

Taxonomy of Chagas Disease Vectors

Subjects: [Zoology](#) | [Parasitology](#)

Contributor: Cleber Galvão

Chagas disease is a neglected tropical disease caused by the protozoan *Trypanosoma cruzi* and transmitted mainly by members of the subfamily Triatominae.

Triatominae

classical taxonomy

molecular taxonomy

integrative taxonomy

1. Triatominae: The Vectors of Chagas Disease

Chagas disease is a neglected tropical disease caused by the protozoan *Trypanosoma cruzi* (Chagas, 1909) (Kinetoplastida, Trypanosomatidae) ^[1]. This disease is found mainly in 21 Latin American countries, where it is mostly vector-borne, more specifically by members of the subfamily Triatominae (Hemiptera, Reduviidae) ^[1]. Triatomines or kissing bugs are hematophagous insects that have a habit of defecating during or after the blood meal—if they are infected with *T. cruzi*, they release the parasite in the feces/urine ^[1]. An estimated 8 million people are infected worldwide, and more than 65 million people at risk of acquiring the disease, which causes more than 12,000 deaths per year, the vector control being the most useful method to prevent new infections ^{[1][2]}.

There are currently 157 species (154 extant species and three fossils), grouped into 18 genera and five tribes (**Table 1**) ^{[3][4][5][6][7]}, being all potential vectors of *T. cruzi*. Taxonomic studies of Triatominae started in the 18th century with the description of *Triatoma rubrofasciata* (De Geer, 1773) (as *Cimex rubro-fasciatus*) ^[8]. Almost two and a half centuries after the description of the first species, we presented for—the first time—a review of the state-of-the-art of taxonomy of the whole subfamily, covering from the initial classic studies to the use of integrative taxonomy, a term formally introduced only in 2005 to describe taxa by integrating information from different data and methodologies ^{[9][10]}.

Table 1. Tribes, genera, and number of species that make up the subfamily Triatominae.

Tribe	Genus	Species (n)
Alberproseniini	<i>Alberprosenia</i>	2
Bolboderini	<i>Belminus</i>	9
	<i>Bolboderia</i>	1
	<i>Microtriatoma</i>	2
	<i>Parabelminus</i>	2

Tribe	Genus	Species (n)
Cavernicolini	<i>Cavernicola</i>	2
Rhodniini	<i>Psammolestes</i>	3
	<i>Rhodnius</i>	21
Triatomini	<i>Dipetalogaster</i>	1
	<i>Eratyrus</i>	2
	<i>Hermanlenticia</i>	1
	<i>Linshcosteus</i>	6
	<i>Mepraia</i>	3
	<i>Nesotriatoma</i>	3
	<i>Panstrongylus</i>	15
	<i>Paratriatoma</i>	2
	<i>Triatoma</i>	81
	<i>Paleotriatoma</i>	1
Total		157

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Studies

For 225 years (1773–1998), the descriptions of triatomine species have been based only on studies of classical taxonomy (using descriptive morphology, comparative morphology, and/or morphometry). Although these analyses are imperative and are present in the description of all species of the subfamily Triatominae, in the last decade, other approaches (such as biochemical [5][11], cytogenetic [5][12], phylogenetic [5][13][14][15][16][17] and/or of reproductive barriers [5]) started to be combined with the characterization of morphology and/or morphometry, employing the integrative taxonomy in the study of these insect vectors.

More than 190 synonymization acts occurred in the subfamily Triatominae [18][19], with the majority of synonymized taxa being described from classical taxonomy. The use of combined analyses for the characterization of a taxon greatly reduces the chances of synonymization (although it does not make it impossible [19][20]). Based on the synonymization events and the importance of multi-analyses for the characterization of a taxon, we will discuss the current issues, applications, and limitations of classical, molecular, and integrative taxonomy.

2.1. Classical Taxonomy

Classical taxonomy underlies most taxonomic studies of species description in the subfamily Triatominae. The morphological and morphometric studies applied in the last described taxa are: morphological study of the head, thorax, abdomen, and male and female genitalia (with optical microscopy (OM) and/or scanning electronic

microscopy (SEM)), and morphometric study of the head, thorax, abdomen and appendices (using OM) [5][6][7][15][16][17][21].

Although the use of morphological and morphometric characters is essential to describe a new taxon (since the diagnosis of the species needs to be made based on specimens that will be deposited, such as vouchers, in entomological collections), evolutionary events of cryptic speciation [14] and phenotypic plasticity [14] present in the subfamily Triatominae can make it difficult to diagnose a taxon only by morphological studies. Classic examples of this can be seen in the genus *Rhodnius* Stål, 1859: *R. montenegrensis* Rosa et al., 2012 [13] and *R. marabaensis* Souza et al., 2017 [15] represent two of the four paraphyletic strains of *R. robustus* Larrousse, 1927 [22][23] (the application of integrative taxonomy allowed description of the species from specimens initially characterized as *R. robustus* [24]). On the other hand, was demonstrated that *R. taquarussiensis* Rosa et al., 2017 (species described by integrative taxonomy [20]) represented only an intraspecific polymorphism of *R. neglectus* Lent, 1954 [19] (from studies of molecular taxonomy combined with experimental crosses it was possible to synonymize the species [19]).

Morphological convergence events can also hinder the classic taxonomy of these vectors [25]. The paraphyletic genus *Triatoma* Laporte, 1832 needs several studies from a taxonomic and systematic point of view [26]. *Triatoma tibiamaculata* (Pinto, 1926), for example, is a species that has morphological characteristics that bring it together and groups it (until now) as a *Triatoma* [27]. However, the generic status of this vector has been questioned several times [22][26][27]—since it presents cytogenetic [28], structural [29] and phylogenetic [26][27] characteristics that bring it closer to *Panstrongylus* (which highlights the importance of studies with integrative taxonomy).

2.2. Molecular Taxonomy

The first phylogenetic trees with molecular markers were published only in 1998 [30], giving rise to the phylogenetic systematics and molecular taxonomy of these vectors. Although no species of triatomine has been described by molecular taxonomy, the combination of phylogenetic analyses with morphological and morphometric studies in species description studies (integrative taxonomy) has been a trend in the last decade [5][13][14][15][16][17], since it provides greater reliability of the specific status of the taxa and allows, above all, to understand the evolutionary history of the species.

In addition to the contributions mentioned above, molecular taxonomy and phylogenetic systematics allowed the evaluation and re-validation of the taxonomic status of some species: reinclusion of *Linshcosteus* Distant, 1904 genus in Triatomini tribe (extinguishing the Linshcosteini tribe) [31]; inclusion of *Psammolestes* Bergroth, 1911 species in the genus *Rhodnius* [31] (proposal not accepted by the scientific community due to the differences that support the generic status of *Psammolestes* [17]); inclusion of the species *T. flavida* Neiva, 1911, and *N. obscura* Maldonado & Farr, 1962 in the genus *Nesotriatoma* Usinger, 1944 [32]; confirmation of the generic status of *Nesotriatoma* [21]; inclusion of species *T. spinolai* Porter, 1934, *M. gajardoi* Frias, Henry & Gonzalez, 1998, *T. eratyrusiformis* Del Ponte, 1929, and *T. breyeri* Del Ponte, 1929 in the genus *Mepraia* Mazza, Gajardo & Jörg, 1940 [32] (partially accepted suggestion, being the *Mepraia* genus currently composed of *M. spinolai*, *M. gajardoi*,

and *M. parapatrica* Frías-Lasserre, 2010 [4][33]; confirmation of the generic status of *Mepraia* [26]; and inclusion of *T. dimidiata* (Latreille, 1811) in the *Meccus* Stål, 1859 genus (genus that later was considered invalid and the *Meccus* species started to be considered as *Triatoma* [26][34][35]).

Although the International Code of Zoological Nomenclature does not consider groupings of triatomines to be complexes or subcomplexes [36], Justi et al. [26] suggests that these groupings should represent monophyletic groups. In the genus *Triatoma*, for example, studies based on phylogenetic systematics evaluated the position of several species that had been grouped mainly by geographic distribution and morphological similarities and proposed regrouping and/or the creation of new monophyletic groups [26][37][38]. Species well defined as natural groups (monophyletic) are currently the *T. brasiliensis* [39][40], *T. sordida* [41], *T. rubrovaria* [41], *T. infestans* [26], and *T. vitticeps* [38] subcomplexes.

2.3. Integrative Taxonomy

The data integration in the integrative taxonomy can be done by cumulation or congruence [42]. The use of combined tools to delimit a species of triatomine occurred for the first time in 1998 by Frias et al. [43] who combined morphological, morphometric, cytogenetic, and reproductive barriers data to describe *M. gajardoii*. However, only in the last decade has the integrative taxonomy has been more applied in the study of these vectors.

This tendency to integrate different analyses to characterize a taxon, made it possible to resolve ancient taxonomic issues, such as the description by *T. mopan* Dorn et al. (2018) and *T. huehuetenanguensis* Lima-Cordón et al. (2019) from specimens initially characterized as *T. dimidiata* [16][17][44][45] and the recent description of *T. rosai* Alevi et al., 2020 from the allopatric population of *T. sordida* (Stål, 1859) from Argentina [5][46][47]. In addition, the specific status of *T. bahiensis* Sherlock & Serafim, 1967 (a species that for more than three decades has been synonymous with *T. lenti* Sherlock & Serafim, 1967 [48]) has been revalidated based on integrative taxonomy [39].

On the other hand, even if the integrative taxonomy provides more robustness in the characterization of the new taxa (decreasing the chance of synonymization), does not prevent this event can occur (as mentioned above for *R. taquarussuensis* which has been synonymous with *R. neglectus* Lent, 1954 [19]). Although morphological, morphometric, and cytogenetic intraspecific variation had been described in the genus *Rhodnius* [49][50], the description of *R. taquarussuensis* was based on these factors [20]. Thus, synonymization event occurred through phylogenetic analyses and experimental crosses [19]. We suggest that integrative taxonomy work should include molecular studies and, whenever possible, reproductive barriers to confirm the taxon specific status following the biological concept of species [51][52][53].

In general, most articles of description based on integrative taxonomy combine only morphological and morphometric data with molecular analyses. However, it is worth mentioning that in 2020 the description of *T. rosai* was published based on morphometric, morphological, molecular data, and experimental crosses that have been combined with information from the literature about the species (cytogenetic data [46][47], electrophoresis pattern [46], cuticular hydrocarbons pattern [54], geometric morphometry [55], cycle, and average time of life [56][57][58]

as well as geographic distribution [\[18\]](#)[\[59\]](#)[\[60\]](#)[\[61\]](#)[\[62\]](#)[\[63\]](#)), becoming the most complete article of species description of the subfamily Triatominae [\[5\]](#).

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