolous mammals in tropical America, as a result of various factors present in the Amazon region during the Cenozoic (Nores 1999), could have provided a considerable variety of 'vacant' nest-type habitats for the triatomines making possible their diversification in the region and their later radiation (*Linshcosteus*) to the Asian continent. In addition, the radiation of species of *Triatoma* in the Old World probably occurred in a period no greater than 350 years, as occurred with *T. rubrofasciata*, species associated with domestic rats spread by boats and ships during the human exploitation of the commercial maritime routes (Patterson et al. 2001). There are those who suggest that Reduviidae did not develop an obligate hematophagy in Africa possibly due to competition from the Cimicidae, an apparently more primitively evolved family whose origin is in east central Africa (Schofield 2000a; Schofield and Galvão 2009).

Requirements for hematophagy

As was mentioned earlier, the morphological, physiology, and behavior adaptations (adaptations and exaptations) inherited and modified by the first predator hemipterans or reduvid ancestors of the triatomines affected and facilitated the hematophagy trait in this subfamily. The predator reduvids had already developed mouthparts for perforation, digestive enzymes for proteins, and behaviors of aggression and ambush towards their prey as well as associations with nidicolous vertebrates (Schofield 2000b; Lehane 2005). It would seem that the path to bloodsucking was already delineated (in the orthogenetic sense) and the trophic reward, the nutritious blood, was the driving force. Nonetheless, other inherent characteristics like the preceding poisonous saliva, the deficient vitamin content of this new food source, and the management of the new metabolites produced by blood digestion (cytotoxic substances) would represent

some of the obstacles that the ancestor or ancestors of the Triatominae would have to surpass.

Rostrum

One of the most important morphological characteristics that facilitated the evolution of hematophagy in Heteroptera was the previous adaptation for perforation (sensu Lehane 2005), which delineated the way for the development of the blood-sucking habit in at least the three families that we mentioned earlier: Cimicidae, Polyctenidae, and Reduviidae. However, some new changes in the buccal apparatus of the ancestral predator reduvids permitted a more efficient extraction of blood by the Triatominae subfamily. If the presently existing predator reduvids are compared with the hematophagous triatomines, some differences in the function and structure of the rostrum can be observed. The mouthparts of the predators, generally short, rugged, strongly chitinous, and in some cases curved, permit an efficient penetration of prey with a hard exoskeleton. Instead of this, the triatomines developed, in modular form, a longer thin, straight proboscis and with membranaceous linkages among the face segments, capable of perforating the relatively soft covering of a vertebrate in search of blood vessels after the penetration (Carcavallo et al. 2000; Lehane 2005).

Saliva

Another obstacle that the triatomines had to hurdle was the poisonous saliva of their reduvid ancestors which would impede the regular consumption of the blood of their hosts. It is widely accepted that to avoid the defensive reactions of their vertebrate hosts, these insects developed a more benign saliva with low protease concentrations (Schofield 2000b). The majority of the predator reduvid bites are very painful for vertebrates due to their markedly proteolytic saliva, which is fundamental for them to paralyze and digest their invertebrate prey. The presence of trypsin transcripts in the sialome of *T. infestans* and *Panstrongylus geniculatus* (Latreille) suggests a role for these molecules very different from the digestive one (Ribeiro et al. 2014). In the same way, it is interesting from the point of view of the evolution of the predator habit to hematophagy that a paralyzing protein has been detected in the saliva of *T. infestans*, a function previously only found in predator insects (Alves et al. 2011). Furthermore, the saliva of the triatomines contains antihemostatics, analgesic proteins, and other small molecules that inhibit blood clotting, ease the penetration of the skin, and neutralize the inflammatory response (Andersen et al. 2005; Assumpção et al. 2012). Thus, this adaptation increased opportunities for survival of the triatomines in the most dangerous

instants of their lives, the moment when they bite and feeds on the host.

Digestive enzymes

Having found and transferred the host's blood to the midgut or mesenteron, these insects had to confront the high protein content of their food. The Triatominae sub-family conserves some digestive characteristics of their entomophagous ancestors, having inherited from the reduvid predators a special mix of digestive proteins for the lysis of blood cells. The phytophagous ancestors of the early reduvids lost their ability to use trypsin, the common digestive protease, because plant sap is virtually without protein and the seeds have strong antitrypsins (Savelkoul et al. 1992; Lehane 2005). In the same way the predator reduvids and the hematophagous triatomines developed the capacity to secrete cathepsins in the intestine to digest the proteins found most abundantly in their food (Lehane 2005; Ribeiro et al. 2014). The cathepsins are a family of proteases normally found in the intracellular lysosomes, which generally become active at low pH (best 5.5 to 6), so that it can be said that the triatomines developed a system to acidify lightly alkaline blood (pH \approx 7.4) (Terra et al. 1996). The finding of proteases (trypsins) in the rectal ampulla of *R. prolixus* is congruent with the loss of their digestive function in triatomines (Ribeiro et al. 2014).

Mutualist microorganisms

Blood as feed, although rich in proteins, does not have all the nutritional elements the triatomines need to survive, and therefore, these insects as bloodsuckers needed to develop a symbiotic relationship with microorganisms that produced vitamin B (thiamine, pantothenic acid, pyridoxine, folic acid, and biotin), which is insufficient in vertebrate blood (Douglas and Beard 1996; Sasser et al. 2013). These symbionts are so important that most bloodsuckers store them in bacteriocytes or mycetocytes (Douglas 1989), cells that coat the ventricle of the mesenteron in the tsetse fly or in specialized organs known as mycetomes, present, for example, in lice (Anoplura) (Burkhart and Burkhart 2006). It is well known that the phytophagous hemipterans frequently host symbionts whose primary function is the synthesis of essential nutrients in specialized cavities or caeca of the mesenteron or in the mycetocytes (McCutcheon et al. 2009; Chapman 2013). Nonetheless, the intestinal symbionts were lost in the predator families of Heteroptera (Dolling 1991), and for this reason, the triatomines are not expected to have inherited from their hypothetical predator ancestor cells or specialized organs to house symbionts. In fact, it has been observed that the triatomine symbionts live freely in the mesenteron lumen and are acquired through the consumption of feces of conspecifics or by cannibalism

(Douglas and Beard 1996; Schaub and Eichler 1998; Eichler and Schaub 2002). Among the intestinal symbionts of the triatomines, much emphasis has been given to *Rhodococcus rhodnii* (Goodfellow & Alderson) for its possible use as a strategy to reduce vectorial competence in these insects (Hurwitz et al. 2012); however, there are other microorganisms that have been isolated from the middle intestine of *R. prolixus*, like the bacteria of the genera *Streptococcus*, *Staphylococcus*, *Corynebacterium*, *Mycobacterium*, *Pseudomonas*, and *Escherichia* (Douglas and Beard 1996). The quick processing of the enormous volume of ingested blood, by means of excretion of large quantities of water and salts as well as the gregarious behavior of the triatomines facilitates the transmission of symbionts among conspecifics (Figueiras and Lazzari 2000; Kollien et al. 2001).

Fore legs

The reduvid fore legs experience interesting morphological modifications related to their different life styles, from predators to bloodsuckers forms. In the first case, their fore legs are usually long and adapted with adhesive organs in the tibia (*fossulae spongiosae*) to trap and manipulate the invertebrate prey (Gorb and Beutel 2001). The presence of this *fossula spongiosa* or spongy pad is a plesiomorphic character in Reduviidae (Weirauch 2005, 2007). Although the fore legs are more simplified in triatomines, some species exhibit similar extendible adhesive organs, which we here will call spongy pads, in both the fore and middle tibia of the adults which permit their scaling smooth surfaces (Gillett and Wigglesworth 1932; Weirauch 2005, 2007), a useful adaptation for hemipterans that fly and live in trees as do species of the *Rhodnius* genus (Beutel and Gorb 2001). Nevertheless, from the adaptive point of view, the absence of these spongy pads in *Eratyrus mucronatus* (Stål) and *D. maximus*, or its appearance in nymphs and adults of *Microtriatoma* and *Parabelminus*, is incomprehensible, while is present only in adults of the rest of the triatomines (Lent and Wygodzinsky 1979; Weirauch 2007). These observations make less plausible the role the spongy pads may have in the adaptation to predate and climb. It is more convenient to use the term 'aptation' to describe these forms, given that their 'function' and 'adaptation' are not obvious. Although this topic will not be furthered in this work, it opens a door for a debate and a second look at the phylogenetic importance of this group's spongy pads. Provisional studies that we have made of the presence of these organs in *E. mucronatus* support this position.

From the entomophagic to hematophagic behavior

Besides the structural aptation previously mentioned, there were also behavioral changes that made

hematophagy possible. The triatomines, in contrast to other hematophagous insects like mosquitoes or tsetse flies, are insects that occupy the host's dwelling, and feed on him during the night while he sleeps. In other words, they are nest-dwelling hematophagous insects. Tree-dwelling vertebrates, like birds, sloths, reptiles, and marsupials of several classes as well as cave or burrow vertebrates, like armadillos, cavies, rabbits, rodents, and bats, are the usual hosts of triatomines. For this reason, underground lairs, nests in hollow trees, bird nests, fallen trees, palm fringes, bromeliaceous plants, cracks in the bark of trees, and similar places lodge these insects.

Probably, the decisive step that permitted the change from predator to bloodsucking habit was a change of behavior (Figure 1). There are other examples where behavior can initiate evolutionary adaptations for an ecological niche (Futuyma 1998). As Mayr (1963) mentions: '...a change to a new niche or adaptive zone is, almost universally, started by a behavioral change.' Other adaptations to a certain niche, particularly the structural ones, according to this theory are fixed in a secondary and ancillary manner, either as adaptations or exaptations (in a functional or effective way). With trophic and habitat selection playing a preponderant role within an adaptive zone - an ethological phenomenon - the importance of behavior is evident at the beginning of new evolutionary events.

Most researchers agree that the change of 'prey' that took place in Triatominae was developed from an association between a reduvid predator and a vertebrate (Schofield 2000b; Lehane 2005), which result into a nidicolous hematophagy. This conclusion is based on phylogenetic studies and the behavioral adaptations in the reduvid predators and triatomines of the present day. The majority of the present-day reduvid predators are normally active hunters, free living, that seek for and attack prey, while others adopt an ambush strategy, waiting for the prey to pass nearby to attack it by surprise, and many of them have been found living in nests and burrows of vertebrates and even feeding on the triatomines (Carpintero 1981). Some of these may have been 'transitional' forms between predator and a hematophagous reduvid (i.e., brother groups to Triatominae). Several authors have suggested that the members of the subfamilies Physoderinae, Reduviinae, Harpactorinae, Emesinae, and Peiratinae are all potentially brother groups to Triatominae within Reduviidae (Lent and Wygodzinsky 1979; Carcavallo et al. 2000; Schofield 2000a, b). Some of the species of these predator subfamilies show morphological similarities with the triatomines, and also behavioral ones, as several of them can apparently feed on blood if they are permitted to do so; nonetheless, our knowledge of their biology is rather poor. Currently, the

solidest evidence for the relationship hypothesis, considering the sampling achieved in the Reduviidae family, suggests the Reduviinae subfamily genera *Zelurus* and *Opisthacidius* as the phylogenetic groups closest to the triatomines (Hwang and Weirauch 2012). Thus, the question arises: do some of these species share morphological, physiological, and behavioral characteristics with the triatomines? It would be interesting to know if these reduvid predators are gregarious in nests, are active at night, prefer to seek prey near vertebrate nest, are attracted by their odors, or share other characteristics with the triatomines. In relation to this, Hwang and Weirauch (2012) note the presence of *Opisthacidius rubropictus* (Herrich-Schaeffer) in bird nests supposedly hunting arthropods, and that it is a taxon that breaks up the monophyly of the subfamily.

The habits of some species within Triatominae link this group with entomophagy. Some triatomines even today feed on invertebrates during their early and adult stages, both in natural and laboratory conditions. For example, some juvenile instars of *E. mucronatus* can feed on hemolymphs of large arachnids (Amblypygi) that dwell in trunks and hollow trees (Gaunt and Miles 2000). There are also reports of *P. geniculatus* feeding on moths during night capture (Garrouste 2009), and *Belminus herreri* (Lent & Wygodzinsky) and *Belminus ferroae* (Sandoval, Pabón, Jurberg & Galvão) have been detected feeding on members of the Blattidae family in Colombian dwellings (Sandoval et al. 2004, 2010). On the other hand, in laboratory conditions, the *R. prolixus* nymphs practice cannibalism and cleptohematophagy (Piñero et al. 1988). Species like *B. herreri* and *Belminus peruvianus* (Herrer, Lent & Wygodzinsky) are incapable of feeding directly off the blood of birds and mammals during their early instars, but can do so on other replete insects through cleptohematophagy or cannibalism (Sandoval et al. 2000). Furthermore, Lorosa et al. (2000) were successful in feeding all the nymph stages of *Triatoma circummaculata* (Stål) and *Triatoma rubrovaria* (Blanchard) with only Blattidae hemolymph under similar conditions; nonetheless, these authors apparently were unable to complete the life cycle of these species due to their needing vertebrate blood to produce a second generation. Pontes et al. (2011) found that *Triatoma pseudo-maculata* (Corrêa & Espinola) can feed on arthropods, specifically on *Periplaneta americana* (Linnaeus), and more recently, Sandoval et al. (2013) carried out, for the first time successfully in Triatominae, the complete life cycle of *B. ferroae* at the expense of hemolymph of *Blaberus* sp.

Certainly, a chain of evolutionary steps leading from the reduvid predator to the bloodsucker existed. Many of these steps were determined by the early contact of the reduvids with vertebrates. The birds and primitive mammals that appeared in the Mesozoic era were not

dominant until the dinosaur extinction (65 Ma); however, their great radiation between the later Cretaceous and early Tertiary must have provided a wide range of new niches for several groups of opportunist arthropod species (Kim 1985; Ericson et al. 2003; Delsuc et al. 2004; Table 1). The new vertebrate species occupied a greater range of ecological niches and practiced a greater variety of life styles than the early reptiles, and many of them were small organisms with the habit of nesting in trees and underground burrows (Ericson et al. 2003; Delsuc et al. 2004; Huggett 2004). It is reasonable to assume that such birds and mammals nests were continually invaded and colonized by several opportunistic arthropods, probably scavengers and saprophages feeding on organic remains and taking advantage of the vertebrate refuge (Lehane 2005). The ancestral reduvid predators were attracted by this abundant prey offer. Presumably, these early triatomines fed on the abundant soft invertebrates in the nests and burrows (e.g., larvae and immature insects), and later tried puncturing and penetrating the skin of the defenseless newly born vertebrates (Carcavallo et al. 1998; Gorla et al. 1997). It is probable that these 'bites' were initially exploratory and only occurred in a casual manner. The close and long association with nidicolous mammals and birds eventually resulted in the specialization of feeding directly and efficiently on vertebrates *per se*, minimizing the time devoted to finding nourishment (Lehane 2005). Aside from providing abundant food and protection from various enemies, the nest also provided a favorable and constant microclimate (Heger et al. 2006). The protection against extreme climatic conditions led to reproduction that depended less on the seasonal changes and an increase in the population density of the early triatomines. Furthermore, the aggregation in closed spaces near the host produced other effects and offered advantages: (i) facilitated mating and the acquisition of symbiotic microorganisms through the consumption of feces of conspecifics and through cannibalism; (ii) permitted the development of an alarm system based on intercommunication with others, which is an advantage when facing predators; (iii) provoked the production and excretion of large quantities of waste with chemical signals that marked the way back to the refuge after foraging (Schofield 2000b).

Conclusions

All the members of the Triatominae subfamily (Heteroptera, Reduviidae) are fit for bloodsucking (hematophagy). Their adaptations, both the inherited adaptations as well as the exaptations modeled by the environment, facilitated and affected the hematophagy since their reduvid predator ancestors until to the present-day triatomines. Certain primitive characteristics, originally developed by the ancestral reduvids, eased and modeled the triatomines' hematophagy. Examples

such as mouthparts, antihemostatic mechanisms, membranaceous connections between segments, saliva, and digestive symbionts are appropriate adaptations for blood consumption and digestion. However, the decisive event which probably made possible the jump from predation to hematophagy was a change of behavior: early association of a reduvid predator with a nesting vertebrate permitted the change from an arthropod prey to a vertebrate host. This intimate and prolonged association with birds and nidicolous mammals eventually developed into a specialization to feed directly and efficiently from the blood of these animals. If we consider that the trophic and habitat selection plays a preponderant role within an adaptive zone, the importance of an ethological phenomenon in the beginning of new evolutionary events is clear. The next important behavioral change of interest to humans, due to the epidemiological implications in the transmission of *T. cruzi*, is the adaptation of these insects to what we anthropocentrically call the 'human habitat'.

Endnotes

^aAccording to Gould and Vrba (1982), the term adaptation has been defined and recognized under two criteria: one of historical genesis (traits or characters fixed by natural selection which in this moment fulfill the function they were fixed for) and another of pragmatic usage (those traits or characters which at this moment do not fulfill the function for which they might have been selected, but are important to the species fitness). These authors point out that there are structures which are useful to an organism but, in contrast to the true adaptations, have not been fixed by natural selection for the function they have now (De Renzi 2009), and assign the term 'exaptation' to these structures. They then unify both concepts adaptation and exaptation, in a broader one called aptation. The consequence of this would be the conclusion that the morphogenesis, due to its own internal laws, generates structures which later on may or may not find usefulness, so that any adaptation must be preceded by an exaptation (De Renzi 2009).

^bOne of the best examples of the effects of exaptation is the feathers and flight-sequential evolution on birds. Feathers are considered an adaptation to solve waterproofing (isolation) and thermoregulation problems (heat loss) in the ancestor of birds and, later, an exaptation for other issues (predation, mimicry, sexual selection; Gould and Vrba 1982). Later, the development of large-contour feathers and their arrangement on the arm arise as adaptations for insect catching and eventually become exaptation for flight (Gould and Vrba 1982). Thus, the feathers along with other features (skeletal ones) may be considered as an exaptation to flight on actual birds, which do not resolve a problem but have an effect in the conquest of a new ecological niche, the aerial strata.

Additional file

Additional file 1: Spanish version.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

FOL, AJPS, CS and EA collaborated on the writing of the manuscript. All authors read and approved the final manuscript.

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