ENTOMOLOGÍA Y VECTORES

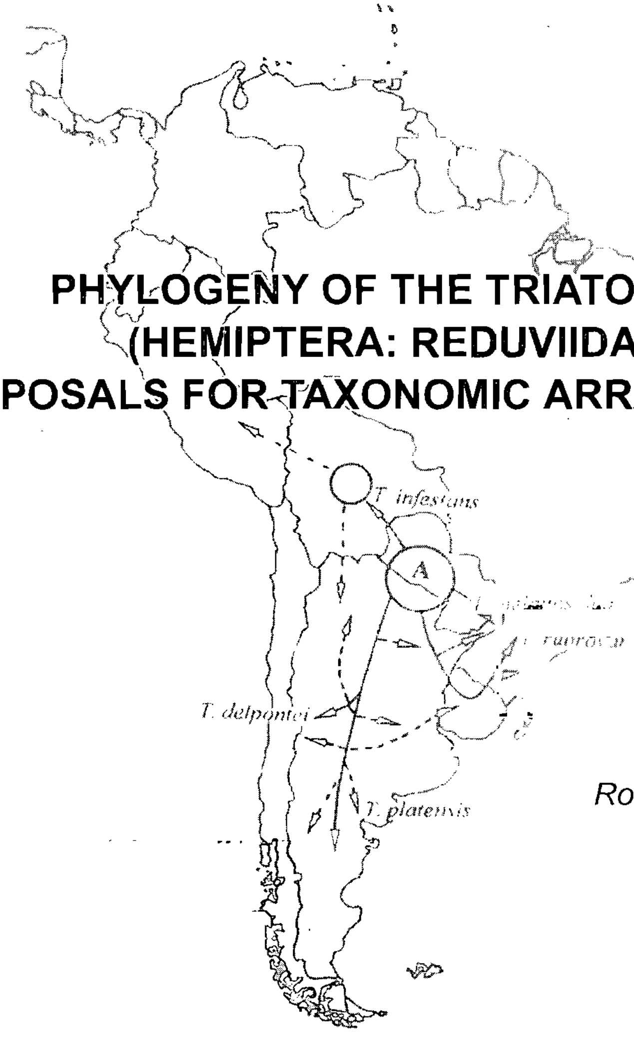
UNIVERSIDADE GAMA FILHO

Diretoria de Ensino e Pesquisa

(Rio de Janeiro, Brasil)

Volume 7, Suplemento 1

Junho, 2000



PHYLOGENY OF THE TRIATOMINAE (HEMIPTERA: REDUVIIDAE). PROPOSALS FOR TAXONOMIC ARRANGEMENTS.

Rodolfo U. Carcavallo
José Jurberg
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François Noireau
Cleber Galvão

ISSN 0328-0381

Entomología y Vectores

Vol. 7, Suplemento 1, junho 2000

EDITORA
GAMA
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(Catalogado na fonte pela Biblioteca Central da Universidade Gama Filho)

Entomología y vectores = Entomologia e vetores /
Universidade Gama Filho. – Vol. 1, n. 1 (jan. 1994) -.–
Rio de Janeiro: Editora Gama Filho, 1994 –
v.: il.

Trimestral. Bimestral até o Vol. 6, n. 6 (1999)
Publicado pelo Instituto de Entomología Salta até o Vol. 4, n. 6.
Descrição baseada em Vol. 5, n. 5 (set./out. 1998).
ISSN 0328-0381.

1. Entomologia – Periódicos. I. Título.

CDD: 595.7005

Os artigos publicados na
Revista Entomología y Vectores
estão indexados:

Zoological Record - UK
Review of Applied Entomology - UK
Library of Congress - USA
Quaterly Bibliography of Major Tropical Diseases - USA

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Os autores e os assinantes do exterior pagarão a anuidade de U$ 60,00 (sessenta dólares) e os assinantes do Brasil R$ 70,00 (setenta reais) em cheque nominal a SUGF, Editora Gama Filho. Banco HSBC Bamerindus - Agência 1018 - Méier - Rio de Janeiro - Conta nº 02592-42. A cópia do comprovante do pagamento deverá ser enviado ao editor, Dr. José Jurberg, Instituto Oswaldo Cruz, Departamento de Entomologia, C. Postal 926, 21045-900 Rio de Janeiro, RJ, Brasil.

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As vésperas do início do novo milênio a Revista Entomologia y Vectores completa seu sexto ano de existência. Foi extremamente gratificante para nós que temos a responsabilidade pela sua edição, bem como pela aceitação cada vez maior pelos entomólogos deste novo meio de divulgação de suas pesquisas.

Nestes seis anos publicamos trinta e seis fascículos abrangendo assuntos diversificados, principalmente aqueles voltados para Entomologia Médica e Veterinária, Acaralogia, Taxonomia, Morfologia, Influência das alterações climáticas, Biologia, Ecologia, Biografia de entomólogos, entre outros assuntos.

Para o sétimo volume correspondente ao ano 2000 algumas alterações sobre as normas de publicação estão sendo divulgadas nas “Informações para os autores”. Estaremos publicando quatro fascículos por ano (março/junho/setembro/dezembro) e suplementos que contemplem os artigos na íntegra de Simpósios e Congressos.

Os Editores

Message for subscribers

Right at the eve of a new millennium, the journal Entomologia y Vectores celebrates its 6th anniversary. It was a pleasure for the current editorial board to carry on the responsability of the edition of the 6th volume and to acknowledge the increased interest by the part of the contributing public, divulgating their research results in our journal.

Thirty six fascicles distributed in six volumes, respectively, covered wide scope entomological subjects such as medical, veterinary, environmental entomology, acarology, taxonomy, morphology, bionomics, behavior, ecology and related subjects such as the influence of climatic alterations in insect life, biographies, among other related subjects.

Little changes are being introduced in the editorial policy for the 7th volume, year 2000th, that have to do with editorial instructions for publication, which will be separately announced in "informations for authors". We will be publishing four fascicles per year (mars, june, september, december). Eventually, suplements that cover annais of symmposia and congresses can be accepted for publication.

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Entomología y Vectores

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Entomología y Vectores, Rio de Janeiro, Vol. 7 (Supl. 1): 1-99, Jun. 2000

PHYLOGENY OF THE TRIATOMINAE (HEMIPTERA: REDUVIIDAE). PROPOSALS FOR TAXONOMIC ARRANGEMENTS.(*)

Rodolfo U. Carcavallo (1/+), **José Jurberg** (1),
Herman Lent (2), **François Noireau** (1) **& Cleber Galvão** (1)

Abstract

Phylogeny of the Triatominae (Hemiptera: Reduviidae). Proposals for taxonomic arrangements - Numerous scientists have emphasized the importance of phylogenetic information in ecosystemic interrelations, population dynamics, and possibilities for control when such populations are harmful to human beings and their health and economy. This work questioned at one and the same time the Henning's theory which considers that the unit of study is not the species or the individual but rather each one of his different periods of evolution called semaphoront, and the definition of species according to Mayr et al. (1953): "*groups of natural populations that reproduce within each other in a real or potential way and that are isolated reproductively from other analogous groups.*" These concepts should be interpreted taking into account not only the biological and

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(*) This study was partially published in the *Atlas of Chagas´ disease vectors in the Americas*, Volume III, pp. 925-970, Editora FIOCRUZ Rio de Janeiro, 1999.

Supported by: convênio FNS/FIOCRUZ nº 123/97, CNPq/IRD e FAPERJ.

genetic but also the geographical and ecological isolation. So exist in the nature many species perfectly identified by morphology able to cross and give fertile hybrids, sometimes with rapid fixation of new intermediate characters, that might be considered as new species by hybridization. This is well known by farmers and breeders of orchideae and aquarium fishes. Among Triatominae, the most noteworthy example may be that of *Triatoma infestans* which produces fertile offsprings with *T. platensis* over several generations. Hybrid forms present morphological intermediate characters between both species after many years.

All Hemiptera Heteroptera feed by sucking organic liquids. According to the food-seeking trends, Schofield (1995) divides them in several groups: the Leptopodomorpha feed on the ground surface; the Gerromorpha on the water surface monocuticle; the Nepomorpha below water; and three categories, Enicocephalomorpha, Dipsocoromorpha and Cimicomorpha, in interstitial habitats.

Species from some families can feed on the blood of vertebrates, like *Anthocoris pilosus* and *Lyctocoris campestris* (family Anthocoridae), *Clerada apicicornis* (family Lygaeidae), the species of the family Cimicidae almost exclusively hematophagous and those of a subfamily of Reduviidae, Triatominae, also highly hematophagous. From this last family, another subfamily the Physoderinae showed facultative hematophagous habits through a South American species, *Cryptophysoderes fairchildi.* According to Terra (1988), the origin of this feeding habit began for the Neoptera which group all winged insects except for Ephemeroptera and Odonata. From here they divide into three lines: Holometabola (all insects with complete metamorphosis), Polyneoptera (including orders like Orthoptera, Dictyoptera and Isoptera), and Paraneoptera (evolutionary line which includes the Hemiptera with fossils found dating to the Permian but with possible ancestors dating to the Devonian). Apparently, the primitive ancestors were sapsucking. Later preying and hematophagous insects appeared, undergoing modifications in their buccal and digestive apparatuses. For this last behavior, they need to find the food source by way of specialized sensors on the antennae and rostrum (Catalá, 1997) and then penetrate blood vessels. The saliva and capacity of elimination of large amount of liquid had to change to allow for the development of bloodsucking.

In this work we present some theories about the possible evolution up to arrive to the Triatominae, subfamily established as monophyletic by Lent & Wygodzinsky (1979) when Carcavallo et al. (1999) sustain its possible polyphyletic origin, considering the characteristics of the five tribes actually admitted. Some genera as *Cavernicola*, *Torrealbaia* and *Psammolestes* have still some anatomical characteristics of predator groups (thick rostrum and anterior femur) similar to different related subfamilies.

Actually the subfamily Triatominae is divided into 17 genera and approximately 130 species. Only one genus, *Linshcosteus* Distant, 1904, is not found in the Americas. Other genera and the great majority of species are American. The tribes and genera known to date are:

Tribe Alberproseniini Martínez & Carcavallo 1977
  Genus *Alberprosenia* Martínez & Carcavallo, 1977

Tribe Bolboderini Usinger, 1944
  Genera *Bolbodera* Valdés, 1910
    Belminus Stål, 1859
    Microtriatoma Prosen & Martínez, 1952
    Parabelminus Lent, 1943

Tribe Cavernicolini Usinger, 1944
  Genera *Cavernicola* Barber, 1937
    Torrealbaia Carcavallo, Jurberg & Lent, 1998

Tribe Rhodniini Pinto, 1926
  Genera *Rhodnius* Stål, 1859
    Psammolestes Bergroth, 1911

Tribe Triatomini Jeannel, 1919
  Genera *Dipetalogaster* Usinger, 1939
    Eratyrus Stål, 1859
    Hermanlentia Jurberg & Galvão, 1997
    Linshcosteus Distant, 1904
    Mepraia Mazza, Gajardo & Jörg, 1940
    Panstrongylus Berg, 1879
    Paratriatoma Barber, 1938
    Triatoma Laporte, 1832

In the present work we suggest the hypothesis that *Alberprosenia*, by the morphological and cuticular characteristics of head, might be considered as separate subfamily if the molecular approach supports it. The position of *Linshcosteus* inside the subfamily Triatominae, previously questioned by other authors, was modified. This genus, which lacks for stridulatory groove and has a rostrum not attaining the prosternum, was separated from the tribe Triatomini. By these sole and fundamental characteristics, we create the tribe Linshcosteusini derived from an unique ancestor not related to any other Triatominae and limited to the Indian subcontinent.

Three genera containing numerous species, *Rhodnius, Panstrongylus* and *Triatoma,* display groups of species with extensive morphological similarities. They constitute specific complexes. In this work we analyse several of them, some previously recognised 30 years ago by Ryckman (1962) but with modifications (*T. protracta* complex), other mentioned by Lent & Wygodzinsky (1979) and Carcavallo et al. (1999), and finally some here studied for the first time. Their geographical distribution, altitudinal dispersion and some data about habitat and feeding sources are provided. The studied complexes and the species integrated are:

Rhodnius pictipes, *R. stali*
Rhodnius prolixus, *R. neglectus, R. robustus, R. nasutus, R. domesticus*
Rhodnius pallescens, *R. ecuadoriensis, R. colombiensis*
Rhodnius dalessandroi, *Rhodnius* n. sp. in process of publication and dedicated to M.A.Miles
Panstrongylus lignarius, *P. humeralis, P. herreri*
Triatoma flavida, *T. bruneri, T. obscura*
Triatoma venosa, *T. dispar, T. carrioni, T. nigromaculata*
Triatoma breyeri, *T. eratyrusiformis*
Triatoma circummaculata, *T. limai*
Triatoma infestans, *T. platensis, T. delpontei, T. rubrovaria, T. melanosoma, T. carcavalloi*
Triatoma sordida, *T. guasayana, T. garciabesi, T. patagonica,*
Triatoma dimidiata, *T. hegneri, T. brailovskyi, T. gomeznunezi*
Triatoma oliveirai, *T. guazu, T. jurbergi, T. williami, T. matogrossensis, T. klugi*

***Triatoma maculata**, T. pseudomaculata*
***Triatoma protracta**, T. sinaloensis, T. peninsularis, T. barberi, T. neotomae, T. nitida, T. incrassata*
***Triatoma phyllosoma* (Genus *Meccus*)**, *T. pallidipennis, T. longipennis, T. mazzottii, T. picturata, T. bassolsae*

For the complex *phyllosoma*, the authors propose to revalidate *Meccus* Stål, 1859 described previously as genus. Out of the external characters, these species have an unique size and shape of testicles, not related to any other *Triatoma* and different to other genera. The species of complex *protracta* showed unique morphological characteristics inside the tribe Triatomini (small insects, pronotum with lateral side straight, interlobar level of the pronotum without a distinct angle or faint, legs short, etc.) For the other specific complexes of *Triatoma* the nominotypical subgenus is maintained until further analyzes allow to classify correctly the complexes *breyeri, circummaculata, dimidiata, flavida, venosa, infestans, sordida, maculata* and *oliveirai*, each of them with peculiar characteristics but still insufficiently studied.

Key words: Phylogeny, Triatominae, specific complexes

Introduction

According to Carcavallo et al. (1999) phylogenetic studies have gained increasing importance along with the expansion of research on the origins and trends of populations of living beings. In addition, the incorporation of new techniques such as histochemical, cytochemical, physiological, ethological, and morphometric studies, in addition to electron microscopy, cytogenetics, and DNA to rank the affinities and differentiation between populations, have expanded the possibilities for knowledge in this field. Numerous investigators have emphasised the importance of phylogenetic information in ecosystemic interrelations, population dynamics, and possibilities for control when such populations are harmful to human beings and their health and/or economy. Phylogeny is thus increasingly related to taxonomy and has helped shed light on these interrelations, grouping similar individuals and populations in categories with different ranks (taxa), with interpretations as to their possible genetic or evolutionary connections.

For many years interrelations were based on morphological characteristics. Klingstedt (1937) contended that taxonomic work was organized in three successive stages:

1) Description of the species and its ordering, which was more or less arbitrary, or the **classificatory stage.**

2) Ordering of the species according to their characteristics, to establish a **typological system.**

3) The **phylogenetic stage**, in which one establishes the definitive relations between known taxa and infers the evolutionary lines based on known or suspected ancestors.

Hennig (1968 and previous editions) disagrees with the idea that phylogenetic systematics are based on morphological systems; neither does he believe that one can establish supremacies of ideal systems without utilizing prior suppositions. Thus, this first stage involving "only classifying" should be viewed in a relative light if it is not accompanied by premises or a hypothesis. All ordering in the final analysis may merely be the observation and expression of natural reality from a special point of view. He also views as a mistake the typological focus of considering similarities, mainly of individuals or species. The author contends that the unit of study **is not the individual**, rather the **semaphoront,** that is, the individual at a given, specific, or special moment in its life trajectory, since each individual displays profound morphological, physiological, ethological, and ecological differences according to the moment at which it is studied, and this has a profound genetic base in each specific case. In other words, some semaphoronts have links of a genetic type between each other (ontogenetic relations) over the course of a time system, constituting an interrelated chain that one can call an **individual**. If in a given place and at different moments we observe an egg, which becomes a larva, then a pupa, and finally the imago of an insect, we can determine that they all have a common genetic relationship and we will have determined that this set of semaphoronts constitutes an individual. Hennig (1968) also explains that between individuals one can establish genetic relations derived from the reproductive process ("tocogenetic relations"), thence emerging a definition of **species** that the same author considers too simplistic: "groups of individuals related through tocogenetic relations". The author views as **phylogenetic relations** the various genetic relations that interconnect different species. The genetic relations that join semaphoronts as individuals, tocogenetic relations that join individuals as species, and ontogenetic relations that interrelate the species are referred to by Zimmermann (see Hennig, 1968) as **hologenetic relations.**

The concept of "species"

In relation to "**species**" , opinions are different according to the approach of several biological major field of studies. For a botanical taxonomist, this word has a meaning of populations of plants with morphological characteristics, specially in flowers and fruits, but not necessarily genetically isolated. As examples, three genera of orchids of different geographical distribution, *Brassavola, Cattleya* and *Laelia* were hybridised, getting a new genus with different species obtained by hybridization, named *Brassoleliocattleia.* Similar observations and results were made by zoologists in systematics and taxonomy of fishes. Several genera (i.e. *Xyphophorus* and *Poecilia*) from different geographical regions, can be hybridized, with offspring with intermediate characters fixed permanently after a few generations. Something similar happens with Triatominae bugs.

According to Mayr et al. (1953) "**species** are groups of natural populations that reproduce within each other in a real or potential way and that are isolated reproductively from other analogous groups". This ensures a certain identity of genetic combinatory possibilities that are typical of a community and that find their expression in morphological (or holomorphological, according to Hennig, 1968), physiological, and ethological characteristics. But the concept of reproductive isolation as defining a species should be interpreted not only as the biological impossibility of fertile offspring, which per se ensures specific separation, but also through geographical or ecological barriers that make mating impossible between populations that are not genetically incompatible. This is particularly important in the subfamily Triatominae, in which there are specific complexes or groups of morphologically similar and genetically interfertile populations which taxonomically are unanimously considered valid species. The most noteworthy example may be that of *Triatoma infestans* (Klug, 1834) and *T. platensis* Neiva, 1913, easily separable based on their external morphology, genitalia, electrophoresis of their lymphatic proteins and isoenzymes, and other modern molecular taxonomic techniques, and which hybridise to produce fertile offspring with which one can experimentally form colonies lasting over several generations. Nevertheless, there are no geographical barriers between the two species, since the former is totally encompassed in the geographic distribution area of the latter. The existing barriers are ecological, since while *T. infestans* is an almost totally domiciliated species, *T. platensis* has remained a sylvatic, bird-nest related species, rarely approaching human dwellings, remaining restricted to the peridomiciliary environment. It is in this peridomiciliary environment that the two species tend to form natural hybrids (Abalos, 1949). But in the taxonomic study of semaphoronts, individuals, or populations, one should keep in mind that what we are seeing are not only genotypes resulting from the predictable combinations of parental DNA, rather phenotypes, that is, the adapting results of the basic genetic conditions to the paratypical environmental conditions, which explain not only many diversities and variations but also many evolutionary aspects related to adaptation.

The Abalo's colony of *T. infestans* x *T. platensis hybrids* lasted several years, remaining intermediate forms only, without specimens with parental characters. A hypothesis is that hybridization could be an important way of speciation within Triatominae. To reinforce this hypothesis, specimens found in nature with intermediate characters between two different species are relatively common and can explain misidentifications and different opinions of taxonomists. Authors are performing laboratory hybridizations trying to prove this hypothesis.

The grouping of species with morphological, physiological, and ethologic similarities through their genetic relationship leads to a broader taxon, the **genus**. But with the current knowledge of a great number of species belonging to genus *Triatoma*, and the additional condition that several of them are morphologically very similar, authors suggest that some division should be needed, based in the International Code of Zoological Nomenclature, using an intermediate taxon, the subgenus, as commonly employed in other entomological groups as Diptera (Culicidae and other families), These and the higher taxa correspond to associative creations within a more or less abstract system, and scientists thus tend to differ as to their validity, limits, reach, and definitive contents. The **tribes, subfamilies**, and **families** have been the object of similar views, which explains the diversity of opinions as to their number and validity.

Origin of Hemiptera and Reduviidae

The Triatominae constitute a subfamily of Reduviidae (Hemiptera, Heteroptera) characterized by their obligatory haèmatophagy, at least in the adult stage for mating and reproduction. There was once na attempt to rise Triatominae to the level of family by Pinto (1926), the subject was also widely discussed by Lent (1936, 1941). Today, there is a general consent to consider Triatominae a subfaly of Reduviidae. The haematophagy is not unique in the Hemiptera order, since it is also present in the Cimicidae, Polyctenidae, and some Lygaeidae. Other subfamilies of Reduviidae like the Physoderinae also optionally take blood meals.

Nearly all of the Hemiptera feed by sucking organic liquids, whether of plant or animal origin; in the latter case they can prey on other invertebrates (almost all of the reduviids) or even small vertebrates, like some Hemiptera of the Belostomatidae family. Not only the phytophagous and entomophagous cases but also predators of other prey have occupied not only the respective niches, but also a large number of habitats and have adapted to nearly all ecosystems, both terrestrial and aquatic. Schofield (1995) established the food-seeking trends of some groups: the Leptopodomorpha feed on the ground surface, the Gerromorpha on the water surface monocuticle, Nepomorpha below water, and Enicocephalomorpha, Dipsocoromorpha, and primitive Cimicomorpha in interstitial habitats.

Humans are frequently bitten when they inadvertently touch some hemipterans. Particularly painful accidental bites are those of the Reduviidae, especially the subfamilies Harpactorinae, Apiomerinae, Echtrichodinae, and Peiratinae, as well as Belostomatidae. Some groups of predators and phytophagous insects also display aggressive behaviour, biting and feeding on bare human skin if they are allowed to (Anthocoridae, Miridae, Lygaeidae). In the first of the aforementioned families, predator species like *Anthocoris pilosus* (subfamily Anthocorinae) and *Lyctocoris campestris* (subfamily Lyctocorinae) feed on the blood of vertebrates living in the habitats they share (Stys & Daniel, 1956, Stys, 1973). Cobben (1978) recalls the close relationship between Anthocoridade and the highly haematophagous family Cimicidae. *Clerada apicicornis* is a species of Lygaeidae frequently reported as having hematophagous habits, although it has not lost its behavior of preying on insects, including Triatominae of the genus *Rhodnius* (Tonn & Otero, *fide* Carcavallo et al., 1999).

Considering their common origin according to information summed up by Terra (1988), for the Neoptera (all winged insects except for Ephemeroptera and Odonata), there are three lines along which they evolved: Holometabola, Polyneoptera, and Paraneoptera. The **Holometabola** include all of the orders with complete metamorphosis (egg, larva, pupa, and adult). The **Polyneoptera** include orders like Orthoptera, Dictyoptera, and Isoptera. The **Paraneoptera** constitute an evolutionary line which includes the Hemiptera, with fossils found dating to the Permian but with possible ancestors dating to the Devonian (Fig. 1). Apparently, the primitive

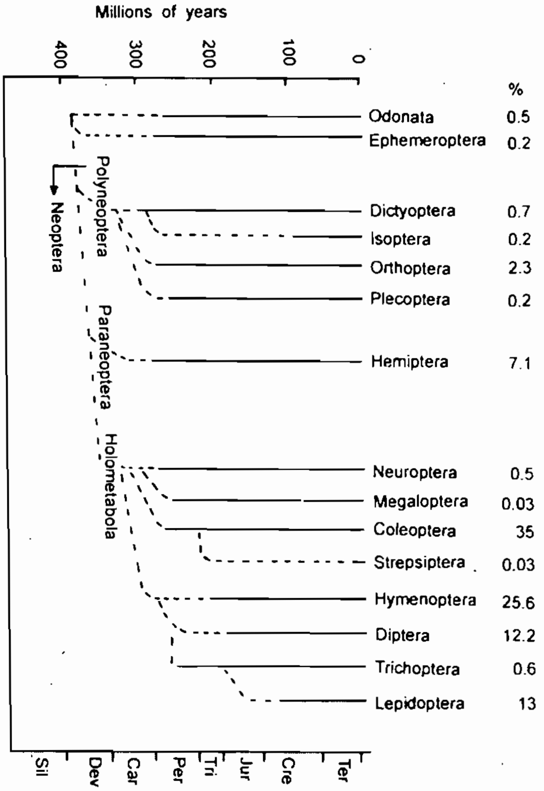


Figure 1: Phylogenetic relations of the major insect orders and approximate numbers of living species as percent of total insects (860.000 species) (from Terra, 1988).

ancestors common to Homoptera and Heteroptera were sap-sucking insects, with this type of feeding behaviour that has survived in the first of the aforementioned suborders. In order to adapt to this type of diet and feeding, it was necessary to undergo a change in the alimentary canal to allow for concentrating the ingested liquid.

It is believed that the preying and hematophagous insects evolved from these sap- and phloem-suckers, undergoing modifications in their buccal and digestive apparatuses. In the former, the adaptation allowed for perforation of soft tissues through modifications in the stylets; in the latter, through the loss of the peritrophic membrane and the appearance of the microvillous membrane for efficient absorption of solutes (Terra, 1988). In addition, they need to find the food source, first the host and then the nutrient fluid (blood). They appear to perform all of this by way of highly specialised sensors on the antennae and rostrum (Catalá, 1997) and the stylets. Friend & Smith (1985) describe the feeding behaviour of *Rhodnius prolixus* Stal, 1859, and we feel it is relevant to quote several paragraphs from their study to show to what extent bloodsucking is a process that is highly differentiated from other forms of feeding by the Heteroptera: "Despite the great importance of thermal signals, both visual and olfactory stimuli as well as perhaps vibration or contact can produce the search (Wigglesworth & Gillet, 1934). Such non-thermal signals probably have an influence on natural feeding and are presumably important when there are no temperature gradients. It is known that *T. dimidiata* feeds on cold-blood animals like snakes and toads (Zeledón et al. 1970; Schofield, 1979). We have observed that after a thermal signal disappears, *R. prolixus* keeps it proboscis extended and attempts to probe any available surface for a short period of time... Under such conditions, *R. prolixus* generally penetrates the membrane and feeds until satiated... A temperature gradient is only necessary at a critical point in the feeding process... A contact between the tip of the proboscis and a hard surface is necessary to activate the next phase of feeding behaviour: operation of the mandibular and maxillary stylets. The stylets have not been observed to extend to the tip of the proboscis if a surface cannot be reached. If an adequate surface is contacted, the insect uses its mandibles to penetrate it; this is performed by an alternating movement of the mandibles. These are sharply pointed and equipped with curved teeth measuring 3 microns in *R. prolixus* and 5-6 microns in *T. infestans*... The mandibles do not penetrate very deeply; and subsequent penetration, which is deeper in the host tissues, is done by the maxilla. The latter is pushed inwards and outwards in different directions, while the saliva flows constantly from its tips (Friend & Smith, 1971). At regular intervals of 5-10 seconds, the left maxilla slides backwards and its tip bends outwards, exposing the space between the two maxillae. The morphology of the maxillary tips and the mechanism forming the "functional mouth" were described by Bernard (1974) in his studies on *T. infestans*. One or more strokes of the pharyngeal pump take place while the mouth is open and the liquid enters the alimentary canal... This activity takes place when the insect tastes its diet, determining its convenience (or availability). Each stroke of the pharyngeal pump of a fifth-stage *R. prolixus* nymph can absorb some 60 nanoliters of food ... the anterior alimentary canal and the epipharyngeal sensors have a volume of less than 5 nanoliters, so that one stroke is more than sufficient to place the food in contact with the chemoreceptors involved in tasting it... This sampling, which can take place in less than a second ... probably occurs as a routine part of penetration and may be the main way by which the triatomines obtain information on fluids at the maxillary tip. Each of the maxillae is innervated by three dendritic neuronal processes whose cell bodies are located on the stylet situated at the base of the maxilla... responding to: lateral bending, longitudinal compression, and extension, respectively. Although these responses are modified by changes in temperature and moisture (Bernard et al., 1970), it appears that the three dendrites are mechanoreceptors ... the maxillary groping phase culminates in vivo when the insect locates a blood vessel; *T. infestans* (and undoubtedly all the triatomines) feed on vessels (Lavoipierre et al. , 1959). As long as the vessel is penetrated by the serrated maxillary tips, the functional mouth probably remains inside the vessel during feeding; the retracted tip of the left maxilla probably avoids it from being removed during feeding. The tip can also help keep the blood vessel from collapsing (Cobben, 1978)".

This physiological scheme is performed through structures that can change from one species to another. The extremities of the right and left maxillae in *T. maculata* (Erichson, 1848) have differences whose form and structure were described by Cobben (1978). The right stylet has a tapered tip and a curvature towards the left, while the internal preapical area has an abruptly widened edge. This widening presses against the point of articulation of the left maxilla when the right stylet protrudes and the left retracts.

Studies of this type of activity and strategy in non-haematophagous Reduviidae, like some species of Harpactorinae and Emesinae, show some similarities, but the entire structure needs to be stronger in order to pierce surfaces harder than bird or mammal skin, like the chitin of some arthropods. The mandibles have a spatula-shaped apex, with either a rough, serrated, or fingerprint-like outer surface. Cobben (1978) suggests that this change indicates a greater functional relationship between the mandibular and maxillary stylets than in the Gerromorpha and Nepomorpha. In some Harpactorinae one observes that "there is a greater penetration of the mandibles than would be necessary if it were only a matter of attaching the mouthparts to the prey's cuticle. The flat lateral stylets are apparently adapted to penetrate more easily through an intersegmental fold and from a more horizontal angle of attack. Furthermore, they can guide the maxillary bundle beyond a short distance inside the host, thus helping to determine the direction of the food sample" (Cobben, 1978). "The fluid food is taken by some primitive Emesinae probably through mechanical laceration of the host tissues (mainly spiders) by a maxillary bundle that lacks movable halves. The other Reduviidae presumably employ approximately the same strategy as the Harpactorinae, that is, protrusion of the right maxillary stylet frontwards of the left, combined with the retraction of the latter" (Cobben, 1978).

The saliva had to change to allow for the development of bloodsucking. In the predators the saliva has a marked proteolytic effect, which was lost in the bloodsuckers, where the saliva has no digestive functions and the bite must be painless in order for the blood to be completely ingested.

Bloodsucking also requires a rapid turnover of the enormous amount of blood generally ingested by the Triatominae, and the insect immediately excretes a large amount of water and salts to decrease its weight. In addition, haemolysis of the erythrocytes is performed by way of a haemolytic factor (Azambuja et al., 1983). It is generally agreed that these physiological adaptations appeared relatively recently in the evolution of the Heteroptera, yet they are very profound processes, including synthesis of carbohydrases and proteases by the insect.

The emergence and evolution of the Heteroptera families of Hemiptera and the Reduviidae subfamilies have been the object of several hypotheses, some of which we review in this Chapter.

Miles (1972) describes four types or forms of feeding among the Heteroptera, based on the salivary function and food source:

1. with stylets in a sheath (Pentatomomorpha that feed on vascular plants);
2. through laceration and liquid flow (Pentatomomorpha that feed on seeds, phytophagous Miridae);
3. predation (several, including most of Reduviidae)
4. bloodsucking.

In the opinion of the aforementioned author, the four forms evolved in the above order, beginning with a pre-hemipteran bite-and-suck mechanism associated with the Thysanoptera. This theory is based on modifications in a study by Goodchild (1966) (see Cobben, 1978), and the scheme in Figure 2, in which there emerge first (and with question marks) the Coleorrhyncha, with the development of sheathed stylets and mesophilic feeding, by which they are considered true Hemiptera. One of the three lines evolves with the posterior joining of the midgut and hindgut, giving rise to the Heteroptera. The latter display various forms of feeding, with the appearance of laceration and liquid flow. The terrestrial groups split into two main branches in their evolution: Pentatomomorpha and Cimicomorpha. From the latter emerge several preying and hematophagous forms (Cimicidae, Reduviidae) and others that return to feeding on plants, like Miridae and Tingidae.

China & Miller (1959) proposed an evolutionary scheme starting from a Proto-Heteroptera derived from Thysanoptera, a trunk from which several main branches emerge early. One group of them form the families grouped as Cimicomorpha, which are divided in predatory forms and those that return to plant feeding. From the first group emerge Reduviidae and Cimicidae, as bloodsuckers.One branch of the Cimicomorpha splits off early to form a family, Joppeicidae, and later ends up bifurcating into two more: Reduviidae and Phymatidae. We should recall that in the opinion of several hemipterologists, the latter is merely considered a subfamily of Reduviidae. These authors limit themselves to the scheme in Figure 3, which stops at the family level, and there are thus no observations on the evolution to haematophagy.

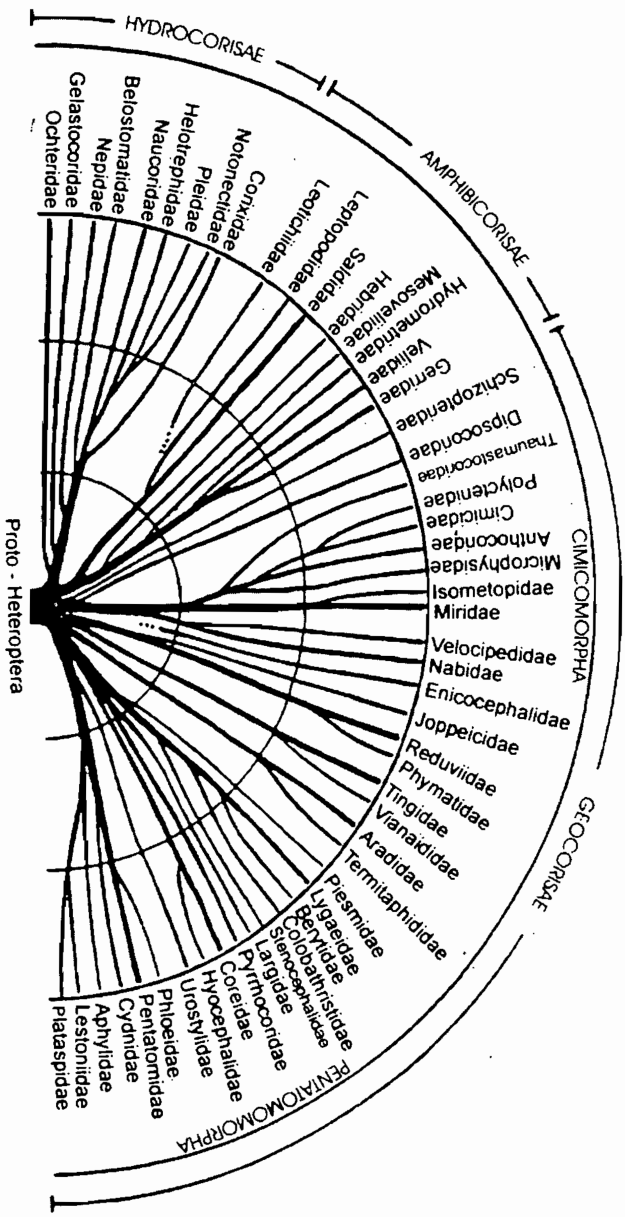


Figure 2: Evolutionary relationships of Hemiptera based on physiology of feeding (from Miles, 1972).

Contrary to Miles, Cobben (1978) contends that the first mechanism to appear may have been "rasping-filtering" in Gerromorpha, Enicocephalomorpha, and some Dipsocoromorpha and Nepomorpha. From this type of mechanism there may have evolved lacerating or biting followed by liquid flow in the Leptopodomorpha, some Dipsocoromorpha, Nepomorpha, and Reduvioidea and primitive Cimicomorpha *stricto sensu* (all with preying habits). From this level on there may have emerged both the phytophagous (part of the Miridae, Tingidae, Thaumastocoridae, and Pentatomomorpha) and haematophagous insects (Reduviidae:

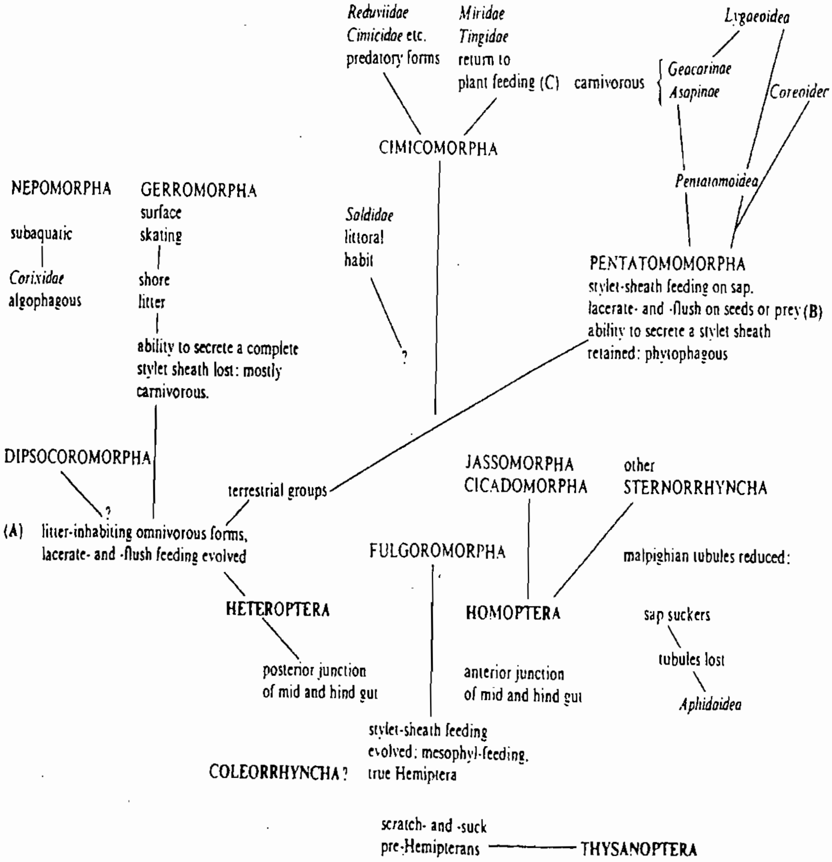


Figure 3: Evolutionary branches of Hemiptera Heteroptera from a Proto-Heteroptera (from China & Miller, 1959).

Triatominae, Cimicomorpha *stricto sensu*: Cimicidae). Cobben provides numerous studies on the evolutionary trends in the mouthparts of the Heteroptera. One of his diagrams shows the evolution of the most important mouthparts, establishing a comparison between Gerromorpha (with the basic original structures) and other Heteroptera, amongst which the Reduvioidea. He sums up the process as follows: "...a number of changes in the feeding apparatus, particularly the gradual loss of maxillary barbs, anticipated the advance from predatory to hematophagous and phytophagous feeding. A dorsal and ventrally closed maxillary bundle, functioning as a syringe, and an increased ability to protrude the mandibles were apparently preadaptative, enabling plant-feeding to develop". Based on a detailed anatomical study of the mouthparts of numerous families, genera, and species, he constructs the hypothetical phylogeny of the Heteroptera.

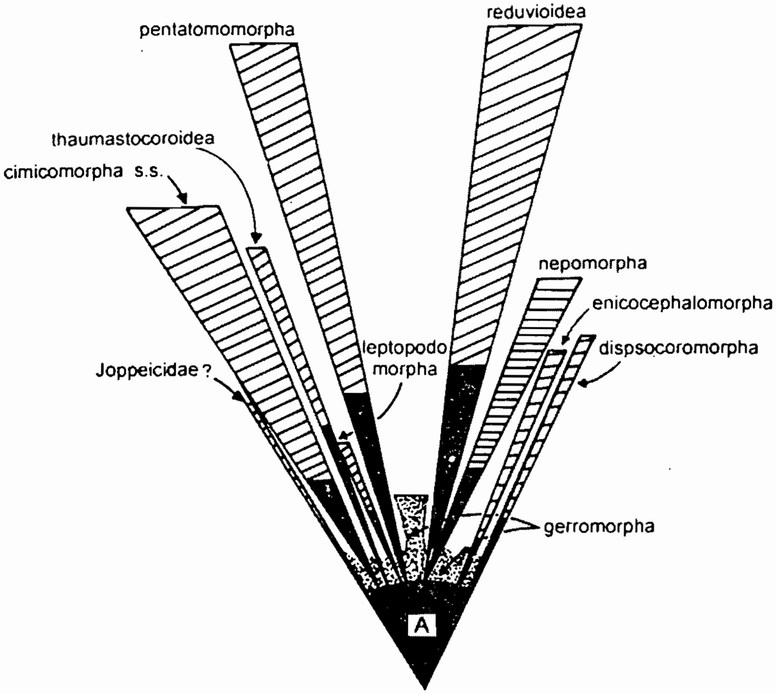


Figure 4: Diagram of hypothetical phylogeny of heteroptera after Cobben (1968) with names of the respective taxa. Terrestrial groups are obliquely lined (from Cobben, 1978).

He also tabulates and quantifies the plesiomorphic, intermediate, and apomorphic characteristics, displayed in a bar graph with comparative frequencies (Fig. 6). But Cobben still has doubts, despite the abundant information he presents, and proposes another diagram of the hypothetical phylogeny in the same study (Figs. 4 and 5), in which the greatest difference is in Reduvioidea, although he leaves his questions open: "The general problem of phylogeny and the relative position of the branchings of the major taxa is shifted in the Figure to sector 'A'. For each of the phyletic lines A-H, one must first construct the respective archetype before attempting a cladistic solution. If the scheme proposed generally reflects the true image of past history, then I am not being overly optimistic in believing that one day we may succeed in solving the phylogeny of the Heteroptera. The final solution might be to interconnect the 8 archetypes and the common archetype by way of a branch diagram. All of the archetypes probably shared gerrhomorphic characteristics and were thus not very different from each other. In

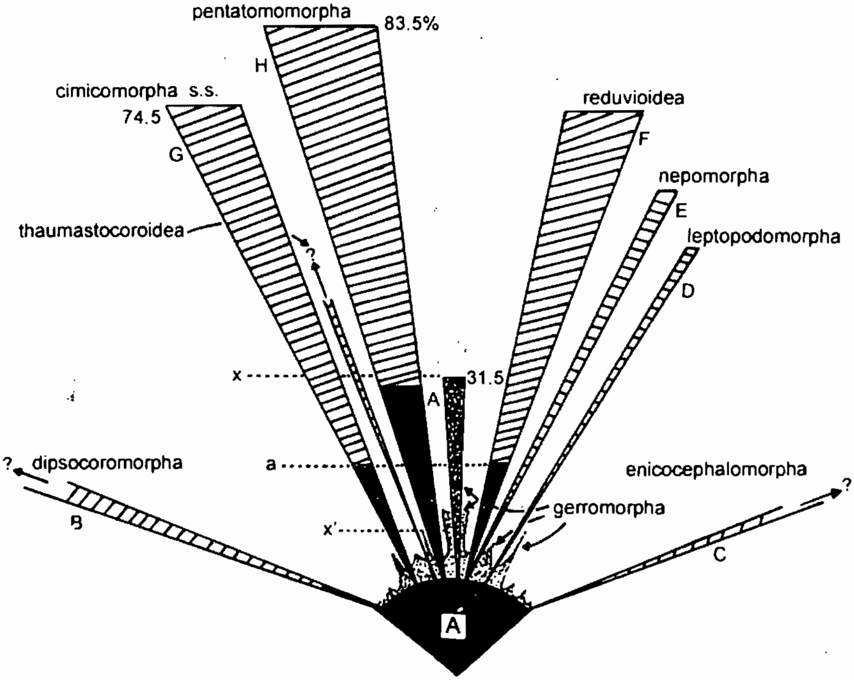


Figure 5: Modification made by Cobben (1978) of the diagram of Fig. 4.

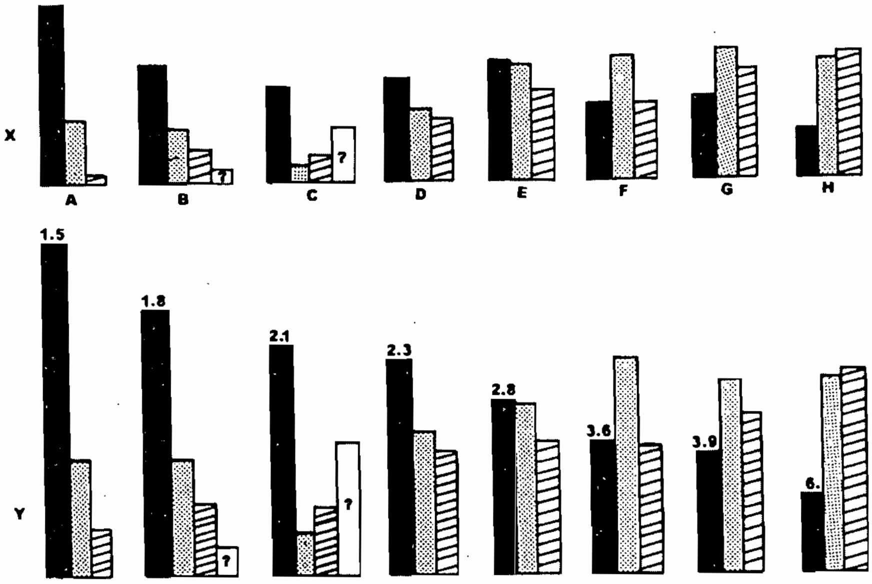


Figure 6: Frequency of plesiomorphous (black column), intermediate (stipped) and apomorphous (lined) characters. A: Gerromorpha. B: Dipsocoromorpha. C: Enicocephalomorpha. D: Leptopodomorpha. E: Nepomorpha. F: Reduvioidea. G: Cimicomorpha *sensu str.*. H: Pentatomomorpha.

order for a cladistic analysis to be meaningful it will be necessary to identify the plesiomorphic elements in each gerrhomorphic family."

The morphological characteristics allowing one to situate a Heteroptera in the Reduviidae family are usually the lateral insertion of the four-segmented, generally filiform antennae, although there are exceptions (for example, Physoderinae, which has claviform segments), a three-segmented rostrum or proboscis that does not extend beyond the prosternum, the almost constant presence of the stridulatory groove, a well-marked neck, and presence of Brindley's glands in bridles located on the lateral edge of the metathorax. The Reduviidae family is universally distributed, and the majority of its subfamilies, genera, and species prey on other arthropods with a buccal apparatus adapted to pierce the hard chitinous exoskeleton of their prey. A list of Heteroptera families and subfamilies is shown in Table I.

Table I

Families of Hemiptera-Heteroptera according to China & Miller (1959) and subfamilies of Reduviidae according to Maldonado Capriles (1990) and Schuh & Slater (1995). These taxa have undergone changes on several occasions and what is showing in the table is only by way of illustration.

FAMILIES OF HETEROPTERA	SUBFAMILIES OF REDUVIIDAE
Plastamidae Dallas, 1851	
Lestoniidae (China, 1955)	
Cydnidae (Billberg, 1820)	
Pentatomidae (Leach, 1815)	
Aphylidae (Bergroth, 1906)	
Urostylidae Dallas, 1851	
Phloeidae (Amyot & Serville, 1843)	
Coreidae (Leach, 1815)	
Stenocephalidae Dallas, 1852	
Hyocephalidae Bergroth, 1906	
Lygaeidae (Schilling, 1829)	
Pyrrhocoridae (Amyot & Serville, 1843)	
Largidae (Amyot & Serville, 1843)	
Piesmatidae (Amyot & Serville, 1843)	
Thaumastocoridae Kirkaldy, 1908	
Berytidae Fieber, 1851	
Colobahristidae (Stal, 1866)	
Aradidae (Spinola, 1837)	
Termitaphididae Myers, 1924	
Joppeicidae Reuter, 1910	
Tingidae (Costa, 1838)	
Vianaididae Kormilev, 1955	
Enicocephalidae (Stal, 1860)	
Phymatidae (Laporte, 1832) (*)	
Elasmodemidae Lethierry & Severin, 1896 (*)	
Reduviidae Latreille, 1807	

(A)	(B)	
+	-	Apiomerinae (Amyot & Serville, 1843)
+	+	Bactrodinae (Stal, 1866)
+	+	Centrocniminae Miller, 1956
+	+	Cetherinae Jeannel, 1919
+	+	Chryxinae Champion, 1898
+	-	Diaspidinae Miller, 1959
+	-	Ectinoderinae (Stal, 1866)
+	-	Echtrichodinae Spinola, 1850
+	-	Elasmodeminae Lethierry & Severin, 1896
+	+	Emesinae Spinola, 1850
+	+	Hammacerinae (Stal, 1859)
+	+	Harpactorinae Spinola, 1850
+	+	Holoptilinae (Amyot & Serville, 1843)
+	+	Manangocorinae Miller, 1954
+	+	Peiratinae (Stal, 1859)
+	+	Phimophorinae Handlirsch, 1897
-	+	Phymatinae (Laporte, 1832)
+	+	Physoderinae Miller, 1954
+	-	Pseudocetherinae
+	+	Reduviinae Spinola, 1850
+	+	Saicinae (Stal, 1859)
+	+	Salyavatinae (Stal, 1859)
+	+	Sphaeridopinae (Pinto, 1927)
+	+	Stenopodainae Stal, 1859)
+	+	Triatominae Jeannel, 1919
		- Tribe Alberproseniini Martínez & Carcavallo, 1977
		- Tribe Bolboderini Usinger, 1944
		- Tribe Cavernicolini Usinger, 1944
-		- Tribe Rhodniini Pinto, 1926
		- Tribe Triatomini Jeannel, 1919
+	+	Tribelocephalinae (Stal, 1866)
+	+	Vesciinae

Pachynomidae (Stal, 1873)
Velocipedidae Bergroth, 1891
Nabidae Costa, 1852
Polyctenidae Westwood, 1874
Cimicidae (Latreille, 1804)
Anthocoridae (Amyot & Serville, 1843)
Microphysidae Dohrn, 1859
Miridae (Hahn, 1831)
Isometopidae Fieber, 1860
Dipsocoridae Dohrn, 1859
Schizopteridae (Reuter, 1891)
Hydrometridae (Billberg, 1820)
Gerridae Leach, 1815
Veliidae (Amyot & Serville, 1843)
Mesoveliidae Douglas & Scott, 1867
Hebridae (Amyot & Serville, 1843)
Leotichidae China, 1933
Leptopodidae Costa, 1838
Saldidae (Amyot & Serville, 1843)
Notonectidae Leach, 1815
Pleidae (Fieber, 1851)
Helotrephidae Esaki & China, 1927
Corixidae Leach, 1815
Nepidae (Latreille, 1802)
Belostomatidae (Leach, 1815)
Naucoridae Fallèn, 1814
Gelastocoridae Kirkaldy, 1897
Ochteridae Kirkaldi, 1906

(*) Considered a family or subfamily, according to the authors. (**A**) Subfamilies of Reduviidae accepted by Maldonado Capriles (1990). (**B**) Subfamilies of Reduviidae accepted by Schuh & Slater (1995), **see** Schofield, 1995.

The Origin of the Triatominae

Based on the above, the evolution of haematophagy derived from one or several predatory groups with special types of behaviour both in food-seeking and choice of habitat. From the point of view of feeding, the most important adaptations were the ability to pierce the soft tissues in the skin of vertebrate hosts through a special structure in the stylets; to suck the host painlessly in order to finish the blood meal, taking several minutes; the ability to rapidly eliminate large amounts of water and some solutes after the blood meal; the breakdown and haemolysis of the erythrocytes at the beginning of the digestive process and the lack of anaphylatic reactions in the host. This last condition is not absolute and several triatomine species produce some kind of skin reactions, generally depending of the host and insect (i.e., *Dipetalogaster maxima, Panstrongylus geniculatus* and several species of *Rhodnius* produce severe alergic reactions.

Yet in order to constitute what is currently known under the name Triatominae, an inappropriate term since it is based on three antennal segments when in reality there are four (albeit the term cannot be changed under the rules of the International Code of Zoological Nomenclature), there also need to be some anatomical characteristics: a straight, thin rostrum (there are cases with a thicker rostrum, like *Psammolestes* Bergroth, 1911*)* adpressed to the gula, the third segment of which is upwardly flexible in the feeding position; antennae inserted laterally, almost always filiform; and absence of dorsal abdominal scent glands. All of these traits are apomorphic, and their occurrence in about 130 species (Table II shows those species found in the Americas) distributed in five tribes (six in this paper) and seventeen genera, is one of the some authors' arguments for a monophyletic origin of the subfamily Triatominae. Perhaps the most in-depth analysis of all the information available for sustaining this monophyletic theory is that of Lent & Wygodzinsky (1979), part of whose arguments we quote here: "It was Jeannel (1919) who for the first time formally differentiated the group on a suprageneric level, as the tribe Triatomini. Ever since, these insects have been recognized as a monophyletic group, in most cases as a subfamily. We have attempted to establish the sister group of the Triatominae. The obviously apomorphic traits of the triatomines, viz., the obligatory hematophagous condition and the upwardly flexible third rostral segment when the rostrum is in feeding position are to our knowledge not found in any other reduviid. These characters are autapomorphic and thus of no value for determining relationships with other groups of Reduviidae, but they do establish the Triatominae as a monophyletic group. The absence of dorsal abdominal scent gland openings in the Triatominae (an apomorphy within the Reduviidae) although comparatively uncommon in the family, is also found in all Saicinae and Emesinae as well as in scattered genera placed in the Reduviinae. None of these share any other apomorphic character with the Triatominae, and no close relationship between the former and the latter is postulated. The external genitalia of the Triatominae are of plesiomorphic structure in the less specialized forms (Triatomini) and agree symplesiomorphically with the genitalia of many other reduviids, a fact certainly not helpful for the analysis of relationships. The same applies to the venation of the hemelytra and hind wings. Of possible significance is the combination, unusual for the Reduviidae, of a straight rostrum closely adjoining the gula, and the lateral insertion of the antennae. These features, apomorphic within the Reduviidae, are not restricted to the Triatominae, being also found in some Harpactorinae and Apiomerinae. These groups, however, belong to a different phyletic lineage, the 'harpactorine complex' (Davis, 1961) and are not closely related to the Triatominae. A possible sister group, sharing with the Triatominae a straight rostrum adpressed to the gula and distinctly laterally inserted antennae, is the Physoderinae. The physoderine bugs have dorsal abdominal glands as opposed to their absence in the Triatominae, and although the rostrum is straight and closely parallel to the gula as in the Triatominae, the third rostral segment is apparently not capable of flexing upward when the insects are feeding. Regarding feeding habits, however, Carcavallo & Tonn (1976) mentioned *Cryptophysoderes* -the only Western Hemisphere physoderine- as being of '*hábitos optativos hematófagos*'. If the haematophagous habits of *Cryptophysoderes* were confirmed, even as facultative, the hypothesis of a sister group relationship between the Triatominae and the Physoderinae would be strengthened because the bloodsucking habit is derived within the Reduviidae and can be assumed to have arisen only once in the family."

The opinion of Lent & Wygodzinsky (1979), previously defended by Usinger (1944), has favourable and unfavourable aspects and opinions. The possibility of a single origin for the combination of anatomical, physiological, and ethological factors is difficult to explain, considering the combination of plesiomorphic and apomorphic traits that differentiate the tribes and genera, as well as the geographical distribution, which is typical and characteristic for some groups. The evolution from a predator behaviour to haematophagism shows currently some intermediate aspects. Thick rostrum and femora, as predator morphological conditions, are present in three genera: *Cavernicola, Torrealbaia* (both belonging to tribe Cavernicolini) and *Psammolestes* (tribe Rhodniini). To reinforce the existance of transitional behaviors, *T.*

Table II

Checklist to the Triatominae Tribes, Genera, Subgenera, specific complexes and species in the Americas with some comments

Tribe Alberproseniini Martínez & Carcavallo, 1977. Probably should be considered in the future as a subfamily.

Genus *Alberprosenia* Martínez & Carcavallo, 1977

Species: *A. goyovargasi* Martínez & Carcavallo, 1977
- *A. malheiroi* Serra, Atzingen & Serra, 1980

Tribe Bolboderini Usinger, 1944

Genus *Bolbodera* Valdéz, 1910
Species: *B.scabrosa* Valdés, 1910

Genus *Belminus* Stål, 1859
Species: *B. rugulosus* Stål, 1859
- *B. costaricensis* Herrer, Lent & Wygodzinsky, 1954
- *B. herreri* Lent & Wygodzinsky, 1979
- B. laportei *Lent, Jurberg & Carcavallo, 1995*
- *B. peruvianus* Herrer, Lent & Wygodzinky, 1954
- *B. pittieri* Osuna & Ayala, 1993

Genus *Microtriatoma* Prosen & Martínez, 1952
Species: *M. trinidadensis* (Lent, 1951)
- *M. borbai* Lent & Wygodzinsky, 1979

Genus *Parabelminus* Lent, 1943
Species: *P. carioca* Lent, 1943
- *P. yurupucu* Lent & Wygodzinsky, 1979

Triba Cavernicolini Usinger, 1944

Genus *Cavernicola* Barber, 1937
Species: *C. pilosa* Barber, 1937
- *C. lenti* Barrett & Arias, 1985

Genus *Torrealbaia* Carcavallo, Jurberg & Lent, 1998
Species: *T. martinezi* Carcavallo, Jurberg & Lent, 1998

Tribe Rhodniini Pinto, 1926

Genus *Psammolestes* Bergroth, 1911
Species: *P. coreodes* Bergroth, 1911
P. arthuri (Pinto, 1926)
P. tertius Lent & Jurberg, 1965

Genus *Rhodnius* Stal, 1859
Specific complex: *R. prolixus* Stål, 1859
R. domesticus Neiva & Pinto, 1923
R. nasutus Stål, 1859
*R. neglectus*Lent, 1954
R. robustus Larrousse, 1927
Specific complex *R. pictipes* Stål, 1872
R. stali Lent, Jurberg & Galvão, 1993
Specific complex *R. pallescens*, Barber, 1932
R. colombiensis Mejía, Galvão & Jurberg, 1999
R. ecuadoriensis Lent & León, 1958
Specific complex *R. dalessandroi* Carcavallo & Barreto, 1976
Rhodnius sp. n. Carcavallo, Rocha, Galvão & Jurberg in Valente et al. (in preparation)
Species: *R. brethesi* Matta, 1919
R. neivai Lent, 1953
R. paraensis Sherlock, Guitton & Miles, 1977

Tribe Triatomini Jeannel, 1919

Genus *Dipetalogaster* Usinger, 1939
Species: *D. maxima* or *maximus* (Uhler, 1894)
(both names are currently used by specialized scientists)

Genus *Eratyrus* Stål, 1859
Species: *E. cuspidatus* Stål, 1859
E. mucronatus Stål, 1859

Genus *Hermanlentia* Jurberg & Galvão, 1997
Species: *H. matsunoi* (Fernández Loyza, 1989)

Genus *Mepraia* Mazza, Gajardo & Jörg, 1940
Species: *M. spinolai* (Porter, 1934)
M gajardoi Frías, Henry & González, 1998

Genus *Panstrongylus* Berg, 1879
Specific complex: *P. lignarius* (Walker, 1873)
P.humeralis (Usinger, 1939)
P. herreri Wygodzinsky, 1948
Species: *P. guentheri* Berg, 1879
P. chinai (Del Ponte, 1929)
P. diasi Pinto & Lent, 1946

P. geniculatus (Latreille, 1811)
P. howardi Neiva, 1911
P. lenti Galvão & Palma, 1968
P. lutzi (Neiva & Pinto, 1923)
P. megistus (Burmeister, 1835)
P. rufotuberculatus (Champion, 1899)
P. tupynambai Lent, 1942

Genus *Paratriatoma* Barber, 1938
Species: *P. hirsuta* Barber, 1938

Genus *Triatoma* Laporte, 1832

Specific complex *T. circummaculata* (Stål, 1859) This complex needs further studies
T. limai Del Ponte, 1929
Specific complex *T. flavida* Neiva, 1911 This complex needs more studies
T. bruneri (Usinger, 1944)
T. obscura (Maldonado Capriles & Farr, 1962)
Specific complex *T. dimidiata* (Latreille, 1811)
T. brailovskyi Martínez, Carcavallo & Peláez, 1984
T. hegneri Mazzotti, 1940
T. gomeznunezi Martínez, Carcavallo & Jurberg, 1994
Specific complex *T. sordida* (Stål, 1859)
T. guasayana Wygodzinsky & Abalos, 1949
T. patagonica Del Ponte, 1929
T. garciabesi Carcavallo, Cichero, Martínez, Prosen & Ronderos, 1967
Specific complex *T. breyeri* Del Ponte, 1929
T. eratyrusiformis Del Ponte 1929. The original name *"eratyrusiforme"* was changed by Lent & Wygodzinsky, 1979
Specific complex *T. venosa* (Stål, 1872)
T. carrioni Larrouse, 1926
T. dispar Lent, 1950
T. nigromaculata (Stal, 1859) This species should give the name to the complex but some characters do not fit completely with it.
Specific complex *T. infestans* (Klug, 1834)
T. platensis Neiva, 1913
T. delpontei Romaña & Abalos, 1947
T. rubrovaria (Blanchard, 1843)
T. melanosoma Martínez, Olmedo & Carcavallo, 1987
T. carcavalloi Jurberg, Rocha & Lent, 1998
T. infestans-like Dark Morph Noireau, 1999
Specific complex *T. oliveirai* Neiva, Pinto & Lent, 1939
T. matogrossensis Leite & Barbosa, 1953
T. williami Galvão, Sousa & Lima, 1965
T. guazu Lent & Wygodzinsky, 1979
T. jurbergi Carcavallo, Galvão & Lent, 1998
T. klugi Carcavallo, Jurberg, Lent & Galvão, 2000
Specific complex *T. maculata* (Erichson, 1848)
T. pseudomaculata Correa & Esspínola, 1965
Specific complex *T. protracta* (Uhler, 1894)
T. barberi Usinger, 1939
T. incrassata Usinger, 1939

T. neotomae Neiva, 1911
T. nitida Usinger, 1939
T. peninsularis Usinger, 1940
T. sinaloensis Ryckman, 1962

Species (more studies are needed to decide if they belong to any specific complex):

T. arthurneivai Lent & Martins, 1940
T. bolivari Carcavallo, Martínez & Peláez, 1987
T. brasiliensis Neiva, 1911
T. costalimai Verano & Galvão, 1959
T. deanei Galvão, Sousa & Lima, 1967
T. gerstaeckeri (Stål, 1859)
T. indictiva Neiva, 1912
T. lecticularia (Stål, 1859)
T. lenti Sherlock & Serafim, 1967
T. melanocephala Neiva & Pinto, 1923
T. mexicana (Herrich-Schaeffer, 1848)
T. petrocchiae (Pinto & Barreto, 1925) Described as "*petrocchi*"
T. recurva (Stål, 1868). This species should be studied very careful for its taxonomic position, because it shares some
Intermediate characters with genus *Dipetalogaster*
T. rubida(Uhler, 1894)
T. rubrofasciata (De Geer, 1773) Type species of *Triatoma* Laporte, 1832
T. ryckmani Zeledón & Ponce, 1972
T. sanguisuga (Le Conte, 1855)
T. tibiamaculata (Pinto 1926) Described in the genus *Eutriatoma* of which was the type species, currently a synonym of *Triatoma*
T. vitticeps (Stål, 1859)
T. wygodzinskyi Lent, 1951

Genus *Meccus* Stål, 1859

Species: *M. phyllosoma* (Burmeister, 1835)
M. longipennis (Usinger, 1939)
M. mazzottii (Usinger, 1941)
M. pallidipennis (Stål, 1872)
M. picturata (Usinger, 1939)
M. bassolsae (Alejandre Aguilar, Nogueda Torres, Cortez Giménez, Jurberg, Galvão & Carcavallo, 1999)

rubrovaria and *T. circummaculata* were reared during all the nymphal stages feeding Blattaria (Lorosa et al., 2000). However, for getting a second generation these species need vertebrate blood. In other words: apparently, at least in these two species, haematophagism is not necessary for the life cycle from first to fifth instar nymph, but is needed for sexual fertility and ovarian development.

Bargues et al (2000), studying nuclear rDNA-based molecular clock of the evolution of Triatominae, conclude that "The results presented here cannot be directly viewed in terms of the evolution of haematophagy since neither the 18S nor ITS-2 genes are known to be involved in blood-sucking behaviour, but they do lend strong support to arguments for a polyphyletic origin of Triatominae". These authors find divergence between Rhodniini and Triatomini and consider that the origin of North American *Triatoma* species and the South American ones are linked with different ancestors and derived independently. In addition, the variability of different populations of *T. dimidiata* is considered as "normal" in this paper, because authors agree that the origin could be placed in the North of South America, and migration and speciation could happened after the joining of North and South America through the isthmus of Panama.

The genus *Linshcosteus* Distant, 1904

The genus *Linshcosteus* Distant, 1904 is only found in India; Gorla et al. (1997), Schaefer (1998), Schofield (1988), and Schofield (2000) placed doubts about its inclusion in the Triatominae subfamily. The last publication considers that this genus is aberrant within the Subfamily. These doubts are not new: Lent & Wygodzinsky (1979) commented " The abbreviated rostrum combined with the absence of a stridulatory groove is an apomorphic condition unique among the Triatomini, but we have not been able to determine the cladistic relatioships between *Linshcosteus* and the remaining genera of the tribe" The ancient condition of both morphological characters, the abbreviate rostrum not extending to level of proesternum, and the absence of stridulatory groove, characters permanently found in all known species of this genus and also in nymphs, plus the agreement of "aberrant" within the tribe (Schofield, 2000 even considers that is aberrant for the subfamily) let us take the decision to separate *Linshcosteus* in as single new tribe, Linshcosteusini.

Linshcosteusini Trib. Nov.

General morphological characters as typical in the subfamily Triatominae. The characters that are considered enough to establish the new taxon are: a) the rostrum, very short, not attaining neither the prosternum not the posterior border of the head; b) the absence of stridulatory groove. unique case in triatomines; c) the body conspicuously flattened, as not found in any genus of the tribe Triatomini; d) the head and thorax densely beset with setiferous granules, character only found in Alberproseniini within the triatomines. As a not morphological argument, the geographical distribution of all species, limited to India, fact that can be considered as a monophyletic origin, with a local ancestor. Future studies using DNA techniques might allow to change the status to the subfamily level.

Key to the tribes of Triatominae

1- Stridulatory groove absent. Rostrum not attaining the prosternum.. Linshcosteusini Trib. Nov.
- Stridulatory groove always present. Rostrum attaining clearly the prosternum..2
2- Genae clearly surpassing the apex of clypeus ....Bolboderini Usinger, 1944
- Genae not surpassing the apex of clypeus 3
3- Short head, pre and postocular regions of same length, eyes very large ....Alberproseniini Martínez & Carcavallo, 1977
- Head longer than wide, anteocular region generally (not always) than postocular. Eyes of moderate size 4
4- Head ovoid and convex in dorsal view; femora very wide...Cavernicolini Usinger, 1944
- Head never ovoid and convex; femora not very wide 5
5- Antennal insertion near the apex of head. Postocular region with callosities and setiferous tubercles ....Rhodniini Pinto, 1926
- Antennal insertion far from the apex of head. Postocular region without lateral callosities.............................Triatomini Jeannel, 1919

Note: Alberproseniini might belong to another subfamily. Authors are developing this hypothesis

Other genera of Triatominae

From the genus *Triatoma* Laporte, 1832, only a few species close to *T. rubrofasciata* (De Geer, 1773) are found outside the Americas; the other genera of the subfamily are strictly American; *Dipetalogaster* Usinger, 1939; *Paratriatoma* Barber , 1938, and two homogeneous groups of *Triatoma* species are only found in North America (United States and Mexico) and only one species in Central America: *T. protracta* (Uhler, 1894) and the closest species and the specific complex of *T. phyllosoma* (Burmeister, 1835), which includes six species. *Bolbodera* Valdés, 1910 is a genus found only in Cuba, and the two species of the genus *Parabelminus* Lent, 1943 were only found in the Atlantic Forest east of the Serra do Mar, between Rio de Janeiro and Bahia, Brazil.

Genus *Eratyrus* Stal, 1859 has a broad geographical distribution in the Americas, in intertropical areas between Mexico and Bolivia, but it is relevant to situate the primitive form in relation to the orogenic movements around the end of the Tertiary and early Quaternary which gave rise to the Andes Range, since in South America *E. cuspidatus* Stål, 1859 is only found west of the Andes, while *E. mucronatus* Stål, 1859 extends eastward from the Andes. In addition, the emergence of the Central American isthmus began in the Quaternary, and *E. cuspidatus*, which reaches as far as southeast Mexico (State of Chiapas) can only have spread from Colombia in this latter period. This indicates that the speciation process began after said orogenic phenomena occurred, when the mountain chain became a geographical barrier to interbreeding and the previously non-existent isthmus joined South and North America. Based on this it would be possible to situate the origin of one of the species or an ancestor of both in the northwestern part of South America.

The adaptation of some triatomines to a given type of food source and habitat appears to be linked to a situation prior to haematophagy, when the reduviid fed on soft forms of invertebrates that swarmed in nests (caterpillars, larvae, spider bellies) and later began to attempt to pierce the skin of small vertebrates. It is possible that during a first stage in these nests, haematophagy was optional, and until the saliva changed to make it painless it was only used against newborn (and thus defenseless) vertebrates, which the insects would attack with a special form of predation. It was only when the saliva became painless and adaptations occurred for the haemolysis and digestion of the erythrocytes that a process of haematophagy as we know it today could have begun. Yet this phenomenon may have occurred in nests and dens of various vertebrates, producing a separation that may have been related initially to biogeographic and bioclimatic factors, and in a second stage there may have been a preference or selection that separated the populations with obligate or heavily preferred food sources (stenophagous) from others with less strict feeding requirements and more diversified sources (euryphagous). In other words, this hypothesis proposes a polyphyletic origin for the Triatominae (Schofield, 1988, 1995).

The statement from the previous paragraph is a hypothesis that helps explain the close relationship between species from genus *Psammolestes* Bergroth, 1911 and nests of Dendrocolaptidae birds, between *Cavernicola pilosa* Barber, 1937 and mammals from the order Chiroptera (bats), between *Microtriatoma trinidadensis* (Lent, 1951) and the biocenosis of large epiphytic bromeliads, between *Panstrongylus geniculatus* (Latreille, 1811) and subterranean edentates of the family Dasypodidae which they accompany from southern Mexico to northern *Argentina*, and between all species of the complex *Triatoma protracta* (Uhler, 1894) and close species with the nests of spiny rats from genus *Neotoma*. It also helps explain the existence of a genus that is atypical in its anatomy, *Linshcosteus,* (with a rostrum that does not reach the stridulatory groove in any of its five species) and in its geographical distribution in the Indian subcontinent.

Schofield & Dujardin (1999) pointed out that "in primitive terms, we can envisage an adaptative process from a free-living predatory form to a nest-dwelling haematophagous form, and we can supose that this has happened several times within the Reduviidae to give rise to the various tribes of Triatominae. Such a trend has been associated with various morphological, biochemical and reproductive changes, but can also be envisaged as a typical evolution of demographic strategy (*sensu* Rabinovich, 1974) from r-strategist (free-living predators adapted to relatively unstable conditions of habitats and food-supply) to K-strategist (nest-dwelling predators exploiting a more stable habitat and food-supply) (Schofield & Dolling, 1993). Within the Triatominae there are several lines of evidence to suggest that this adaptative process has been relatively recent. The absence of authochthonous species from Africa (Gorla et al., 1997) dates them post continental separation, and they could not have followed our proposed evolutionary route before the advent of nest-building mammals and birds in the neotropics, which already places them in the post-cretaceaous period. Their frequent association with rodents would suggest them to have evolved well after the mid tertiary period and, from their relative lack of divergence from the basic reduviid form, we see no reason to suggest that they would have evolved even prior to the quaternary period." Schofield & Dujardin (1999) consider that some predatory conditions are not completely lost in Triatomini, as some species that feed on invertebrates during the earlier development stages (some Bolboderini, *Eratyrus mucronatus* and *Dipetalogaster maxima* among others). Recently Lorosa et al. (2000) found that *Triatoma rubrovaria and T. circummaculata,* can complete the whole nymphal development feeding in Blattaria only. There are other species which bites remain painful to the vertebrate hosts as the bites of other predatory Reduviidae do. The symbiotic fauna of Triatomini, needed as in all obligate bloodsuckers to provide essential vitamins that are lacking in their diet, is inconsistent and lives haphazardly in the gut lumen instead of storing it in the mycetome (as Nycteribiidae, Hippoboscidae, Cimicidae, Polyctenidae, Anoplura and Rhynchophthirina) or intracellularly (as Glossinidae, Streblidae, Nycteribiidae, Hippoboscidae and Mallophaga).

The polyphyletic origin hypothesis also helps explain the major anatomical differences found between some of the tribes and their noteworthy similarity to taxa from other subfamilies.

Alberproseniini, with the preocular region reduced to a minimum, as long as or shorter than the postocular region, very large eyes, and a flat body, reminds one of the appearance of the head and overall shape of some Cetherinae like, between many others, *Homalocoris*

Figure 7: *Homalocoris varius* Perty.

varius Perty (Fig. 7). However, more studies are needed. The shape, size, relationships and cuticular structure of the whole head, and specially on the anteocular region of *Alberprosenia* (Fig.8) is so different to any other found in Triatominae genera and species, that we are working with the hypothesis that this genus belongs to other subfamily, probably new (Alberproseniinae?). For comparison, authors show partially the anteocular region of *Triatoma mazzottii* Usinger 1941 (Fig. 9). To take the decision, authors are waiting results from DNA studies currently performed in two different laboratories.

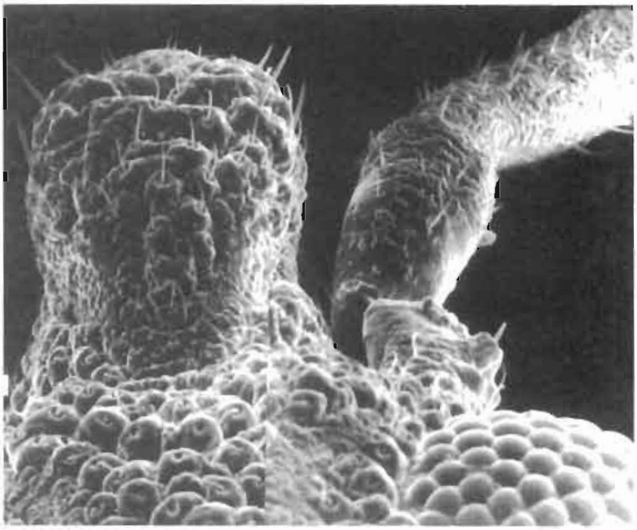


Figure 8: Anteocular region of *Alberprosenia malheiroi* Serra, 1987. See the cuticular structure no existing in any other Triatominae (SEM X400).

Genus *Psammolestes* Bergroth, 1911 (Fig. 10) has many of the anatomical characteristics of the second genus of Physoderinae described in the Americas: *Harpinoderes* Martínez & Carcavallo, 1988 (Fig. 11), whose main differences are the slightly claviform antennal segments. Morphological similarities as these could be related or not with phylogenetic relationships started by a common ancestor or could be by a evolutionary convergence phenomenom.

The tribe Bolboderini is an interesting case to reinforce the polyphyletic theory because their phalic structures are completely different from those of the other Triatominae tribes (Lent & Jurberg,

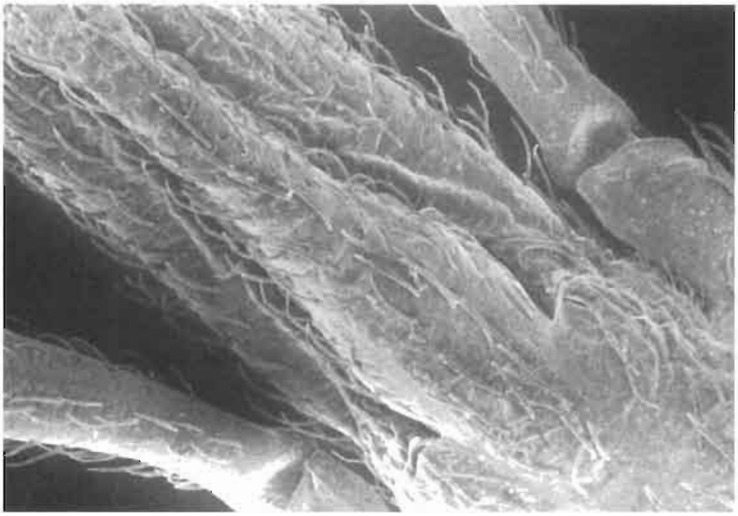


Figure 9: Anteocular region of *Triatoma mazzottii*. Cuticular structure common to all Triatominae genera and species, except *Alberprosenia*.

Figure 10: *Psammolestes coreodes* Bergroth, 1911.

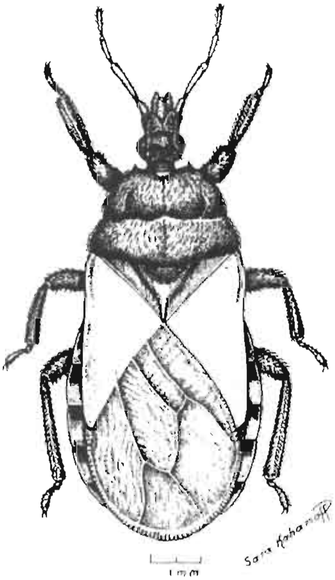


Figure 11: *Harpinoderes cicheroi* (Physoderinae) a possible case of evolutionary convergence with the Triatominae of Fig. 10, or phylogenetic relationships.

1984). The small size of all genera and species and the different general shape with other Triatominae are arguments to follow further studies of this particular tribe.

Microtriatoma Prosen & Martínez, 1952 is a genus of the tribe Bolboderini which has many similarities to a Reduviinae, *Aradomorpha championi* Lent & Wygodzinsky, 1944. As summed up by Schofield (1995): "This species of Reduviinae is so similar to Triatominae that it was at one time erroneously classified as a new species of *Microtriatoma* (Sherlock & Guitton, 1982)" (Figs. 12 and 13).

The other genera of Bolboderini share the characters of the male genitalia but each one has a typical aspect as *Bolbodera* Valdés, 1910 (Fig. 14), *Belminus* Stål, 1859 (Fig. 15) and *Parabelminus* Lent, 1943 (Fig, 16)

Figure 12: *Microtriatoma borbai* Lent & Wygodzinsky, 1979.

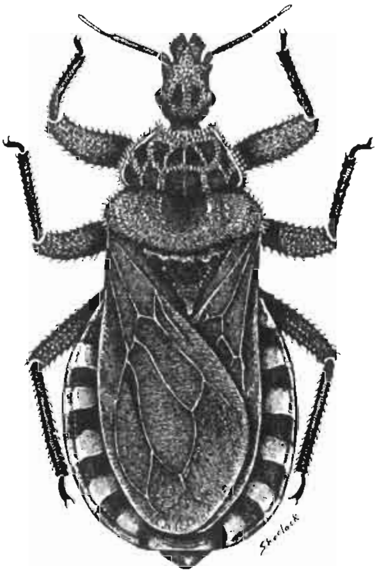


Figure 13: *Aradomorpha championi* Lent & Wygodzinsky, 1944, a Reduviinae so similar to the Triatominae of Fig. 12 that was wrongly described as *Microtriatoma pratai.* Another case of evolutionary convergence or phylogenetic relationships.

Figure 14: ***Bolbodera scabrosa*** **(Valdés, 1910).**

Figure 15: ***Belminus laportei*** **Lent, Jurberg & Carcavallo, 1995.**

Figure 16: ***Parabelminus carioca*** **Lent, 1943.**

The tribe Cavernicolini was thought as monotypical, and its genus *Cavernicola* Barber, 1937, has two species with a heavily convex head, a large postocular area with a well-demarcated interocular sulcus, and strong, broadened anterior femora, (Figs. 17 and 18) suggesting that the loss of its predatory condition is very recent. A recently described reduviidae, *Torrealbaia martinezi* Carcavallo, Jurberg & Lent, 1998 (Fig. 19), has traits similar to Reduviinae, Piratinae, and even Harpactorinae, (from this last subfamily is interesting the similar general shape with genus *Amphilobus* Klug, 1834) although these subfamilies are taxonomically thought as far apart from each other and Triatominae. Probably, hemipterologists should study carefully and with new techniques (as DNA) relationships between subfamilies of Reduviidae. The shape of the head and the two anterior femora and overall appearance of *Torrealbaia* bear a striking similarity to *Cavernicola*. This could be explained by an exceptional evolutionary convergence, or taking into account the origin of this strange reduviid, Venezuela, it could suggest a phylogenetic relationship in which the new species could represent the form most similar to the ancestors (predators) and *Cavernicola* represents the evolutionary form towards

Figures 17 and 18: Heads of *Cavernicola pilosa* Barber, 1937 and *C. lenti* Barrett & Arias, 1985(SEM).

Figure 19: *Torrealbaia martinezi* Carcavallo & Lent, 1998 a Cavernicolini which shares some predatory characters with Reduviinae and Harpactorinae.

hematophagy, but without a complete morphological differentiation. Schofield (2000) points out that Cavernicolini is perhaps the group first adapted to haematophagism. However, it is the tribe with more characters linked to predation.

Schofield (1995), based on then-unpublished studies by Guimarães & Ribeiro and Catalá, refers to the other two tribes of Triatominae: "Amongst the most compelling (studies) is the recent discovery of fundamental differences in salivary components between the Rhodniini and Triatomini, as well as important differences in sensorial patterns which suggest origins for these two tribes. In a sense therefore, the subfamily Triatominae is perhaps best seen as a utilitarian grouping defined on the basis of their bloodsucking habits and adaptations associated with this diet, rather than a cladistic classification of individuals sharing a common ancestral form".

The current situation of the species and specific complexes

The range of the species and even the genera of Triatominae is constantly changing in number, based on reviews of the material and new approaches and tools with which studies are performed. Some genera are monotypical and thus pose no taxonomic problem with the only species known thus far. These genera are: *Bolbodera* Valdés, 1910, *Torrealbaia* Carcavallo, Jurberg & Lent, 1998, *Dipetalogaster* Usinger, 1939, *Paratriatoma*, Barber, 1938, and *Hermanlentia* Jurberg & Galvão, 1997. There are genera in which the species are highly similar to each other, and distinguishing between them is a task for specialists. Such is the case of *Eratyrus* Stal, 1859, *Belminus* Stal, 1859 , *Microtriatoma* Prosen & Martínez, 1952, *Parabelminus* Lent, 1943, *Psammolestes* Bergroth, 1911, and *Linshcosteus* Distant, 1904. Other genera have only two species, with good traits for distinguishing them, like *Alberprosenia* Martínez & Carcavallo, 1977, *Cavernicola* Barber, 1937 and *Mepraia* Mazza, Gajardo & Jörg, 1940. Finally, there are three genera with numerous species described, some of which show great similarities: *Rhodnius* Stal, 1859, *Panstrongylus* Berg , 1879, and *Triatoma* Laporte, 1832. The species which have extensive morphological similarities constitute the so-called **specific complexes.**

Genus *Mepraia* species are *M. spinolai* (Porter, 1934) and *M. gajardoi* Friás, Henry & González, 1998. Both populations are similar even though they have good characters for differentiation. One character of males is the alary polymorphism. In *M. spinolai* it could be related to geographic distribution and demographic strategy, according to Schofield et al. (1998): "adults from costal populations are invariably wingless, whereas inland populations show balanced alary polymorphism between wingless females and males that are either winged or wingless... An X-linked mutation is proposed to inhibit wing development. Field studies of population demography indicate that male alary polymorphism is advantageous in the desert environment of northern Chile"

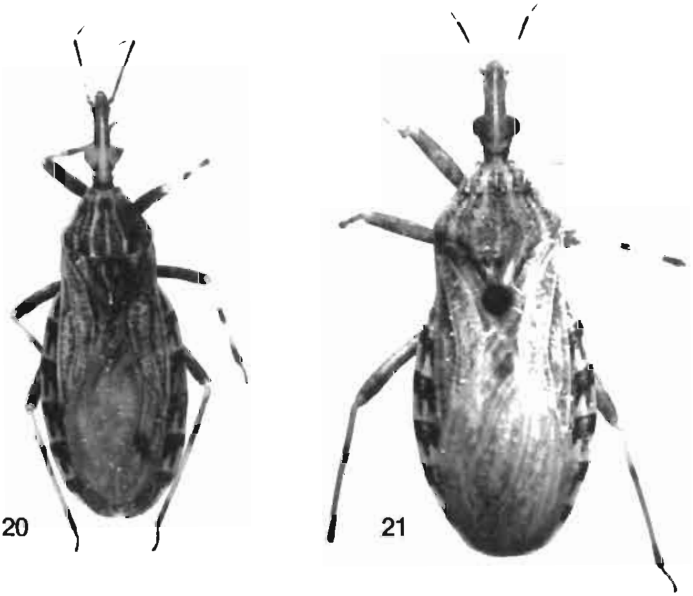
Genus *Rhodnius* Stål, 1859

According to Carcavallo et al. (1999), *Rhodnius* has only one specific complex, that of *R. prolixus* Stal, 1859. The species belonging to it, in addition to the nominotypical one, are *R. robustus,* Larrousse, 1927, *R. neglectus* Lent, 1954, and *R. nasutus* Stal, 1859. The studies performed, both morphometrically and through cross-breeding in the laboratory and by analysis of isoenzymes (Galíndez et al., 1994, 1997; Harry et al., 1992) determined that the differences between *R. prolixus* and *R. robustus* are almost undetectable in many populations, while in others a specific differentiation is possible. This suggests that there are areas with geographical or ecological barriers, while in others hybridization is frequent, and thus the specific differences are much less apparent. In this paper we consider the existence of other specific complexes within the genus *Rhodnius.*

Schofield & Dujardin (1999) consider that the possible origin of this genus could be "during the quaternary from a predatory form of reduviid occupying arboreal habitats in the Amazon-Orinoco rainforest" These authors gave the opinion of T.V. Barrett, as a personal communication, suggesting an ancestral form similar to extant Stenopodinae. "For such a predator, vertebrate nests in the region would offer shelter from climatic extremes together with more abundant supplies of invertebrate prey that could be captured by opportunistic ambush. Moreover, within the nests, the diet of invertebrate fluids could be supplemented by vertebrate blood – progressively more so as the organs involved in feeding on vertebrates became more appropriately adapted. Eventual adaptation to obligate haematophagy would be associated with several physiological and behavioral changes (Schofield, 1988) including greater reliance on the hosts for dispersal. This implies that the current species distribution of the genus would be strongly influenced by the distribution and migratory patterns of key host species"

***Rhodnius pictipes* complex** (Figs. 20, 21)

Schofield & Dujardin (1999) suggested that "within the genus, the form closest to the original would be best represented by a geographically widespread and relatively generalist species such as *Rhodnius pictipes.*" This species has the widest geographical distribution within the genus and is closely related to *R. stali* Lent, Jurberg & Galvão, 1993. *R. pictipes* was found from the extreme North of South America to Peru and Bolivia, near the border with Argentina, where it is possible its prevalence. *R. stali* seems to be an species derived from the former one, including characters of the genitalia: these two species are exceptions within the genus, with

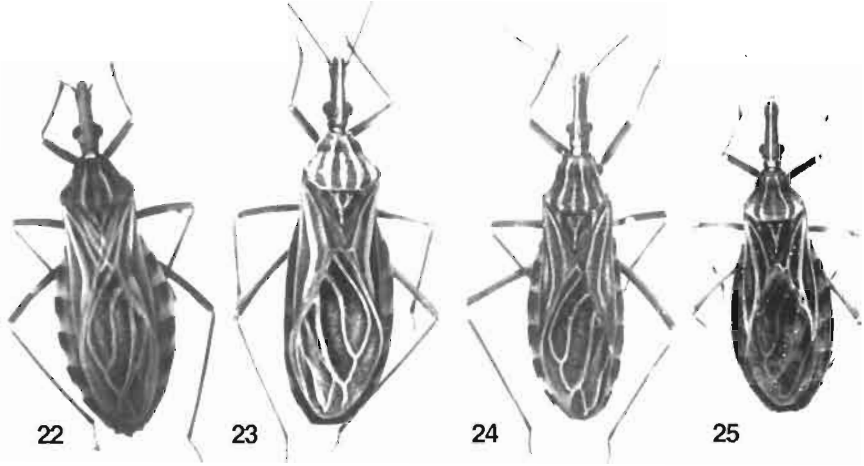


Figures 20 and 21: *Rhodnius pictipes* (20) shares a specific complex with *R. stali* (21).

phallosome support, anatomical character absent in all the other *Rhodnius* species. Jurberg (1995) considers that *R. pictipes* and *R. stali* could be the link between tribe Rhodniini and the other tribes, because the presence of the phallosome process. According to the relationships with hosts and habitats, (Carcavallo et al., 1998) *R. pictipes* Stal, 1872 was found in palm trees *Acrocomia sclerocarpa, Copernitia australis, Orbignya speciosa, Jessenia policarpa, Maximiliana regia, Scheelea sp., Attalea sp.*as well as in the Bromelid *Aechmea sp.* Feeding sources seem to be birds, bats, marsupials, rodents and lizards. In relation to human habitats, this species is found in corrals, pigeon and chicken coops and occasionally inside hoses attracted by light. *R. stali* was found in palm trees without mention of species and the feeding sources would be mammals and birds. It is attracted by light, too.

Rhodnius prolixus *complex* (Figs. 22-25)

Another specific complex already mentioned is *R. prolixus* (Fig. 22) with *R. robustus* (Fig. 23), *R. neglectus* (Fig. 24) and *R. nasutus* (Fig. 25). No closely related with these aspecies, a fifth one could be included, *R. domesticus.* Even though it has enough morphological



Figures 22-25: *Rhodnius prolixus* complex includes the nominotypical species (22), *R. robustus* (23), *R. neglectus* (24) and *R. nasutus* (25). *R. domesticus can also be included in this complex.*

characters to consider it as a single and isolated taxon. *R. prolixus,* according to Schofield & Dujardin (1999) "evolved through radiative adaptation from a discrete Amazonian population" Same authors point out that this species has a "wide but a highly discontinuous distribution". Even though this species is domiciliated in most of its geographical distribution, it maintains a wild cycle. Recent discussions on the validity of *R. robustus* (Galíndez et al., 1994, 1998; Harry et al., 1992; Schofield & Dujardin, 1999) suggested that populations of these two species would hybridise frequently, specially in palm trees where both species share the habitat. Out of other many habitats, including bird nests and mammal shelters, *R. prolixus* was found in the palm tress *Copernitia tectorum, Mauritia flexuosa, M. minor, Acrocomia sclerocarpa, A. aculñeata, Orbignya speciosa, Maximiliana elegans, Sabal mauritiaformis, Attalea humboldtiana, Scheelea sp., Coccos nucifera, Oenocarpus batana, Leopoldina piassaba, Jessenia policarpa, J. batana*, and trees *Samanea saman, Chlorophora sp., Agamia agami, Euxenura maguari, Ttheristicus caudatus, Cercibis oxycerca, Caracaya plancus* and *Polyborus plancus.* (Carcavallo et al., 1998). In wild environment the feeding sources are opossums (50%), rodents (17%), lizards (9%), birds (7%), mixed (16%) and in domestic environment, human (91%), dogs (4%) (Pifano, 1973). *R. robustus* shares some of the palm trees already mentioned as *R. prolixus* habitats. And its feeding sources are almost the same: rodents, marsupials, bats, lizards, frogs, when found near a human habitat, they feed on man, being 10 % of the samples positive for this source (Rosell et al., 1977). *R. neglectus* was found in palm trees *Orbignya martiniana, Acrocomia sclerocarpa, A. macrocarpa, Mauritia vionifera, Scheelea phalerata, Arecastrum romanzoffianum, Syagrus oleracea*, plus hollow trees and microhabitats of birds, marsupials, rodents and bats. Studies of feeding sources performed by Barreto (1967, 1968, 1971) and Forattini et al. (1971) showed a marked preference for avian blood, followed by marsupials, rodents and bats. Similar findings showed *R. nasutus,* (Espínola, 1985) found in the palm tree *Copernitia cerifera* and, as the former species, occasionally found in chicken coops, corrals or inside houses. The possible dispersion and evolution of this specific complex would be from an ancestor in the north of the South American rain forest. From there, and by active and passive transportation (eggs glued to bird feathers) there was an evolution of a single form that evolved to speciation in palm trees, hollow trees, bird nests and mammal shelters, when there existed barriers or some level of isolation, giving in some extremes of the geographical distribution or in some special habitats as human houses, specific differentiation between *R. prolixus* and *R. robustus,* but remaining a wide area where both forms are found together with intermediate forms. Under this point of view, the difficult to classify many specimens is related with the presence of the former species rather than hybridations between *R. prolixus* and *R. robustus.* Later, there were geographical isolations of populations: to the East, *R. neglectus,* to the North-East, *R. nasutus,* to the South-East, remaining in the costal region, *R. domesticus. R. domesticus* has different habitats that the other species of the complex: it is found mainly in bromelids plants, rodent nests, marsupial shelters, hollow trees, under bark and associated with *Echimys braivillei, E. dasythrix, Phynomys dasvelheix, Didelphis marsupialis* and *Marmosa cinerea* (Lent & Wygodzinsky, 1979, Espínola, 1985). Soares et al. (1998) found a new method to study *R. prolixus* interpopulation variability and to distinguish this species from *R. robustus* using salivary heme proteins (nitrophorins) electrophoresis in starch gel.

R. prolixus was found in Mexico (Oaxaca and Chiapas), Colombia (Antioquia, Arauca, Boyaca, Caqueta, Casanare, Cesar, Cundinamarca, Guajira, Huila, Magdalena, Meta, Norte Santander, Putumayo, Santander, Tolima, Vichada), Surinam, Guyana, French Guiana, Venezuela (all the satates), Trinidad, Brazil (Amazonas, Goiás, Pará, Rio de Janeiro?), Panama?, Costa Rica, Nicaragua, Honduras, El Salvador, Bolivia (Santa Cruz), Equator (Esmeraldas, Manabi, Napo, Zamora-Chinchipe), at altitudes from the sea level to 2.700 m.a.s.l. *R. robustus* was found in Bolivia (Pandos, Santa Cruz), Brazil (Amazonas, Pará, Maranhão, Goiás), Colombia (Santander, Norte Santander), Equator (Napo), Venezuela (Mérida, Falcon, Tachira, Cojedes, Apure, Barinas, Bolivar, Monagas, Sucre, Yaracuy), Peru (Cajamarca, Loreto, Madre de Dios), French Guiana, at altitudes from the sea level to 1.100 m.a.s.l. *R. neglectus* is prevalent in Brazil, on the states of Bahia, Mato Grosso, Minas Gerais, Goiás, São Paulo, Paraná, Maranhão, Pernambuco, between the sea level and 800 m.a.s.l. *R. nasutus* is restrictes to the Noth east of Brazil, on the satates of Ceará, Piauí, Rio Grande do Norte, Paraíba and Maranhão, between the sea level and 700 m.a.s.l. *R. domesticus* is a species found only at the East of Brazil, on the states of Espirito Santo, Bahia, Rio de Janeiro, Santa Catarina, Paraná, Sao Paulo, Maranhão, Piauí, Minas Gerais, at altitudes from almost the sea level to 800 m.a.s.l. (Carcavallo et al. , 1998). Findings of *R. prolixus* in Central America and Mexico are thought to be related with human accidental infestation from specimens carried from Venezuela (Zeledón, personal communication; Schofield 2000)

Rhodnius pallescens **complex** (Figs. 26, 27)

Other complex developed probably from *R. pictipes*, in relation to the forest of the Andes foothills rather than the Amazon plains or Mato Grosso ecosystems. The evolution would start from South to North, appearing first *R. ecuadoriensis* Lent & León, 1958, in Peru (Tumbes, Piura, Cajamarca, La Libertad, San Martin?) and Equator (Manabi, Guayas, Loja), the new species *R. colombiensis* Mejía, Galvão & Jurberg 1999 from Colombia (Tolima) and *R. pallescens* Barber, 1932 in Colombia (Bolivar, Sucre), Belize, Costa Rica, Venezuela (Zulia and Falcon) and Panama, where is the most important Chagas´ disease

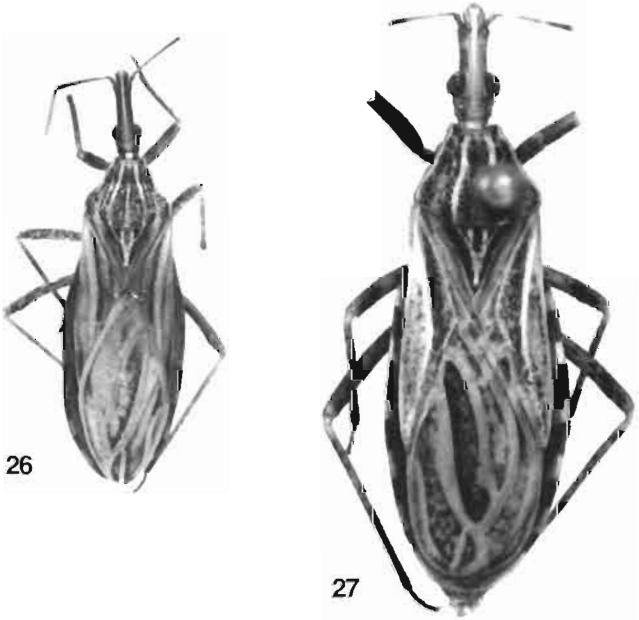


Figure 26: *R. pallescens* and *R. ecuadoriensis* (27) are part of an specific complex with the recently described *R. colombiensis*.

vector. It is possible that the dispersion would be facilitated by the feeding preference on *Didelphis marsupialis* and Caviidae (Rodentia). Currently, *R. ecuadoriensis* has invaded human houses but maintains a wild cycle in the palm tree *Elaeis guineensis* and trunks of trees (Cornejo Donayre, 1958; Lumbreras, 1960; Lazo, 1985; Carcavallo et al., 1999). *Rhodnius pallescens* is found in houses and some wild habitats as burrows and caves of Dasypodidae, palm trees *Scheelea zonensis,* hollow trees with *Didelphis marsupialis, Tamandua tetradactyla, Nyctomys sumichrasti, Caluromys derbianus, Proechymys semispinosus,* Sciuridae and Sauria. 45% of the studied samples were positive for *Didelphis* blood (Christensen et al., 1978, 1980; Sousa, 1972, Carcavallo et al., 1999). *R. colombiensis* from Tolima is a species of this complex that need more ecologic and biologic studies.

Another possible specific complex

R. dalessandroi Carcavallo & Barreto, 1976 was found only once in Colombia (Meta) at approximately 300 m.a.s.l., in a palm tree *Jessenia policarpa* but its feeding sources are unknown. Recently a new species very similar was found in Pará, Brazil and it is in process of publication, after which there could be the chance to consider another specific complex (Valente et al., 2000 in press, species named in homage to M.A. Miles)

Comments on the genus *Rhodnius*

Other species of the genus *Rhodnius* do not have enough similar characters to be included in specific complexes. *R. brethesi* Matta, 1919 is found in Venezuela (Territory Amazonas) and Brazil (Amazonas, Pará) at less than 500 m.a.s.l., in palm trees *Leopoldina piassaba* and in caves of *Dasypus novemcinctus.* Mascarenhas (1991) found that feeding preferences are reptiles and rodents. *R. neivai* is restricted to the dry and very dry forest in the North of South America, Venezuela (Lara, Falcon, Zulia) and Colombia (Cesar), at less than 300 m.a.s.l., frequently found in houses, being found in the wild environment by the first time in 1975, in palm trees *Copernitia tectorum, Scheeles ap.* and trunks of dead trees (Carcavallo et al., 1976, 1999). *R. paraensis* Sherlock, Guitton & Miles, 1977, very different morphologically to the other *Rhodnius* species (as *R. neivai* and *R. dalessandroi*) is found in Brazil (Para), almost at sea level, in rodent and marsupial shelters and having *Echimys crisurus* and *Didelphis marsupialis* as principal feeding sources (Sherlock et al., 1977, Miles et al., 1981)

According to previous information, the geographical distribution and specific differentiation would be related to hosts linked to the feeding preference. According to that, two different ways would have happened, one, following the dispersal of marsupials, specially Didelphidae, the other, more eclectic, related to birds, mammals and reptiles sharing the habitats, mainly palm trees, with the bugs.

New tools have been used to study the evolution and taxonomic status of the genera and species of Rhodniini: quantitative morphometry, isoenzyme analysis and mitochondrial DNA sequences. According to Galíndez, 1994, 1998; Dujardin et al, 1999; Chávez et al., 1999; Schofield & Dujardin, 1999), there are three principal groups of *Rhodnius* species, considering morphometry and isoenzymes: 1) *pictipes, stali, brethesi;* 2) *neglectus, nasutus, prolixus* (domestic); d*omesticus* and *neivai* could be clustered with these species; 3) *pallescens, ecuadoriensis, colombiensis.* Catalá & Schofield (1994) studied the antennal sensilla patterns and found similarities between *pictipes* and *ecuadoriensis* and two pairs: *robustus + prolixus* and *neglectus + nasutus.* Studies of DNA sequences were done sequencing the 16S small subunit rRNA gene of four species and by analysis based on the large subunit rRNA gene and the cytochrome-B gene fragment of seven species. Stohard et al. (1998) found three groups: 1) *pictipes;* 2) *ecuadoriensis;* 3) *prolixus* and *nasutus.* Lyman et a. (1999) showed three complexes: 1) *pictipes + brethesi;* 2) *pallescens + ecuadoriensis;* 3) *prolixus+ neglectus+ robustus.* Schofield & Dujardin (1999) quoted data from F. Monteiro & C.B. Beard (personal communication) using D2 nuclear DNA sequence information with a larger number of specimens that showed that the Tolima form (later described as *R. colombiensis*) clusters with *ecuadoriensis* and *pallescens,* adding *nasutus* near *neglectus* and including *domesticus* and *neivai* in the *robustus-prolixus-neglectus-nasutus* clade. *R. neivai* is morphologically different and ecologically isolated and therefore we consider the comment "although bootstrap support for the placement of *R. neivai* was poor" correct, and we do not consider this species as phylogenetically related to any other of the currently known *Rhodnius* species. The new species in press (Valente et al., 2000) from Brazil, Pará, is very similar to *R. dalessandroi* as previously mentioned and it is possible that further studies may place these two species in another complex in the future, in spite of the distance between their respective geographical distribution, but both connected with the Amazonian basin.

Schofield & Dujardin (1999) show two diagrams of *Rhodnius* species relationships, that we consider useful and probably very near the real interconnections.

The possible origin and dispersion of the three specific complexes are shown in the map of Figure 28.

Figure 28: Possible routes for dispersion of some species of *Rhodnius* which are included in three specific complexes.

Genus *Psammolestes* and its relation to *Rhodnius*

Psammolestes coreodes and *Ps. tertius* were placed by Monteiro & Beard (quoted by Schofield & Dujardin (1999) as personal communication) at the base of the *robustus* clade, in spite that with all other techniques "none... has fully resolved the relationship between *Rhodnius* and *Psammolestes*, since cladistic analysis based on isoenzymes or morphometry gives a variable position for *Psammolestes* either within or external to the other Rhodniini. Several studies, including analysis of salivary nitrophorins show that populations of *R. robustus* of the extreme Northern and Southern areas of its geographical distribution have great variability, having the southern forms similarities with *R. prolixus* from domestic environment.

Even though the DNA studies, it is difficult to understand relationships between the two genera of Rhodniini. If we accept the possibility of an ancestor related to a reduviid similar to Stenopodinae for *Rhodnius,* the morphological characters of *Psammolestes* (Fig. 10) remind some predatory behaviour not completely lost and linked, apparently, to other subfamily as Physoderini, one of which genera, *Harpinoderes* (Fig. 11), is very similar. The two characters considered to include *Psammolestes* in the tribe Rhodniini are the antennal insertion, near the apex of head, and the presence of postocular callosities. But these characters are neutralized by the strong and wide rostrum and femora with predatory characteristics, completely different to the thin and slender rostrum and legs of *Rhodnius.*

Panstrongylus lignarius complex

The genus *Panstrongylus* Berg, 1879 was studied by Lent & Wygodzinsky (1979), who constructed a cladogram (Fig. 29, Tab. III) to establish the relations between the traits in plesiomorphic and apomorphic states, thus situating each species in a phylogenetic scheme.. The complex *P. lignarius* (Walker, 1873), to which belong, in addition to the nominotypical species (Fig. 30), *P. humeralis* (Usinger, 1939) and *P. herreri* Wygodzinsky, 1948 is the only specific complex of this genus. Although the three species display great morphological and chromatic similarity, *P. humeralis* is the easiest to distinguish due to both its taxonomic characteristics and its geographical isolation, being confined to the Republic of Panama, almost at the sea level. On the other hand, the other two species are so similar that it is often difficult to distinguish between them. *P. lignarius* is known from the Amazon Basin: Brazil (Amazonas, Pará, Goiás, Maranhão); Guyana; Surinam up to the dry tropical forest in Venezuela (Portuguesa), between the sea level and 600 m.a.s.l.. *P. herreri*, on the other hand, is known from Peru, from almost the sea level to 1600 m.a.s.l. (Amazonas, San Martin, Piura, Cajamarca), where it is prevalent in both the high and low forests, between the Huallaga and Marañón rivers, but also having reaching the drier Pacific watershed. Of the three in the specific complex, this latter species is the one with the highest domiciliation indexes and is considered the second most important species in Peru in epidemiological terms (Calderón et al. , 1985).

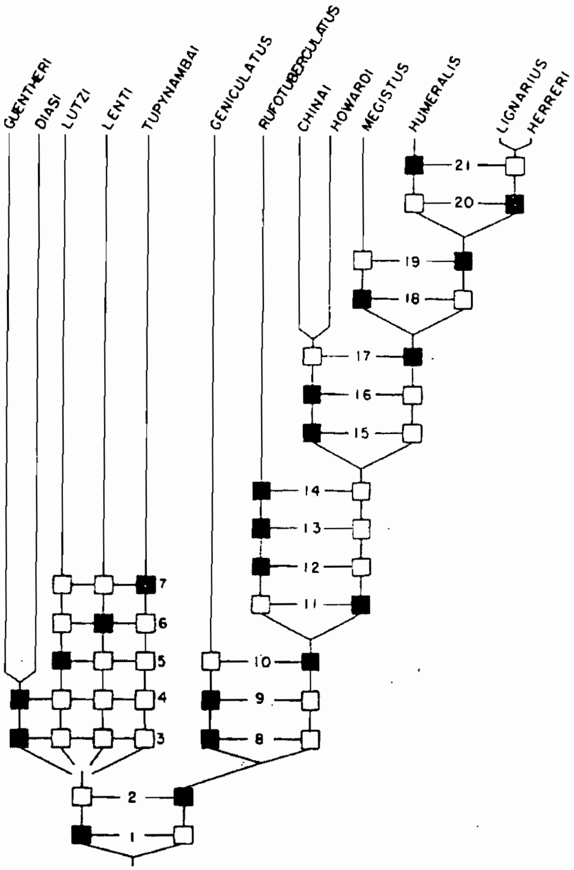


Figure 29: Cladogram for the species of genus *Panstrongylus* according to Lent & Wygodzinsky (1979). The cladogram is completed with Table 2.

Table III

Characters used to construct the cladogram shown in figure 29

Character	Plesiomophic state	Apomorphic state
1. Eyes of male	Large; ratio eye/synthlipsis 1:1.1-1.75	small; ratio eye/synthlipsis 1:2.0-2.3
2. Overall color pattern	Simple	Complex
3. Discal and lateral tubercles of pronotum	Present	Obsolete or absent
4. Endosoma processes of male genitalia	Denticulate	Not denticulate
5. Connexival segments with dark spots	All	Only III and IV
6. Granules of under surface of fore femur	At most in three pairs	Much more numerous
7. First rostral segment	Slightly to distinctly shorter than second	As long as or longer than second
8. Pattern of abdominal venter	Simple	Complex
9. Sides of postocular	Conspicuously rounded	Almost straight
10. Apicolateral process of antenniferous tubercle	Present	Obsolescent or lost
11. Jugae	Blunt	Hooklike
12. Male genitalia with	1+1 endosoma processes	2+2 endosoma processes
13. Clypeus	Not bilobed apically	Bilobed apically
14. Dorsal setae of head and thorax	Not scalelike	Many scalelike
15. Denticles of femora	Present	Absent
16. Vesica of male genitalia	With less specialized structure	Semiglobose, heavily sclerotized
17. Scutellar spine	Elongate cylindrical	Short, blunt
18. Endosoma processes	Only apically denticulate	Almost entirely denticulate
19. Third article of antennae	As long as second	Distinctly shorter than second
20. Assessory sublateral tubercles of pronotum	Absent	Present
21. Posterior process of scutellum	Without heavy hump basalty	With haevy hump basalty

Caracteres usados para construir o cladograma da Figura 21.10

Caráter	Estado plesiomórfico	Estado apomórfico
1- Olhos do macho	grandes, relação olho-região interocular 1: 1.1- 1.75	pequeno, relação olho-região interocular 1: 2.0 - 2.3
2- Padrão geral de colorido	simples	complexo
3- Tubérculos discais e laterais do pronoto	presente	ausente
4- Processo do endosoma	denticulado	não denticulado
5- Segmento conexivo com mancha escura	todos	Só III e IV
6- Grânulos da superfície inferior do fêmur anterior	com no máximo três pares de grânulos	muito mais numerosos
7- Primeiro segmento do rostro	mais curto que o segundo	tão longo ou maior que o segundo
8- Padráo do abdomen ventral	simples	complexo
9- Bordos postoculares	conspicuamente arredondados	quase retos
10- Processo apico-lateral do tubérculo antenífero	presente	ausente
11- Jugas	obtusas	em forma de gancho
12- Genitália masculina	1 + 1 processo do endosoma	2 + 2 processos do endosoma
13- Clípeo	não bilobado apicalmente	bilobado apicalmente
14- Cerdas dorsais da cabeça e tórax	não escamosas	muitas escamosas
15- Dentículos dos fêmures	presentes	ausentes
16- Vesica da genitália do macho	com pouca estrutura especializada	semiglobosa, altamente esclerotizada
17- Processo do escutelo	alongado e cilíndrico	curto e obtuso
18- Processos do endosoma	só apicalmente denticulados	quase totalmente denticulados
19- Terceiro artículo da antena	tão longo quanto o segundo	mais curto que o segundo
20- Tubérculos acessórios sublaterais do pronoto	ausentes	presentes
21- Processo posterior do escutelo	sem forte saliência basal	com forte saliência basal

The complex *lignarius* may have originated in Amazonia and have spread from there to Panama and Peru. The ecological conditions in the Darien region may have posed a barrier which allowed for the well-defined speciation of *P. humeralis* of not well known habitats. On the other hand, although Lent & Wygodzinsky (1979) report that no intermediate forms have been found, the fact that the eastern limits of

P. herreri reach the Marañón river in Peru leads one to suspect that there may once have been this link through the Amazon basin with the area of *P. lignarius*, of which it is virtually a cryptospecies due to its great similarity. The barriers, in this case are not geographical but ecological, to the extent that *P. herreri* adapted to other habitats (including human dwellings) through its trophic link to Caviidae guinea pigs (Herrer, 1960), while *P. lignarius* is found in palm trees *Scheelea humboldtiana, Sabal sp., Maximiliana elegans* and hollow trees and tree tops, related to some feeding sources as rodents, toucans, spiny rats, *Didelphis marsupialis, Coendu sp., Tamandua tetradactyla and* the bat *Desmodus rotundus*. In the cladogram constructed by Lent & Wygodzinsky (1979), *P. lignarius* and *P. herreri* come together, without plesio- or apomorphic traits that differentiate them.

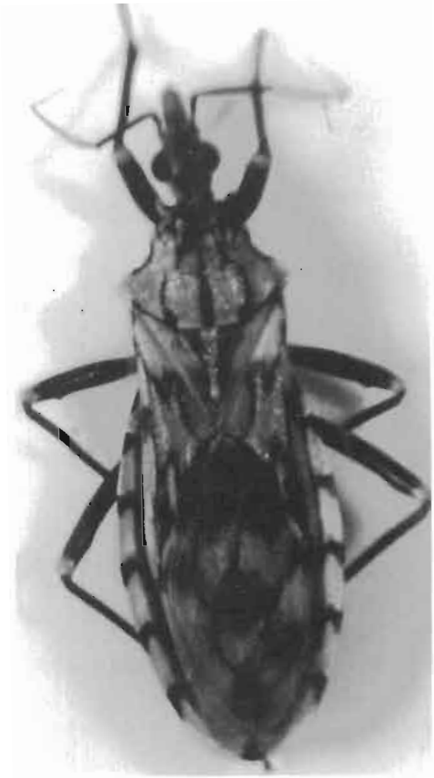


Figure 30: *Panstrongylus lignarius*. The specific complex includes *P. humeralis* and *P. herreri*.

Genus *Triatoma*

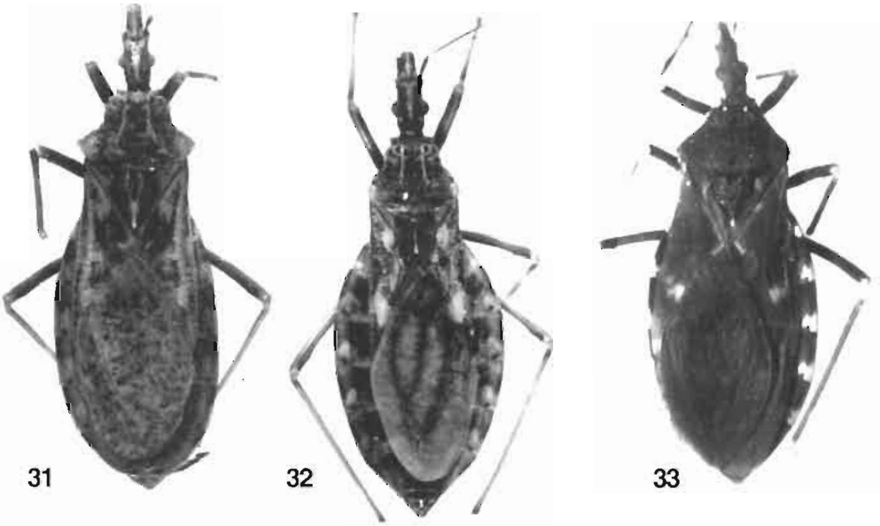
The type species of genus *Triatoma* Laporte, 1832 is *T. rubrofasciata* (De Geer, 1773). It is a pantropical species, being found in the New and the Old World. However, as pointed out by Cai et al. (1994) " There are 10 synonyms under the name *T. rubrofasciata* (Lent & Wygodzinsky, 1979). The stridulum structures of individuals from South China are different from those reported by Lent & Wygodzinsky (loc. Cit.). There are two possibilities: one is that the species exhibits stridulitrum polymorphism; another is that those individuals showing differences on stridulitra structures may represent different species. It is essential to study the *Rubrofasciata* (sic) complex in more detail from a global point of view"

Lent & Wygodzinsky (1979) mentioned various specific complexes in the genus *Triatoma* Laporte, 1832, analysing the morphological traits of the adults and some nymphs. For example, they emphasise the importance of the presence or absence of specialised metatarsal hairs in first-stage nymphs, to the point of suggesting that they may be significant in the specific and generic taxon. The complexes they mention in *Triatoma* are the following: *infestans, circummaculata, protracta, flavida, rubrofasciata, recurva, nigromaculata, dispar, lecticularia,* and *phyllosoma*. Some of them, like the complex *spinolai*, can no longer be considered, since the nominotypical species of the complex has been included in genus *Mepraia*, revalidated by Lent et al. (1994). Lent & Wygodzinsky (1979) think that most of the *Triatoma* species of the Americas can be included in the "*rubrofasciata* group", of eastern origin. Schofield (2000) accept the possibility that *T. rubrofasciata* might be originated in South America. Lent & Wygodzinsky (1979) characterise them by the presence of specialised metatarsal hairs in the first-stage nymphs (although several North American species lack them), and the majority of the fifth-stage nymphs have a longitudinal line of dorsal abdominal tubercles. However, this latter trait loses taxonomic importance, according to the aforementioned authors, because in *T. rubrofasciata* (De Geer, 1773) there are specimens that have the line of abdominal tubercles and others that do not.

***Triatoma flavida* complex** (Figs. 31-33)

Triatoma flavida, Neiva, 1911 (Fig. 31), *T. bruneri* Usinger, 1944 (Fig. 32), and *T. obscura* (Maldonado Capriles & Farr, 1962) (Fig.

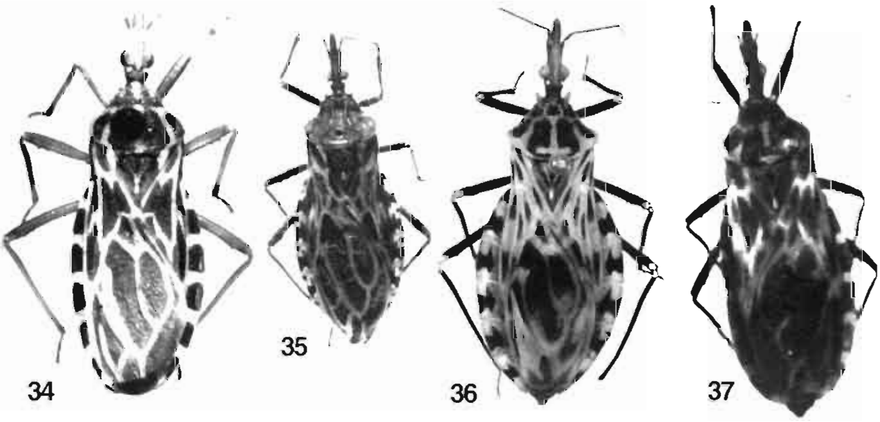
33) form a complex geographically limited to the larger Caribbean islands, with the first two species in Cuba and the third in Jamaica, and all they at altitudes lower than 500 m.a.s.l.. The Cuban species are particularly similar, and some specimens are difficult to distinguish, possibly due to interspecific breeding. *T. bruneri* habitats are caves with mammals (Usinger, 1944) while *T. flavida* was found in domestic and peridomestic environments and, when in wild ecotopes, related to the rodent *Capromys pilorides* (Sotolongo, *fide* Lent & Wygodzinsky, 1979). *Triatoma obscura* is morphologically and chromatically much more differentiated, and although there may have been a common origin for the three, it is impossible with current techniques to establish a chronological phylogenetic relationship. Its habitats is unknown, but it has shown some anthropophilic behaviour.



Figures 31-33: *Triatoma flavida* (31) complex, which includes *T. bruneri* (32) and *T. obscura* (33).

***Triatoma venosa* complex** (Figs. 34-37)

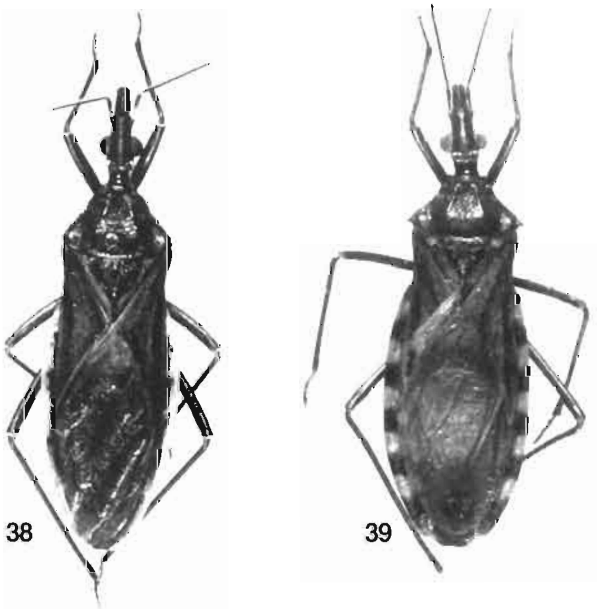
A similar case is that of the complex that includes *T. venosa* (Stal, 1872) (Fig. 34) from Colombia (Boyaca, Santander), Equator (Azuay) and Costa Rica, at altitudes between 500 and 2.550 m.a.s.l., and *T. dispar* Lent, 1950 (Fig. 35), from Costa Rica, Panama, and Equator (Guiayas, Imbabura) at altitudes near the sea level., This complex also includes, with some reservations based on cuticular differences in the abdomen of fifth-stage nymphs, *T. nigromaculata* (Stal, 1859) (Fig. 36), from Venezuela (Aragua, Barinas, Bolivar, Cojedes, Lara, Mérida, Monagas, Portuguresa, Sucre, Yaracuy, Territory Delta Amacuro, federal District), from 300 to 1.000 m.a.s.l.. This complex is not named *nigromaculata*, species described before than *T. venosa*, due to the reservations previously mentioned. This complex could also include *T. carrioni* Larrousse, 1926 (Fig. 37), which is prevalent on both sides of the border between Peru (Piura, Cajamarca, ? intermediate departments) and Equator (El Oro, Cañar, Azuar, Zamora-Chinchipe), from 1.000 to 2.600 m.a.s.l.. The probable origin of this complex is in the forest areas between Ecuador and Colombia. *T. dispar* has not shown a trend towards domiciliation and is apparently linked to Bradipodidae. *T. carrioni* and *T. venosa* have been found colonising, the first in Peru and the second in Colombia. *T. nigromaculata*, which appears to be the most separate of the group, is sylvatic, but specimens have been found on several occasions in peridomiciliary areas and even inside dwellings in Venezuela. There do not appear to be any geographical barriers to explain this group's speciation, which might lead one to think of ecological differences in the sylvatic environment. One should keep in mind that domiciliation is a recent phenomenon.



Figures 34-37: *Triatoma venosa* (34) complex. It includes *T. dispar* (35), *T. nigromaculata* (36) and *T. carrioni* (37).

Triatoma breyeri complex (Figs. 38, 39)

The complex *Triatoma breyeri* Del Ponte 1929 includes two species recognized as such, and allopatric: the nominotypical species (Fig. 38) and *T. eratyrusiformis* Del Ponte 1929 (Fig. 39). Lent & Wygodzinsky include these species in the *spinolai* complex, but the latter was separated from the genus *Triatoma* when genus *Mepraia* Mazza, Gajardo & Jörg, 1940 was revalidated, but the other species have important morphological differences, including the male genitalia, and could not be included in the revalidated genus. Both species were described in the same study, and *breyeri* has priority for naming this specific complex simply because of the page number. This species' geographical distribution is very limited, with peculiar ecological conditions. It appears to be associated with rodents from the family Cavidae in a salty semidesert ecosystem around Salinas Grandes in central Argentina, from 200 to 700 m.a.s.l.. *T. eratyrusiformis* is distributed over a broader area in western Argentina, including central Patagonia, at altitudes between 100 and 800 m.a.s.l..

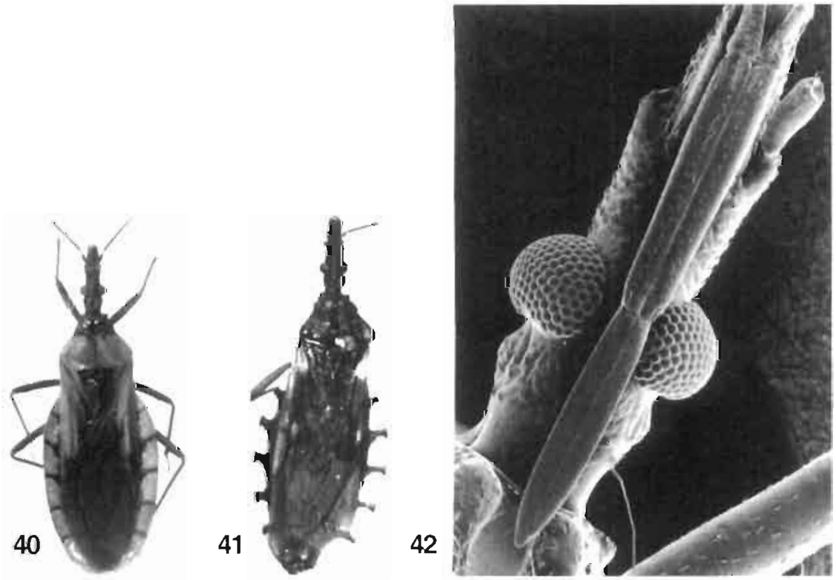


Figures 38 and 39: *Triatoma breyeri* and *T. eratyrusiformis*, a complex which need further studies.

It is a basically rupestrine species associated with edentates and rodents, amongst which *Microcavia australis* Geoffroy. Attempts to breed the two species have led to few nymphs that did not survive beyond the third stages. In central Argentina, and with no known geographical relationship to the rest of the distribution of *T. eratyrusiformis*, one finds populations with morphological differences, such as the lacking spiny humeral angles, but which, according to Lent & Wygodzinsky (1979), might be variable and insufficient to separate them as a different species (*T. ninioi* Carcavallo, Martínez, Prosen & Cichero, 1964, current synonym of *T. eratyrusiformis*).

Triatoma circummaculata **complex** (Figs. 40-42)

It includes only two species, the nominotypical, described by Stål in 1859 (Fig. 40), and *T. limai* Del Ponte, 1929 (Fig. 41). Pinto (1931) included these species in the new genus *Neotriatoma*, taking into account the only case in the genus *Triatoma* of a species with rostrum having the third segment of the same size of the second (Fig. 42) and very strongly flattened dorsoventrally. This

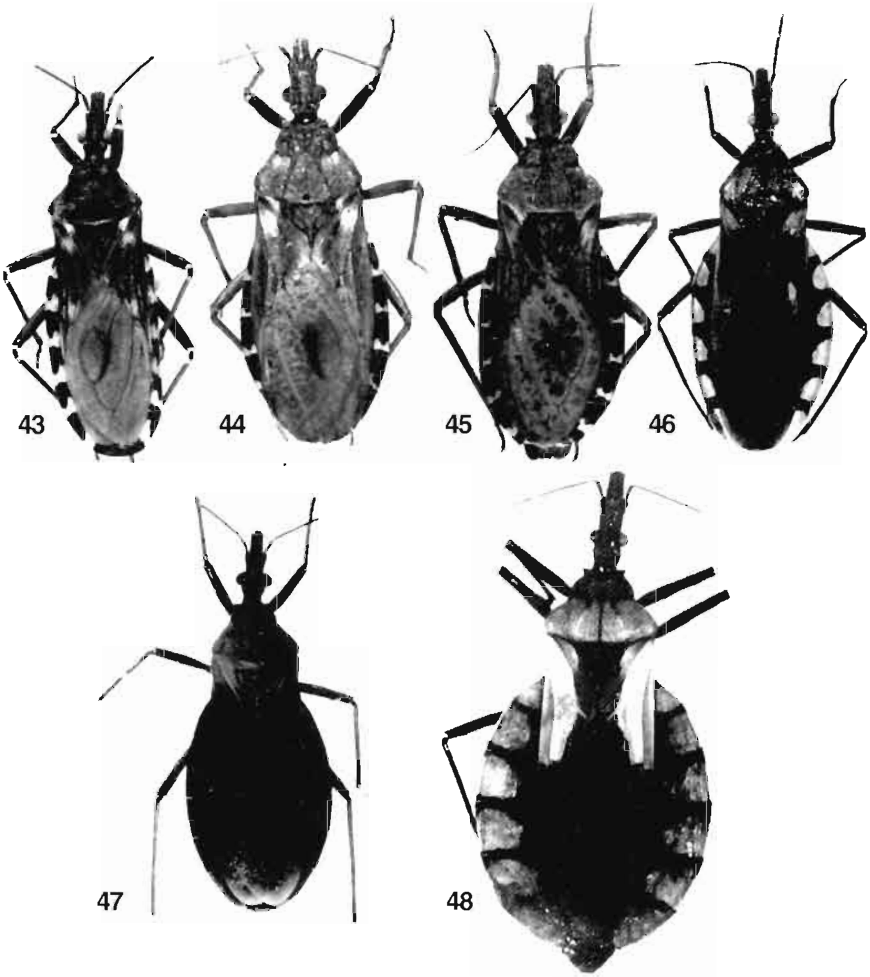


Figures 40-41: The *T. circummaculata* (40) complex is completed with another species, *T. limai* (41). The rostrum with the second and third segments of the same size is the only case in the Tribe Triatomini (42).

character, apparently, only appears in the adult stage, not being present in the nymphs. *T. circummaculata* is restricted to Uruguay and the State of Rio Grande do Sul, in Brazil, while *T. limai* is prevalent in central Argentina, in the provinces of Córdoba and San Luis. Both species are rupestral, linked with rodent and marsupial shelters, lizards and Blattaria.

***Triatoma infestans* complex** (Figs. 43-49)

Many species have been included in the complex *T. infestans*, some of which bear little relationship to each other or to the species for which the complex is named, so that for some the specific taxon may be open to discussion. Carcavallo et al. (1999) follow Usinger et al. (1966), who only include the following with *T. infestans* (Klug, 1834) (Fig. 43): *T. platensis* Neiva, 1913 (Fig. 44), *T. delpontei* Romaña & Abalos, 1947 (Fig. 45), and *T. rubrovaria* (Blanchard, 1843) (Fig. 46), adding another species, *T. melanosoma* Martínez, Olmedo & Carcavallo, 1987 (Fig. 47), originally described as a subspecies of *T. infestans* and later moved to the specific taxon by Lent et al., (1994b). Recently another one was described and should be included in this complex, *T. carcavalloi* Jurberg, Rocha & Lent, 1998 (Fig. 48). The possible ecological barriers between the first three species, sympatric in large areas of central Argentina, the lack of genetic barriers between *T. infestans* and *T. platensis* or *T. delpontei,* and the reproductive and ecological barriers between *T. rubrovaria* and the first three species have been studied in detail by Usinger et al. (1966), who show in short that the three are interfertile to a greater or lesser degree and that although they are sympatric, their habitats do not coincide, except in the peridomicile, where *T. infestans* and *T. platensis* cohabit and sometimes hybridise naturally. Experimental studies by Cortón (*fide* Carcavallo et al. , 1999) and Galvão (unpublished) have shown that *T. melanosoma* is also interfertile with *T. infestans.* But *melanosoma* also displays ecological and geographical isolation from *T. infestans*, since it is present in an area where the latter has never been found. The conclusions presented by Usinger et al. (1966) are quite clear and can be added to the species not mentioned by them, *T. melanosoma* and *T. carcavalloi* "The fact that completely fertile hybrids between *infestans*, *platensis* and *delpontei* are readily produced in the laboratory leads us to re-examine the systematic status of the three. First, each of these three species is defined by constant morphological, color, physiological and ecological characters that do not overlap; no intermediate populations are found. Each has attained reproductive isolation from its siblings. This isolation appears to have been effectuated by geographical and



Figures 43-48: The *Triatoma infestans* complex includes the nominotypical species (43), *T. platensis* (44), *T. delpontei* (45), *T. rubrovaria* (46), *T. melanosoma* (47) and *T. carcavalloi* (48). Wild populations from Bolivia, studied by Noireau (1999) may also be considered as included in this complex ("Dark Morphs").

ecological isolation between *infestans* on the one hand and *platensis* + *delpontei* on the other hand, and by ecological isolation between *platensis* and *delpontei*... In the case of *infestans* versus *platensis* + *delpontei*, which might have started out as an ecological separation (mammal versus avian hosts)... As long as perfect geographical and ecological isolating mechanisms exist between populations separated by a complete morphological and behavioural gap, the fact that genetic barriers to gene exchange have not evolved does not invalidate the status of these populations as good species. We do not think that the potential production of fertile hybrids, under laboratory or other voluntarily or involuntarily man-made conditions, could be taken as a motive for lowering the taxa involved to the level of subspecies."

The hypothesis has been raised that the origin of *T. infestans* may be in an association with rodents from the family Caviidae in the mesothermic valleys of Bolivia (Usinger et al., 1966; Prosen, personal communication, Borda Pisterna, 1985). This fits into a certain logic and is within the realm of the possible, but it does not explain either the great distances separating the other species in the complex from the supposed point of origin nor the major ecological, physiological, and behavioral differences between these species. One hypothesis that would explain all the gaps is that one of the species in the complex or an ancestor spread from the dry subtropical Chaco forest from the South of Bolivia and Paraguay and the North of Argentina. From there, one line spread north, adapting to the association with Caviidae until human intervention, domesticating Guinea-pigs, introduced the insect into dwellings and scattered it over a major portion of South America. This is the species currently known as *T. infestans,* which geographical distribution includes Argentina (Salta, Jujuy, Tucumán, Formosa, Chaco, Santiago del Estero, Santa Fe, Misiones, Corrientes, Entre Ríos, Córdoba, Catamarca, La Rioja, San Juan, Mendoza, San Luis, Buenos Aires, La Pampa, Neuquén, Río Negro, Chubut), Uruguay (Artigas, Salto, Paysandú, Rio Negro, Revira, Tacuarembó). Bolivia (Cochabamba, Potosí, Tarija, Beni, La Paz, Santa Cruz, Chiquisaca), Brazil (Alagoas, Bahia, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Paraiba, Paraná, Pernambuco, Piauí, Rio de Janeiro, Rio Grande do Sul, São Paulo, Santa Catarina, Sergipe), Paraguay (Concepción, San Pedro, Cordillera, Guairá. Caaguazú, Caazapá, Misiones, Peraguarí, Central, Presidente Hayes, Alto Paraguay, Chaco, Nueva Asunción, Boquerón), Peru (Apurimac, Ayacucho, Moquegua, Arequipa, Tacna, Ica, Lima), Chile (in the nine provinces between 18º30´S and 34ª36´S), Equator (? Esmeraldas). This species was found at altitudes between the sea level and 4.100 m.a.s.l. (Borda Pisterna, 1985; Espínola, 1985; Schenone et al, 1985; Lazo, 1985, Gozález Romero, 1985, Franca Rodríguez, 1985; Martínez et al., 1985; Carcavallo et al., 1999). Another evolutionary line spread to the south, preferring nidicolous habitats and ornitophylic feeding, overlaping their geographical distribution but later specializing in two different types of nests, Psittacidae and Dendrocolaptidae (*T. delpontei, T. platensis).T. delpontei* is found in Argentina (Buenos Aires, Catamarca, Córdoba, Corrientes, La Rioja, Salta, Santa Fe, Santiago del Estero, Tucumán, Chaco, Jujuy, Formosa, La Pampa), Bolivia (Santa Cruz), Paraguay (Presidente Hayes) and Uruguay at altitudes between the sea level and 550 m.a.s.l. (Carcavallo et al.,1999, Lent & Wygodzinsky, 1979) *T. platensis* is prevalent at the same Argentinian provinces than the previous species, plus Entre Rios, San Luis, San Juan, Mendoza, Rio Negro and it is also found in the same Department of Paraguay, the West of Uruguay and the South of Bolivia as *T. platensis* and at the same altitude. Even though the different host preference shown in natural habitats, sometimes both two species share the human peridomiciliary environment.

Our hypothesis of an ancestor spread from the Chaco is supported by the recent detection of a new sylvatic *T. infestans* population in this region Chaco (Noireau et al., 1997b). Because of chromatic differences with domestic *T. infestans* (overall darker coloration with small yellow markings on the connexivum), they were named dark morphs (DM). Hollow trees and, to a lower extent Bromeliaceas, constitute their more favourable ecotopes (Noireau et al., 2000b). Such ecotopes suggest a possible association between *T. infestans* DM and rodents. Successful crossing experiments between DM and domestic *T. infestans* from the Chaco point out a reproductive compatibility. Nevertheless continuous gene flow between wild and domestic *T. infestans* populations in the Chaco seems unlikely because of the marked chromatic and morphometric differences as well as differences in mitochondrial DNA and chromosome banding (Noireau et al. 2000a; Monteiro et al., 1999). As showed by cytogenetics and antennal pattern, the DM population would be more closely-related to domestic *T. infestans* from Paraguay, Uruguay, Brazil and Argentina than domestic and sylvatic Andean populations (Noireau et al., 2000a). Likewise, the similarity of habitat between *T. infestans* DM and *T. melanosoma* suggests that both species share ecological traits as habitat and related fauna.

From the Chaco, another line of dispersion was towards the southeast, *T. rubrovaria*, swerving north after crossing the Paraná and Uruguay rivers, adapting to the rupestrian environment and feeding on mammals and reptiles living in rocky lairs. This species, according to Usinger et al. , (1966) shows some type of genetic isolation respect the other species of the complex. However, natural and experimental hybrids with *T. infestans* are relatively frequent. The geographical distribution includes Argentina (Misiones, Corrientes, Entre Rios), Brasil (Rio Grande do Sul) and Uruguay (Artigas, Salto, Paysandú, Rio Negro, Rivera, Tacuarembó), at altitudes lower than 400 m.a.s.l. Recently was described a species, *T. carcavalloi* Jurberg, Rocha & Lent, 1999, with morphological and chromatic similarities with the last species although easy to differentiate because its typical abdominal shape, wing color pattern and genitalia. It is currently restricted to stone fields near peridomiciliary environments in Brazil (Rio Grande do Sul), sharing some ecotopes with *T. rubrovaria*. It seems to exist an obvious phylogenetic relationship between these two species.

Finally, some spread east, being the only population entering the subtropical wet forest, in the extreme Northeast of Argentina (Misiones), at approximately 300 m.a.s.l., inhabiting tree hollows, bark, and other arboreal habitats, near peridomiciliary environments, with no specialised feeding, but taking advantage of their black color to remain hidden in the depths of their ecotopes (*T. melanosoma*). Presumed routes of dispersion of this specific complex are shown in Figure 49.

According to their feeding preferences and habitats, species belonging to the *T. infestans* complex could be classified as follows: **Euriphagous**, without a current preference but probably originated on a relationship to Caviidae. Mainly found in domestic and peridomestic environment, almost completely adapted to human environment, exceptionally found in bird and parakeet nests, hollow trees, cacti *Cereus,* palm tree *Acrocomia macrocarpa*, fig tree, marsupial and rodent shelters: *T. infestans.* **Euriphagous**, with preference to rodent and reptiles leaving in stony fields: *T. rubrovaria,* possibly *T. carcavalloi*. **Euriphagous,** with preference by birds, specially Dendrocolaptidae, but feeding also on marsupials, rodents, pigeon, rabbits, rats and humans: *T. platensis*. **Stenophagous**, with marked relationship to Psittacidae, even though sometimes was found in other habitats and experimentally accepting other feeding sources: *T. delpontei*. **Experimentally euriphagous**, natural feeding sources unknown, habitats on trees, under bark and peridomestics in humid tropical forest: *T. melanosoma*. **Experimentally euriphagous**, found in natural stony ecotopes with rodents, lizards and Blattaria, on which they experimentally fed: *T. carcavalloi*.

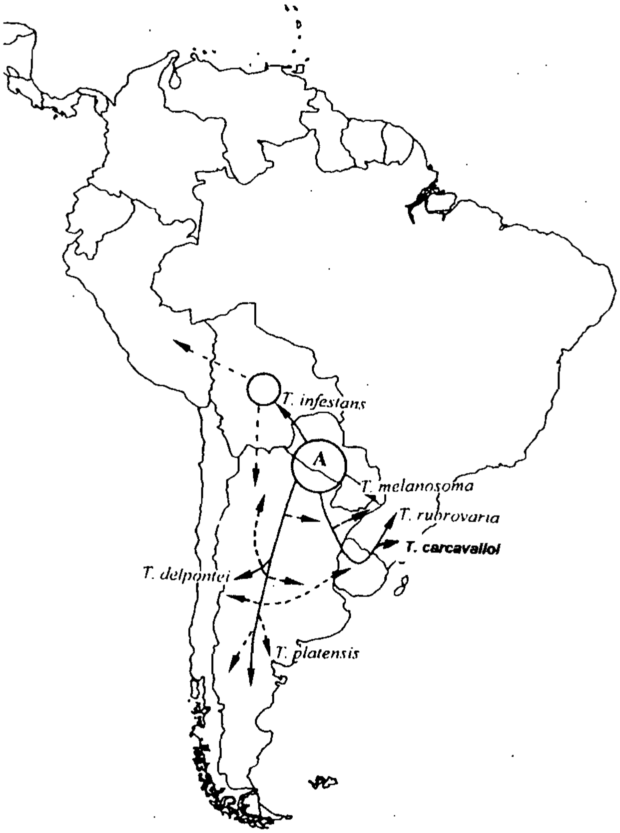


Figure 49: Presumed routes of dispersion and phylogeny of *T. infestans* complex. From Bolivian mesothermic valleys, and possibly by domestication of Caviidae, the nominotypical species dispersed by passive way.

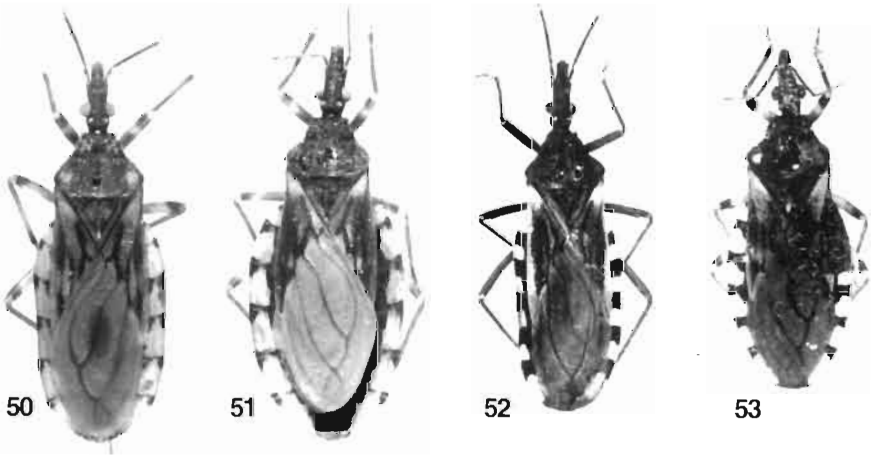
Pereira et al. (1996) studies the enzymatic variability by multilocus enzyme electrophoresis and phylogenetic relatedness among species of this complex and published an unrooted Wagner tree and a UPGMA dendrogram, showing basic relationships of the four species they have considered: *T. infestans, platensis, delpontei* and *rubrovaria.* They submitted izoenzyme patterns to classical phenetic and genetic clustering analysis, concluding that "the genetic distance between *T. infestans* and *T. platensis* was very low compared to that between *T. platensis* and *T. delpontei*...even though there is no doubt that these are definitely separate species". As Panzera et al., (1995) found more cytogenetical similatrity between *T. platensis* and *T. infestans* than between *T. platensis* and *T. delpontei*, Pereira et al., (1996) support the hypothesis of a relatively recent common ancestor for the two first species, "fully consistent with previous studies which recorded complete interfertility between *T. platensis* and *T. infestans* (Abalos, 1949; Franca Rodriguez, 1985) and production of sterile hybrids was observed between *T. infestans* and *T. rubrovaria* (Usinger et al., 1966)".

García (1999) studied the molecular phylogenetic relationships among several species of *Triatoma. T. rubrovaria* is far from *T. infestans* in the parsimonious tree based on combined 12S+16S+COI mtDNA data set. A non expected result was that *T. rubrovaria* and *T.circummaculata* are closely related. Some morphological characters of the last species, as the third rostral segment as long as the second, separate this species and *T. limai* from all other species of the genus *Triatoma.*

***Triatoma sordida* complex** (Fig. 50-54)

In addition to the nominotypical species (Stal, 1859) (Fig. 50), the complex *sordida* includes *T. guasayana* Wygodzinsky & Abalos, 1949 (Fig. 51), *T. patagonica* Del Ponte, 1929 (Fig. 52), and the recently revalidated *T. garciabesi* Carcavallo, Cichero, Martínez, Prosen & Ronderos, 1967 (Jurberg, Galvão, Lent, Monteiro, Lopes, Panzera & Pérez, 1998) (Fig. 53). The complex as a whole has a distribution from northern central Brazil to the Patagonia, including a major portion of Argentina, Paraguay and Bolivia. Several studies have focused on this group of species and their morphology, biology, ethology, geographical distribution, genetics, and isoenzymatic aspects. There is great similarity between the four species, especially between *T. sordida* and *T. garciabesi*. These latter two were considered synonymous for almost twenty years because of their great similarity and great variability in some morphological traits.

Recently, a putative cryptospecies named *T. sordida* group 2 (G2) was included in this complex (Noireau et al., 1998). A multilocus enzyme electrophoresis analysis performed on a *T. sordida* population collected in the Bolivian Chaco made evident the existence of two sympatric biological species occurring within *T. sordida* and the absence of natural hybrids, revealing that mating was not random within the morphological species. The hypothesis of a recent evolutionary divergence between both populations may be supported by the fact that crossing experiments were rarely successful (only 6% of cases between *T. sordida* G2 females - *T. sordida* males and 36% for reciprocal crossings). Genetic distance between them is in agreement with the hypothesis of distinct species. Later, cytogenetics, RAPD and morphometrics confirmed that *T. sordida* G2 was readily separated from the sympatric *T. sordida s.s* (Panzera and Dujardin, unpublished data). On the other hand, relationships between *T.*



Figures 50-53: The *T. sordida* complex includes the nominotypical species (50) plus *T. guasayana* (51), *T. patagonica* (52) and *T. garciabesi* (53). Studies of Noireau (1999) demonstrated the existence of other possible cryptospecies in Bolivia.

sordida G2 and *T. garciabesi* remains unclear. Isoenzymatic patterns of both species reveal fixed differences when no cytogenetic disagreement is detected. Another *T. sordida* population collected in Apolo, a Bolivian locality close to Peru border, sets an additional taxonomic problem. Although its isoenzimatic pattern is similar to *T. sordida s.s.*, cytogenetic differences are observed with both *T. sordida* species from the Chaco and *T. garciabesi.*

The relatively high genetic variability observed for *T. sordida s.s.* and *T. sordida* G2 populations from the Bolivian Chaco, in comparison with *T. sordida* populations from Brazil, might strengthen the hypothesis that the phytogeographical region of the Chaco would be the area where *T. sordida* (and consequently the complex) originated.

The phytogeographical area of the Chaco is a dry subtropical forest occupying eastern Bolivia, western and central Paraguay, and northern Argentina. Four of the species are found there, and the geographical distribution area of the fifth, *T. patagonica,* comes very close to the southern edge of the Chaco region. Although the outside limits of the distribution of *T. sordida* and *T. patagonica* are thousands of kilometers apart, within the area of the complex there are zones in which more than two species overlap, which means to say that the six species in question are partially sympatric. The nominotypical species, *T. sordida s.s.,* would have spread from the Chaco towards the east and northeast, displaying great adaptation to habitats and food sources and invading human dwellings relatively frequently in the wet zones. Natural habitats are palm trees such as *Copernitia australis, Mauritia vinifera, Syagrus oleracea, Orbinya martiana, Arecastrum omanzoffianum, Acrocomia macrocarpa, Scheelea pharelata* and other plants as *Bromelia faustosa, Ficus eumophala* and *Fourcroye gigantea*, where the feeding sources are marsupials *Didelphis marsupialis* and *Lutreolina crassicaudata,* rodents such as *Akodon aviculoides, Cavia aperea, Echimys nigrispinus* and *Rattus norvegicus* and monkeys *Cebus apella.* This species frequently invade domestic and peridomestic environment where they feed on chicken, several domestic animals and humans (Barretto, 1968; Forattini et al., 1971; Rocha e Silva et al., 1977: Noireau et al., 1997a).

T. sordida is the only species detected in bird-nests in the Bolivian Chaco (Noireau et al., 1999). Birds would have ensure the passive transport of nymphal instars among their feathers (as demonstrated by Forattini et al., 1971) explaining the further wide distribution throughout the continent of this species. Its current geographical distribution includes Argentina (Misiones, Corrientes, Chaco, Formosa, Santa Fe), Bolivia (La Paz, Cochabamba, Santa Cruz, Chuquisaca, Tarija and Beni), Brazil (Bahia, Goiás, Mato Grosso, Mato grosso do Sul, Maranhao, Minas Gerais, Paraná, Pernambuco, Piaui, Rio Grande do Sul, Santa Catarina, Säo Paulo), Paraguay (Concepción, Cordillera, Central, Nueva Asunción), Uruguay (Espínola, 1985; Silveira et al., 1984;. Franca Rodríguez, 1985; González Romero, 1985) The altitude varies from the sea level to 1.800 m.a.s.l. (Carcavallo et al., 1999).

T. garciabesi emigrated south and west, being ornitophilic and living in bird nests in trees, shrubs and hollow cacti. It is found in Argentina (Salta, Jujuy, Santiago del Estero, NW. of Santa Fe, NW Formosa, Córdoba, San Luis, Tucumán, Catamarca La Rioja, San Juan, Mendoza) and probably in dry regions of S. Bolivia, at altitudes lower than 1.000 m.a.s.l.. When approaching a peridomiciliary area it colonizes chicken coops and trees where poultry roosted.

Other populations spread south, reaching areas with a continental climate, with major variations in temperature. One of them, *T. patagonica,* reached 46º S latitude, with a geographical distribution including Argentina (Chubut, Rio Negro, Neuquen, Mendoza, La Pampa, Buenos Aires, San Luis, Córdoba, San Juan, La Rioja, Santiago del estero, Catamarca, Salta, Santa Fé, Entre Rios, Corrientes) ans possibly Uruguay, at altitudes between the sea level and 750 m.a.s.l. (Gorla et al., 1993, Carcavallo et al., 1999). It displays a preference for habitats on or close to the ground, under stones in natural crevices, under fallen trunks, in rodent shelters of Caviidae, Cricetidae and Muridae, shelters of Dasypodidae, and sometimes invading the peridomestic environment. This species feeds on the blood of mammals (wild rodents and Dasypodidae, *Graomys sp.,*, sometimes attacking humans in the wild; it does not show a tendency to domiciliate, and in the peridomicile it is almost always found in corrals. *T. guasayana* is perhaps the least specialized of the group, and may therefore be the closest to what might have been the origin of the specific complex. It has been found in almost all imaginable wild habitats, all over the peridomicile, and inside human dwellings, and wherever it colonizes it feeds on any vertebrate, including cold-blooded ones. Its geographical distribution includes Argentina (Buenos Aires, Catamarca, Córdoba, Chaco, Jujuy, La Pampa, La Rioja, Mendoza, Salta, san Juan, San Luis, Santa Fe, Santiago del Estero, Tucumán), Paraguay (Alto Paraguay, Boqueron, Nueva Asunción, Paraguarí, Presidente Hayes), Bolivia (Santa Cruz, Tarija, La Paz) (González Romero, 1985; Martínez et al., 1985; Gorla et al., 1993) at altitudes from the sea level to 900 m.a.s.l. (Carcavallo et al., 1999). The presumed routes of dispersion of this complex are shown in Figure 54.

The phylogenetic relationship between these species could be studied with some new tools. Panzera et al., (1998) has shown, through the amount and distribution of the C-heterochromatic blocks in the chromosomal complement that *"T. sordida"* from Brazil is a different species that *"T. sordida"* from Argentina. The first one has 8-

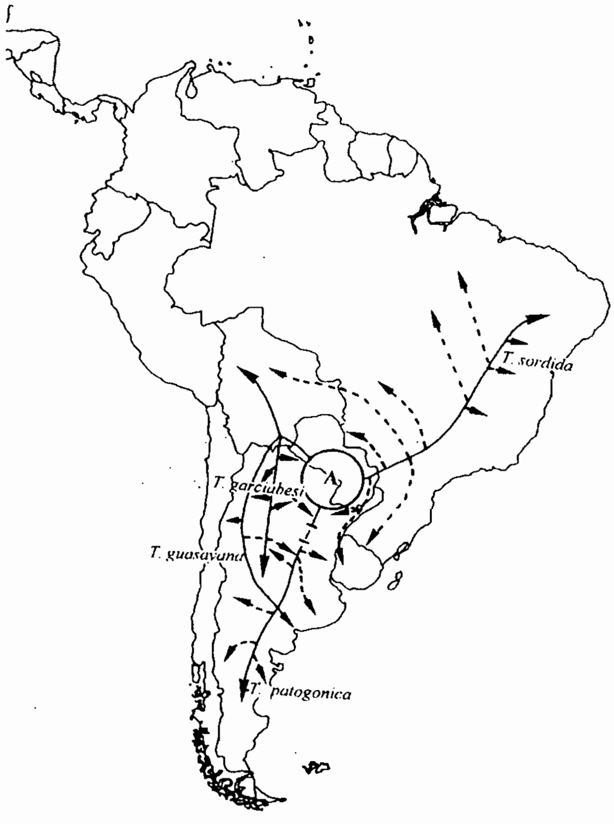


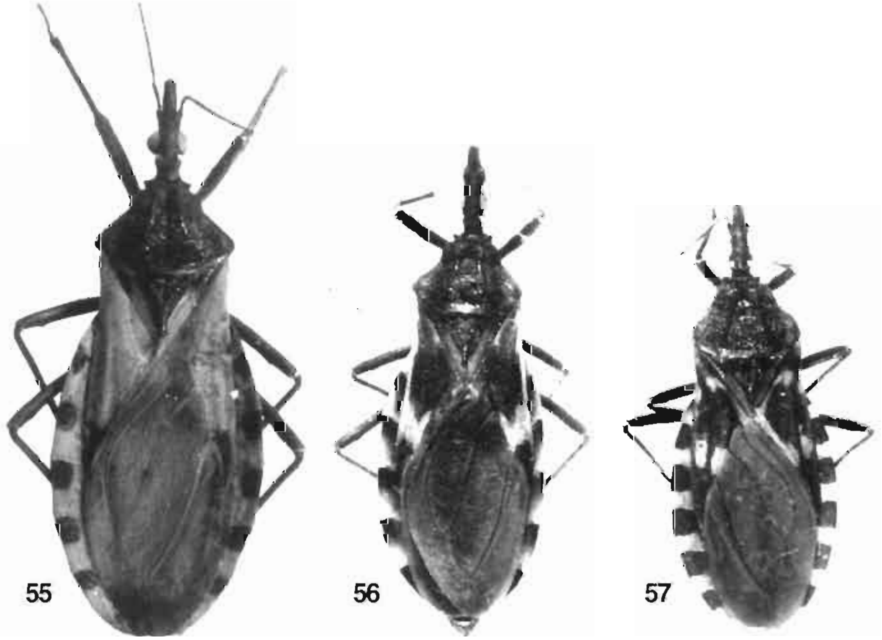
Figure 54: Presumed routes of dispersion and phylogeny of *T. sordida* complex.

10 autosomal pairs with C-blocks and 15-20 % of autosomal C-heterochromatin, while the second showed "zero" in both values. Similar results than the population from Brazil showed *T. patagonica* (10 and 35%, respectively), while *T. guasayana* was negative ("zero" in both values as the population of Argentina, later revalidated as *T. garciabesi*. According to these findings is possible that *T. sordida* and *T. patagonica* share a common origin, while *T. garciabesi* could have a nearer relationship with *T. guasayana*. Garcia (1999) did not include *T. patagonica* in the parsimonious tree based on combined 12S+16S+COI mtDNA, but she confirms that *T. guasayana* is far from two populations of *T. sordida* from Brazil and Argentina. In this case, both populations are closely related, probably because that one from Argentina was from Formosa or Corrientes, and in this case it was *T. sordida,* not *T. garciabesi* the studied specimens.

***Triatoma dimidiata* complex** (Figs. 55-57)

Triatoma dimidiata (Latreille, 1811) (Fig. 55) has a broad geographical distribution, from central Mexico (Campeche, Chiapas, Guerrero, Jalisco, Nayarit, Oaxaca, Puebla, Quintana Róo, San Luis Potosí, Tabasco, Veracruz, Yucatán) to Peru (Tumbes), reaching east as far as Guyana and including Belize, Honduras, Guatemala, El Salvador, Nicaragua, Costa Rica, Panama, Venezuela (Cojedes, Carabobo, Yaracuy, Bolivar, Falcon, Territory Delta Amacuro, Federal District), Colombia (Cundinamarca, Boyaca, Huila, Norte Santander, Magdalena, Casanare, Santander) and Equator (Guayas, Manabi, Esmeraldas, El Oro, Los Ríos, Bolivar, Morona Santiago) (Zeledón, 1985; D´Alessandro & Barreto; 1985; Lazo, 1985). The altitude varies from the sea level to 2.700 m.a.s.l. Based on variations in the morphometric relations and spots on the chorion, two forms were described as species and soon changed to subspecies, "*maculipennis*" in the north and "*capitata*" in the south, which are not accepted by Lent & Wygodzinsky (1979), who contend that there are intermediate forms and great variability. At any rate, we believe that in Mexico there are three species related to *T. dimidiata* with which they form a specific complex that should be studied genetically: *T. hegneri* Mazzotti, 1940 (Fig. 56), from the island of Cozumel at the sea level, in the State of Quintana Róo; *T. gomeznunezi* Martínez, Carcavallo & Jurberg, 1994 Fig. 57), from the State of Oaxaca at 1.000 m.a.s.l., and *T. brailovskyi* Martínez, Carcavallo & Peláez, 1984, from the States of Colima, Nayarit, and Jalisco at altitudes between 100 and 800 m.a.s.l.. The ecologic information for *T. dimidiata* show a great adaptability to several habitats and feeding sources: caves inhabited by marsupials, rodents, bats and other mammals; fences and piles of stones; hollow trees; palm tree *Scheelea sonensis*; shelters of edentata; houses, under floor made of wood; corrals, chicken coops, wood piles; in the soil this species cover itself with little particles (camouflage, Zeledón, 1985). *T. hegneri* is found in rocky ground, related to opossum, and in corrals and chicken coops, feeding domestic animals. Habitats and feeding sources of *T. gomeznunezi* and *T. brailovskyi* are unknown.

Given the plesiomorphic morphological conditions, common to all these species, very similar to those of South American *Triatoma* and completely different from those of *Triatoma* species from Mexico and the United States (*T. phyllosoma* complex and *T. protracta* complex), we support the hypothesis that the origin of the complex



Figures 55-57: *T. dimidiata* (55) shares a specific complex with *T. brailovskyi, T. hegneri* (56) and *T. gomeznunezi* (57).

may be in northern South America. From there, they spread south and east and after the appearance of the Central American isthmus, to the north where, after geographical or more possibly ecological adaptations, they separated, first *hegneri* towards the east, almost at the same time or soon after *gomeznunezi* towards the southeast, and finally, farther north, *brailovskyi* towards the Pacific (Fig. 58).

***Triatoma oliveirai* complex** (Figs. 59-62)

The complex *T. oliveirai* is the proposal we defend based on the comparison of several species from Brazil. The nominotypical, *T. oliveirai* (Neiva, Pinto & Lent, 1939) (Fig. 59) was found in Rio

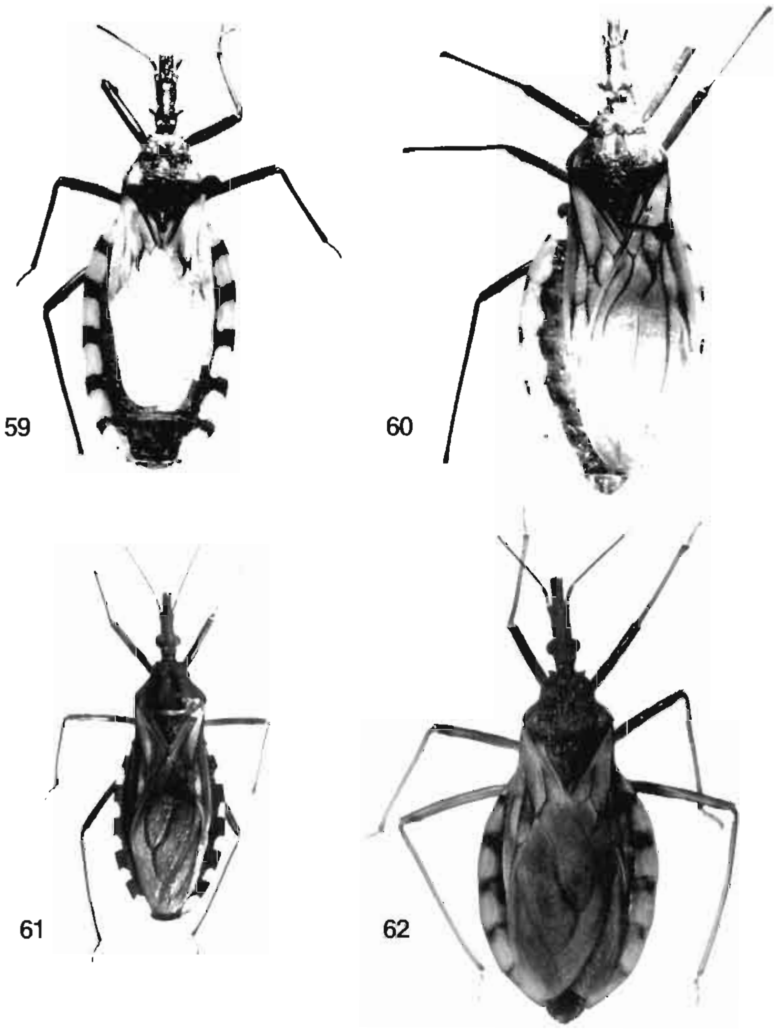
Figure 58: Presumed routes of dispersion and phylogeny of the *T. dimidiata* complex.

Grande do Sul, between 200 and 600 m.a.s.l., in shelters of rodents *Cavia aperea* (Lent & Wygodzinsky, 1979). We include in this complex other species morphologically related with the first one. *T. matogrossensis* Leite & Barbosa, 1953, from Mato Grosso and Mato Grosso do Sul, at altitudes lower than 400 m.a.s.l., probably related to bird nests and mammal shelters. *T. williami* Galvão, Souza & Lima, 1965 (Fig. 60), found in human dwellings in Goiás, Mato Grosso and Mato Grosso do Sul.; being the wild habitats unknown. *T. guazu* Lent & Wygodzinsky, 1979 (Fig. 61) prevalent in Mato Grosso but is the only species of this complex found in other country out of Brazil: the holotype was found in Paraguay (Villarica); wild habitats could be caves with mammals and birds but it was found in peridomestic and domestic environments, colonising at altitudes between 200 and 500 m.a.s.l.. Recently other species were incorporated into this complex that are highly similar to the previous ones, especially to *guazu*, albeit notably different in several traits, including its almost red color in *Triatoma jurbergi* Carcavallo, Galvão & Lent, 1998 (Fig. 62), found in Mato Grosso in caves and houses, at approximately 200 m.a.s.l and *T. klugi* Carcavallo, Jurberg, Lent & Galvão 2000, from Rio Grande do Sul, at 750 m.a.s.l. in basaltic formations. This complex is very homogeneous in its characteristics, all of the species tend to invade rural peridomestic environments but not the human dwellings, and their sylvatic habitats and food sources have been insufficiently studied. The origin of this complex, which is very limited geographically, may be in the wooded areas and the Pantanal ecosystems of Mato Grosso, Brazil..

The possible relationship between these specific complexes could be analysed under different points of view. The second part of this research is being developed with a multidisciplinary approach, including the comparison of different DNA markers for genera and specific complexes, and also for some samples of subfamilies near Triatominae. The possibility of the validity of subgenera in *Rhodnius* and *Triatoma* is another hypothesis which is being developed using different techniques.

Triatoma maculata complex

Triatoma maculata (Eichson, 1848) was found in Venezula (all he States except Táchira and Territory Delta amacuro, Colombia (Atlántico, Cesar, Guajira, Vichara), Brazil (Roraima), Surinam, Guyana, French Guiana, Aruba, Bonaire and Curaçao. Its habitats are palm trees *Attalea humboldtiana, Attalea sp., Acrocomia sp., A. sclerocarpa, Scheelea sp., Copernitia tectorum, Sabal sp., Coccos nucífera;* bird nests: *Mycteria americana,* Furnariidae, Dendrocolaptidae, dead and hollow trunks, bromelids plants, corrals, chicken and pigeon coops. Human dwellings. In wild habitats it is

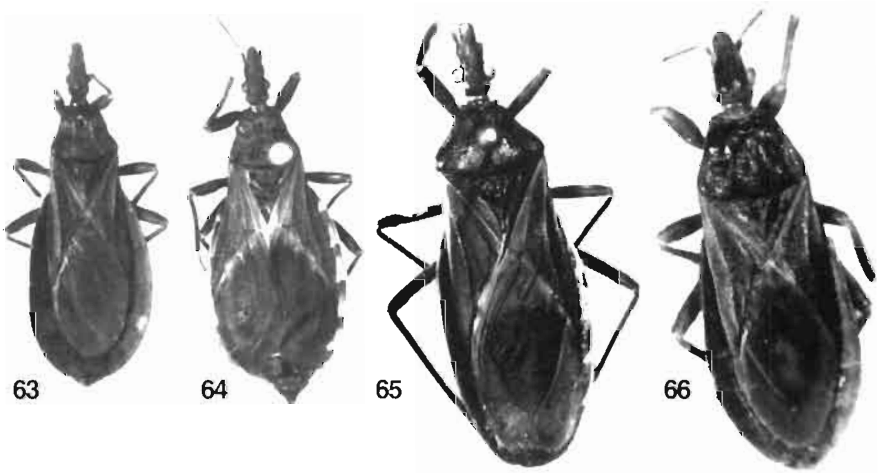


Figures 59-62: *T. oliveirai* (59) shares a specific complex with *T. williami* (60), *T. guazu* (61), *T. jurbergi* (62), *T. matogrossensis* and *T. klugi*.

related to *Didelphis marsupialis, Tamandua tetradactyla, Dasypus novemcinctus, Sygmodon sp.* and several bats and birds..*T. pseudomaculata* Correa & Espínola, 1964 is very similar and was missclassified during many years. It is prevalent in Brazil (Alagoas, bahia, Brasilia, Ceará, Goiás, Minas Gerais, Paraiba, Pernambuco, Piauí, Rio Grande do Norte, Maranhào, Sergipe, Mato Grosso do Sul). Its habitats are rodent and marsupial shelters, hollow trees, corrals, chicken coops, stables, human dwellings (Lent & Wygodzinsky, 1979; Espínola, 1985; Carcavallo et al., 1999)

Triatoma protracta complex

The complex *T. protracta* (Uhler, 1894) (Fig. 63) was studied in detail by Ryckman (1962) and Usinger et al., (1966) and has three other species, which are *T. barberi* Usinger, 1939 (Fig. 64), *T. peninsularis* Usinger, 1940 (Fig. 65), and *T. sinaloensis* Ryckman, 1962 (Fig. 66). The nominotypical species was separated into 5 allopatric subspecies by Ryckman (1962). The studies on interbreeding and the geographical distribution of the species led to the maps produced by the latter study cited above and shown in Figures 67, 68 and 69, raising the hypothesis on the possible distribution routes and lines of speciation



Figures 63-66: The classic four species included in the *T. protracta complex*: the nominotypical species (63), *T. barberi* (64), *T. peninsularis* (65) and *T.* sinaloensis (66). Morphological characters, only found in this groups plus other three species that authors have included in the complex.

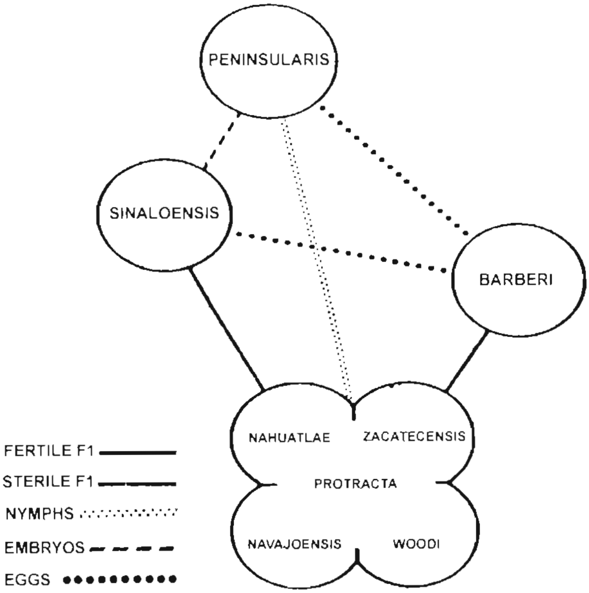
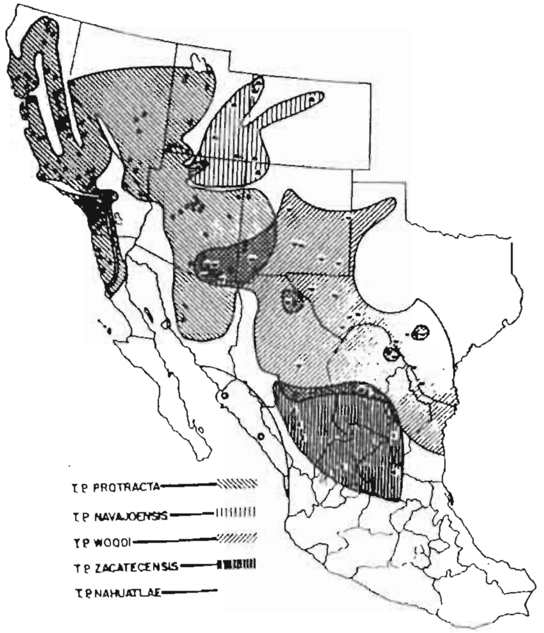


Figure 67: Interbreeding relationships of the four previously treated species from Usinger et al., (1966).

(Fig. 70), starting from a possible ancestor located in southeastern Mexico, approximately in Chiapas. Studies on breeding between these species have shown the great biological affinity between them, ranging from fertile F1 offspring of *T. protracta* and *T. barberi* to infertile offspring of *T. protracta* and *T. sinaloensis,* with partial infertility or only oviposition in other combinations, like those of *T. barberi* and *T. sinaloensis* or *T. barberi* and *T. peninsularis*. As noted by Usinger et al., (1966), *T. peninsularis* and *T. sinaloensis*, which are the most similar populations, do not interbreed, while *T. protracta* and *T. barberi*, which are the most different morphologically, produce fertile offspring. The speciation process may have occurred due to geographical separations, since they are all allopatric and are ecologically very similar, with a strong tendency in nearly all of the species to live in nests of rodents from genus *Neotoma*, which are also their main food source. *T. barberi* is the only one found in peridomiciles, feeding on chickens or entering human dwellings in Mexico (Colima, Hidalgo, Jalisco, Michoacan, Morelos, Oaxaca, Puebla, Guerrero, Tlaxcala, Guanajuato, Querétaro,



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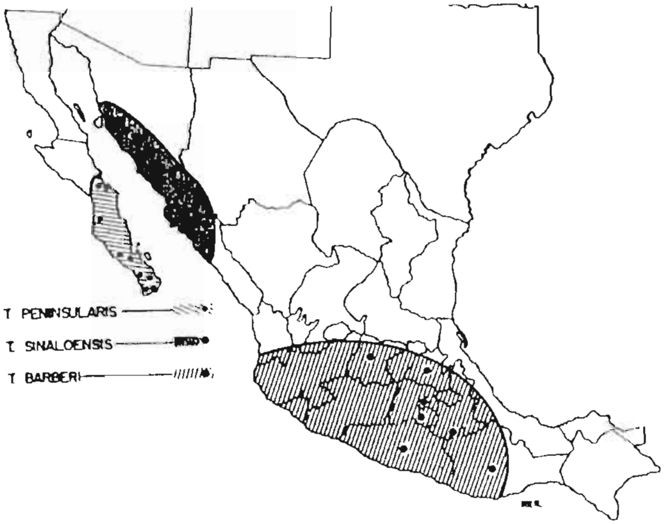

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Figures 68 and 69: Geographical distribution of *Triatoma protracta* subspecies proposed by Ryckman (1962) (68), and other species of the complex (69) (Ryckman,1962; Usinger et al.,1966).

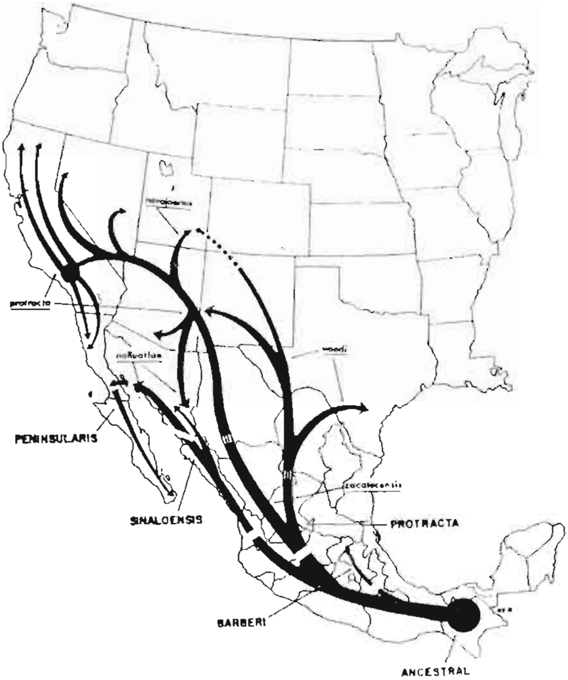
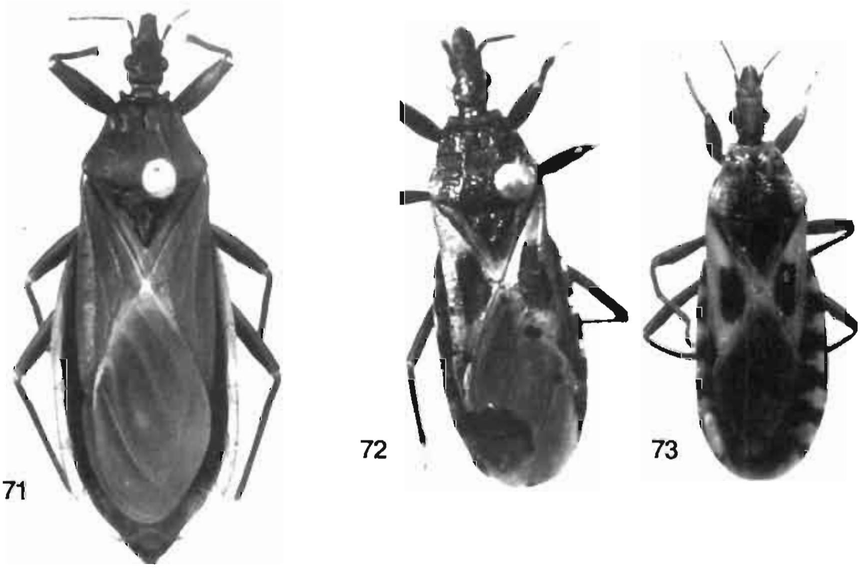


Figure 70: Presumed routes of dispersion and phylogeny of the *T. protracta* complex from Ryckman (1962).

Federal District, from almost the sea level to 1.900 m.a.s.l.. *T. peninsularis*is found only in Mexico (Baja California Sur), at altitudes lower than 200 m.a.s.l.. *T. sinaloensis* is prevalent in Mexico, too, but on the states of Sonora and Sinaloa, between 100 and 300 m.a.s.l.. We add other three species to this complex, as treated later.

Other three species have the same morphological characters of the *T. protracta* complex (pronotum with lateral side straight, without a distinct angle at the interlobar level, not diverging much posteriorly, and with short legs): *T. incrassata* Usinger, 1939 (Fig. 71), *T. neotomae* Neiva, 1911 (Fig. 72) and *T. nitida* Usinger, 1939 (Fig. 73). All they have the same habitats than the other species of the complex, nest or shelters of rodents, specially of those belonging to the genus *Neotoma*. These species are found in Mexico, two of them expanding towards USA and one, the only of the complex, to Central America. *T. incrassata* is found in Mexico (Sonora, though there is a mention at the Mexico Valley) and USA (Arizona), at altitudes between 700 and 1300 m.a.s.l. *T. neotoma* is prevalent in Mexico (Nuevo León, Tamaulipas) and USA (Arizona, California, New Mexico), between 300 and 1.000 m.a.s.l.. *T. nitida* has a geographical distribution atypical for this complex, because it includes from the Mexican State of Yucatan to Costa Rica, being prevalent in Guatemala and Honduras. According to the morphological characters, the geographical distribution and the ecological habitats and niches, we support the hypothesis that these three species should be included in the *Triatoma protracta* complex.

The species of this complex extending from Mexico North toward the USA are *T. incrassata, T. neotomae* and the nominotypical one. *T. protracta,* divided into five allopatric subspecies by Ryckman (1962): *T.p.protracta,* from Mexico (Baja CaliforniA Norte, Sonora) and USA (California, Arizona, Nevada, Utah); *T.p.nahuatlae,* from Mexico (Pacific coast of Sinaloa and Sonora); *T.p. zacatecensis* from Mexico (Chihuahua, Durando Coahuila, San Luis Potosí, Nuevo León, Zacatecas, at the central plateau); *T.p. navajoensis* from USA



Figures 71- 73: Other three species included in the *T. protracta* complex: *T. incrassata* (71), *T. neotomae* (72) and *T. nitida* (73).

(Arizona, Colorado, New Mexico, Utah, at the high Colorado Plateau); and *T.p. woodi* found on the Rio Grande basin: Mexico (Coahuila, Chihuahua, Nuevo León, Tamaulipas) and USA (Arizona, Texas, New Mexico) (Ryckman, 1962; Lent & Wygodzinsky, 1979).

The morphological characters of these species are exceptional not only in the genus *Triatoma* but in all genera of the tribe Triatomini. We consider that these characters, the geographical distribution and some ecological factors give enough arguments to separate them from the "typical" *Triatoma.*

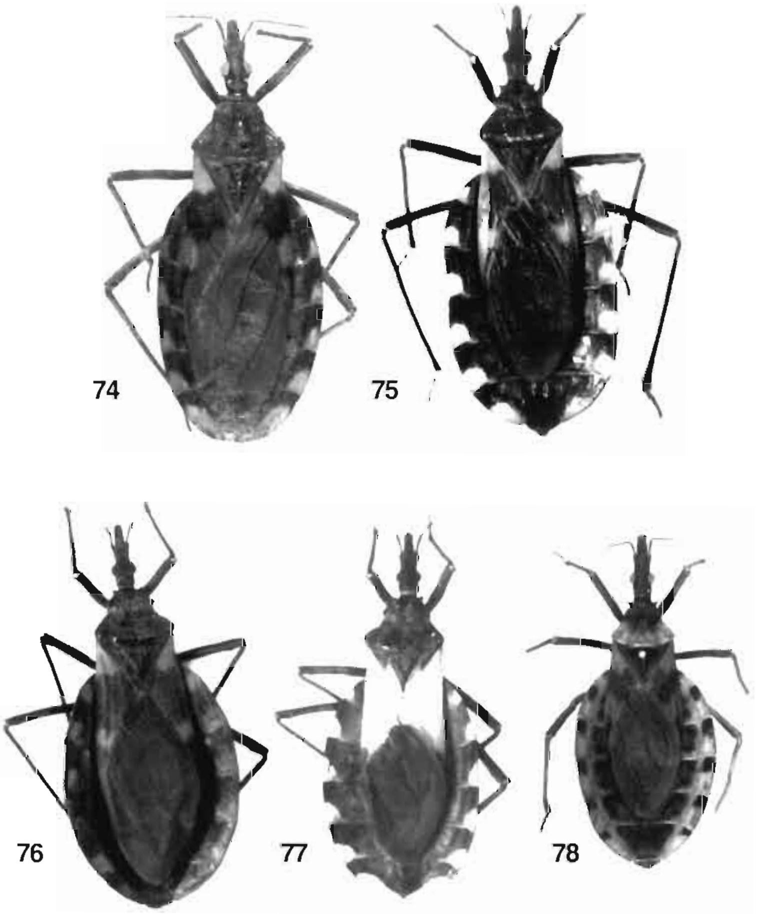
The *Triatoma phyllosoma* complex = *Meccus* Stål, 1859 reval. (Figs. 74-78)

Triatoma phyllosoma (Burmeister, 1835) (Fig. 74) lends its name to a specific complex consisting of various allopatric species, all of which existing only in Mexico, mostly in the southwest. They were considered subspecies by Usinger (1944) and Usinger et al., (1966). Lent & Wygodzinsky (1979) keep five of these populations, promoting them to species status and synonymizing two others. Thus, the range currently consists of these five species, plus another recently published: *T. longipennis* Usinger, 1939 Fig. 75), (Aguascalientes, Colima, Chihuahua, Jalisco, Nayarit, Sinaloa, (?)Yucatán, Zacatecas, between 200 and 1.600 m.a.s.l.); *T. mazzottii* Usinger, 1941(Fig. 76), (Guerrero, Jalisco, Michoacán, Nayarit, Oaxaca, from 200 to 1.100 m.a.s.l.); *T. pallidipennis* (Stal, 1872) (Fig. 77) (Nayarit, Jalisco, Colima, guerrero, Michoacán, Mexico, Puebla, Morelos, Zacatecas, Querétaro, Veracruz, from almost the sea lebvel to 1.700 m.a.s.l.); *T. picturata* Usinger, 1939 (Fig. 78), (Nayarit, Jalisco, Colima, Oaxaca, from 400 to 1.200 m.a.s.l.) and *T. bassolsae* Alejandre Aguilar et al., 1999 (Puebla, at 1.100 m.a.s.l.), plus the nominotypical species, *T. phyllosoma* (Oaxaca). Isolated studies on hybridizations performed by Mazzotti & Osorio (1942) showed that interfertility is frequent in this group. According to Usinger et al. (1966), "In any case, *Triatoma phyllosoma* is considered to be a polytypic species of the type with abrupt steps rather than gradual morphological differences and with complete rather than partial interfertility between allopatric populations." Lent & Wygodinsky (1979) contend that such observations do not reinforce the possibility of the complex members being subspecies, since interfertility between populations under laboratory conditions is not a valid indicator of taxonomic status. The same authors give an excellent perspective on the origin and situation of this complex: “We do not doubt that the members of **the *phyllosoma* complex share a recent common ancestor not shared by any other species**, and thus constitute a **monophyletic group**”. Ecologically, *T. longipennis* is found in domestic and peridomestic environments plus caves with bats (Lent & Wygodzinsky, 1979). *T. mazzottii* is found in rodent nests of *Neotoma sp.* and shelters of Dasypodidae. Occasionally invades houses or peridomestic environments- *T. pallidipennis* is related to rodents *Neotoma* and armadillos *Dasypus;* sometimes it is found in chicken coops, corrals and human dwellings. Identical habitats has *T. phyllosoma,* while *T. picturata* is currently known only from peridomestic environments.

We consider that, according to the arguments given by Lent & Wygodzinsky (1979) and the group of morphological characters that are found only in this complex (the largest size in the genus *Triatoma,* the extremely wide connexivum in all the species, the thoracic tubercles unusually prominents and the width of the abdomen, approximately one third of the total length, all these species could be considered as a genus. There are important differences in the structure and shape of testicles between *Meccus* and *Triatoma* that might allow to consider both in the taxon of genera. Differences of these types were found by Silva & Schreiber (1969) in 4 genera and 11 species; by Lent, Jurberg & Galvão (1994) to revalidate the genus *Mepraia* Mazza, Gajardo & Jörg, 1940 and Gonçalves et al., (1987). Having in mind that *T. phyllosoma* was described by Burmeister in the genus *Conorhinus* but later it was taken by Stål (1859) as type species for his new genus *Meccus,* we hereby revalidate the last genus (Figs. 79,80,81).

Genus *Meccus* Stål, 1859 (Figs. 74-78)

Species very large, of sizes between 27 and 40 mm. Head longer than pronotum, not strongly convex dorsally; antenniferous tubercles short, remote from eyes. Anteocular region subcylindrical approximatively 3 times longer than the postocular. Pronotum with conspicuous and unusually prominent discal and lateral tubercles. Abdomen one third as wide as the total length, with small hemelytra that leave a large dorsal abdominal surface no covered, including the three last urotergites. General color black, with specific markings of different colors. Stal erected the genus in 1859, based in two species, *phyllosoma* and *mexicana* the first of Burmeister and the second of H. Schaeffer. He starts the diagnosis saying that " the body is pilous with noticeable constriction on the middle of the thorax."



Figures. 74- 78: *Triatoma phyllosoma* complex (Genus *Meccus* Stål, 1859). Nominotypical species (74), *M. longipennis* (75), *M. mazzottii* (76), *M. pallidipennis* (77), *M. picturata* (78). Recently was described another species, *M. bassolsae.* Morphological characters, the general aspect and size of all the species of this complex, allow to support thr hypothesis of revalidation of *Meccus* Stal, 1859.

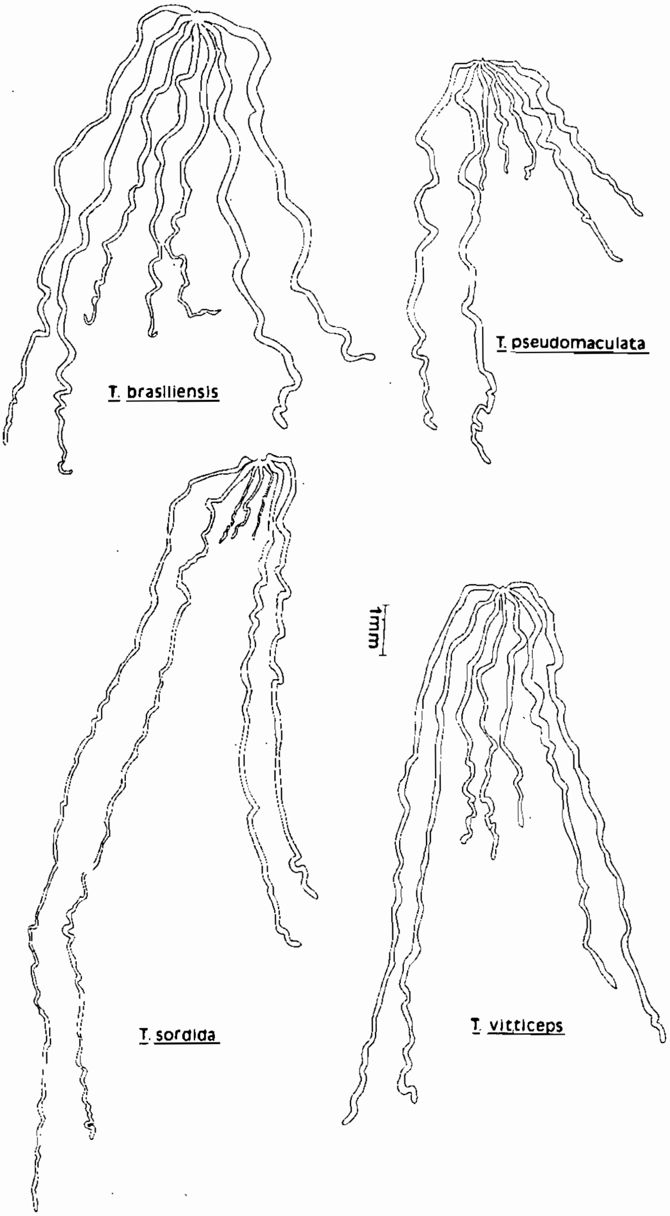


Figure 79: Testicular follicles of four species of *Triatoma* Laporte, 1832 (Gonçalves et al., 1987).

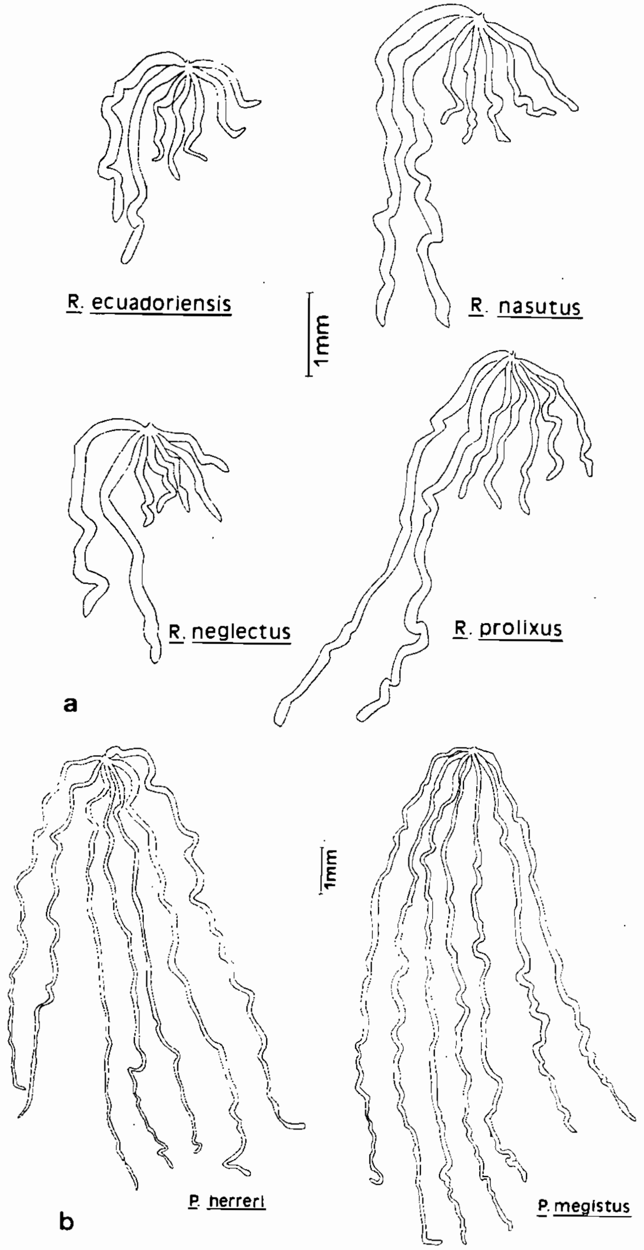


Figure 80: Testicular follicles of Triatominae. a: *Rhodnius* Stal,1859; b: *Panstrongylus* Berg, 1879 (Gonçalves et al., 1987).

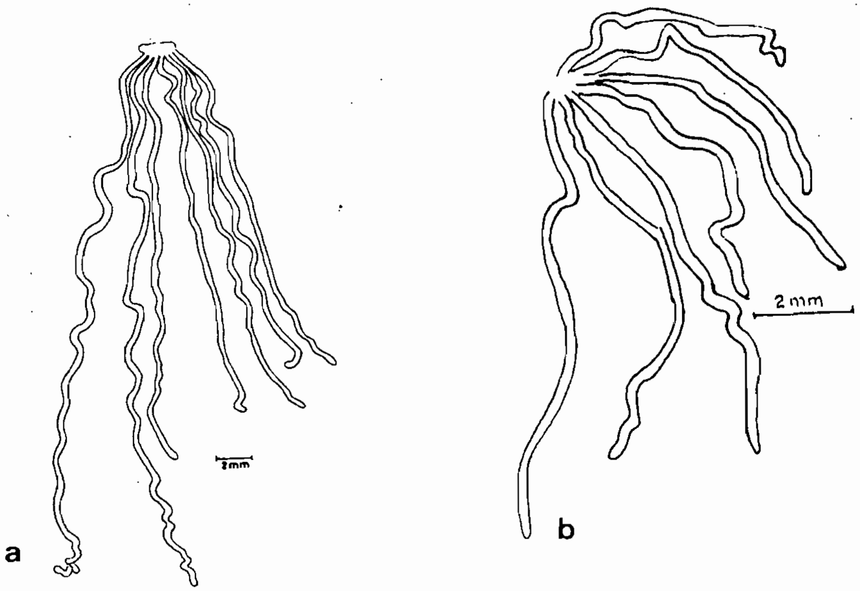
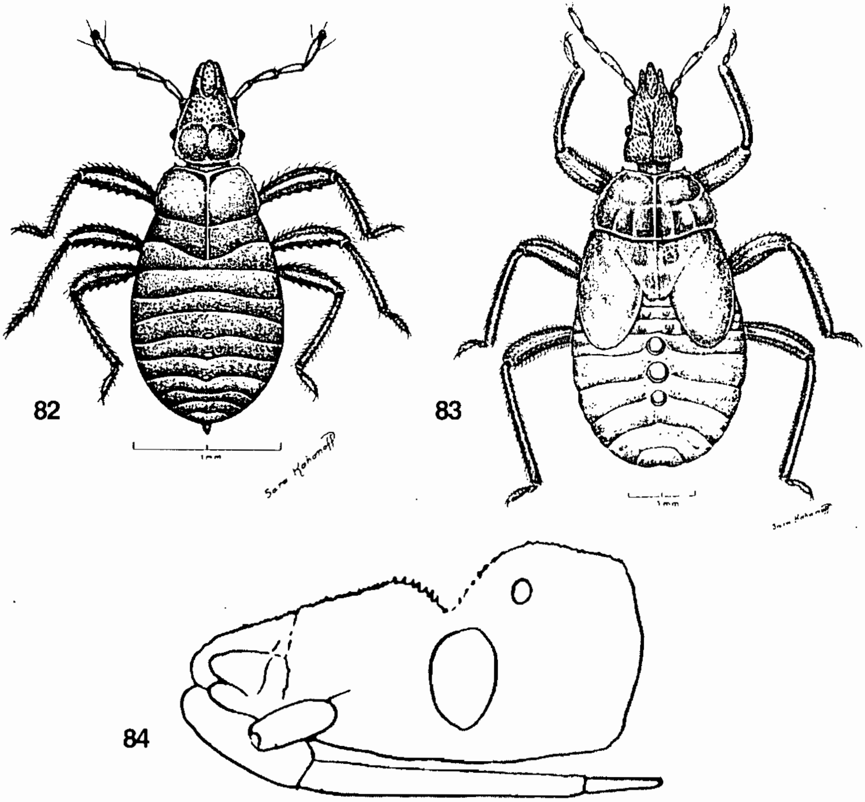


Figure 81: Testicular follicles of Triatominae. a: *Meccus* Stal, 1859; b: *Mepraia* Mazza, Gajardo & Jörg, 1940 (Lent et al., 1994).

Considerations about a sister subfamily for Triatominae

Lent & Wygodzinsky (1979) considered the possibility of the existence of a sister subfamily for Triatominae. They considered that Physoderinae was the most appropriate candidate, having in mind morphological characters and the observation of hematophagism on the only species known in 1979 *Cryptophysodered fairchildi* Wygodzinsky & Maldonado Capriles, 1972. The redescription of this species plus the description of the nymphal stages (Figs. 82-84) published by Martínez and Carcavallo (1989), and the new genus and species *Harpinoderes cichero* Martínez & Carcavallo (1989), allow to consider that Triatominae and Physoderinae are closely related, probably through some ancestor sharing bird nests, from which both, *Harpinoderes* and *Psammolestes* could had their evolution. In the other hand, *Torrealbaia* a Cavernicolini with common characters with other subfamilies of Reduviidae, including one relatively far, as Harpactorinae, demonstrates that the theory of a polyphyletic origin for Triatominae has enough arguments to follow further research, necessary for confirmation of any hypothesis.



Figures 82-84: A sister subfamily, Physoderinae, shows several characters very similar to Triatominae. The study of *Cryptophysoderes fairchildi* shows some similarities in Nymph I (82), Nymph V (83) and the adult head (84) with some Triatominae species.

Conclusion

New techniques of studying Triatominae populations, currently used and possibly a routine in the future, allow investigators to put together a rich information and therefore, to support some theories with more elements than in the past. Information coming from different fields as morphology, morphometry, ecology, physiology, ethology, chemistry, genetics, DNA, etc., probably will show a comprehensive picture of this puzzle that currently is the origin and evolution of Chagas´ disease vectors.

With present information, several publications including the present report consider with doubts the inclusion of *Linshcosteus* in the Triatominae subfamily. Similar considerations were made about the two species of *Alberprosenia*, genus currently included as a tribe (Alberproseniini) but with enough differences to support the hypothesis that in the future, it could be considered as a separate subfamily.

The specific complexes in genera *Rhodnius, Panstrongylus* and *Triatoma,* even though are not taxa included in the International Code of Zoological Nomenclature, are practical groups with similar morphological characters. However, when those characters are too different to the average of the species, as the cases of *Triatoma phyllosoma* and their related species, authors consider that is better separate them through a valid taxon, the genus. The authors propose revalidate the genus *Meccus* Stål, 1859. Further studies are needed to decide about other complexes as *protracta, breyeri, circummaculata, flavida* and *sordida.*

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ISSN 0328-0381

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Zeledon, R., 1997. Infecção do inseto vetor pelo *Trypanosoma cruzi*. Volume 1: 271-278 In **Atlas dos Vetores da Doença de Chagas nas Américas** (R. U. Carcavallo, I. Galíndez Girón, J. Jurberg & H. Lent eds). Editora FIOCRUZ, Rio de Janeiro.

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ENTOMOLOGÍA Y VECTORES

ISSN 0328-0381

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