UNIVERSIDADE ESTADUAL DE CAMPINAS
INSTITUTO DE BIOLOGIA

Vinicius Fernandes de Paiva

Estudo taxonômico e análise cladística de espécies neárticas do gênero *Triatoma* (Hemiptera, Reduviidae, Triatominae)

Taxonomic study and cladistic analysis of nearctic species of *Triatoma* genus (Hemiptera, Reduviidae, Triatominae)

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Tese apresentada ao Instituto de Biologia da Universidade Estadual de Campinas como parte dos requisitos exigidos para a obtenção do Título de Doutor em Biologia Animal, na área de Relações antrópicas, Meio ambiente e Parasitologia.

Thesis presented to the institute of Biology of the University of Campinas in partial fulfillment of the requirements for the degree of doctor in Animal Biology, inthe Concentration Area of Anthropic Relations, Environment and Parasitology

Orientador: Prof. Dr. João Aristeu da Rosa

ESTE ARQUIVO DIGITAL CORRESPONDE À VERSÃO FINAL DA TESE DEFENDIDA PELO ALUNO VINÍCIUS FERNANDES DE PAIVA E ORIENTADA PELO PROFESSOR DOUTOR JOÃO ARISTEU DA ROSA.

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Os membros da Comissão Examinadora acima assinaram a Ata de Defesa, que se encontra no processo de vida acadêmica do aluno

Dedico este trabalho ao meu pai, minha mãe, ao meu irmão e à minha companheira,
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Resumo

Na subfamília Triatominae são descritas 157 espécies, distribuídas em 18 gêneros e 5 tribos. Devido à sua importância em saúde pública, como vetores da doença de Chagas, a subfamília tem recebido a atenção dos taxonomistas. Identificar corretamente os gêneros e as espécies é muito importante para a vigilância epidemiológica e controle desses vetores. Dentre os 18 gêneros de triatomíneos somente em *Triatoma, Panstrongylus* e *Paratriatoma* foram descritas subespécies. Ao longo dos anos aproximadamente quarenta subespécies foram descritas na subfamília Triatominae, portanto, no primeiro artigo, apresentamos novas informações da literatura sobre essas subespécies. Embora várias dessas tenham sido sinonimizadas, evidenciamos que algumas subespécies podem ser válidas. Realizamos também, no segundo artigo, por meio de informações genéticas, citogenéticas e com base no exame dos espécimes, a transferência de *Triatoma lecticularia* (Stål, 1859) para o gênero *Paratriatoma* com a nova combinação resultante: *Paratriatoma lecticularia* (Stål, 1859) (Reduviidae: Triatominae). Por fim, no terceiro artigo, embora os complexos de espécies não sejam formalmente reconhecidos pelo ICZN, por meio de análise filogenética com dados moleculares e morfológicos mostramos a possível relação dos grupos *T. dispar, T. protracta* e *T. phyllosoma* e seus respectivos complexos. Por meio dos estudos realizados reiteramos também a manutenção do complexo *T.nitida/T.rubida* e o restabelecimento do complexo *T. recurva.*

Abstract

In the subfamily Triatominae, 157 species are described, distributed in 18 genera and 5 tribes. Due to its importance in public health, as vectors of Chagas disease, the subfamily has received the attention of taxonomists. Correctly identifying genera and species is very important for epidemiological surveillance and control of these vectors. Among the 18 genera of triatomines, only *Triatoma, Panstrongylus* and *Paratriatoma* have subspecies. Over the years approximately forty subspecies have been described in the subfamily Triatominae, therefore, in the first article, we present new information from the literature on these subspecies. Although several of these subspecies have been synonymized, we have shown that some subspecies may be valid. We also carried out, in the second article, through genetic and cytogenetic information and based on the examination of the specimens, the transfer of *Triatoma lecticularia* (Stål, 1859) to the genus *Paratriatoma* with the new resulting combination: *Paratriatoma lecticularia* (Stål, 1859) (Reduviidae: Triatominae). Lastly, in the third article, although the species complexes are not formally recognized by the ICZN, through a phylogenetic analysis using molecular and morphological data we elucidated the relationship of the *T. dispar, T. protracta,* and *T. phyllosoma* groups and their respective complexes. We also reinforced the maintenance of the *T.nitida/T.rubida* complex and the reestablishment of the *T. recurva* complex.

Sumário

1. Introdução

1.1 Triatomíneos na transmissão da doença de Chagas

Em 1907, o médico brasileiro Carlos Ribeiro Justiniano Chagas, foi a região Norte de Minas Gerais executar uma campanha contra a malária durante a construção da Estrada de Ferro Central do Brasil, concomitantemente investigou a infestação de insetos hemípteros hematófagos em áreas rurais da região (Chagas, 1909). Esses insetos se ingurgitavam de sangue durante a noite, muitas vezes no rosto das pessoas. Foi relatado por Carlos Chagas que os insetos vetores só permaneciam nas habitações enquanto o homem ali residia. De casas abandonadas os insetos logo desapareciam, pela ausência de alimentação (DIAS et al., 2002). A espécie que invadia as casas, podendo ou não se domiciliar, era *Panstrongylus megistus* (Burmeister, 1835), como escrito por Carlos Chagas:

> "E' o hematofago referido um hemiptero heteroptero, da família Reduviidae, gênero *Conorhinus*. A espécie é, provavelmente, *megistus* Burm. (Est. 9). O estudo do inseto, especialmente a biolojia delle, vai sendo feito na seção de zoolojia do instituto, pelo Dr. Arthur Neiva, que do assunto, quando oportuno, dará conhecimento exato" (CHAGAS, 1909, p. 160).

Carlos Chagas encontrou um protozoário no intestino de alguns espécimes desse hemíptero, pensando inicialmente se tratar de uma espécie já existente de *Trypanosoma*. No entanto, com uma pesquisa mais aprofundada pôde concluir que se tratava de uma nova espécie devido à morfologia variada, denominada inicialmente de *Schizotrypanum cruzi* e posteriormente *Trypanosoma cruzi* (CHAGAS, 1922). Retornando à Lassance, em 1909, Carlos Chagas verificou que *T. cruzi* infectava humanos e animais, encontrando o parasito em um gato doméstico e em uma criança chamada Berenice (CHAGAS, 1909; VIANNA, 1911). Com todas essas informações, Chagas desvendou o ciclo da doença, que a denominou como "nova tripanozomiase humana" e que posteriormente ficou conhecida como doença de Chagas (CHAGAS, 1922). Após a importante descrição do protozoário *Trypanosoma cruzi*, da doença que ele provoca e que os vetores são insetos da subfamília Triatominae, estudos diversificados incluindo a biologia, taxonomia, filogenia e a distribuição desses insetos vetores passaram a ser realizados.

Passados noventa e seis anos da descrição do *T. cruzi* e dos vetores triatomíneos, Poinar (2005) demonstrou que a associação entre esses insetos e o gênero *Trypanosoma* é bastante antiga sendo estimada como antecedendo à Era terciária (20 a 45 milhões de anos atrás), como no caso da espécie fóssil *Triatoma dominicana* e *Trypanosoma antiquus* que foram encontrados preservados em âmbar e, fornecem, portanto, a primeira evidência fóssil de uma associação entre vetores triatomíneos e parasitos tripanosomatídeos.

1.2 Subfamília Triatominae

Com mais de 7.000 espécies em todo o mundo, a família Reduviidae (Insecta: Heteroptera) forma a terceira maior família da ordem Hemiptera compondo um dos mais diversos grupos de insetos (WEIRAUCH, et al 2014). Sob o ponto de vista taxonômico, os vetores da doença de Chagas estão incluídos na ordem Hemiptera, subordem Heteroptera, família Reduviidae, subfamília Triatominae (LENT e WYGODZINSKY,1979). Possuem desenvolvimento hemimetábolo, isto é, passam por cinco estádios ninfais antes da fase adulta. As ninfas diferenciam-se dos adultos por não possuírem os órgãos reprodutivos completamente desenvolvidos, hemiélitros e ocelos não desenvolvidos. O 5º estádio apresenta diferenciação sexual externa, já descrita na literatura, enquanto os adultos apresentam genitália masculina e feminina (ROSA et al. 1992). Na subfamília são reconhecidas 157 espécies, distribuídas em 18 gêneros e 5 tribos (SCHOFIELD E GALVÃO, 2009; OLIVEIRA, ALEVI, 2017; DORN et al 2018; DALE, JUSTI, GALVÃO 2021). Dentre as cinco tribos: Alberproseniini, Bolboderini, Cavernicolini, Rhodniini e Triatomini, as duas últimas são muito mais diversas e epidemiologicamente relevantes (JUSTI, 2016).

O gênero *Triatoma* foi descrito por Laporte em 1832. Porém, a etimologia do gênero foi baseada em um espécime com um segmento da antena ausente, possuindo apenas três dos quatro segmentos antenais. Ao examinar novos espécimes, e percebendo seu engano, ele mudou o nome do gênero para *Conorhinus,* contudo, pelo princípio da prioridade, *Triatoma* prevaleceu (LAPORTE, 1832; SCHOFIELD E GALVÃO, 2009). A primeira espécie descrita pertencente à subfamília foi *Triatoma rubrofasciata* (De Geer 1773), que permanece atualmente como espécie-tipo de gênero *Triatoma* (SCHOFIELD E GALVÃO, 2009).

Os triatomíneos são encontrados nas Américas, com registros de algumas espécies de *Triatoma* no Velho mundo e de *Linshcosteus* spp. que ocorrem na Índia (SCHOFIELD & GALVÃO, 2009). A América do Sul representa o “hotspot” de biodiversidade, principalmente nas áreas tropicais e subtropicais, com crescente aumento de espécies em proximidade à linha do Equador (LENT & WYGODZINSKY, 1979). Atualmente, estão incluídas 81 espécies em *Triatoma,* das quais aproximadamente 40 estão distribuídas nas Américas Central e do Norte (RAMSEY et al., 2015; BERN et al., 2019; PAIVA et al., 2022).

Os complexos e subcomplexos são agrupamentos de espécies devido principalmente às semelhanças morfológicas, ajudando na identificação específica e sistemática (CARCAVALLO, et al 2000; SCHOFIELD; GALVÃO, 2009). Com o intuito de entender as relações filogenéticas e taxonômicas na subfamília Triatominae, diversos estudos têm sido feitos analisando caracteres morfológicos, morfométricos e genéticos (RYCKMAN, 1962; RYCKMAN, CASDIN,1976; ROSA, et al 1999; PATTERSON, et al 2001; ALDANA, 2011; GARDIM et al 2014; JUSTI et al 2014; OLIVEIRA et al 2017). O agrupamento de espécies de triatomíneos em “complexos” teve início com o trabalho de Ryckman (1962), em que as espécies *Triatoma protracta* (Uhler, 1894); *Triatoma incrassata* Usinger, 1939; *Triatoma sinaloensis* Ryckman*,*1962 e *Triatoma barberi* Usinger*,* 1939 foram incluídas no complexo *Triatoma protracta.* Posteriormente *Triatoma neotomae* Neiva, 1911, *Triatoma nitida* Usinger*,* 1939, *e Triatoma peninsularis* Usinger*,* 1940, também foram incluídas nesse complexo (SCHOFIELD E GALVÃO, 2009). O complexo *Triatoma lecticularia* foi proposto com as seguintes espécies: *Triatoma lecticularia* (Stål, 1859)*, Triatoma recurva* (Stål, 1868), *Triatoma gerstaeckeri* (Stål, 1859), *Triatoma indictiva* Neiva, 1912, *Triatoma rubida* (Uhler, 1894), e *Triatoma sanguisuga* (Leconte, 1855) (LENT & WYGODZINSKY, 1979; SCHOFIELD E GALVÃO, 2009).

As pesquisas sobre a origem dos triatomíneos do velho mundo com a subfamília Triatominae são de grande interesse, já que são intimamente relacionados a Triatomini como *Triatoma rubrofasciata* (HYPŠA et al 2002; CERETTI JUNIOR, et al. 2008). Análises mostram parafilia entre Rhodniini e Triatomini, com divergência aproximada de 83 milhões de anos atrás (MARCILLA, et al 2002). Os clados neárticos de Triatomini, possivelmente diversificaram-se de um ancestral não-triatomíneo, de um “Triatomíneo neártico”, ou ainda divergiram independentemente (PATTERSON et al. 2001, HYPŠA, et al 2002). A possível origem de triatomíneos neotropicais se dá a partir de derivações de triatomíneos neárticos, aferida “pela estreita relação genética de *Panstrongylus* spp. e *Triatoma vitticeps* (Stål, 1859) com o ramo norte-americano de *Triatoma*, por meio das relações com o grupo *Triatoma protracta* (Uhler, 1894) e *Triatoma dimidiata* (Latreille, 1811)” (CERETTI JUNIOR, et al. 2008).

O grupo *T. phyllosoma* possivelmente derivou de uma linhagem de *T. dimidiata*, pois apresenta caracteres morfológicos, dados biogeográficos e análises filogenéticas em comum. Porém, as ligações com o complexo *T. protracta* aparentemente parecem menos evidentes (SCHOFIELD E GALVÃO, 2009). Como sugerido por Guhl e Schofield (2005), as possíveis ligações entre a linhagem *T. dimidiata-T. phyllosoma* podem ser representadas por *T. gerstaeckeri* e *T. nitida*, uma vez que ambos apresentam algumas características intermediárias. Análises sugerem ainda que *T. sordida* diversificou mais recentemente que *T. protracta,* corroborando a hipótese de que triatomíneos sul-americanos possuam ancestrais norte-americanos (PATTERSON et al 2001, CERETTI JUNIOR, et al. 2008). Baseado nesses estudos, hipóteses conflitantes suportam Triatominae como um grupo monofilético (PATTERSON e GAUNT, 2010), ou propõem uma origem polifilética para a subfamília (SCHOFIELD e GALVÃO, 2009). Influenciando nas interpretações sobre a origem da hematofagia em Reduviidae, podendo levar a crer em um evento evolutivo único ou em múltiplas transições evolutivas independentes (HWANG, WEIRAUCH, 2012).

Mesmo que a filogenia das espécies ofereça informações valiosas para a definição específica, ainda há dúvidas a serem esclarecidas e uma delas é a possível confusão na identificação morfológica entre as espécies norte-americanas, exemplificada principalmente pelos complexos *T. protracta* e *T. lecticularia* (proposto por Schofield e Galvão (2009)), levando ao questionamento do real posicionamento taxonômico dessas espécies dentro de seus complexos e em relação ao gênero *Triatoma* (HYPŠA, 2002; JUSTI, et al 2014). Assim, seja pela importância do melhor conhecimento da taxonomia e filogenia do grupo como metodologia de trabalho para outras áreas, incluindo estratégias de controle, ou pela carência de estudos atualizados e mais abrangentes sobre a taxonomia e filogenia de *Triatoma*, justifica-se o presente estudo. Os resultados obtidos propõem a transferência de *T. lecticularia* para *Paratriatoma lecticularia* como nova combinação, uma revisão de todas as subespécies de Triatominae e uma filogenia com dados morfológicos e moleculares (6 genes) de 23 espécies a fim de estabelecer uma hipótese para os grupos e complexos neárticos de *Triatoma.*

1.3 Espécies neárticas

Dipetalogaster maxima (Uhler, 1894)

Morfologicamente essa espécie é a maior da subfamília Triatominae, descrita por P.R. Uhler (1894), a partir de espécimes do extremo sul da península de Baja California, México. Esse gênero monotípico possui conexivo duplo (membrana pregueada), interessante adaptação que permite uma expansão muito maior do abdômen. Como essa espécie geralmente não vive associada a ninhos ou em tocas de vertebrados, a capacidade de ingerir uma grande quantidade de sangue nas alimentações é um mecanismo de sobrevivência. O abdome do adulto não alimentado é plano (RYCKMAN E RYCKMAN, 1967). Foi originalmente descrita no gênero *Conorhinus*. Também foi considerada como pertencente aos gêneros *Triatoma* e *Eutriatoma* (LENT & WYGODZINSKY, 1979).

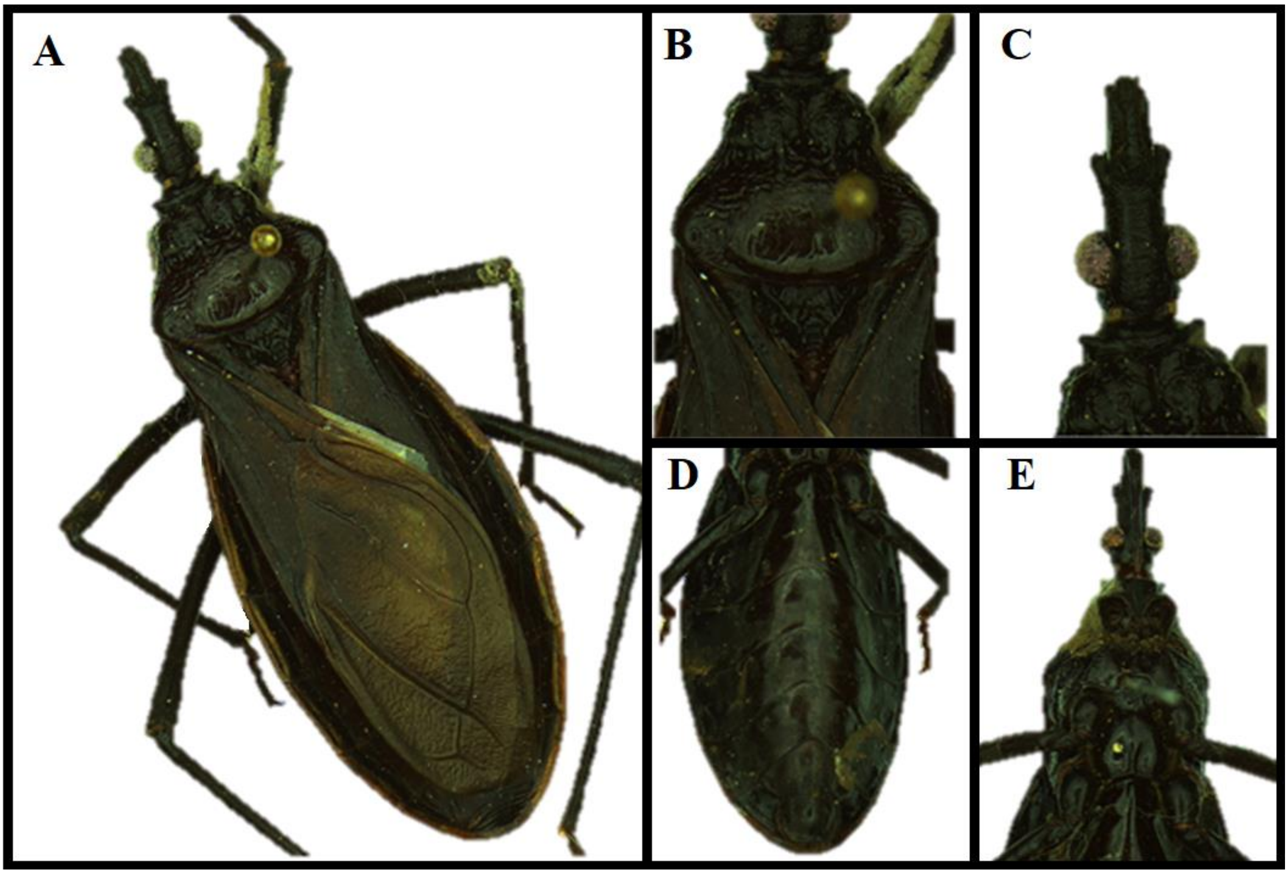

Figura 1. Espécime macho de *Dipetalogaster maxima* da coleção Rodolfo Carcavallo (n° 1555, CTIOC 2754). A. Hábito dorsal; B. Pescoço, pronoto e escutelo; C. Cabeça em vista dorsal; D. Abdômen do macho em vista ventral; E. Cabeça, prosterno, metasterno e mesosterno em vista ventral. Fotos não estão em escala.

Paratriatoma hirsuta Barber, 1938

Esse gênero é relacionado a *Triatoma,* porém é distinto na aparência geral (Usinger, 1944). *Paratriatoma* foi descrito por Barber, 1938, que ao descrever o gênero mencionou “a notável hirsuticidade do corpo e apêndices”. Posteriormente Ryckman (1967), descreveu quatro subespécies geográficas do oeste da América do Norte.

Paratriatoma hirsuta kamiensis Ryckman 1967, é um nome geográfico proposto para os indivíduos da região da antiga nação indígena Kamia, no sudeste da Califórnia. A terminação ‘ensis’ indica a natureza geográfica do nome (Ryckman, 1967). *Paratriatoma* *hirsuta papagoensis* Ryckman 1967, representa os espécimes da região da antiga nação indígena Papago, no sul do Arizona e no norte de Sonora, no México (Ryckman, 1967). *Paratriatoma hirsuta pimae* Ryckman 1967, inclui os indivíduos da região da antiga nação indígena Pima, no centro do Arizona (Ryckman, 1967). *Paratriatoma hirsuta yumanensis* Ryckman 1967, descreve os indíviduos que habitam a região da antiga cultura indígena Yuman na Baja California Norte (Ryckman, 1967).

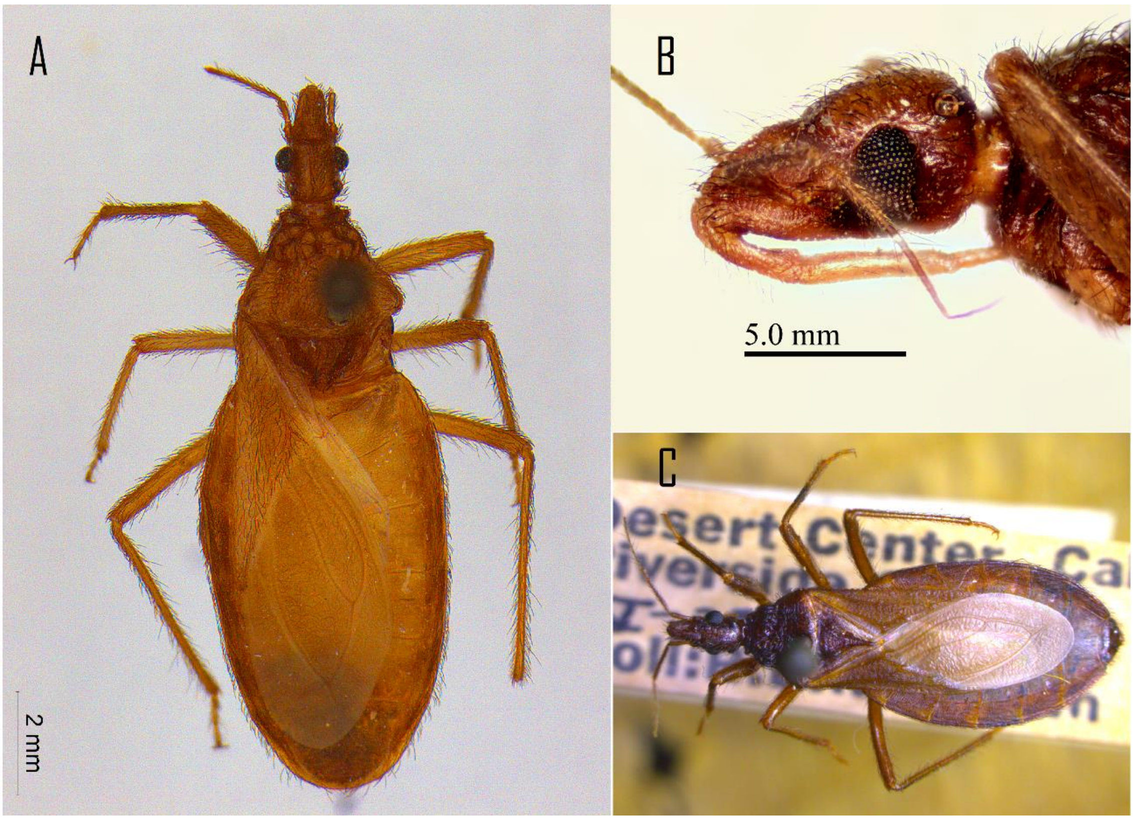

Figura 2. Espécimes de *Paratriatoma hirsuta.* A. Hábito dorsal de um espécime da coleção Rodolfo Carcavallo (n° 2729, CTIOC 2729); B. Cabeça em vista lateral (foto de José Manuel Ayala Landa); C. Hábito dorsal de um espécime da coleção Entomológica de Referência - USP (n°E5026).

Paratriatoma lecticularia (Stål, 1859)

Os espécimes de *P. lecticularia* são variáveis em tamanho, forma, cor e extensão das manchas no conexivo. Em geral, a cor é marrom escura, com manchas laranjas ou amarelo-alaranjadas no pronoto, pleura, cório, conexivo e superfície ventral do abdome. Pilosidade bem desenvolvida em todo o corpo, incluindo cório (LENT e WYGODZINSKY, 1979). É uma espécie não restritiva quanto às fontes alimentares, mas são associados à *Neotoma* spp. (Rodentia: Cricetidae) e *Otospermophilus variegatus* (Rodentia: Sciuridae) (JURBERG E

COSTA, 1989). É uma espécie que possui registro de ocorrência nos EUA e México, sendo encontrada em ambientes antropizados, em oco de árvores, muros e camas (LENT e WYGODZINSKY, 1979). É encontrada naturalmente infectada por *T. cruzi* (BERN et al 2011). Neiva (1911), descreveu *Triatoma occulta* a partir de espécimes pequenos do Texas, posteriormente Usinger (1944) propôs uma nova combinação *Triatoma lecticularia occulta. Triatoma lecticularia floridana* Usinger, 1944 (Representa um nome geográfico para uma população subespecífica de *lecticularia* no estado da Flórida) foi descrito baseado somente em 1 espécime que possuía manchas diferentes no pronoto e olhos maiores. *Triatoma l. floridana* e *T. l. occulta* foram sinonimizadas (LENT e WYGODZINSKY, 1979) e precisam de novas análises morfológicas.

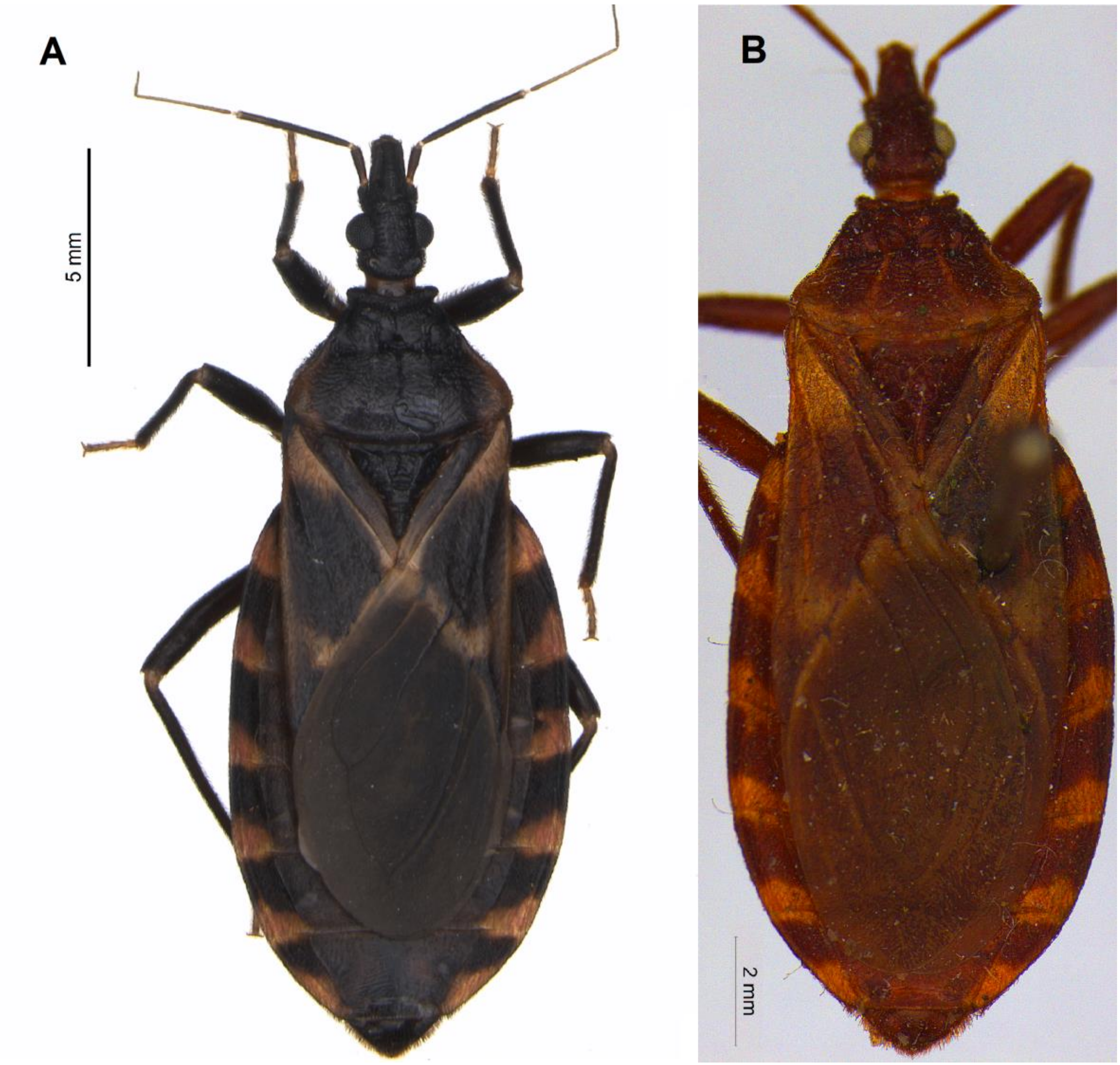

Figura 3. Espécimes fêmeas de *P. lecticularia.* A. Hábito dorsal de *P. lecticularia* (CTA 137); B. Hábito dorsal de *T. lecticularia occulta* (espécime da Uhler collection, Parátipo USNM24708 depositado no LNIRTT (CTIOC 6129)).

Triatoma barberi Usinger, 1939

Triatoma barberi é considerada a espécie endêmica mais importante na transmissão da doença de Chagas no México, pois apresenta ampla distribuição (14 estados) e hábitos peridomésticos e domésticos (EVANGELISTA-MARTÍNEZ et al 2010; PETERSON et al 2002).

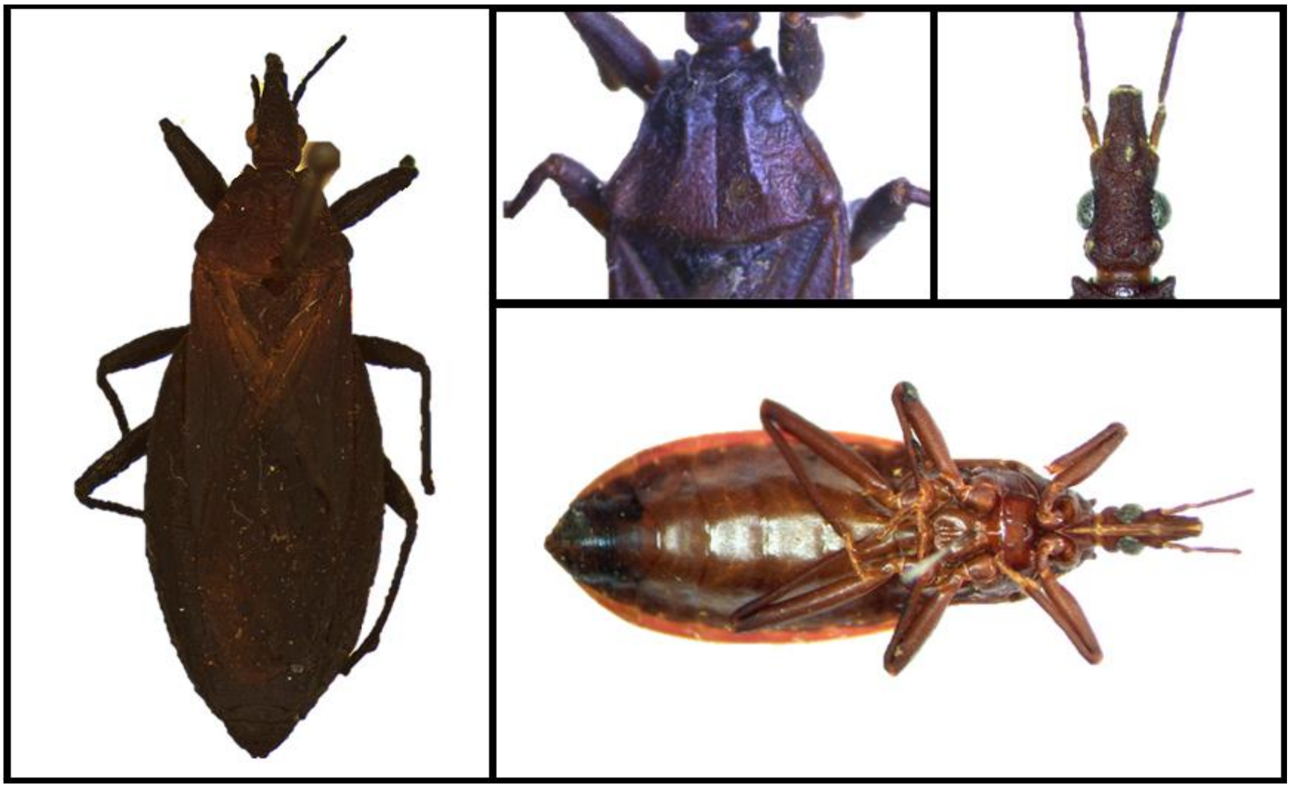

Figura 4. Espécimes fêmea de *T. barberi.* A. Hábito dorsal (coleção Rodolfo Carcavallo (CTIOC 4810)); B. pescoço e pronoto (Coleção Entomológica de Referência (n°E6238, tubo 8)); C. Cabeça em vista dorsal (foto de José Manuel Ayala Landa); D. Hábito ventral da fêmea (foto de José Manuel Ayala Landa). Fotos não estão em escala.

Triatoma gerstaeckeri (Stål, 1859)

Sabe-se que a espécie apresenta coloração do marrom escuro até o preto, com manchas amarelas ou amarelo-alaranjadas no pescoço, cório e conexivo. Cerdas curtas, escassas e pouco visíveis. Possui distribuição nos EUA (New Mexico, Texas) e México (Chihuahua, Nuevo Leon, Tamaulipas, San Luis Potosí, Coahuila).

Já foi registrada no peridomicilio, encontrada naturalmente infectada por *T. cruzi* e possui como hospedeiros naturais roedores do gênero *Neotoma* Say e Ord, 1825. Espécimes pequenos de *T. gerstaeckeri* possuem semelhança morfológica ao *Triatoma indictiva* Neiva, 1912 (LENT e WYGODZINSKY,1979).

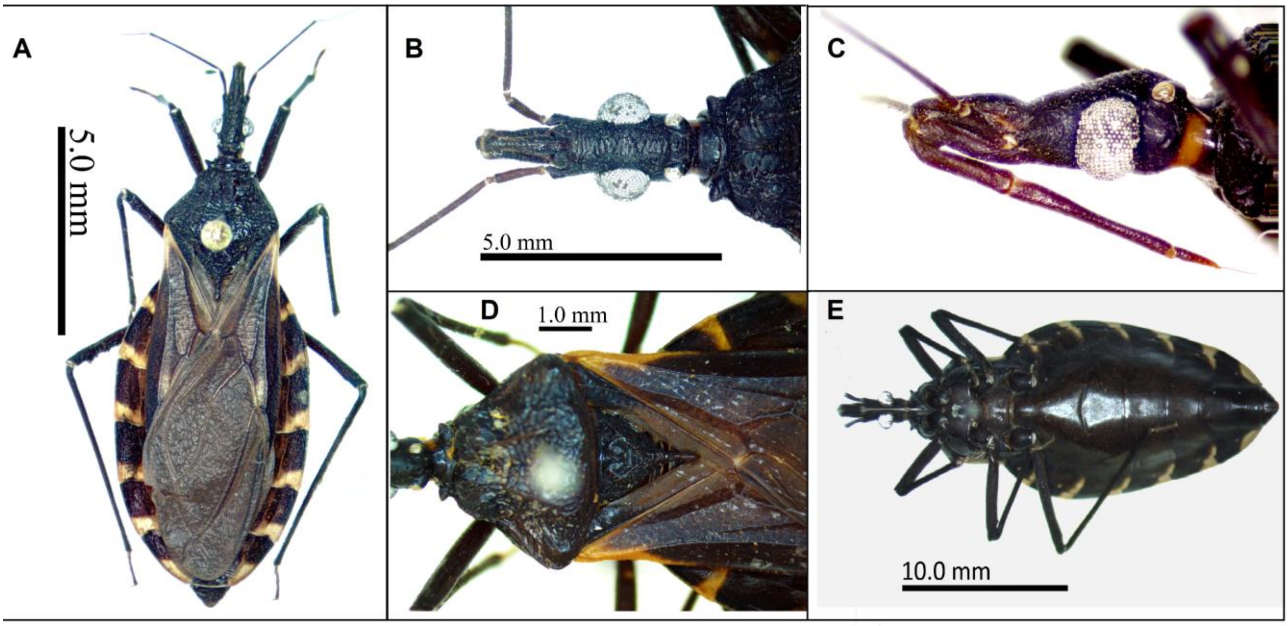

Figura 5. Espécime fêmea de *T. gerstaeckeri.* A. Hábito dorsal; B. Cabeça em vista dorsal; C. Cabeça em vista lateral; D. Pronoto e escutelo em detalhe, vista dorsal; E. Hábito ventral (fotos de José Manuel Ayala Landa).

Triatoma incrassata Usinger, 1939

Na descrição original, Usinger (1939) afirmou que essa espécie pode ser distinguida por sua cabeça curta, olhos grandes e base fortemente robusta do tylus (proeminência central na parte frontal superior da cabeça de alguns hemípteros, anteclípeo). A espécie é de distribuição restrita, sendo registrada em Sonora (Localidade tipo: Valle de México), México e no Arizona, EUA (BERN et al 2011). Espécie com poucos registros de ocorrência e dados escassos. *Triatoma incrassata apachensis* Ryckman, 1962 foi caracterizado como uma população de barbeiros do sudeste do Arizona. Uma área que anteriormente fazia parte da nação Apache (Ryckman, 1962). Posteriormente foi sinonimizada com *T. incrassata* devido aos caracteres diferenciais elencados por Ryckman não serem suficientes para manter o status subespecífico (LENT e WYGODZINSKY,1979).

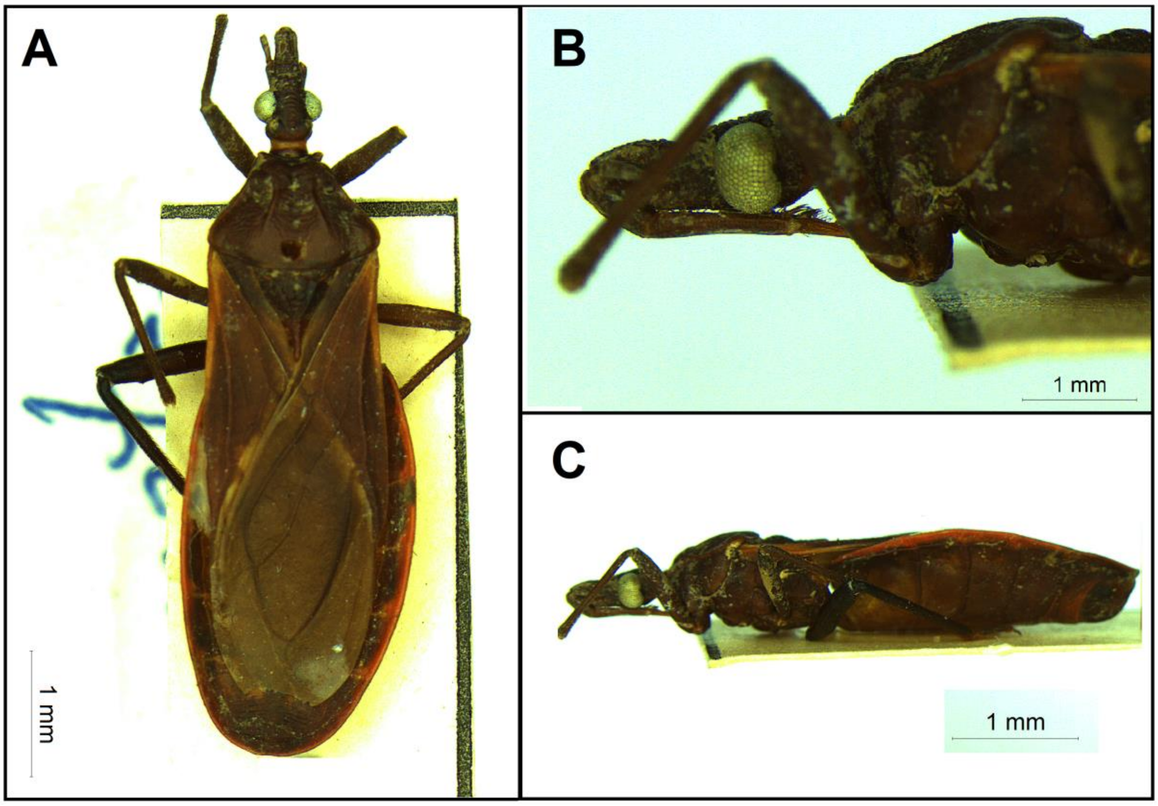

Figura 6. Espécime macho de *T. incrassata.* A. Hábito dorsal; B. Cabeça em vista lateral; C. Hábito em vista lateral (espécime da coleção Rodolfo Carcavallo (CTIOC 5426).

Triatoma indictiva Neiva, 1912

Possui coloração do corpo de marrom escuro a preto, as manchas no conexivo podem variar do laranja ao vermelho, dependendo da preservação do inseto; a base e a região do clavo do cório levemente manchadas, pronoto geralmente de coloração uniforme. Pilosidade escassa, mas visível sobre a superfície do abdômen e nas pernas (LENT e WYGODZINSKY,1979). Encontrada naturalmente infectada por *T. cruzi* (PIPPIN, LAW E GAYLOR 1968).

Neiva descreveu essa espécie a partir de espécimes provenientes do Arizona e Texas (Kerrville), baseando-se em quatro espécimes machos e uma fêmea na publicação de 15 de janeiro de 1912, na revista Brazil-Medico:

> “Rostro castanho claro. Antennas, cabeça e thorax escuros; sendo este mais claro no angulos da região posterior. Chóreo com a base e o apice possuindo manchas claras; a parte central, porém, é escura, como tambem a membrana. Connexivo escuro, com estreitas estrias avermelhadas; ventre castanho, assim como as pernas; os tarsos são de colorido mais claro” (NEIVA, 1912, p.22).

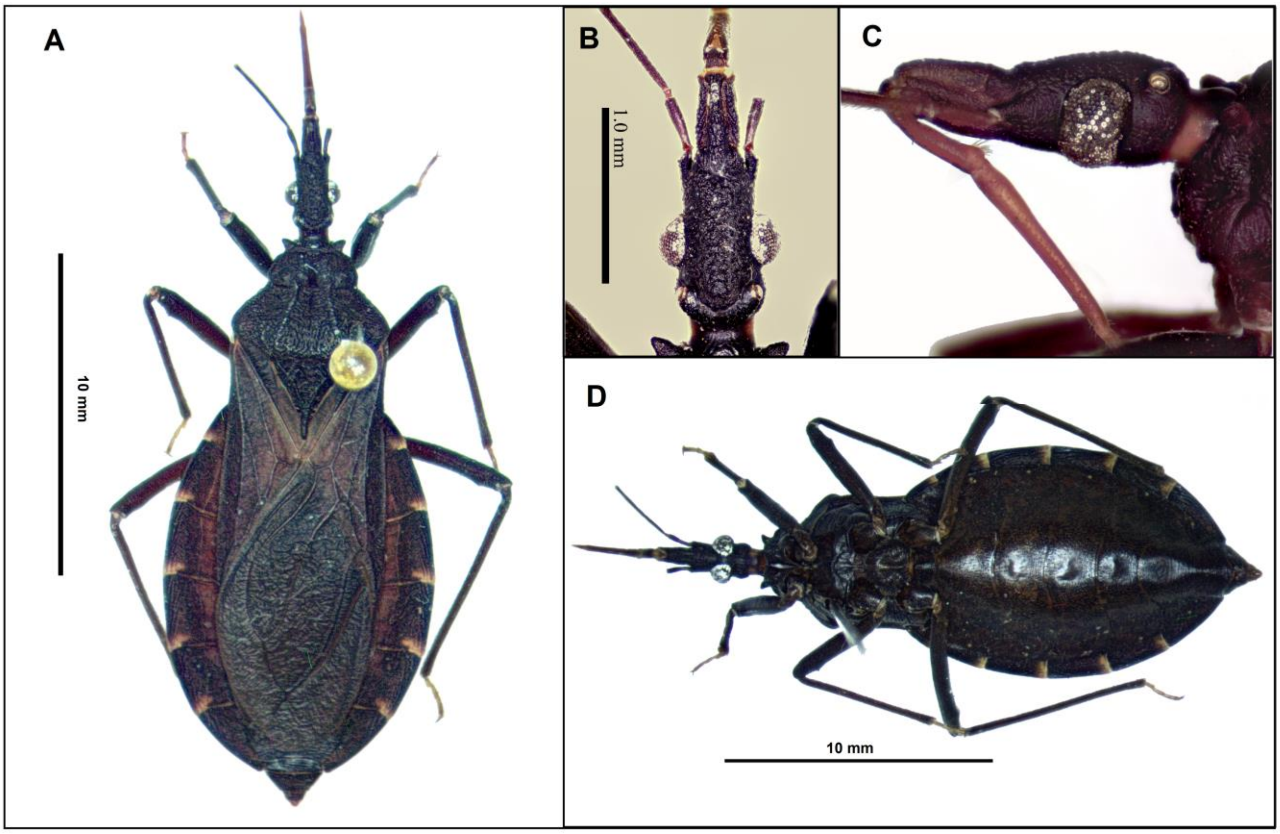

Figura 7. Espécime fêmea de *T. indictiva.* A. Hábito dorsal; B. Cabeça, vista dorsal; C. Cabeça, vista lateral; D. Hábito ventral (fotos de José Manuel Ayala Landa).

Triatoma neotomae Neiva, 1911

Foi descrita por Neiva a partir de três espécimes adultos coletados no Texas em maio de 1904 por H.S. Barber. Apresentam lábio castanho, com o último segmento muito piloso. Ângulos anteriores do pronoto são poucos acentuados, assim como os ângulos da porção posterior. Parte mediana do pronoto atravessada por duas estrias protuberantes, divergentes. Cório amarelado, com uma mancha escura larga no meio e outra comprimida no ápice, membrana escura. Conexivo com manchas alaranjadas. Superfície do corpo reluzente (NEIVA 1911).

Provavelmente o primeiro encontro da espécie no Texas foi feito por E.A. Schwarz em 1898, quando ainda não havia sido descrita e referida da seguinte forma: “bloodsucking bugs without giving the identity” (THURMAN 1944). A espécie é comumente encontrada junto a ninhos de roedores do gênero *Neotoma* e é facilmente infectada experimentalmente por *T. cruzi* (WEINSTEIN e PRATT 1948).

Lent e Wygodzinsky (1979), deixam certa dúvida quanto à validade das espécies *Triatoma nitida* e *T. neotomae*, por apresentarem várias similaridades morfológicas. Lent e Jurberg

(1992), a fim de encontrar caracteres distintivos, estudaram a genitália masculina e concluiram que os parâmeros, extensão mediana da placa basal, processo do gonóporo, processo do endosoma e o processo mediano do pigóforo possuem diferenças. O espécime utilizado por Lent e Jurberg, (1992) está representado na Figura 8A.

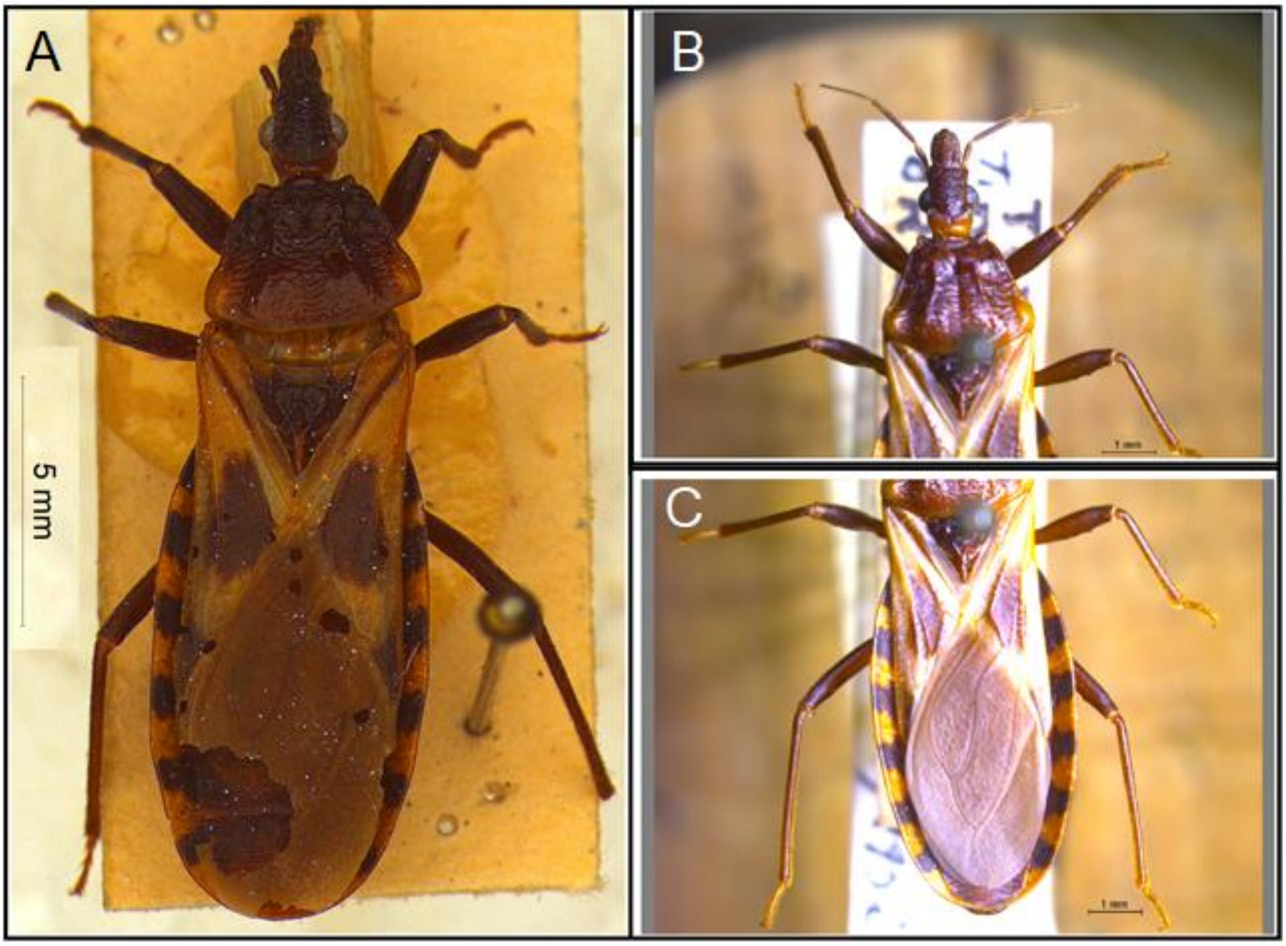

Figura 8. Espécimes machos de *T. neotomae.* A. Espécime coletado em 1934, depositado no LNIRTT (CTIOC 7094); B, C. espécime proveniente de colônia mantida por Ryckman, atualmente depositado na Coleção entomológica de referência (n°E5025).

Triatoma nitida Usinger, 1939

Cor geral marrom escuro a preta, com manchas laranja-amareladas na cabeça, pescoço, pronoto, acetábulo, cório e conexivo, com cerdas curtas, inaparentes. Possui notável semelhança morfológica com *T. neotomae*. Encontrada naturalmente infectado por *T. cruzi*. Possui distribuição na Guatemala, Honduras, Costa Rica e México (LENT e WYGODZINSKY, 1979).

A espécie é considerada silvestre, podendo invadir residências, mas não as coloniza. Em laboratório apresentou longo período de desenvolvimento e pequeno número de defecações após o repasto (GALVÃO, JURBERG e LENT, 1996).

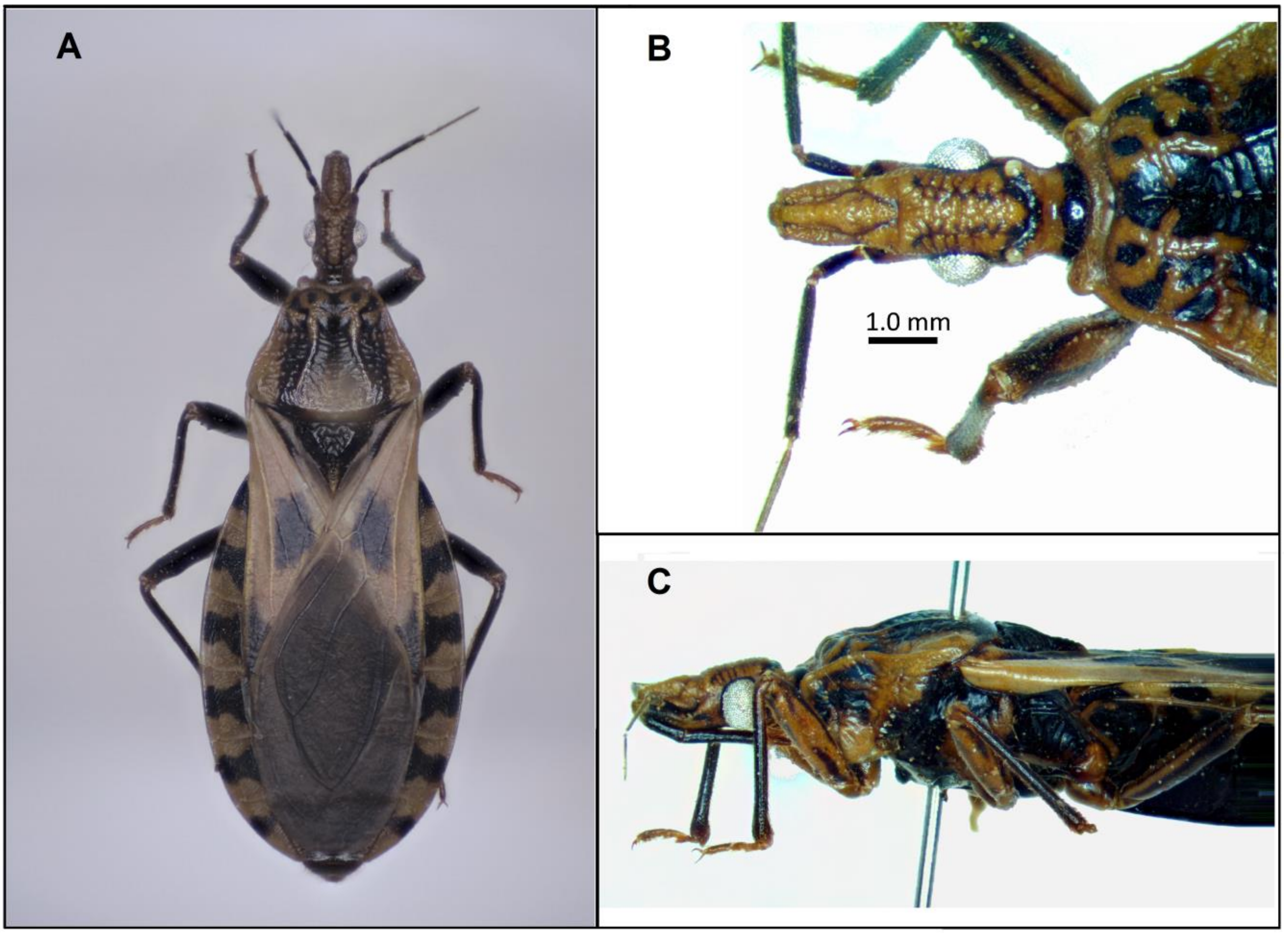

Figura 9. Espécime fêmea de *T. nitida.* A. Hábito dorsal; B. Cabeça em vista dorsal; C. Cabeça, tórax e parte do conexivo em vista lateral (Fotos de José Manuel Ayala Landa)

Triatoma peninsularis Usinger, 1940

Possui cabeça uniformemente convexa dorsalmente em todo o seu comprimento, não impressa na base do "tylus" (anteclípeo). Olhos pequenos, menores que a porção pós-ocular da cabeça. Pronoto mais curto do que a cabeça (USINGER, 1940). Intimamente próximo ao complexo *Triatoma protracta*, mas apresenta um tamanho menor do que a subespécie *T. protracta woodi*. Usinger (1944), reconsiderou o status de subespécie *T. protracta peninsulares.* Posteriormente, Ryckman, (1962) revalida o status específico. A espécie habita uma área desértica, pedregosa, quente, associada ao roedor *Neotoma* e é encontrada naturalmente infectada por *T. cruzi* (LENT e WYGODZINSKY, 1979).

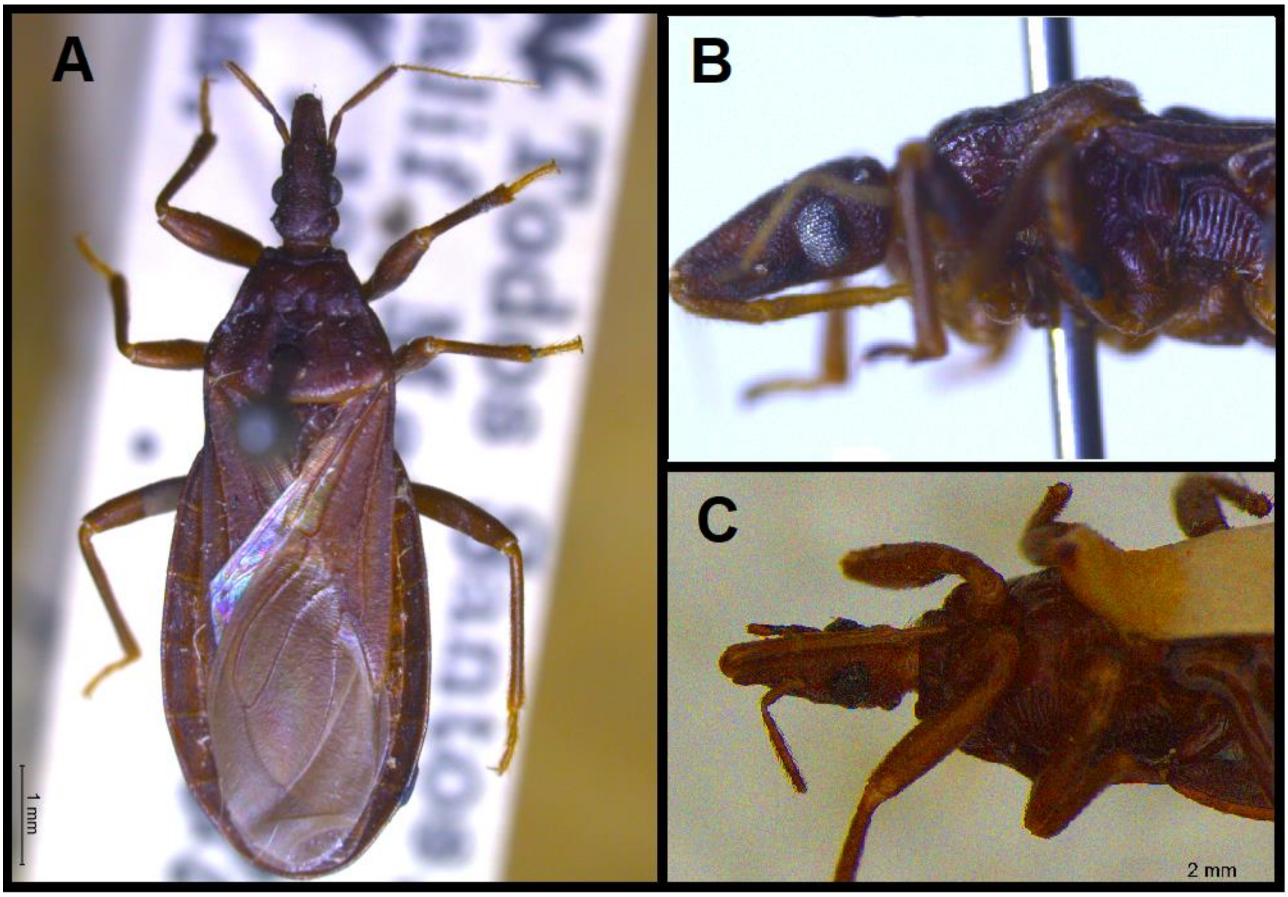

Figura 10. Espécimes machos de *T. peninsularis.* A. Hábito dorsal (depositado na Coleção entomológica de referência da USP (n°E5036)); B Cabeça e mesosterno em detalhe, vista lateral (depositado na Coleção entomológica de referência da USP (n°E5037)); C. Cabeça e tórax, vista ventral (Alótipo, depositado na Coleção Herman Lent (n°2759)).

Triatoma protracta (Uhler, 1894)

A cor geral do corpo é marrom escura a preto, possuem pernas curtas e grossas (LENT e WYGODZINSKY, 1979). É uma espécie que possui estreita associação com roedores *Neotoma* spp.*,* criando condições ideias para a manutenção da transmissão silvestre de *T. cruzi* (SHENDER, et al 2016). *Triatoma protracta* é amplamente distribuído no Sudeste dos EUA e Norte do México. Quatro subespécies foram descritas:

Triatoma protracta woodi Usinger, 1939 é uma homenagem patronímica ao falecido Dr. Sherwin F. Wood. Ocorre nos estados de New Mexico e Texas (EUA), e possui coloração geral do corpo acastanhada (USINGER, 1939). *Triatoma protracta nahuatlae* Ryckman, 1962, é uma denominação feita em homenagem à antiga nação indígena de Nahuati, na costa de Sinaloa, no México. É a menor das subespécies (RYCKMAN, 1962). *Triatoma protracta navajoensis* Ryckman, 1962 é em homenagem à Reserva Indígena Navajo e às áreas adjacentes de ambiente semelhante no Arizona, Colorado, Novo México e Utah.

Possui o maior tamanho entre as subespécies. *Triatoma protracta zacatecensis,* cujo epíteto subespecífico homenageia a população que habita o planalto norte-central do México, terra natal da antiga nação indígena Zacateca. Possui tamanho intermediário entre *woodi* e *nahuatlae* (RYCKMAN 1962; LENT e WYGODZINSKY, 1979).

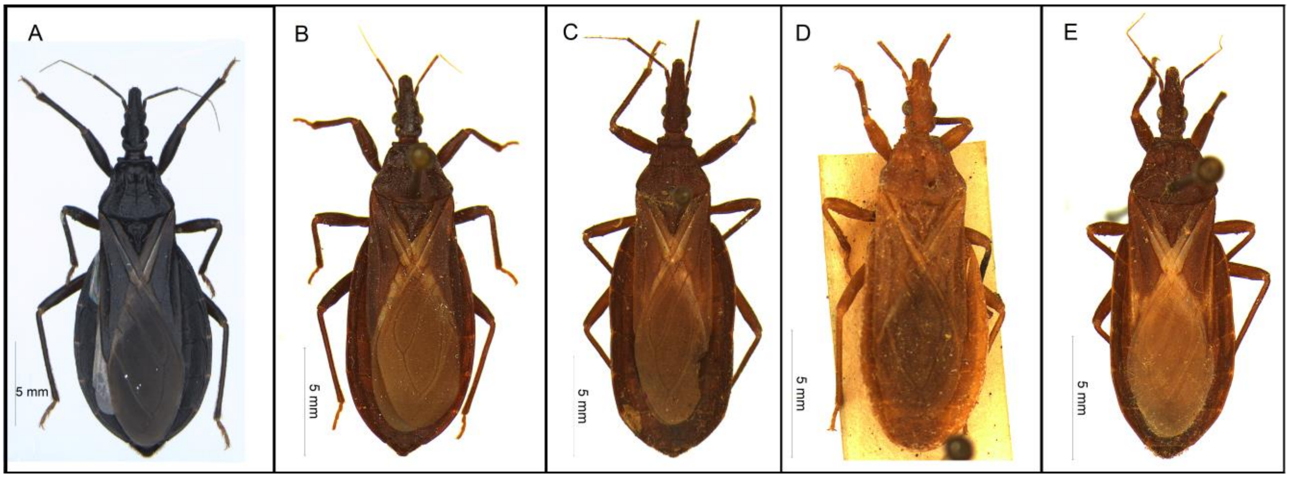

Figura 11. Espécimes das subespécies de *T. protracta.* A. *T. protracta protracta* (Coleção JMSB CTA148); B. *T. p. nahuatlae* (depositado na Coleção do LNIRTT); C. *T. p. navajoensis* (depositado na Coleção Rodolfo Carcavallo, n°4846, CTIOC 10282); D. *T. p. woodi* (depositado na Coleção do LNIRTT CTIOC 10304); E. *T. p. zacatecensis* (depositado na Coleção Rodolfo Carcavallo n°4865, CTIOC 10305).

Triatoma recurva (Stål, 1868)

Em espécimes de museus e em adultos não alimentados, o abdômen largo se curva para cima na região do conexivo. Essa é uma característica bastante marcante dessa espécie, originando a nomeação de *Conorhinus recurvus* Stål, 1868. Cor geral de marrom escuro a preto, conexivo com manchas amarelo-alaranjadas ao longo da margem externa. Cerdas curtas e esparsas, imperceptíveis (LENT e WYGODZINSKY, 1979). As pernas dessa espécie são delgadas e bastante alongadas. A espécie é encontrada naturalmente infectada por *T. cruzi* e ocasionalmente pode invadir domicílios humanos (MARTÍNEZ-IBARRA et al 2012). *Triatoma recurva nigricollis* Ryckman & Ryckman, 1967 (nigr = escuro, preto. (L.) collis = morro, collinus). Essa subespécie escura de *Triatoma recurva* pode ser encontrada na região montanhosa de Sinaloa e Nayarit, México, derivando o nome *nigricollis*. São sinonímias da espécie: *Conorhinus recurvus* Stål, 1868, *Triatoma longipes nigricollis* Usinger, 1944, e *Triatoma recurva nigricollis* Ryckman & Ryckman, 1967 (RYCKMAN 1986; LENT e WYGODZINSKY, 1979).

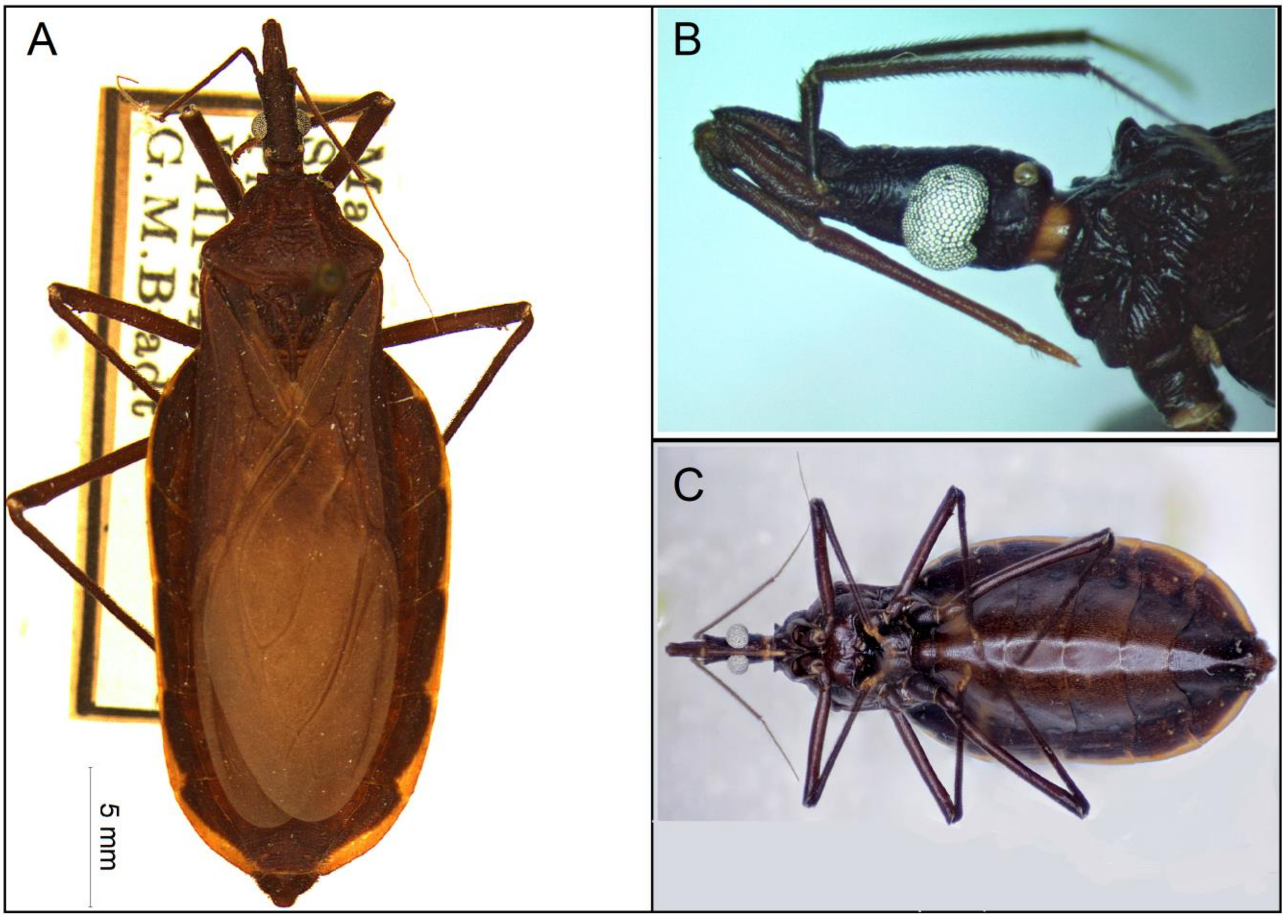

Figura 12. Espécime fêmea de *T. recurva*. A. Hábito dorsal (Espécime do Arizona, depositado na Coleção do LNIRTT CTIOC, determinado por Lent); B. Cabeça em vista lateral (Foto de José Manuel Ayala Landa); C. Hábito ventral (Foto de José Manuel Ayala Landa)

Triatoma rubida (Uhler, 1894)

Quando P.R. Uhler descreveu *Conorhinus rubidus* proveniente da extremidade de Baja California Sur, ele mencionou que a espécie era de cor avermelhada, sugerindo o nome *rubida* (RYCKMAN 1986). Cor geral do corpo castanho-avermelhado claro ou escuro, com manchas em vermelho a amarelado no pescoço, pronoto, cório e conexivo; Cabeça rugosa, não perceptivelmente granulosa; pronoto e cório em alguns casos totalmente escuros. Cerdas são imperceptíveis, curtas, esparsas (LENT e WYGODZINSKY, 1979). É uma espécie que pode invadir domicílios humanos e estar infectada por *T. cruzi* (MARTÍNEZ-IBARRA et al 2012).

Triatoma rubida cochimiensis Ryckman, 1967 é uma subespécie proposta para a subpopulação que habita a região da antiga nação indígena Cochimi, na península da Baja California. *Triatoma rubida jaegeri* Ryckman 1967 é uma subespécie, assim denominada em homenagem ao falecido Dr. Edmund C. Jaeger. Essa população melânica foi descrita em Pond Island, no Golfo da Baixa Califórnia. *Triatoma rubida sonoriana* Del Ponte, 1930 é uma subespécie geográfica presente no estado de Sonora, no México. *Triatoma rubida uhleri* Neiva, 1911 é uma subespécie denominada em homenagem ao hemipterista P.R. Uhler. *Triatoma ocellata* Neiva, 1914 (Etimologia: (L.) ocellatus com olhos pequenos) é um sinônimo júnior de *T. r. uhleri* (RYCKMAN 1986). Essas subespécies foram sinonimizadas por Lent e Wygodzinsky 1979, porém recentemente alguns autores sinalizaram para a validade de pelo menos 3 subespécies (RAMSEY et al 2015; PFEILER et al 2006; MONTEIRO et al 2013).

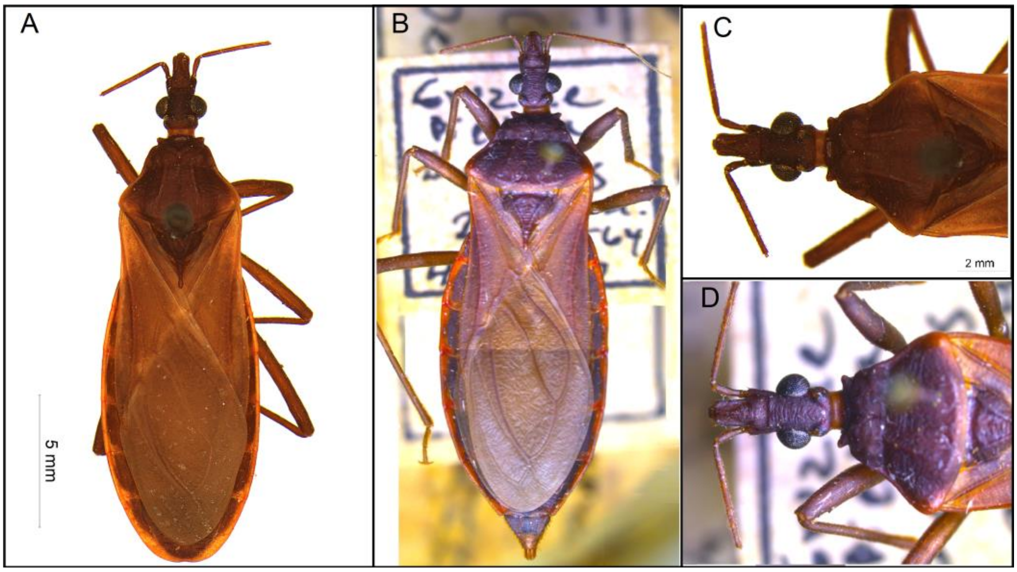

Figura 13. Espécimes de *T. rubida.* A. *Triatoma r. rubida,* macho, hábito dorsal (depositado na Coleção do LNIRTT); B. *Triatoma r. sonoriana,* fêmea, hábito dorsal (depositado na Coleção entomológica de referência (n°E12754, suporte 511))*;* C. Cabeça de *T. r. rubida*, vista dorsal (depositado na Coleção do LNIRTT); D. Cabeça de *T. r. sonoriana*, vista dorsal (depositado na Coleção entomológica de referência (n°E12754, suporte 511)).

Triatoma sanguisuga (LeConte, 1855)

Possui como características diagnósticas: cor geral de marrom escuro a preto, cabeça e tórax granulosos, antenas delgadas com o primeiro segmento muito mais curto do que a cabeça, tórax triangular, manchas amareladas a avermelhadas no pescoço, pronoto, hemiélitro e conexivo (seis manchas vermelhas de cada lado no conexivo conectando com os esternitos), cerdas esparsas. Invade residências humanas no intuito de se alimentar e é encontrado naturalmente infectado por *T. cruzi* (LECONTE, 1855; LENT e WYGODZINSKY, 1979).

No trabalho de descrição da espécie os espécimes eram provenientes da Georgia, (EUA) e John Le Conte discorreu ainda sobre a dor e as implicações que a picada desse inseto causa:

> "Este inseto, inflige uma ferida muito dolorosa. É notável também por sugar o sangue de mamíferos, principalmente crianças. Conheço sua mordida seguida de sérias consequências, o paciente não se recupera de seus efeitos há quase um ano" (LE CONTE, 1855, P. 404).

À época o agente etiológico da doença de Chagas não havia sido descrito, portanto, hipoteticamente, este pode ter sido o primeiro relato da transmissão vetorial (por *T. sanguisuga*) de *T. cruzi* nos EUA.

Essa espécie é muito variável quanto ao tamanho e formas cromáticas. *Triatoma sanguisuga ambigua* Neiva, 1911 ((L.) ambiguus = duvidoso), foi proposta como uma subespécie da Flórida. *Triatoma sanguisuga texana* Usinger, 1944*,* tem seu nome subespecífico relativo à região geográfica em que foi encontrada, o estado americano do Texas (RYCKMAN, 1986). Dados moleculares apontam para a existência de uma subespécie, que pode ser nova, da Louisiana (DE LA RUA, STEVENS, DORN, 2011).

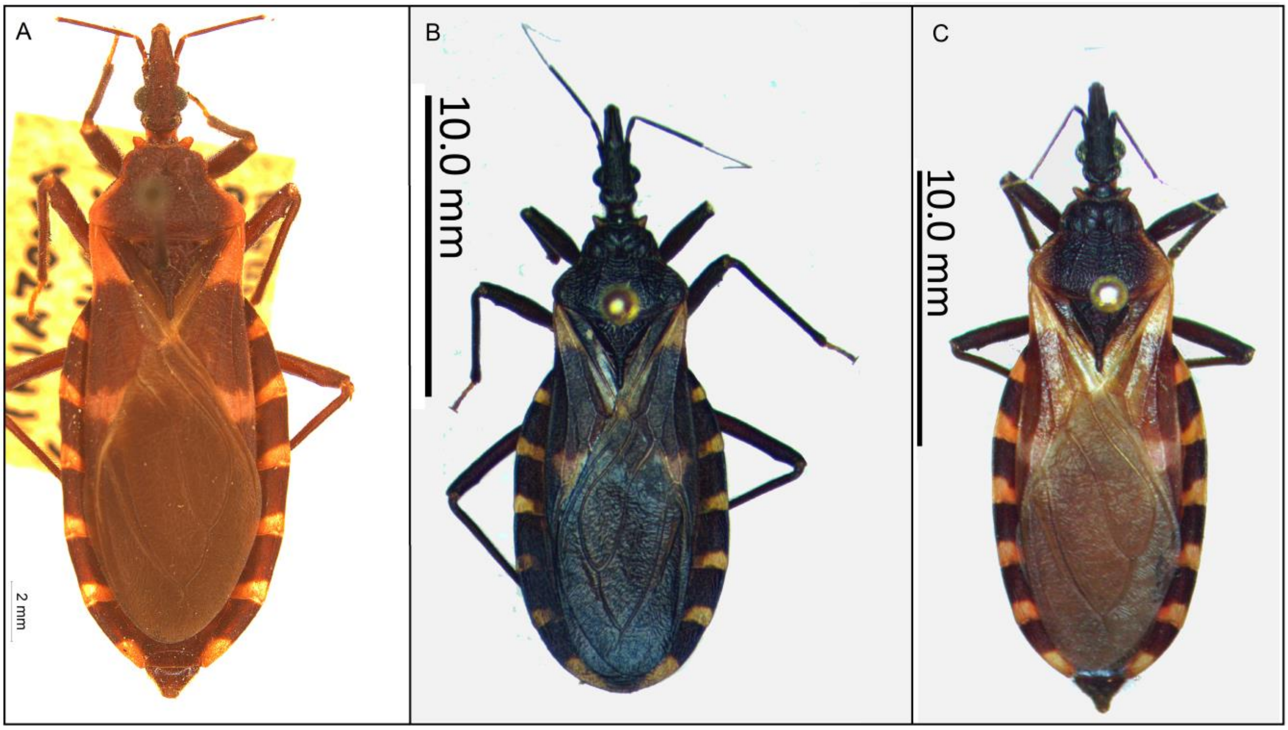

Figura 14. Espécimes de *T. sanguisuga,* com diferenças cromáticas. A. Hábito dorsal (depositado na Coleção do LNIRTT CTIOC); B. Hábito dorsal (Foto de José Manuel Ayala Landa); C. Hábito dorsal (Foto de José Manuel Ayala Landa).

Triatoma sinaloensis Ryckman, 1962

É uma espécie bem pequena (10 a 13 mm), possui coloração castanha. Cabeça curta, sem depressão na região posterior da sutura do clípeo; pronoto polido, sem tubérculo discal, ângulos anteriores arredondados; sem manchas pronunciadas no conexivo. Considerada silvestre e habita área costeira e desérticas de Sinaloa e Sonora, no México. É naturalmente encontrada infectada com *T. cruzi* e em associação com o roedor do campo *Neotoma phenax* Merriam e *Neotoma albigula* Hartley. (RYCKMAN 1962; LENT e WYGODZINSKY, 1979).

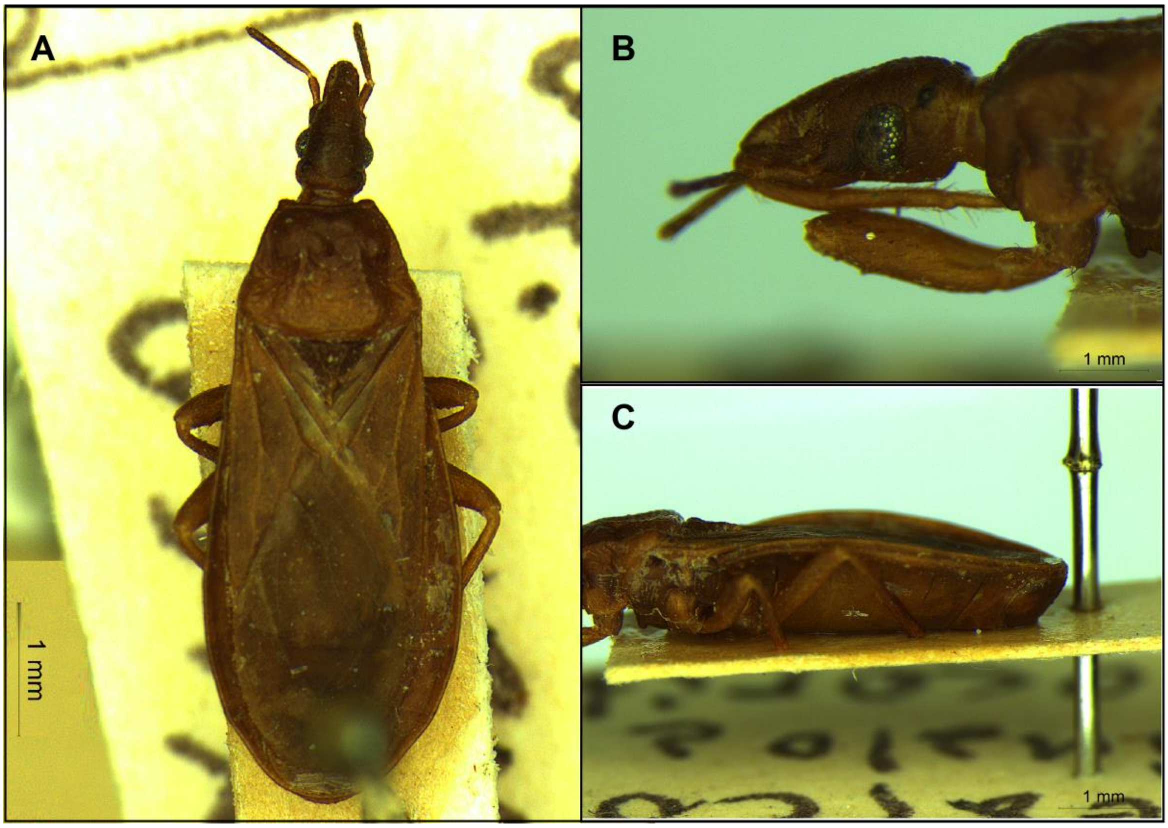

Figura 15. Espécime macho de *T. sinaloensis.* A. Hábito dorsal (Espécime de Mocorito, Sinaloa, México, determinado em 1969 por Rodolfo Carcavallo, depositado na Coleção do LNIRTT CTIOC 5191); B. Cabeça em vista lateral; C. Corte do pronoto, escutelo, conexivo e esternitos em vista lateral.

2. Objetivos

2.1. Geral

-Revisar os aspectos taxonômicos dos complexos *Triatoma lecticularia* e *Triatoma protracta* (propostos por Schofield e Galvão, 2009).

2.2. Específico

-Verificar a validade taxonômica dos gêneros e espécies dos complexos de *Triatoma* por meio dos caracteres morfológicos da cabeça, tórax e abdômen.

-Tecer hipóteses sobre as relações filogenéticas entre as espécies e seus complexos, aplicando abordagem cladística, baseada em dados morfológicos e moleculares.

3. Resultados

A tese apresenta-se dividida em três capítulos. Explicitamos na tese o papel dos triatomíneos na transmissão da doença de Chagas, posteriormente abordamos os aspectos taxonômicos desses vetores e por último discorremos resumidamente sobre todas as espécies que, de alguma forma, fizeram parte do objetivo do trabalho. Essas espécies faziam parte dos complexos *Triatoma protracta* e *Triatoma lecticularia,* proposto por Schofield e Galvão (2009). Os Materiais e métodos utilizados foram inseridos em cada Capítulo, respectivamente.

O primeiro capítulo traz o artigo “A review of the taxonomy and biology of Triatominae subspecies (Hemiptera: Reduviidae)”, publicado na revista Parasitology Research, abordando taxonomicamente todas as subespécies incluídas nos gêneros *Panstrongylus, Paratriatoma e Triatoma.*

No segundo capítulo incluímos o artigo “Formal assignation of the kissing bug *Triatoma lecticularia* (Hemiptera: Reduviidae: Triatominae) to the genus *Paratriatoma*”, publicado na revista Insects. Nesse artigo apresentamos a nova combinação *Paratriatoma lecticularia* através da compilação de dados moleculares, morfológicos e citogenéticos. Esse artigo representa um passo importante na taxonomia, pois seu antigo complexo de espécies foi destituído.

O terceiro capítulo compreende uma extensa análise cladística de 23 espécies neárticas, por meio de caracteres morfológicos e moleculares (CytB, COX1, COX2, 16S, 18S e 28S). Como esses dados são extensos, foram incluídos em “Supporting Information Appendix 1”, ao final da tese. Esse capítulo também foi organizado em formato de artigo científico em inglês, para posterior publicação.

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Capítulo I

Artigo científico publicado na revista Parasitology Research

A review of the taxonomy and biology of Triatominae subspecies (Hemiptera: Reduviidae)

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Abstract

Due to its public health importance, as vectors of Chagas disease, the subfamily Triatominae, has received the attention of taxonomists. Knowing how to correctly identify these insects is of paramount importance for the surveillance and control of these vectors. Over many years, more than 40 triatomine subspecies were proposed. Infraspecific taxa are accepted as real entities in nature and recognized as biologically significant. Infraspecific diversity and population subdivision are frequently confused with the underlying mechanisms that lead to the formation of new species and species-level diversity. The distinction between infraspecific and interspecific divergence processes has received far less attention than species delimitation. In this work, new literature data on subspecies included in the subfamily Triatominae are presented. Data were compiled about *Triatoma brasiliensis, Triatoma breyeri, Triatoma circummaculata, Triatoma dimidiata, Triatoma incrassata, Triatoma infestans, Triatoma phyllosoma, Triatoma protracta, Triatoma recurva, Triatoma rubida, Triatoma sanguisuga, Triatoma vitticeps, Panstrongylus megistus, Paratriatoma hirsuta,* and *Paratriatoma lecticularia* subspecies. Although several of these subspecies have been synonymized, herein we emphasize that some subspecies may be valid. Therefore, further studies are needed on the taxonomy, evolution, phylogeny, biogeography, ecology, physiology, and behavior of species to reinforce, or to invalidate the infraspecific status in the subfamily.

Key words: Chagas disease, Taxonomy, synonymy, infraspecific taxa

Introduction

Carlos Chagas described the protozoan *Trypanosoma cruzi* (Chagas, 1909), including its pathology, causes, and possible vertebrate hosts and vectors (Chagas 1909). Chagas disease is the parasitic zoonosis with the greatest impact in Latin America (Kratz 2019) and is mainly transmitted through vectors, blood transfusion, congenital means, and contaminated food (infected kissing-bugs crushed together with açai or sugarcane juice, for example) (Mattos et al. 2017). Observations about the blood-sucking insect *Panstrongylus megistus* (Burmeister, 1835) generated great interest for medicine since it was shown to be the first vector of this trypanosomiasis (Neiva 1910). Currently these vectors are included in the order Hemiptera, suborder Heteroptera, family Reduviidae, subfamily Triatominae (Lent and Wygodzinsky 1979), counting 157 species and 2 subspecies, distributed in 18 genera and five tribes: Alberproseniini, Bolboderini, Cavernicolini, Rhodniini, and Triatomini (Table 1) (Dujardin et al. 2002; Galvão et al. 2003; Schofield and Galvão 2009; Paiva et al. 2021; Dale, Justi and Galvão 2021).

Species are the basic units of biological organization and due to the universality of the subject, taxonomists are required to define the species. According to the International Zoological Nomenclature Code (ICZN 1999), subspecies are accepted and named according to the trinomial format. The subspecies concept goes back to the 19th century and was coined to describe geographic variations or morphological polymorphisms among species that are not sufficient to determine a new taxon. Subspecies are natural populations ("geographic populations") belonging to a single mother species with visible and easily observable characteristics (Dujardin et al. 2009).

In Triatominae, over the years, species and subspecies have been described according to their geographic locations, hosts, morphological characters, or in homage to a researcher (Ryckman 1986; Galvão et al. 2003). Triatomine species and subspecies are being continuously redefined because they exhibit a relatively high degree of morphological plasticity (Dujardin et al. 1999; Schofield and Galvão 2009). Morphology (or its variations, e.g., colours, shape, patterns) or molecular data alone should not in itself lead to the erection of a new species name. Modern approaches, and especially quantitative ones, must be applied before reaching a consensus. At the same time, clear and usable morphological characters should be described (Bargues et al. 2010). The main morphological classification of this subfamily is based largely on the review by Lent and Wygodzinsky (1979), where many subspecies were invalidated or placed as species, creating a gap in the knowledge about subspecies of triatomines. Later studies (including molecular data) showed that many subspecific taxa exclusions were not appropriate (Galvão et al. 2003; Pfeiler et al. 2006; Mas-Coma and Bargues 2009; De la Rua, Stevens, Dorn 2011; Costa et al. 2013; Espinoza et al. 2013; Monteiro et al. 2013; Ramsey et al. 2015; Alevi et al. 2018; Martínez-Ibarra et al. 2020).

The aim of the present work is to list and discuss the subspecies included in the subfamily, clarifying the current situation of Triatomines in view of the new literature data.

Results

The subspecies of *Triatoma*

In the genus *Triatoma*, more than 40 subspecies have been proposed (Table 1), representing approximately 50% of the total number of taxa of the genus. This percentage of subspecies is due to the phenotypic polymorphism common in triatomines, that is, the adaptation of the phenotype to the environment (Nattero et al. 2013; Lunardi et al. 2017). The phenotype is a direct result of gene expression; however, phenotypic expression may undergo physiological, morphological, or morphometric changes in response to environmental pressures (Bitner-Mathé et al. 1995; Dujardin et al. 1997; Ayala et al. 2011). Some populations, due to their morphological aspects, resulted in descriptions of subspecies, for which the following subspecies are presented.

Triatoma brasiliensis subspecies

Initially three subspecies were described, *Triatoma brasiliensis brasiliensis* Neiva, 1911, *Triatoma brasiliensis melanica* Neiva and Lent, 1941, and *Triatoma brasiliensis macromelasoma* Galvão, 1956*. Triatoma brasiliensis* is currently one of the main vectors of Chagas disease in the Brazilian semiarid region (Silveira and Vinhaes 1999). In 1941, Neiva and Lent described *T. b. melanica* as a subspecies based on chromatic variations. Later, in Costa et al. (2006), *T. melanica* was elevated to species status through comparisons of its morphology, biology, ecology, crossing experiments, allozymes, and mtDNA sequences with those of other members of the *T. brasiliensis* species complex. *T. b. macromelasoma* had a knocked down status and was named by Lent and Wygodzinsky (1979). According to the authors, the differences noted earlier were not sustained due to the intermediate forms between being common in nature. In Costa et al. (2013), the status of subspecies of *T. b. brasiliensis* and *T. b. macromelasoma,* was confirmed and redescribed by crossing experiments and morphological, biological, ecological, and molecular analyses. The distinction between *T. b. brasiliensis* and *T. b. macromelasoma* is the most complex among representatives of the *T. brasiliensis* subcomplex (Costa et al. 2013) however, studies show well-defined genetic (Monteiro et al., 2004) and morphological aspects (Oliveira et al. 2020).

Triatoma breyeri subspecies

Triatoma breyeri Del Ponte 1929, is a South American triatomine, found in Argentina in the provinces of Catamarca, Córdoba, and La Rioja. A population identified as *T. breyeri* was found near Mataral, Cochabamba, Bolivia, but a cytochrome b sequence appears to diverge approximately 4% from the original Argentinean specimens, which according to the literature is enough to separate two subspecies (Pfeiler et al. 2006; Justi et al. 2014; Monteiro et al. 2018). Eduardo Del Ponte received a female specimen, 1930, from the "Museo de Historia Natural" that agreed with the type of *T. breyeri*, but the connexivum had black spots that reach the edge, trapezoid-shaped spots, with a larger and more visible external base and was named *Triatoma breyeri dallasi*, and attributed to the province of La Rioja (Del Ponte 1930). There was no formal synonymization of the subspecies (Lent and Wygodzinsky 1979), so it is considered synonymous (Galvão et al. 2003). In this case, it is necessary to clarify if the molecular differences pointed out by the studies correspond to the specimens described as *T. breyeri dallasi*, because if so, the subspecies status can be revalidated. Therefore, a larger sample is necessary for better inference.

Triatoma circummaculata subspecies

Triatoma circummaculata (Stål, 1859) possess an overall color varying from dark brown to black, with markings that can vary from orange to red in the pronotum, corium, and connexivum. With restricted distribution to the south of Brazil, Uruguay, and Argentina (Lent and Wygodzinsky 1979). *Triatoma limai* Del Ponte, 1929 has been described in comparison with *Triatoma sordida* (Stål, 1859), demonstrating obvious differential morphological characters (Del Ponte 1930). However, *T. limai* is obviously closely related to *T. circummaculata,* differentiating only in the light-yellow areas of the connexivum, eyes slightly larger, and head, in profile, higher posteriorly (Lent and Wygodzinsky, 1979). Carcavallo et al. (1967) concluded that both taxa corresponded to the same species, thus proposing the subspecies *Triatoma circummaculata limai* Del Ponte, 1929. However, despite little evidence, Lent and Wygodzinsky (1979) returned the specific status of *T. limai.*

Triatoma dimidiata subspecies

The phylogenetic species *Triatoma dimidiata* (Latreille, 1811) presents one of the biggest problems for the genus taxonomy (Dorn et al. 2018). Arthur Neiva considers it the most variable morphology, with observations ranging from large spots on the corium to their absence (Neiva 1914). *Conorhinus macullipenis* (Stål, 1859) was originally described, and later categorized as subspecies *Conorhinus dimidiatus macullipenis* (Champion, 1811), which Neiva (1914) confirms is now in the genus *Triatoma,* including the two subspecies *T. d. dimidiata* and *T. d. macullipenis*. The morphological differences between these subpopulations were described in detail and led to the conclusion that they may be intercrossing (Lent and Jurberg 1985). *Triatoma capitata* (Usinger, 1941) was described and shortly afterwards it was transferred to the subspecies *Triatoma dimidiata capitata* (Usinger 1944). In the revision carried out by Lent and Wygodzinsky (1979), the subspecies were synonymized. Mas-Coma and Bargues (2009) argue that the level of genetic divergences between these three groups of haplotypes supports the re-validation of the three subspecies. These issues were also discussed in Dorn et al. (2018), and Lima-Cordón et al. (2019).

Triatoma hegneri Mazzotti, 1940 presents peculiar chromatic characteristics of insular isolation. The *Triatoma hegneri* Internal Transcribed Spacer 2 (ITS-2) gene differs by only three mutations in comparison with *T. d. maculipennis*. Experimental crosses are known to produce fertile hybrids between *T. dimidiata* and *T. hegneri* (R.E. Ryckman unpublished, apud: Bargues et al. 2008). The subspecific status of *Triatoma dimidiata hegneri* could be verified because analysis separates it as a very close but evolutionary lineage (Bargues et al. 2008; Mas-Coma and Bargues 2009).

Triatoma incrassata subspecies

The type-locality of *Triatoma incrassata* Usinger, 1939 is the “Valley of Mexico” near Mexico City, presenting restricted distribution, with specimens captured in the state of Sonora (Mexico) and Arizona (USA) (Bern et al. 2011). Specimens from Arizona were described (based on three specimens) as *Triatoma incrassata apachensis* Ryckman, 1962, and specimens from Mexico as the nominotypical subspecies *Triatoma incrassata incrassata*. Lent and Wygodzinsky (1979) examined the type of *incrassata*, as well as a specimen from Arizona (Santa Rita Mountains) and concluded that the general color of the body and the size of the specimens are not sufficient to support the two subspecies.

Ryckman (1962) comments that when superficially examining *T. i. apachensis*, it can be confused with a large, dark, and introgressive hybrid (*Triatoma protacta woodi* X *T. protracta protracta*) that also occurs in the same area in Arizona. These hybrids created in the laboratory are very similar to *T. i. apachensis* in size and color pattern. However, they can be distinguished by the deep transverse groove in the post clypeal suture region and by the posterior increase in the clypeus in *T. incrassata*; which, if present, is not as pronounced in *T. protracta*. However, *T. incrassata* is an extremely poorly sampled species (e.g., GBIF returns nine occurrence results), so even though there was a synonymization, more data on these subspecies should be collected for further statements.

Triatoma infestans subspecies

Triatoma infestans (Klug, 1834) is the main vector of Chagas disease, having a wide geographical distribution and high capacity for domiciliation (Forattini 1980). An entirely melanic form of Misiones (Argentina), was originally described as a subspecies, *Triatoma infestans melanosoma* Martinez, Olmedo and Carcavallo, 1987, and later proposed as a species, *Triatoma melanosoma* (Lent et al. 1994). A second dark form, discovered in the Bolivian Chaco, has been described simply as a 'dark morph' of *T. infestans* (Noireau et al. 1997). Some studies support the idea that the 'dark morphs' or '*T. melanosoma*, are different ecotypes and not different species (Dujardin et al. 1999). Monteiro et al. (1999), using molecular data (mtCytB gene), cytogenetics, and allozymes did not detect differences between these two taxa, suggesting that *T. melanosoma* could represent no more than an inbred founder population of *T. infestans* where a putative melanic allele has become fixed. Gumiel et al. (2003), propose the synonymization of *T. melanosoma* with *T. infestans* based on geometric morphometry of the hemelytron.

Triatoma infestans erythrophtalmus Noé & Silva, 1949, included mutant red-eye specimens and was later synonymized with *T. i. infestans* (Galvão 2003; Ryckman 1971b).

Triatoma phyllosoma subspecies

Triatoma phyllosoma (Burmeister, 1835), according to Usinger, Wygodzinsky and Ryckman (1966) "is considered to be a polytypic species of the type with abrupt steps rather than gradual morphological differences and with complete rather than partial infertility between allopatric populations". Initial morphological evidence has supported the rank of species for *T. pallidipennis* (Stål, 1872), *T. longipennis* (Usinger, 1939), *Triatoma mazzotti* (Usinger, 1941), and *T. picturata* (Usinger, 1939). However, some authors considered as subspecies *T. phyllosoma pallidipennis, T. phyllosoma longipennis*, *T. phyllosoma mazzotti*, *T. phyllosoma picturata,* and the nominotypical *T. p. phyllosoma* (Martínez-Ibarra et al. 2015, 2017; Mazzotti and Osorio 1942; Usinger 1944; Usinger, Wygodzinsky and Ryckman 1966).

These subspecies have been inter-crossed with each other under laboratory and wild conditions, and hybrids have been obtained (Mazzotti and Osorio 1942; Martínez-Ibarra et al. 2009; 2015, 2017; Villalobos et al. 2011). DNA sequence (ITS-2, COI, Cyt*b*) studies support the proposal that the subspecies are valid, indicating a recent common ancestor (Mas-Coma and Bargues 2009; Bargues, Zuriaga & Mas-Coma 2014; Martínez-Ibarra et al 2015, 2017). In a review by Lent and Wygodzinsky (1979), the subspecies were raised to a specific rank, however, the author did not provide logical explanations for this. Nevertheless, Rengifo-Correa et al. (2021) implement the cohesion species concept, validating the species status of *T. bassolsae, T. longipennis, T. mazzottii, T. pallidipennis, T. phyllosoma*, and *T. picturata*.

Triatoma phyllosoma usingeri Mazzotti, 1943 was also described, which represents an intermediate form between *T. p. pallidipennis* and *T. p. picturata* (Mazzotti 1943). *Triatoma phyllosoma intermedia* Usinger, 1944 is closely related to *T. p. picturata,* but differs in the great reduction in orange markings, the short hemelytra, and pubescent pronotal disk (Usinger 1944). These last two taxa were synonymized by Lent and Wygodzinsky (1979).

Triatoma protracta subspecies

Triatoma protracta is a polytypic species, and the typical form of *protracta* is widely distributed in the southwestern USA and northern Mexico. The overall color of this form is dark brown or black (Lent and Wygodzinsky, 1979). Usinger (1939) proposed the name *T. protracta woodi* for the light-colored population of New Mexico and Texas. *T. protracta navajoensis* Ryckman is morphologically the largest of the five subspecies recognized, its distribution is restricted to the high Colorado Plateau. *Triatoma protracta nahuatlae* Ryckman is black and is morphologically the smallest of the five subspecies. It appears to be adapted to the west coast of the states of Sonora and Sinaloa, Mexico. *Triatoma protracta zacatecensis* Ryckman, is black and intermediate in size between *T. p. woodi* and *T. p. nahuatlae* and is distributed throughout the central Mexican Plateau. Although among *T. protracta* specimens intermediate morphotypes can be found between subspecies, *P. woodi* is admittedly polymorphic and in *P. zacatecensis* and *P. nahuatlae* the morphological differences are extremely tenuous. All subspecies and infrasubspecific (entity below the rank of subspecies, e.g.: smooth egg and rough egg) populations of *T. protracta* have been shown able to interbreed (Ryckman 1962; Lent and Wygodzinsky 1979).

Triatoma peninsularis (Usinger, 1940) was described as a species and has also been treated as a subspecies (Usinger, 1944). *T. peninsularis* is an isolated species that occupies in the Baja California Sur (Lent and Wygodzinsky 1979). Therefore, these species appear to possess a recent common origin. These species produced unfeasible F1 nymphs when mated with *T. p. woodi*. When *T. peninsularis* was mated with the subspecies of *T. protracta*, only sterile eggs, embryos, or weak F1 nymphs that died in the first or second instar were obtained (Ryckman 1962; Usinger, Wygodzinsky and Ryckman 1966; Lent and Wygodzinsky 1979).

The *Triatoma protracta* complex has raised many taxonomic doubts since it was proposed. Many species and subspecies have no pre-or post-zygotic barrier, resulting in many hybrids. Several abnormalities were observed for the crossing of these subspecies (Ryckman, 1971b). A robust phylogeny is necessary for this group of superspecies.

Triatoma recurva subspecies

Triatoma recurva (Stål, 1868) has been described as *Conorhinus recurvus* and is a comparatively large insect (25.5-30 mm). *Triatoma longipes* Barber, 1937 is a junior synonym of this species. Usinger (1944) described a subspecies *T. longipes nigricollis* from Nayarit, Mexico based on a single specimen, which differs from typical *'recurva'* by having a nearly black color, with the connexivum broadly bounded with orange-yellow and slightly larger eyes. Lent and Wygodzinsky (1979), observed that the general color of the specimens in the collections varied in intensity from dark brown to black according to the state of preservation of the samples. The authors found similar yellow areas in the connective in Mexican and Arizona specimens, and similar eye measurements in both populations, therefore concluding that '*nigricollis'* should not be kept as a valid name.

Triatoma rubida subspecies

Triatoma rubida includes five natural subspecies: *T. rubida rubida* (Uhler), *T. rubida uhleri* (Usinger, 1944), *T. rubida sonoriana* (Usinger, 1944), *T. rubida cochimiensis* Ryckman, 1967, *T. rubida jaegeri* Ryckman, 1967, based on morphological criteria and lack of reproductive barriers (Ryckman 1967). Through a pioneering comparative electrophoretic study of the *T. rubida* complex, using the specimen's hemolymphs, differences in the analyzed protein bands were demonstrated (Adams and Ryckman, 1969). *Triatoma rubida* is very close to the *T. protracta* complex because it has ten autosomes in the haploid condition. In addition, an F1 nymph (fifth instar) was obtained from interspecific mating between *T. barberi* male and *Triatoma rubida uhleri* female (Usinger, Wygodzinsky and Ryckman 1966).

Although they were synonymized by Lent and Wygodzinsky (1979), in a more recent study Ramsey et al. (2015) consider that *T. rubida* has five proposed subspecies, according to their morphological characteristics. These five subspecies are distributed in northern and northwestern Mexico, with *T. r. rubida* and *T. r. uhleri* occurring in the United States (Lent and Wygodzinsky 1979). Biological parameters of *T. r. sonoriana* and *T. r. uhleri* demonstrated that they can mate and generate offspring with potentially superior biological characteristics (Martínez-Ibarra et al. 2020). Molecular analyses indicate that at least one of the subspecies, *T. rubida cochimiensis*, has greater than 9% (d > 9%) sequence divergence for *Cytb* and COI from *T. r. uhleri* / *T. r. sonoriana* (Pfeiler et al. 2006; Espinoza et al. 2013). New literature data suggest that the synonym of *T. r. cochimiensis* should be removed, and it may now be considered a full subspecies (Monteiro et al. 2013). Further analysis is needed to conclude the specific status of the other subspecies.

It should also be emphasized that Patton and Cragg (1913), reported *Conorhinus rubrofasciatus* var. *mexicana,* Neiva as “Proboscis, head, and pronotum chestnut brown; scutellum, which ends in a slender point, of the same color. Corium and membrane dark brown... Connexivum with dark dots separated by ochraceous lines. Ventral surface of body and legs dark brown”, however, these characters alone do not allow it to be distinguished from other morphotypes. This subspecies is synonymized (Lent and Wygodzinsky, 1979).

Triatoma sanguisuga subspecies

Triatoma sanguisuga (Leconte, 1855) is quite variable in relation to size and chromatic variability. In most areas where they occur, specimens are approximately 20 mm long, but in southern Texas and Florida the specimens are smaller (16 mm). Five morphological subspecies (*T. s. occidentalis, T. s. texana, T. s. lateralis, T. s. ambigua, T. s. indictiva*) were described historically based on the size of the dorsal habitus, eyes, and distribution of the connexival markings. However, *T. s. occidentalis* and *T. s. indictiva* were later synonymized and raised to specific status*, Triatoma indictiva* Neiva 1912, respectively. *Triatoma sanguisuga lateralis*, was described and later synonymized with *T. sanguisuga* (Usinger 1944; Lent and Wygodzinsky 1979). Lent and Wygodzinsky (1979) also rejected the two remaining subspecies because “the distinguishing characters used are minor and populations are not separated by a distinctive gap geographically or in characters”. *Triatoma sanguisuga texana* was first described by Usinger (1944) from a specimen collected near Uvalde, Uvalde County, Texas. This subspecies is found naturally infected with *T. cruzi* and collected in dens of the woodrat *Neotoma micropus* Baird, 1855. Davis et al. (1943) report *T. sanguisuga ambigua* Usinger, 1944 as being naturally infected with *T. cruzi* in Texas (Pippin, Law and Gaylor 1968). It is possible that an intergrading zone in Gainesville, Florida, produces intermediate forms between typical *T. sanguisuga* and *T. sanguisuga ambigua* (Mead, 1965). Therefore, robust sampling across the state is necessary for better understanding of the forms (Lent and Wygodzinsky 1979).

Based on *cyt*b divergence, the genetic distance appears to support the existence of a subspecies of *T. sanguisuga* in Louisiana. Neither of the two proposed subspecies has been previously reported in Louisiana: *T. sanguisuga texana*, and *T. sanguisuga ambigua,* and corroborating evidence based on morphology and interfertility would further support the existence of subspecies (De la Rua, Stevens, and Dorn 2011; Usinger 1944).

Triatoma vitticeps subspecies

Triatoma vitticeps (Stål, 1859) is an endemic species in Brazil, found in the States of Bahia, Rio de Janeiro, Espírito Santo, and Minas Gerais (Galvão et al. 2003). *Triatoma chagasi* Brumpt and Gomes, 1914 was described using specimens from Serra do Cabral, Minas Gerais (Marassá and Barata 2000), but was later synonymized with *T. vitticeps* (Lent and Wygodzinsky, 1979). Interestingly, Eduardo Del Ponte described two very similar species to *T. vitticeps*, which are *Triatoma holmbergi and Triatoma neivai* (Del Ponte, 1923). Later, the same author proposed, analyzing the differences of the two species with *T. vitticeps* (*T. chagasi*), that these taxa were the subspecies *Triatoma chagasi holmbergi* and *Triatoma chagasi neivai* ("Plate I, drawings B and C") (Del Ponte 1930). These subspecies are considered synonymized by Lent and Wygodzinsky (1979). Of these subspecies, we do not know the type-localities, but Alevi et al. (2018) show, through different mitochondrial genes, high intraspecific variation from different populations, ranging from 2.3% to 7.2%, suggesting that the subspecies might be valid.

The subspecies of *Panstrongylus*

Panstrongylus Berg is easily defined by the insertion of the anteniferous tubercles close to the anterior margin of the eyes (Lent and Wygodzinsky, 1979). The genus is considered one of the most important epidemiologically because of its considerable synanthropy and ability to domicile (Peixoto et al. 2020).

Panstrongylus megistus subspecies

The typical morphotype of *P. megistus* overall presents the color black, with reddish markings on the neck, pronotum, scutellum, corium, and connexivum (Lent and Wygodzinsky 1979). In 1959, Lucena describes the subspecies *Panstrongylus megistus leucofasciatus.* This subspecies also has overall black coloration, but with white markings in the pronotum, at the apex of the scutellum, at the base and at the apex of the corium, and transversal markings in the connexivum (Lucena and Lima-Borba 1977). Lucena (1959), and Ryckman (1971b) treat these specimens as natural mutants. This subspecies has been synonymized (Galvão et al. 2003; Gonçalves et al. 2009). *Triatoma megista* var. *wernickei* Del Ponte, 1930 is synonymous with *P. megistus.*

The subspecies of *Paratriatoma*

Barber, in 1938 created a new monotypic genus and species of the subfamily Triatominae, known as *Paratriatoma hirsuta* (Table 1), featuring an elongated oval head, slightly shorter than pronotum, and entire body and legs sparsely covered with long, coarse hairs. In his description it was reported that a specimen from Mojave "attacked" a man to obtain food (Barber 1938). Recently, the genus stopped being monotypic with the inclusion of *Paratriatoma lecticularia* (Paiva et al., 2021).

Paratriatoma hirsuta subspecies

Ryckman 1967, described four subspecies: *Paratriatoma hirsuta hirsuta* Barber 1938, *Paratriatoma hirsuta kamiensis* Ryckman 1967, *Paratriatoma hirsuta papagoensis* Ryckman 1967, *Paratriatoma hirsuta pimae* Ryckman 1967, and *Paratriatoma hirsuta yumanensis* Ryckman 1967, based on coloration of the wings and head. The gradient of coloration of the wings and head varies from light brown to black (Ryckman 1967). Hybrids between light and dark parental populations resulted in intermediate F1 progeny, with segregation in the F2 generation. When examining this variation between localities, there is evidence to indicate that natural selection is shaping populations to meet different ecological conditions (Ryckman 1971a). Therefore, a molecular study of these populations is needed to infer their genetic distances, which may assist in the systematics of these subspecies.

Paratriatoma lecticularia subspecies

Paratriatoma lecticularia was originally described as *Conorhinus lecticularius* Stål, 1859, and later treated as *Triatoma lecticularia* by Usinger, 1944. Recently, combining molecular, morphological, and cytogenetic data, a new combination was made: *Paratriatoma lecticularia* (Paiva et al., 2021). The specimens of '*T. lecticularia'* are variable in size, shape, color, and the extension of markings. The small specimens from Texas were described as a *Triatoma occulta* Neiva, 1911. Usinger (1944), proposed a new combination, *T. lecticularia occulta*. Specimens with intermediate parameters were visualized, hindering the subspecies status. Usinger also described *T. lecticularia floridana*, based on a single specimen with unusually pronotal markings and eyes wider than half the synthlipis. The '*floridana'* subspecies was synonymized at the time (Lent and Wygodzinsky 1979), but additional specimens are needed to decide on the taxonomic status of these Florida specimens.

Conclusions

The subfamily Triatominae originated in a tropical environment, where most of the species occur in the neotropical region (Galvão et al., 2003). Most diversity is restricted to Latin America, where approximately 135 species have been described (Gorla and Noireau 2017). Some evidence supports the idea that triatomines evolved relatively recently from predatory reduviidae, for example, *Triatoma recurva* manage to reach adulthood feeding only on cockroach hemolymph (Schmidt, Dorn, and Klotz 2019). In several countries in the Americas, various vector species are found naturally infected with *T. cruzi* (Bern et al., 2011; De la Rua et al., 2011; Espinoza et al., 2013; Kofoid and Whitaker 1936; Pippin, Law and Gaylor 1968) and many species are found in urbanized or peridomicile areas (Gorla and Noireau 2017; Cantillo-Barraza et al., 2020).

The diversification events found in *Triatoma* are closely linked to climatic and geological changes caused by the uplift of the Andes in South America and by variations in sea level in North America (Justi, Galvão, Schrago 2016). Therefore, it is assumed that the ancestors of the *T. protracta* complex reached the north through Central America. Upon reaching southern Mexico, a part of the ancestral population developed into the current *T. barberi* (and the closely allied *T. incrassata*), while the forms that moved along the coast became smaller, developing into *T. sinaloensis* and later migrating to Baja California, as indicated, to give rise to the closely related *T. peninsularis* (Usinger, Wygodzinsky, Ryckman 1966). There is a chance that the formation of the Baja California peninsula influenced the separation of the three subspecies of *T. rubida* and of *T. sinaloensis* from *T. peninsularis* (Justi, Galvão, Schrago 2016). All this diversity found in triatomines leads to the definition of species and to some questions raised by the *Triatoma protracta* complex, where *T.*

sinaloensis and *T. peninsularis,* very similar populations, will not interbreed, while the two most distinct, *T. barberi* and *T. protracta,* produce fertile descendants.

In the "*Triatoma infestans* complex", in these species, in addition to clear morphological differences in all instars, we also noticed an ecological isolation, different ecological niches (*Triatoma delpontei* and *Triatoma platensis* in bird nests and *T. infestans* living almost exclusively in association with humans) and overlapping species distribution. However, calling these full species is difficult because of the high degree of interfertility in the laboratory and the occasional hybrids found in the field (Usinger, Wygodzinsky, Ryckman 1966). In Costa et al. (2013), the status of subspecies of *T. b. brasiliensis* and *T. b. macromelasoma,* was confirmed and redescribed, but Guerra et al. (2019) showed that the genotypic characteristics analyzed may suggest that *T. b. macromelasoma*, *T. brasiliensis,* and *Triatoma juazeirensis* are the same species, possibly resulting from the introgression processes that these species underwent during the homoploid hybridization process.

Some morphological characters utilized for identification of species are affected by morphological plasticity in association with environmental changes. The minor morphological changes between populations of the same species can lead to erroneous identification, such as the presence of morphotypes in some species (Schofield and Galvão 2009). The few synapomorphic characters are important limitations in characterizing the morphological variability between different species of the tribe. Identification of some characters of species with complex interpretation results in inconsistency and errors in morphological identification (Hernández et al., 2020). Infraspecific taxa are subdivisions of species, where their status depends specifically on "their" species. This makes the status of infraspecific taxa crucially dependent on how species are considered (species concepts) (Reydon and Kunz 2021). The different subspecies have documented biological and behavioral parameters. These parameters, such as defecation time after feeding (Martinez-Ibarra et al., 2015, 2017, 2020; Nogueda-Torres et al., 2021), explain the practical importance of the subspecies, in addition to justifying different control strategies for each population. Already in cases of phenotypic plasticity, the changes are restricted to morphological changes (color, shape, or size), which does not justify the elevation of specific status, but these variations can indicate an initial process of divergence (Dujardin et al., 1999; Nattero et al., 2013; Rivas et al., 2021). In Triatominae there is no consensus on the parameters needed to differentiate phenotypic plasticity and a subspecies (Mas-Coma et al., 2009). Therefore, if possible, integrative taxonomy is recommended to corroborate these findings.

In this article considerations are made of taxa that have been neglected several times, and therefore demonstrate the need for more assertive criteria to infer the 'status' of the taxa. According to the information provided, it can be concluded that all taxa need a better inference to validate or not the subspecies, which would lead to 157 (154 extant and 3 fossils) species and 2 subspecies of Triatominae. Consequently, more studies about taxonomy, evolution, phylogeny, biogeography, ecology, physiology, and behavior of species are needed to reinforce, or to invalidate the infraspecific status in the subfamily, being that one of the primary steps in either control program is the proper identification of vectors and understanding of their genetic and population structures (Hernández et al., 2020).

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Conflict of Interest
The authors declare no conflict of interest.

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Capítulo II

Artigo científico publicado na revista Insects

Formal assignation of the kissing bug *Triatoma lecticularia* (Hemiptera: Reduviidae: Triatominae) to the genus *Paratriatoma*

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Simple Summary: The genus *Paratriatoma* is closely related to the paraphyletic genus *Triatoma*—the most diverse and relevant in the epidemiology of Chagas disease. Molecular phylogenetic treatments consistently place the species *Triatoma lecticularia* (Stål, 1859) as sister to the genus *Paratriatoma*. To determine its correct taxonomic assignment, we examined the morphology of several specimens, including types, and cytogenetic data for both taxa. The observations clearly support the transfer of *Triatoma lecticularia* (Stål, 1859) to the genus *Paratriatoma*, with the resulting new combination: *Paratriatoma lecticularia* (Stål, 1859) comb. nov. (Hemiptera: Heteroptera: Reduviidae: Triatominae).

Abstract: The subfamily Triatominae (Hemiptera: Reduviidae) comprises hematophagous insects that are vectors of Chagas disease; including species assigned to the genera *Triatoma* and *Paratriatoma*. Initial examination of *Triatoma lecticularia* revealed the hirsuteness covering the entire body—a characteristic and striking feature of members of the genus *Paratriatoma*—and a systematic study revealed several other morphological characters that are in diagnostic alignment with *Paratriatoma*. Based on the examination of several specimens (including the lectotype), and with additional support of molecular and cytogenetic data, we propose the formal transferal of *Triatoma lecticularia* (Stål, 1859) into the genus *Paratriatoma* with the resulting new combination: *Paratriatoma lecticularia* (Stål, 1859) comb. nov. (Hemiptera: Reduviidae: Triatominae).

Keywords: Taxonomy; vectors; Heteroptera; Triatomini; North America

1. Introduction

Hematophagous insects of the subfamily Triatominae can transmit Chagas disease (American Trypanosomiasis). Currently, the subfamily comprises 5 tribes, 18 genera and, 156 species [1,2]. The Tribe Triatomini Jeannel, 1919 includes the genera *Dipetalogaster* Usinger, 1939; *Eratyrus* Stål, 1859; *Hermanlentia* Jurberg & Galvão, 1997; *Mepraia* Mazza, Gajardo & Jörg, 1940; *Nesotriatoma* Usinger, 1944; *Panstrongylus* Berg, 1879; *Paratriatoma* Barber, 1938; and *Triatoma* Laporte, 1832.

Of these, the paraphyletic genus *Triatoma* is the most diverse with 82 described species [1], and the most relevant in the epidemiology of Chagas disease [3]. Historically there has been disagreements concerning the subgeneric (formal and informal) rankings within *Triatoma*. Since the 1960s, species have been grouped into complexes and subcomplexes based on morphological, geographical, ecological, and, more recently by molecular data [4-9]. One of such groupings is the *Triatoma lecticularia* complex, that has been proposed to include the Neartic species – *T. lecticularia* (Stål, 1859), *T. sanguisuga* (LeConte, 1856), *T. gerstaeckeri* (Stål, 1859), *T. indictiva* Neiva, 1912, *T. recurva* (Stål, 1868), and *T. rubida* (Uhler, 1894) [4,8]. However, some studies show that the *Triatoma lecticularia* complex is not well supported [6,10].

Triatoma lecticularia was originally described as *Conorhinus lecticularius,* based on specimens from Carolina (Museum Schaumburg), India Orientalis (deposited in Musei Berolinensis) [11]. *Triatoma lecticularia occulta* (Neiva, 1911) and *T. lecticularia floridana* (Usinger, 1944) were subspecific morphotypes proposed by the authors for specimens that showed a small variation in some morphological characters, such as the size of the head and eyes and the color pattern of the body [12,13]. Typical T. *lecticularia* specimens have an elongate-oval, shiny body, with the entire surface clothed by distinct decumbent hairs. Overall color piceous, with orange or orange-yellow markings on pronotum, pleura, corium, connexivum, and ventral surface of the abdomen [11]. It presents karyotype 2n=22 (20A+XY), the same as *Paratriatoma* [14].

The genus *Paratriatoma* is closely related to *Triatoma* and can be distinguished by the ovoid shape of the head, absence of arcuate interocellar sulcus, absence of femoral spines or tubercles and, mainly, by the remarkable hirsuteness of the body and the appendages [15]. The monotypic species, *Paratriatoma hirsuta* Barber 1938 is closely associated with pack/ wood rats of the genus *Neotoma* in the Sonora Desert [16]. Five subspecies (*P. hirsuta hirsuta, P. h. kamiensis* Ryckman 1967, *P. h. papagoensis* Ryckman 1967, *P. h. pimae* Ryckman 1967, and *P. h. yumanensis* Ryckman 1967) have been described based on noted differences in coloration of the wings and head [17]. Subsequent analysis revealed that each subspecies represents a chromatic form and is restricted to a limited geographical area [4].

In the current study, we show that the morphology of *Triatoma lecticularia* reconciled with molecular and cytogenetic data are entirely concordant with the genus *Paratriatoma* Barber, 1938 [3,18,19], and propose the new combination: *Paratriatoma lecticularia* (Stål, 1859), comb. nov. (Hemiptera: Heteroptera: Reduviidae: Triatominae).

2. Material and methods

2.1. Material examined

The male lectotype of *T. lecticularia* deposited in the Humboldt Museum für Naturkunde, Berlin, Germany (Figure 1, Table 1), and five males and five females of *T. lecticularia* deposited in Triatomine collection “José Maria Soares Barata”, Universidade Estadual Paulista (UNESP), Araraquara, São Paulo, Brazil (Figure 2-4, Table 1), were directly examined. The type specimen of *Paratriatoma hirsuta* deposited in U.S. National Entomological Collection, National Museum of Natural History, Smithsonian Institution, Washington DC, was also studied. Four specimens of *P. hirsuta* deposited in the “Coleção de Triatomíneos do Instituto Oswaldo Cruz, Fiocruz, Brazil” (Figure 5, Table 1), two specimens of “Coleção Entomológica de Referência, Faculdade de Saúde Pública, Universidade de São Paulo, Brazil” (Figure 6, Table 1), and ten specimens deposited in Ayala-Landa personal collection (Figure 7, Table 1), were used to compare with *T. lecticularia*.

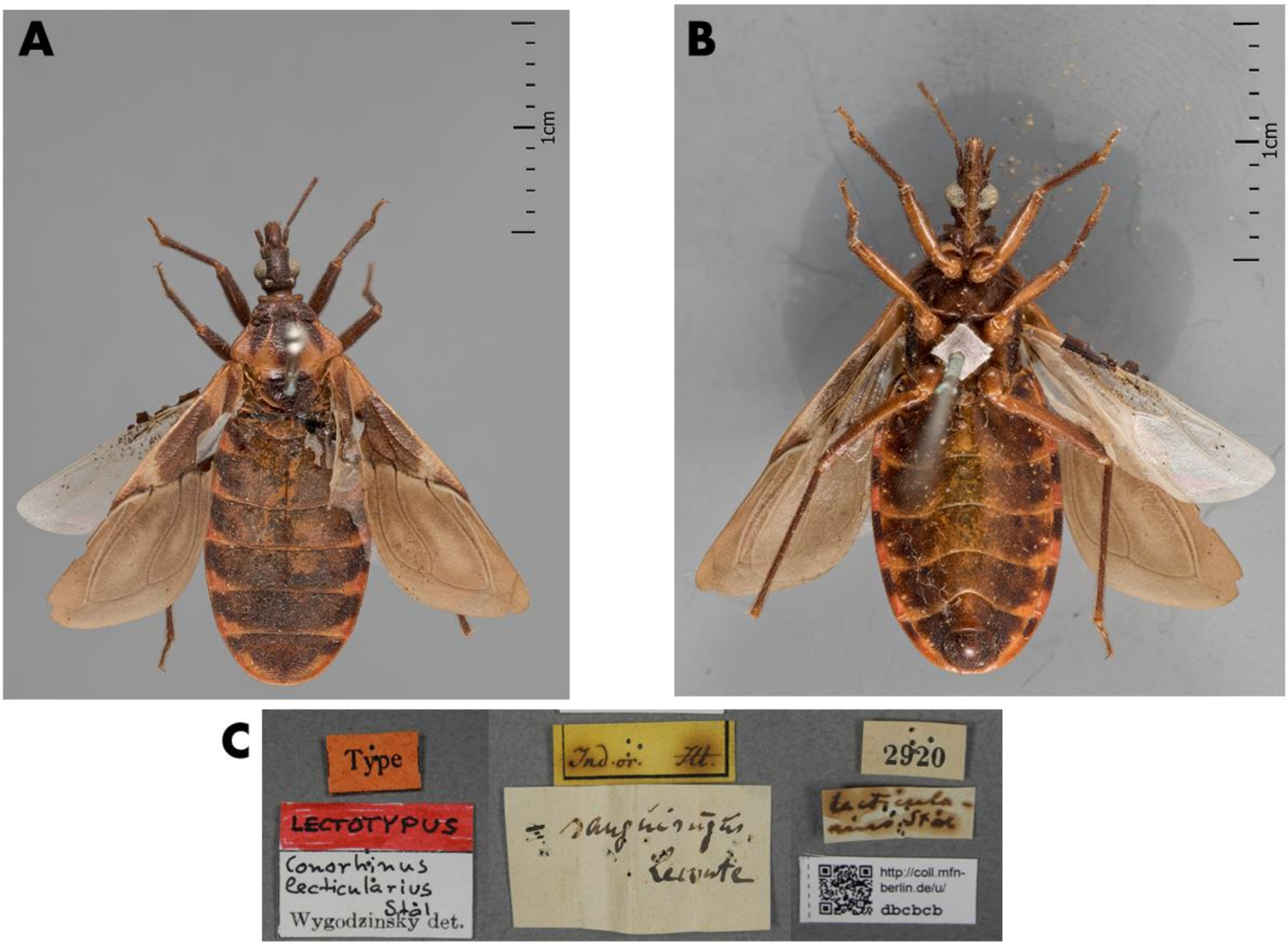
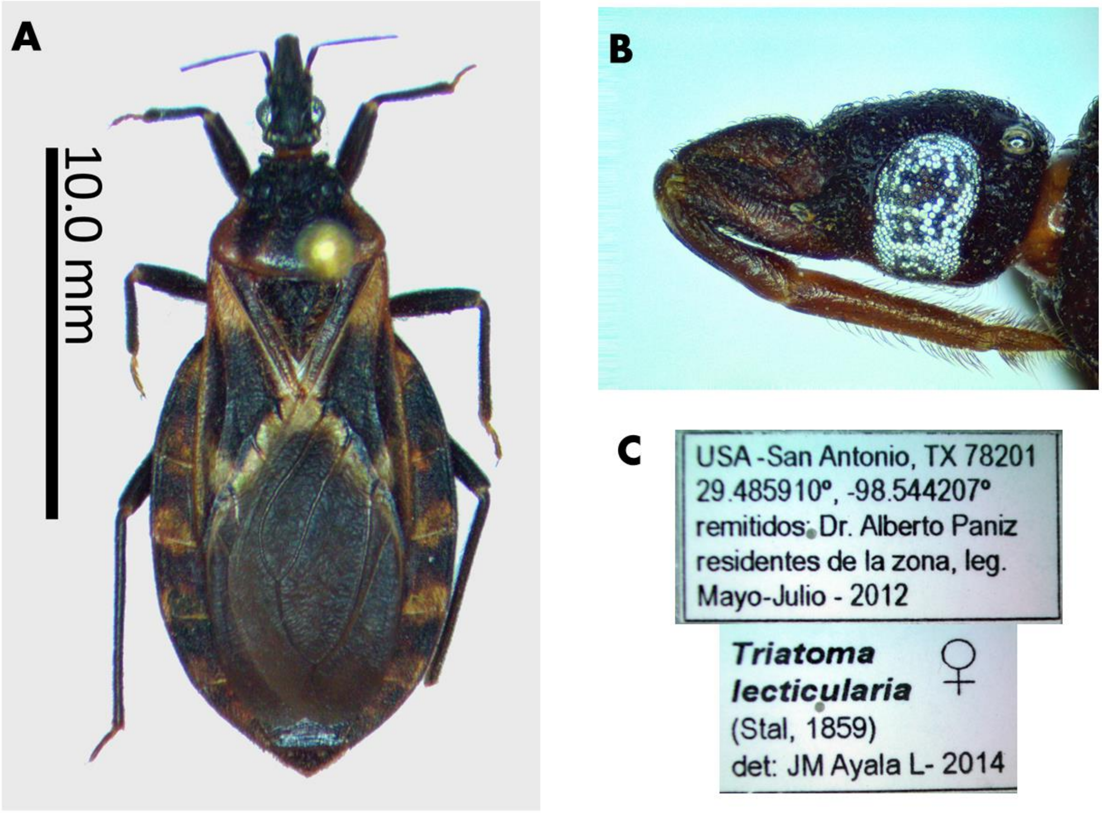


Figure 1. The lectotype of *Paratriatoma lecticularia* comb. nov. deposited in Natural History Museum of Berlin, Germany. A: Dorsal view, B: Ventral view, C: Label of specimen. At the ZMHB the photos were provided by Dr. Jürgen Deckert.

Table 1. Information about the specimens examined, including the collection that is deposited.

Scheme 2920.	Collection	Additional Information
Paratriatoma lecticularia comb. nov.	Humboldt Museum für Naturkunde, Berlin, Germany.	Male, Lectotypus, 2920
Paratriatoma lecticularia comb. nov.	José Manuel Ayala-Landa personal collection	San Antonio, TX78201, USA, Female
Paratriatoma lecticularia comb. nov.	Triatomine collection “José Maria Soares Barata”, Universidade Estadual Paulista (UNESP), Brazil.	Male and female, CTA137
Paratriatoma hirsuta	U.S. National Entomological Collection, National Museum of Natural History, Smithsonian Institution, Washington DC	Type No. 52747 USNM, UCR_ENT 00007957, Mojave Cal.8.23.35
Paratriatoma hirsuta	Coleção de Triatomíneos do Instituto Oswaldo Cruz, Fiocruz, Brazil.	Male, H. Lent det., CTIOC 11976, N° 2729. Female Coleção Rodolfo Carcavallo, n° 1724, CTIOC N° 6229
Paratriatoma hirsuta	Coleção Entomológica de Referência, Faculdade de Saúde Pública, Universidade de São Paulo, Brazil	Female Suporte 141, tubo 2 n° E5027 Desert Center, Calif. Riverside Couty 28/11/50. Col. R.E. Ryckman. Female Suporte 141, tubo 1 n° E5026 Desert Center, Calif. Riverside Couty 28/11/50. Col. R.E. Ryckman. Reared 1952
Paratriatoma hirsuta	José Manuel Ayala-Landa personal collection	Joshua Tree National Park, USA- California. Female.



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remitidos: Dr. Alberto Paniz
residentes de la zona, leg.
Mayo-Julio - 2012

Triatoma lecticularia ♀
(Stal, 1859)
det: JM Ayala L- 2014

Figure 2. Specimen of *Paratriatoma lecticularia* from Texas, USA. A: Dorsal habitus of specimen. B: Lateral view of head. C: Label of specimen.

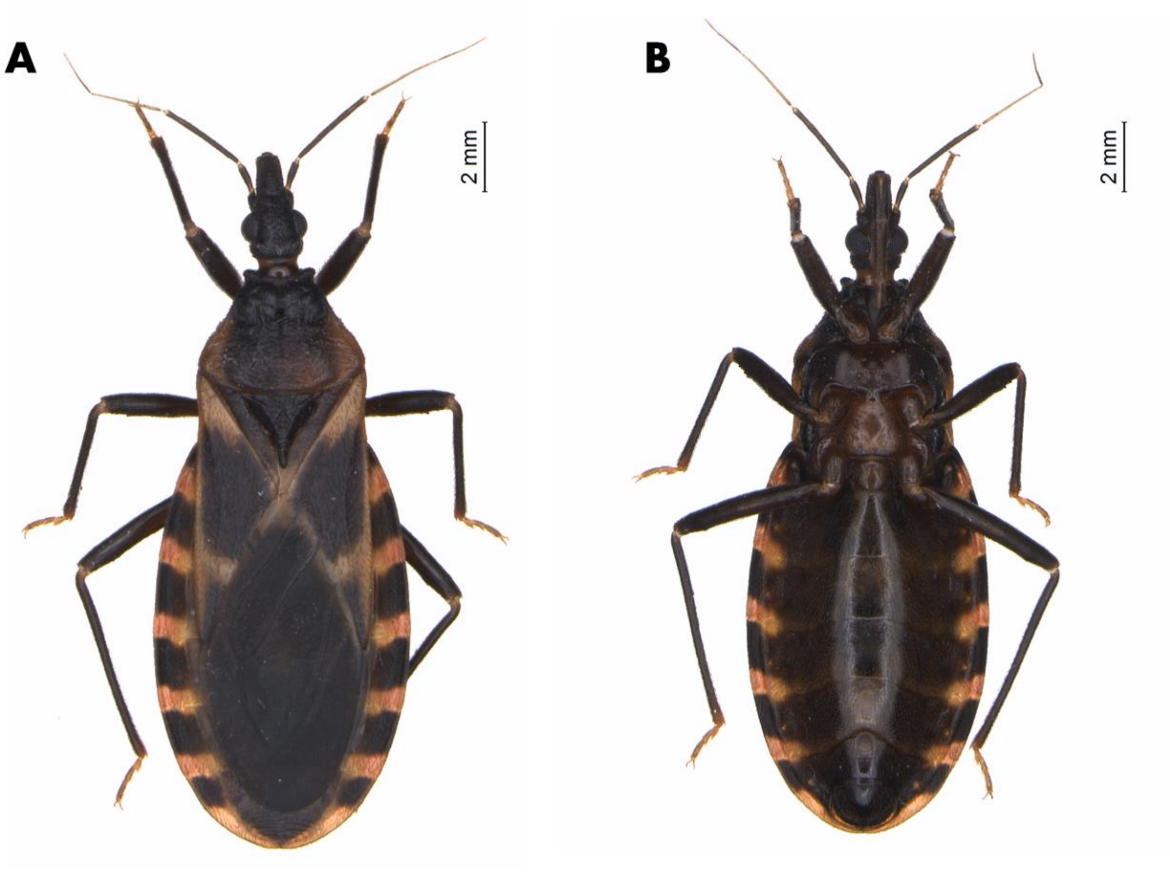

Figure 3. Male specimen of *Paratriatoma lecticularia* from CTJMSB CTA137. A: Dorsal habitus. B: Ventral view.

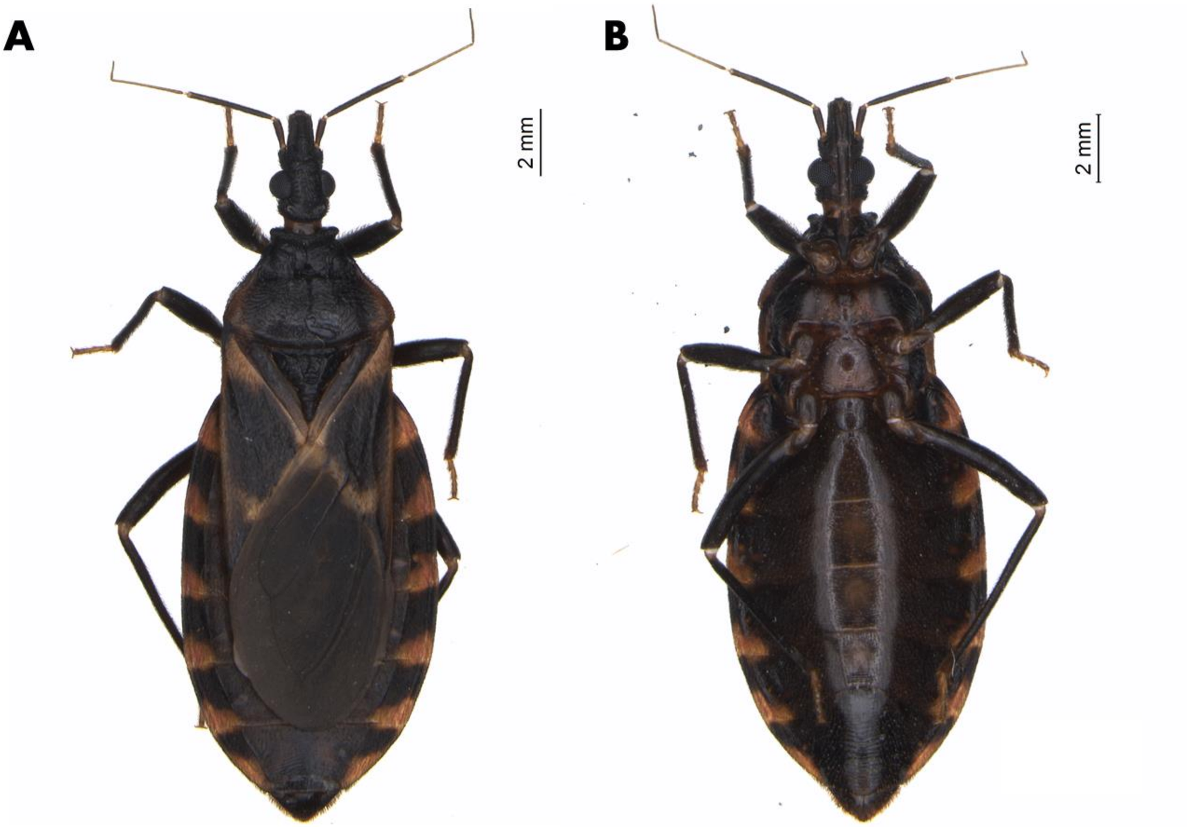

Figure 4. Female specimen of *Paratriatoma lecticularia* from CTJMSB CTA137. A: Dorsal habitus. B: Ventral view.

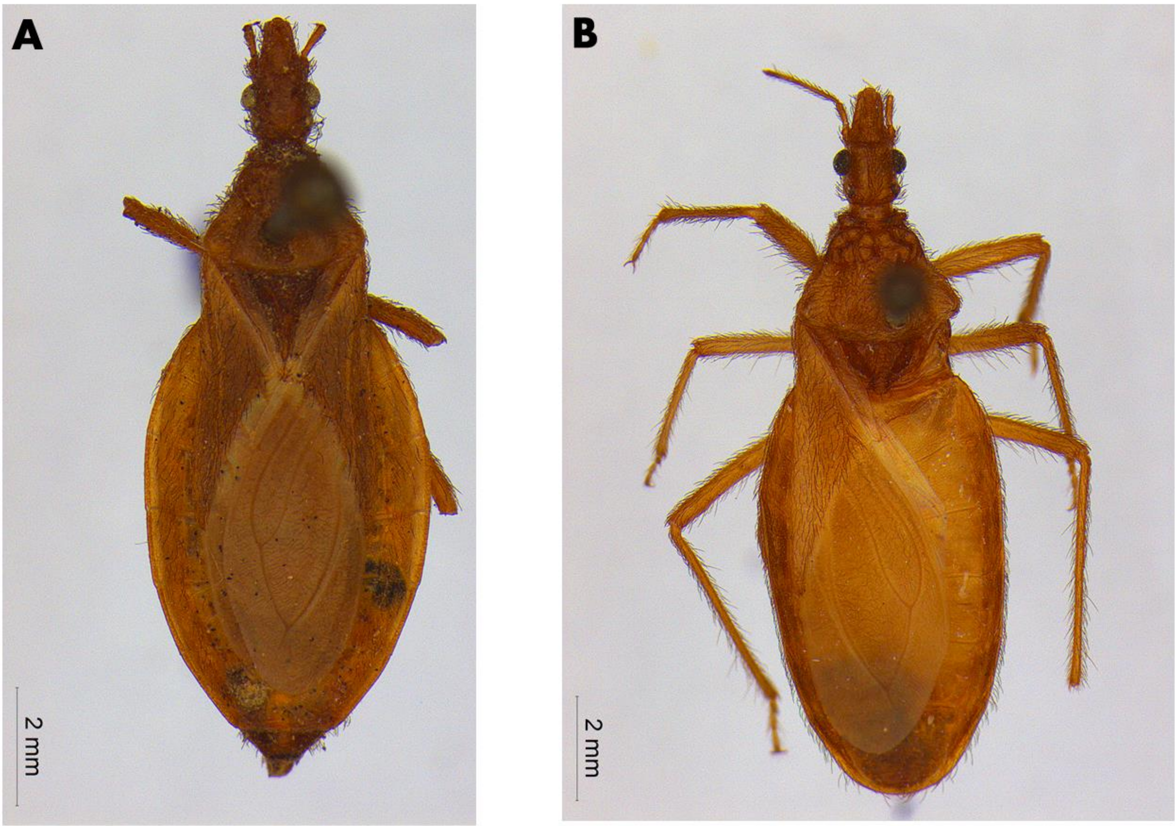

Figure 5. Specimen of *Paratriatoma hirsuta* from CTIOC. A: Dorsal habitus of female specimen. B: Dorsal habitus of male specimen.

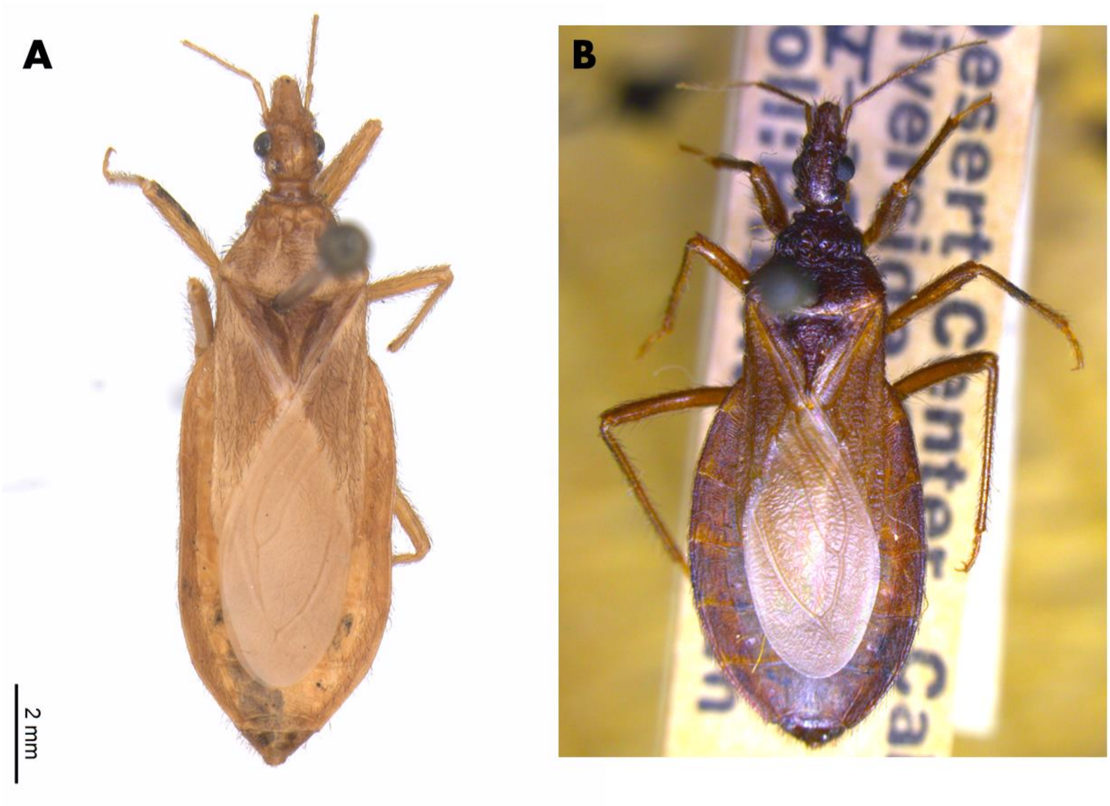

Figure 6. Specimen of *Paratriatoma hirsuta* from CER-USP. A: Dorsal habitus of female specimen. B: Dorsal habitus of female specimen.

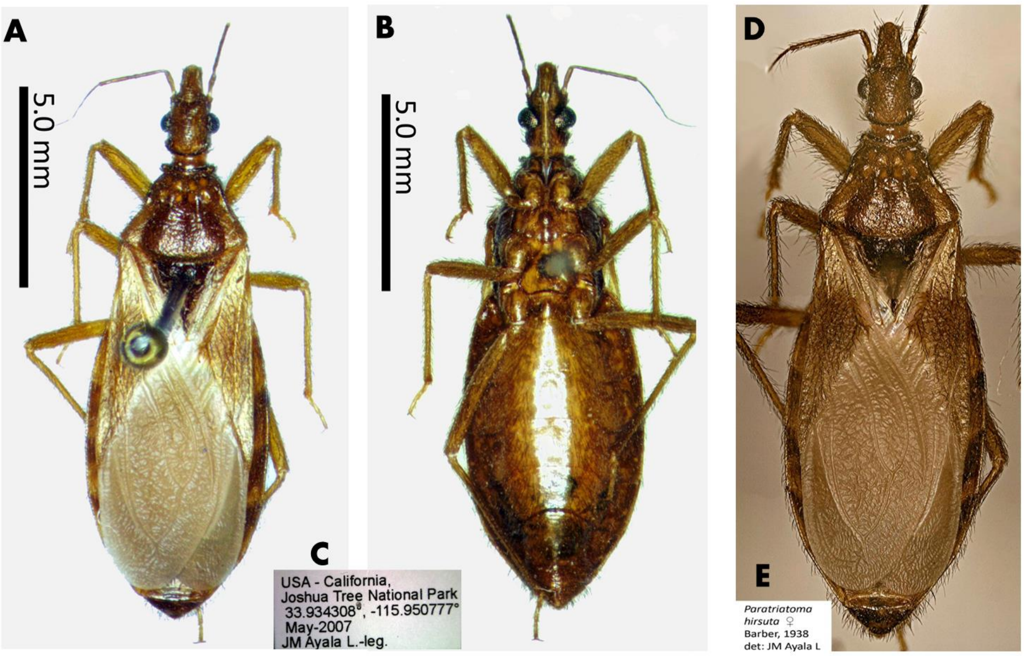

Figure 7. Specimens of *Paratriatoma hirsuta* from California, USA. A: Dorsal habitus of specimen. B: Ventral view. C: Label of specimen. D: dorsal view. E: Label of specimen.

2.2. Morphological study

Photographs were made using a professional camera and Leica M205C stereomicroscope and were processed with the software Leica LAS (version 4.9). Type specimens were examined through photographs, and label information is provided (Table 1). Based on Barber's original (1938) description of the genus *Paratriatoma,* the major features distinguishing *Paratriatoma* from species in *Triatoma* include the ovoidal shape of the head, the absence of an arcuate interocellar sulcus, the absence of femoral spines or tubercles, and the intensely hirsute body and appendages. Another apomorphy is noted in the plates of the dorsal and ventral connexivum of the urosternite overlaping the mesal portion of the ventral plate of the connexivum, with a distinct membrane interpolated between the edge of the connexival plate and the lateral edge of the urosternum (Figure 8).

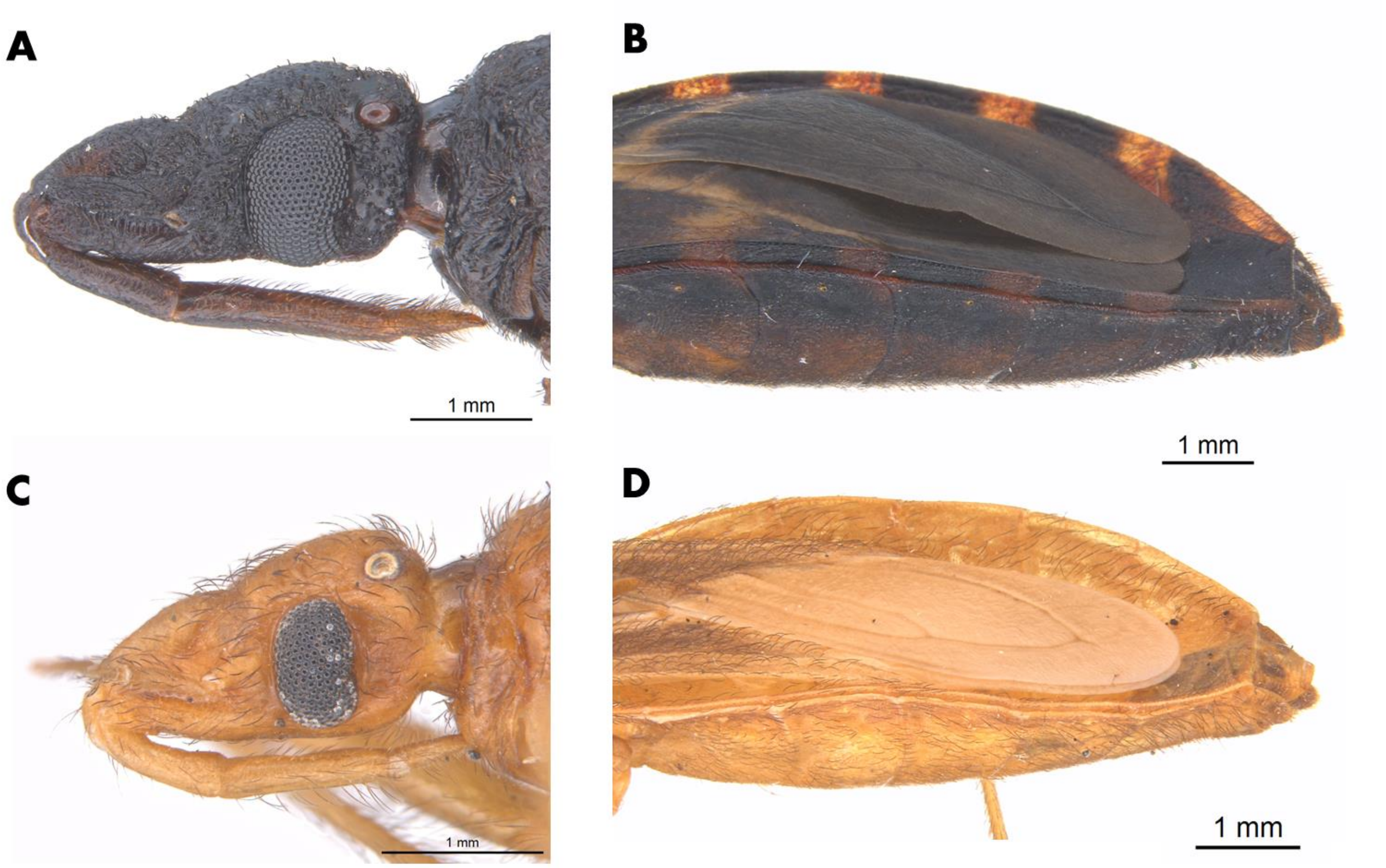

Figure 8. Head and conexivum of *P. lecticularia* and *P. hirsuta.* A: Head in lateral view of *P. lecticularia.* B: lateral view of connexivum of *P. lecticularia,* evidencing your membrane, apomorphic character of the genus. C: Head in lateral view of *P. hirsuta.* D: lateral view of connexivum of *P. hirsuta.*

3. Results

3.1. Taxonomic Hierarchy

Class Insecta Linnaeus, 1758, Order Hemiptera Linnaeus, 1758, Family Reduviidae Latreille, 1807, Subfamily Triatominae Jeannel, 1919, Tribe Triatomini Jeannel, 1919, *Genus Paratriatoma lecticularia* (Stål, 1859), comb. nov. (Figure 1).

Synonyms

Conorhinus lecticularius Stål, 1859 [original description]; *Conorhinus lenticularius* Stål, 1868; *Conorhinus variegatus* Stål, 1872; *Conorhinus heidemanni* Patton and Cragg, 1913; *Conorhinus occulata* Patton and Cragg, 1913; *Conorhinus lectularius* Neiva, 1914; *Triatoma heidemanni* Neiva, 1911, 1914. Blatchley, 1926. Pinto, 1931. Usinger, 1943; *Triatoma occulta* Neiva, 1911, 1914; *Triatoma sanguisuga* Neiva, 1914; *Triatoma lecticularius* Usinger, 1944; *Triatoma lecticularius occulta* Usinger, 1944; *Triatoma lecticularius floridana* Usinger, 1944.

3.2. Morphological characterization of *Paratriatoma*

Ovoidal shape of the head, scarcely shorter than pronotum, eyes rather small not strongly projected. Anteocular region longer than postocular, transversely impressed behind the strongly elevated clypeus. Ocelli slightly elevated, widely separated. Antennae inserted closer to eyes than to apex of the head, as in *Triatoma.* Pronotum somewhat wider than long. Scutellum devoid of a discal depressed area, prolonged into a cylindrical, apical process. Legs rather short, scarcely incrassate, mutic. The entire body and the appendages sparsely covered with long, coarse hairs.

3.3. Morphological characterization of *P. lecticularia* comb. nov.

Coloration. Overall color piceous, with orange or orange-yellow markings on pronotum, pleura, corium, connexivum, and ventral surface of abdomen (Figures 1, 2, 3 and 4). Head uniformly dark, neck uniform light color (Figure 8). Pronotum dark with 1+1 orange bands on lateral margins of the posterior lobe, posterior margin of pronotum is lighter colored in some specimens; in some specimens, dark areas of posterior lobe of pronotum reduced to one wide median and 1+1 sublateral stripes, with orange color extending as 1+1 wide lateral and 1+1 submedian spots occupying carinae and triangularly widened posteriorly, confluent behind with lateral markings (Figures 3, 4). Pleura dark. Scutellum dark. Corium with a large central spot of general color, with basal and subapical spots orange-yellow, and the outer border is narrowly bordered with light color. Legs dark, but with coxae in many cases lightened. Venter with orange-yellow markings at the level of light-colored connexival markings, covering intersegmental sutures and extending along lateral borders of urosternites; in some cases, entire venter tinged with orange, especially on basal half (Figures 1, 3 and 4). Connexival segments dark, posteriorly with orange-yellow spot narrowly extending across intersegmental suture onto anterior portion of following segment; extension of light markings variable (Figure 1, 8B).

Morphological features. The body surface clothed with distinct decumbent hairs. *Head* (Figures 2 and 8) granulose, ovoidal shape, conspicuously convex; slightly less than twice if width across eyes and slightly shorter than pronotum. Anteocular region about three times as long as postocular, postocular with sides convex, converging posteriorly. Eyes in lateral view attaining or slightly surpassing the level of under but not attaining the level of upper surface of head. Antenniferous tubercles situated on posterior third of anteocular region, comparatively close to eyes. First antennal segment falling short of apex of clypeus. Rostrum conspicuously hairy, especially on second and third segments; first segment attaining level of apex of antenniferous tubercle, second attaining level of neck. The third segment of the rostrum smaller than the first, which is smaller than the second. *Pronotum* (Figure 1), narrow anteriorly, becoming wider posteriorly and extending onto humeri; posterior margin of pronotum possess submedian carinae and collar with anterolateral processes; Anterior lobe without discal or lateral tubercles. Posterior lobe rugose, with conspicuous dark setae on entire surface; submedian carinae evanescent posteriorly. Humeral angles rounded, slightly elevated. Anterolateral angles short, rounded apically. *Scutellum* (Figure 1) with central portion only very slightly depressed, limited by irregular carinae; apical process shorter than main body of scutellum, setose, tapering distally, its apex deflected. *Hemelytra* reaching nearly to apex of abdomen. *Corium* completely with conspicuous adpressed black setae. *Legs* hairy, rather short. Fore- and mid-femora with 2+2 very short denticles subapically. Tibiae of first and second pair of males with small spongy fossulae, absent in female. *Spiracles* remote from connexival suture (Figure 9). *Venter* conspicuously pilose (Figure 1). *Connexivum* with distinct adpressed setae. In unfed specimens, the plates of the dorsal and ventral connexivum of the urosternite overlaps the mesal portion of the ventral plate of the connexivum, with a distinct membrane interpolated between the edge of the connexival plate and the lateral edge of the urosternum (Figure 8). This membrane is not normally visible in museum specimens, in which the ventral plates of the connective appear exceptionally narrow, as they are partially covered by urosternites. Urosternites VIII, IX and X form the female external genitalia (Figure 9).

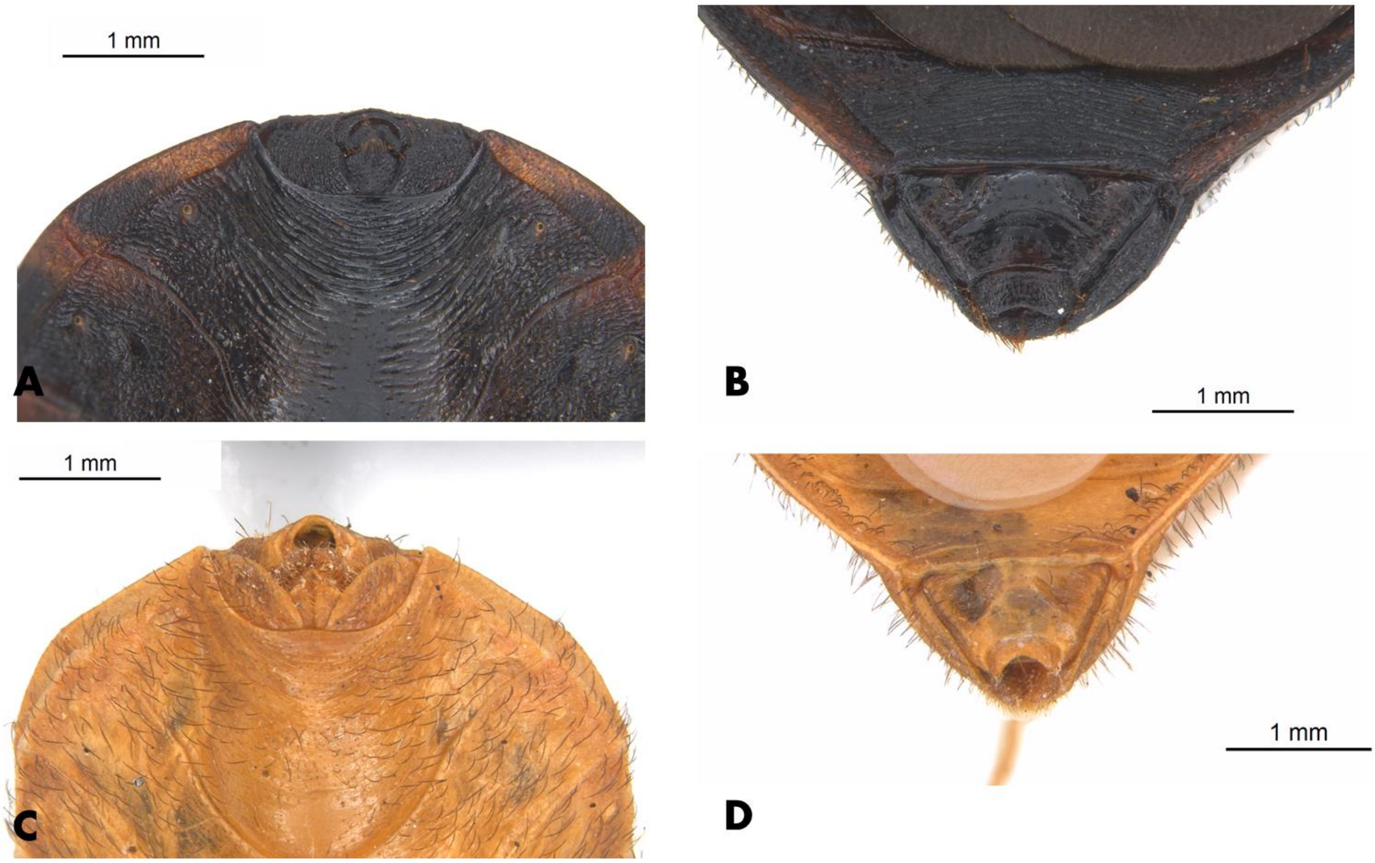

Figure 9. Morphological similarities of the female external genitalia of *P. lecticularia* and *P. hirsuta.* A: Ventral view of external genitalia of *P. lecticularia.* B: Triangular shape of the posterior view of external genitalia of *P. lecticularia.* C: Ventral view of external genitalia of *P. hirsuta.* D: Triangular shape of the posterior view of external genitalia of *P. hirsuta.*

A synonymized *T. l. floridana* form distinguished by its paler coloration and large eyes. A synonymized *T. l. occulta* are extreme forms, smaller in body and eye size.

Vestiture. Pilosity well developed on entire body including corium (Figures 1 and 2).

4. Discussion

4.1. Transfer of *Triatoma lecticularia* to *Paratriatoma*

Stål (1859) described this species as *Conorhinus lecticularius*, and the specimen label states the locality as “India Orientalis” (Figure 1). The insect bears an obviously erroneous locality label because does not occur in the East Indies [4]. The type specimen housed in the Berlin Museum. In 1872, Stål synonymized his *lecticularius* with *variegatus*, a synonym of *rubrofasciata*. Later, Neiva set *lecticularius* in the synonymy of *sanguisuga* [20]. Lent and Wygodzisnky synonymized the subspecies *T. l. occulta* and *T. l. floridana* with *T. lecticularia,* and later appointed a lectotype (Figure 1) [4].

The distribution of *Paratriatoma lecticularia* (Stål, 1859) comb. nov. includes the United States (Arizona, California, Florida, Georgia, Illinois, Kansas, Louisiana, Maryland, Missouri, New Mexico, South Carolina, Tennessee, and Texas) and Mexico (Nuevo Leon), in ecotopes with widely variable climatic conditions, from humid forests to valleys and deserts. The species is found associated with the terrestrial rodent *Neotoma micropus* Baird, and rock squirrel *Spermophilus variagatus* (Erxleben) [21], whereas *Paratriatoma hirsuta* (Figures 6 and 7) is thought to be obligate ectoparasites of the pack rats or wood rats *Neotoma lepida* Thomas, *Neotoma fuscipes macrotis* Thomas, and *Neotoma albigula* Hartley. In human dwellings, *Paratriatoma hirsuta* is found under cracks in the wall, beds, and wooden hollows, and has been found naturally infected by *Trypanosoma cruzi* (Chagas, 1909) [16,21].

Lent and Wygodzinsky determined that the *Triatoma lecticularia* complex included *T. lecticularia*, *T. sanguisuga*, and *T. indictiva* [4] and later Schofield and Galvão [8] added *T. gerstaeckeri, T. recurva, and T. rubida* to the complex. Monteiro et al. [6] proposed that the North American Clade (North of Tehuantepec) of *Triatoma protracta* (Uhler, 1894), *Triatoma barberi* Usinger, 1939, *T. lecticularia*, *Paratriatoma hirsuta* Barber, 1938 and *Dipetalogaster maxima* (Uhler, 1894), comprised a separate species group changing the classification of "complexes" of several species. Nevertheless, as hypothesized by Lent and Wygodzinsky [4], *Paratriatoma* is close to the *Triatoma protracta* complex, so the *T. protracta* complex can be considered one of the sister groups to *Paratriatoma,* despite having the membrane structure of the connexivum apomorphic (Figure 8).

Cytogenetically, the typical autosome number (A) in triatomines is 20. *Paratriatoma lecticularia* differs from other north American species in both chromosome complement and behavior of the sex chromosomes. *Paratriatoma lecticularia* presents the karyotype 2n=22 (20A+XY)—the same as *Paratriatoma hirsuta*. All the other species in the *T. lecticularia* complex exhibit karyotype 2n = 23 (20A+X1X2Y). Considering that *T. rubida* present 2n = 23 and *P. lecticularia* and *P. hirsuta* 2n = 22, it was hypothesized that the ancestor of these triatomines had 22 chromosomes, and during the divergence of *T. rubida* and others, probably an agmatoploidy of the X sex chromosome occurred [14,19].

Justi et al. [3] performed a molecular phylogeny of Triatomini, recovering a clade that includes the genera *Hermanlentia*, *Paratriatoma*, and *Dipetalogaster* + *Linshcosteus* + Northern Hemisphere *Triatoma* (BS = 88, PP = 1); *P. hirsuta* + *P. lecticularia* were considered sister species in phylogeny. Using Bayesian analysis (with six fossils calibrations), Justi et al. [18] proposed *P. hirsuta* and *P. lecticularia* as sister species (with high support =1). Kieran et al. [22] analyzed 40 species of Triatomini using Ultraconserved

Elements (UCEs) and ribosomal dataset and based on the best likelihood tree concluded that *Paratriatoma hirsuta* and *P. lecticularia* are sister species and are included in the *protracta* clade.

In addition to the morphological characters mentioned in the results, reconstruction of the ancestral character state of the fossula spongiosa in males puts *P. hirsuta* and *P. lecticularia* in the same clade [22] and, the structure of the plates and membrane of connexivum are characteristic of *Paratriatoma* (Figure 8), being apomorphic with the Triatomini tribe. Combining morphological, molecular and cytogenetic data, Paratriatoma *lecticularia comb. nov.* does not belong to *Triatoma*.

Paratriatoma lecticularia occurs from the south-central to the Atlantic coast of the USA and can be collected in houses, kennels, woodrat nests *(Neotoma)* and squirrels. It has been reported as a nuisance species, commonly found in well-built dwellings in central Texas. *Paratriatoma hirsuta* occurs in the western United States, collected from arid regions in woodrat nests and human dwellings, has been described as “attacking human”, in addition to being of public health importance due to allergic reactions caused by your bite [13,23]. Both species proved to be a competent vector of *T. cruzi* experimentally. Colonization and invasion of dwellings by triatomines is an important factor in vector transmission, as it increases the chance of feeding potentially infected vectors in humans [23,24]. With the marked loss of their habitats, caused by deforestation and unplanned urbanization, major changes in the epidemiology of Chagas disease are expected. However, we know that a strong and sustained surveillance system is the best strategy. In this dynamic world, making predictions is not easy, so with all the knowledge about the biology, morphological, molecular and cytogenetic taxonomy of triatomine, we can plan public health control in a world with an uncertain future [25].

4.2. Dichotomous key for species of *Paratriatoma*

Head, body and appendages with numerous broad, curved, semi-erect setae; head very strongly convex dorsally; small eyes; antenniferous tubercles inserted near the anterior edge of the eye; anterior femurs without denticles; absent spongy fossulae; legs short and robust, the posterior femurs less than six times longer than broad; first segment of the rostrum less than twice the length of the third; general body coloration light to dark brown *Paratriatoma hirsuta* (Fig. 5, 6, 7)

Head strongly convex dorsally, especially between eyes; antenniferous tubercles elongate, comparatively close to eyes; body clothed with numerous black setae, conspicuous on head; overall color piceous, with orange or orange-yellow markings on pronotum, pleura, corium, connexivum, and ventral surface of abdomen; tibiae of first and second pair of males with small spongy fossulae, absent in female *Paratriatoma lecticularia* (Fig. 1, 2, 3, 4)

5. Conclusions

The genus *Paratriatoma* is closely related to the paraphyletic genus *Triatoma*—the most diverse and relevant in the epidemiology of Chagas disease. Initial examination of *Triatoma lecticularia* revealed the hirsuteness covering the entire body—a characteristic and striking feature of members of the genus *Paratriatoma*—and a systematic study revealed several other morphological characters that are in diagnostic alignment with *Paratriatoma*. Molecular phylogeny treatments consistently place the species *Triatoma lecticularia* (Stål, 1859) as sister to the genus *Paratriatoma*. To determine its correct taxonomic assignment, we examined the morphology of several specimens, including types, and cytogenetic data for both taxa. The observations clearly support the formal transferal of *Triatoma lecticularia* (Stål, 1859) into the genus *Paratriatoma* with the resulting new combination: *Paratriatoma lecticularia* (Stål, 1859) comb. nov. (Hemiptera: Reduviidae: Triatominae).

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Capítulo III

Artigo preparado para submissão na revista Acta Tropica

Revisiting North American species groups of Triatominae (Hemiptera: Reduviidae): combined phylogeny of molecular and morphological data

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Abstract

Triatoma phyllosoma, Triatoma protracta e Triatoma dispar groups includes 35 species of kissing bugs, with many involved in anaphylactic reactions or transmission of *Trypanosoma cruzi*. Although complexes are not formally recognized by the ICZN, they are reported to represent monophyletic groups. We propose that these three groups have six complexes: *Triatoma dispar, Triatoma protracta, Triatoma nitida, Triatoma phyllosoma, Triatoma recurva*, and *Triatoma dimidiata*. The species of these complexes are *T. dispar, T. nigromaculata/T. boliviana, T. carrioni, Triatoma venosa, T. protracta, T. incrassata, T. peninsularis, T. sinaloensis, T. barberi, P. lecticularia, P. hirsuta, D. maxima, T. nitida, T. neotomae, T. rubida, T. ryckmani, T. bolivari, T. bassolsae, T. longipennis, T. mazzottii, T. pallidipennis, T. phyllosoma, T. picturata, T. indictiva, T. mexicana, T. sanguisuga, T. gerstaeckeri, T. recurva, T. dimidiata, T. hegneri, T. brailovskyi, T. gomeznunezi, T. mopan*, and *T. huehuetenanguensis.* Through a Bayesian analysis we concatenate morphological (73 somatic characters) and molecular data (CytB, COX1, COX2, 16S, 18S, and 28S) evidencing the relationship of the *T. dispar, T. protracta,* and *T. phyllosoma* groups by checking their respective complexes. We also reinforced the maintenance of the *T.nitida/T.rubida* complex and the reestablishment of the *T. recurva* complex.

Introduction

The Triatominae subfamily comprises insects that are recognized vectors of *Trypanosoma cruzi.* However, further vector-borne diseases suggest that triatomines may be competent vectors for other pathogens (Vieira et al., 2018). Studies also show their capacity to cause allergies and anaphylactic reactions (Beatty et al., 2021). Currently, 157 taxa of this subfamily are described (Dale et al., 2021). In North America, 35 species of these Reduviidae have been recorded (Bern et al., 2019; Espinoza et al., 2013).

Due to the public health importance of triatomines as vectors, many studies on taxonomy and systematics have been carried out (Lent and Wygodzinsky, 1979; Ramsey et al., 2015; Monteiro et al., 2018; de Paiva et al., 2021). The term "species complex" is commonly used in triatomine systematics, but these groups were proposed at a time when phylogenetic hypotheses were very scarce (Monteiro et al., 2018). Traditionally 'complexes' have been used to designate groups defined mainly by morphological similarities and geographical distribution (Lent and Wygodzinsky, 1979; Schofield and Galvão, 2009). Over the years, these complexes have been reassessed and restructured according to new information provided by molecular, cytogenetic, morphological/morphometric and biogeographic data (Pita et al., 2016; Alevi et al., 2017; Monteiro et al., 2018; Rengifo-Correa et al., 2021). Although complexes and subcomplexes are not formally recognized by the International Code of Zoological Nomenclature, they are reported to represent monophyletic groups (ICZN, 1999; Justi et al., 2014).

In North America, according to Schofield and Galvão (2009), the Triatomini has been assembled in *rubrofasciata* group, in the complexes *Triatoma rubrofasciata, T. protracta, T. lecticularia, T. phyllosoma,* and two subcomplexes (*T. dimidiata* and *T. phyllosoma*). According to Monteiro et al., (2018), the genus *Triatoma* has the 'species groups' *T. protracta, T. nitida, T. phyllosoma* (complexes *T. phyllosoma* and *T. dimidiata*), and *T. rubrofasciata*, including 31 species. Where many species, such as *Triatoma neotomae, T. incrassata, T. indictiva, T. peninsularis, T. sinaloensis, T. gerstaeckeri, T. recurva,* and *T. sanguisuga* had an uncertain *status* within the species group or complexes. However, recently more information has been released about North American species groups (Kieran et al., 2021; Rengifo-Correa et al., 2021).

Using a broad set of morphological and genetic data, we present a topologically corroborated phylogeny for North American *Triatoma* species. Using DNA sequence and external morphology data from the specimens, we evaluated the species now established in complexes and groups. We provide photos and comments about some species. We also present, an update of groups and complexes of North America (*Triatoma* species).

Material and Methods

Species used and Identification

The present study had as its starting point the manuscript of Schofield and Galvão (2009), and we selected the complexes *T. protracta, T. lecticularia* and *T. phyllosoma* to investigate. For this purpose, the species *Paratriatoma lecticularia, P. hirsuta, Triatoma rubida T. recurva, T. sanguisuga, T. gerstaeckeri, T. indictiva, T. protracta, T. sinaloensis, T. peninsularis, T. neotomae, T. nitida, T. incrassata, T. barberi, Dipetalogaster maxima, T. picturata, T. ryckmani,* and *T. mazzottii,* were used. For the external group we use *Triatoma carrioni, T. dispar, T. nigromaculata, Brontostoma colossus* (Ectrichodiinae), and *Leogorrus litura* (Reduviinae). The specimens used in the morphological analysis are referred in Table 1.

Table 1. List of specimens used in morphological analysis

Species	Collection	Label Information
Brontostoma colossus	TC-JMSB[3]	?
Leogorrus litura	TC-JMSB	Abunã, RO, BR, X.13, Col. Oliveira, J. Malaise. Gil-Santana det.
Dipetalogaster maxima	CTIOC[2]	Mexico Baja California, Coleção Rodolfo Carcavallo (1555), CTIOC 2754
Paratriatoma lecticularia	HMNB[5], TC-JMSB	Male, Lectotypus, 2920; CTA137
Paratriatoma hirsuta	CTIOC	H. Lent det., CTIOC 11976, N° 2729; Coleção Rodolfo Carcavallo, n° 1724, CTIOC N° 6229, LAB 69
Triatoma barberi	CTIOC	Coleção Rodolfo Carcavallo. Mexico, Guerrero, CTIOC 4810.
Triatoma carrioni	CTIOC	Coleção Rodolfo Carcavallo (1849), CTIOC 4841; Ryaboca Huintõn Peru 1952. Coleção Rodolfo Carcavallo CTIOC 4840
Triatoma dispar	CTIOC	Estac. Pitilla 700m. Santa Cecilia, Costa Rica, 1988, n° 2347, CTIOC 8687; Santa Cecilia, P.N. Guanacaste. Prov.

		Guana, Costa Rica. N°2348, CTIOC 8688
Triatoma gerstaeckeri	CER[1]; CTIOC	Suporte 502 tubo 07 n° E12636. A.Loyda Nva. Td Guerrero Tamaulipes 8/V/65; Confort, Texas, Coleção Ayala
Triatoma indictiva	JMA-L	Texas: Uvalde, Co., Garner St. Pk. June 1982, at light. G.G Young
Triatoma incrassata	CTIOC	CTIOC 5426
Triatoma mazzottii	CTIOC	CTIOC 7010, 3992, México, Guerrero, Det. Carcavallo 1984.
Triatoma neotomae	CER[1], CTIOC[2]	Macho Suporte 140 Tubo 10 n°E5025. Texas USA. Reared R.E.Ryckman; CTIOC 7094, Las Animas. Dr. Cass N.L. Novermbro 34.
Triatoma nigromaculata	CTIOC	Venezuela, Apure, Mantecal, CTIOC 5256. Rodolfo Carcavallo Det. 1968.
Triatoma nitida	CER, CTIOC	Suporte 509 tubo 07 n°E12726. Paso Ancho Panamá?. 1967. Col. J. Gutierrez; Suporte 509 tubo 08 n°E12727; CTIOC 5262 5261, Guatemala, Coleção Rodolfo Carcavallo (4201, 4202).
Triatoma peninsularis	CER, CTIOC	Suporte 142 tubo 01 n°E5036. Todos Santos T.S. Baja California. Mexico. Jul.57. Col. Ryckman, Spencer; Det. Usinger 1950, Alotipo, n° 2759, Col.16/7/38. Coleção Herman Lent
Triatoma picturata	TC-JMSB[3]	CTA 286
Triatoma protracta	JMA-L[4], TC-JMSB	Pleasanton, CA. USA, W. Lagoon Rd. 318ft. may, 2005; CTA148
Triatoma recurva	CER, CTIOC	Suporte 142 tubo 5 n° E5040. Arizona.

		Madera, Can. Santa Rita. VII/55. F.X. Williams; Ft. Grant, Arizona, Pinaleno 1917; Madrona Cyn. Ranger Station Rincon Pima CO. Arizona. Det. H. Lent
Triatoma rubida	CER, CTIOC	Suporte 511 tubo 10 N° E12754 Cruz de Diedra, Guaymas. 20/VI/64. A.Vado; Globe Arizona 1935 Parker; E. Dias 1937 H. Lent
Triatoma ryckmani	CTIOC	Choluteca (Depto.) Honduras 25/11/93 Col. Elisco Santos Fêmea Progreso, Guatemala, n° fiocruz 3000
Triatoma sanguisuga	CTIOC, TC-JMSB	Dallas, CO. Texas. 08/03/47 J.C. Elkins; Confort, Texas. COL. JMA-L
Triatoma sinaloensis	CER, CTIOC	Suporte 141 tubo 6 n°E5031; Suporte 141 tubo 5 n°E5030; Rodolfo Carcavallo Det. 1969. Mexico, Sinaloa, Mocorito, CTIOC 5191

[1]CER = Coleção Entomológica de Referência, Faculdade de Saúde Pública, Universidade de São Paulo, Brazil; [2]CTIOC = Coleção de Triatomíneos do Instituto Oswaldo Cruz, Fiocruz, Brazil; [3]TC-JMSB = Triatomine collection “José Maria Soares Barata”, Universidade Estadual Paulista (Unesp), Brazil; [4]JMA-L = José Manuel Ayala-Landa personal collection; [5]HMNB= Humboldt Museum für Naturkunde, Berlin, Germany.

Morphological data

The morphological dataset consists of 73 characters. The survey of characters was carried out based on the morphological study of the specimens and the matrix was built from Lent and Wygodzinsky, (1979); Weirauch, (2008); Gil-Santana, (2014); Rivas et al., (2017); Rodrigues, (2018), with modifications, therefore the polarization of the characters followed the criteria adopted by the authors mentioned above. The morphological matrix was made with Mesquite (Maddison and Maddison, 2021), and is provided as ‘Supporting Information Appendix 1’. The characters were examined under a stereoscopic microscope Leica, which had a computer interface enabling the use of the LAS software, observing the external morphology of the head, thorax (including legs), hemelytra and abdomen. The characters were binary and multistate, being considered non-additive (Goloboff, 1997). We use equal weights in the analysis of morphological characters. All specimens were compared to the type-specimens, and only used specimens that matched the type.

Molecular data

We accessed the sequences available in the Genbank of the CytB (641bp), COX1 (1184bp), COX2 (602bp), 16S (509bp), 18S (735bp), and 28S (577bp) markers (Table 2). Alignments were made in the MEGA (Tamura et al., 2021) software, with the ClustalW tool, and trimmed with manual adjustment as required. The molecular matrix is provided as ‘Supporting Information Appendix 1’. jModeltest (Darriba et al., 2012) was used to assess the best-fit model for each of the markers.

Table 2. Genes and Genbank accession numbers of the 23 species used in the analysis

Species	CYTB	COX1	COX2	16S	18S	28S	Reference
Brontostoma colossus	NC_024745.1	KM044501.1	NC_024745.1	KU764538.1	KM278219.1	KM278219.1	Kocher et al 2014; Forthman &Weirauch 2017
Leogorrus litura				FJ230386.1	FJ230459.1	FJ230540.1	Weirauch & Munro 2009
Dipetalogaster maxima	KC249226.1	KC249305.1	MT556654.1	KC248968.1	KC249092.1	KC249134.1	Justi et al., 2014; Aguilera-Uribe et al., 2020
Triatoma lecticularia	KY305709.1	NC_050326.1	MT556650.1	KC249029	KC249111.1	KC249175.1	Curtis-Robles et al., 2018; Aguilera-Uribe et al., 2020; Justi et al., 2014
Paratriatoma hirsuta				FJ230443.1	FJ230521.1	FJ230604.1	Weirauch & Munro, 2009
Triatoma barberi	MT556655.1	MT556655.1	MT556655.1	MW045681.1	MW045728.1	MW045639.1	Aguilera-Uribe et al., 2020; Kieran et al., 2021
T. carrioni			KC249420.1	MW045685.1	MW045732.1	MW045642.1	Justi et al., 2014. Kieran et al., 2021.
T. dispar		MN620835.1					Basset, Y. Unpublished.
T. gerstaeckeri	MT702373.1	KF516486.1				KF188622.1	Kilgore et al., Unpublished. Powell et al., Unpublished. Kjos et al., 2013.
T. indictiva	KY305720.1						Curtis-Robles et al., 2018.
T. incrassata				MW045688.1	MW045737.1	MW045647.1	Kieran et al., 2021
T. mazzottii	MT556651.1	MT556651.1	MT556651.1	AY035446.1	AJ243333.1		Aguilera-Uribe et al., 2020. Hypsa et al., 2002. Bargues et al., 2000.
T. neotomae				MW045695.1	MW045747.1	MW045655.1	Kieran et al., 2021.
T. nigromaculata					MW045748.1		Kieran et al., 2021.
T. nitida	MT556667.1	MT556667.1	MT556667.1	JX872239.1			Aguilera-Uribe et al 2020. De la Rúa et al., Unpublished.
T. peninsularis				MW045698.1	MW045752.1		Kieran et al., 2021.
T. picturata	MT556661.1	MT556661.1	MT556661.1	MW045700.1	AJ243332.1		Aguilera-Uribe et al., 2020. Kieran et al., 2020. Bargues et al., 2000
T. protracta	KF188621.1	MT556662.1	MT556662.1	KT231827.1	MW045755.1	MW045659.1	Kjos et al., 2013. Aguilera-Uribe et al., 2020.

							Zhang et al., 2016. Kieran et al., 2021.
T. recurva	MT556663.1	MT556663.1	MT556663.1	FJ230417.1	FJ230496.1	FJ230577.1	Aguilera-Uribe et al., 2020. Weirauch & Munro 2009.
T. rubida	MT556664.1	MT556664.1	MT556664.1	AY185842.1		GQ853391.1	Aguilera-Uribe et al., 2020. Sainz et al., 2004. Patterson & Gaunt 2010.
T. ryckmani				JX872249.1	MW045757.1		De la Rúa et al., Unpublished. Kieran et al., 2021.
T. sanguisuga	MT556653.1	MT556653.1	MT556653.1	JX890269.1	MW045758.1	MW045661.1	Aguilera-Uribe et al., 2020 De la Rúa et al., Unpublished. Kieran et al., 2021.
T. sinaloensis							

Data analyses

We performed a Bayesian analysis with MrBayes v3.2.7a (Ronquist et al., 2012) with concatenated dataset using partition for morphological and molecular data (MIXED (STANDARD:1-73, DNA:74-4321)). We conducted two independent runs with four chains for 10 million Markov chain Monte Carlo (MCMC) generations sampling every 500 trees with 25% burn-in. The markers CytB, COX1, COX2, 16S, 18S, 28S presented the best models HKY+I+G, GTR+I+G, TIM2+I+G, TVM+I+G, TPM1uf+I and TVM+G, respectively. When it was not possible to use the best model, we used the next best model interpretable by the MrBayes (morphology nst=1 rates=invgamma; CYTB nst=2 rates=invgamma; COX1 nst=6 rates=invgamma; COX2 nst=6 rates=invgamma; 16S nst=6 rates=gamma; 18S nst=2 rates=gamma; 28S nst=6 rates=gamma). Bayesian analyses with and without topological constraints of *Triatoma neotomae* and *Triatoma nitida* were needed to incorporate results from morphological data (Lent and Jurberg, 1992; Lent and Wygodzinsky, 1979).

Results

Phylogenetic hypotheses

The recovered phylogenies derived from the combined morphological and molecular datasets are presented in Fig. 1 for unconstrained topology and, Fig. 2 for constrained topology. In both phylogenetic trees four clades were presented representing the groups *protracta, phyllosoma,* and *dispar*.

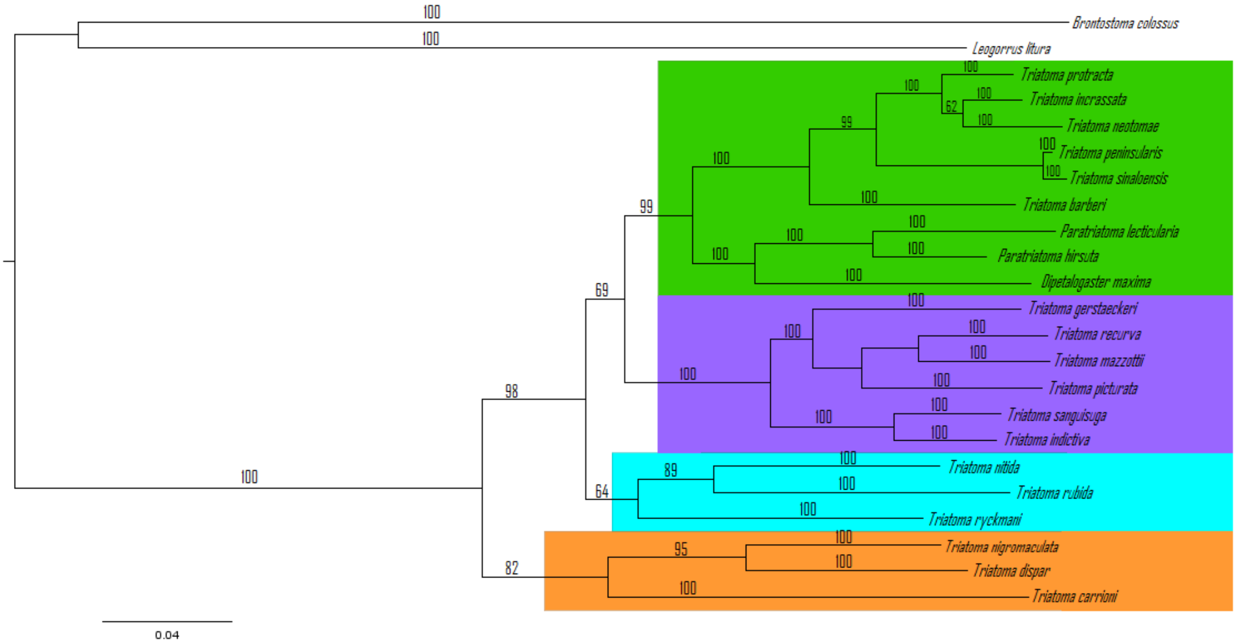

Fig 1. Unconstrained topology by bayesian analysis shows four clusters.

In the unconstrained topology, clade 1 recovered the species ((*T. protracta* + (*T. incrassata* + *T. neotomae*) + (*T. peninsularis* + *T. sinaloensis*) + *T. barberi*)) + ((*P. lecticularia* + *P. hirsuta*) + *D. maxima*)). All branches of the clade had high supports (100, prob_percent), except for *T. incrassata* + *T. neotomae* (62, prob_percent). Clade 2 recovered the species *T. gerstaeckeri, T. recurva, T. mazzottii, T. picturata, T. sanguisuga,* and *T. indictiva,* with high support (100, prob_percent) in the whole clade. Clade 3 recovered the species *T. nitida, T. rubida, T. ryckmani,* with low support for clade (64, prob_percent). Clade 4 recovered the species *T. nigromaculata, T. dispar,* and *T. carrioni*, with 82% support in clade.

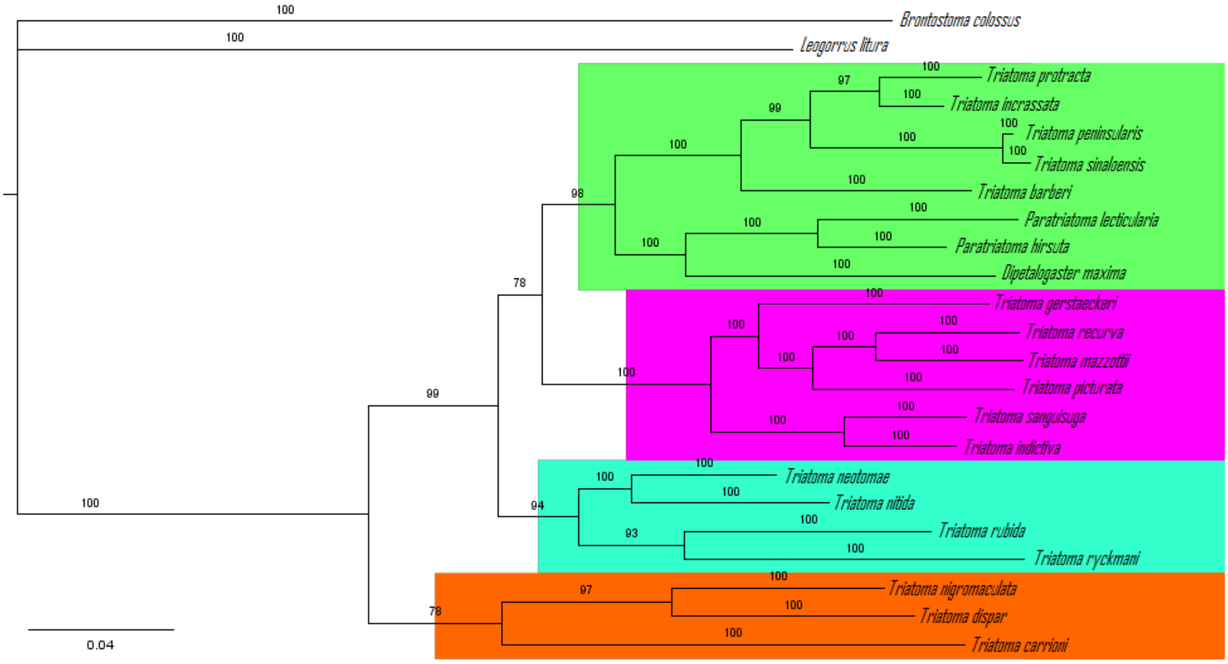

Fig 2. Restricted topology of *Triatoma neotomae* and *T. nitida* by Bayesian analysis shows four species groupings with greater supports

In the constrained topology, clade 1 recovered the species ((*T. protracta* + *T. incrassata* + (*T. peninsularis* + *T. sinaloensis*) + *T. barberi*)) + ((*P. lecticularia* + *P. hirsuta*) + *D. maxima*)). With the clade branches having high support (100, prob_percent). Clade 2 recovered the species *T. gerstaeckeri, T. recurva, T. mazzottii, T. picturata, T. sanguisuga,* and *T. indictiva,* with high support (100, prob_percent) in the whole clade. Clade 3 recovered the species *T. neotomae* + *T. nitida* (100, prob_percent) + *T. rubida* + *T. ryckmani* (93, prob_percent). Clade 4 recovered the species *T. nigromaculata, T. dispar,* and *T. carrioni*.

Proposition of group and complex arrangements

We observed clear separations into monophyletic groups of the species tested. We were unable to sample all species from the complexes covered, so based on previous studies (Lent and Wygodzinsky, 1979; Schofield and Galvão, 2009; de la Rúa et al., 2014; Dorn et al., 2018; Monteiro et al., 2018; Rengifo-Correa et al., 2020; Kieran et al., 2021), were proposed the following groups and species complexes (Table 3).

Table 3. Groups *T. dispar, T. protracta* and *T. phyllosoma* and their complexes

Group	Complex	Species
T. dispar[1]	*T. dispar*[1]	*T. dispar, T. nigromaculata/T. boliviana*[2], *T. carrioni, Triatoma venosa*[1]
T. protracta[2]	*T. protracta*	*T. protracta, T. incrassata, T. peninsularis, T. sinaloensis, T. barberi, P. lecticularia, P. hirsuta, D. maxima*
	T. nitida[2]/*T. rubida*[7]	*T. nitida, T. neotomae, T. rubida, T. ryckmani, T. bolivari*[2,4]
T. phyllosoma[3]	*T. phyllosoma*[3]	*T. bassolsae*[1,2], *T. longipennis*[1,2], *T. mazzottii, T. pallidipennis*[1,2], *T. phyllosoma*[1,2,4], *T. picturata*
	T. recurva[3]	*T. indictiva, T. mexicana*[4,6], *T. sanguisuga, T. gerstaeckeri, T. recurva*
	T. dimidiata[1,2]	*T. dimidiata*[1], *T. hegneri*[1], *T. brailovskyi*[1,4], *T. gomeznunezi*[1], *T. mopan*[5], *T. huehuetenanguensis*[6]

Keys to references: [1]Schofield and Galvão (2009); [2] Monteiro et al., (2018); [3]Lent and Wygodzinsky (1979); [4]Kieran et al., (2021); [5]Dorn et al, (2018); [6]Rengifo-Correa et al., (2020); [7]de la Rúa et al., (2014).

The *Triatoma protracta* complex recovered the *T. protracta, T. incrassata, T. peninsularis, T. sinaloensis*, *T. barberi*, *P. lecticularia, P. hirsuta*, and *D. maxima* species. The *Triatoma nitida* complex recovered the *T. nitida, T. neotomae, T. rubida, T. ryckmani*, and *T. bolivari* species. The *Triatoma phyllosoma* complex contains the species *T. bassolsae, T. longipennis, T. mazzottii, T. pallidipennis, T. phyllosoma,* and *T. picturata.* The *Triatoma recurva* complex possess the species *T. indictiva, T. mexicana, T. sanguisuga, T. gerstaeckeri,* and *T. recurva.* The *Triatoma dimidiata* complex recovered the species *T. dimidiata, T. hegneri, T. brailovskyi, T. gomeznunezi, T. mopan,* and *T. huehuetenanguensis.* The *Triatoma dispar* complex (used as an external group in this study) has the species *T. dispar, T. nigromaculata/T. boliviana, T. carrioni,* and *Triatoma venosa.*

Discussion

The Triatominae family has 18 genera, with *Triatoma, Rhodnius* and *Panstrongylus* being the most important epidemiologically (Cantillo-Barraza et al., 2021). In these species a high degree of phenotypic plasticity is observed, resulting in several subspecies (Bern et al., 2019). Therefore, we only portray the subspecies in de Paiva et al., 2022).

Since the 1962s, species have been reunited into groups and complexes based on morphological, geographical, and ecological data (de Lucena, 1970; Lent and Wygodzinsky, 1979; Ryckman, 1962). Historical disagreements about generic classifications (formal and informal) within *Triatoma* remain in constant assessment (Espinoza et al., 2013; Pita et al., 2016; Alevi et al., 2017; Monteiro et al., 2018; Kieran et al., 2021; Rengifo-Correa et al., 2021).

As an external group were used the *Triatoma dispar* complex which includes the species *T. dispar, T. nigromaculata, T. boliviana, T. carrioni,* and *Triatoma venosa. Triatoma boliviana and T. nigromaculata* were included in this complex by Monteiro et al., (2018) and Schofield & Galvão, (2009), but these species can be synonymous (Aldana et al., 2018). However, the molecular phylogeny supports the monophyly of the *Triatoma dispar* complex (Santillán-Guayasamín et al., 2020).

One of such groupings is the *Triatoma lecticularia* complex (Lent and Wygodzinsky, 1979; Schofield and Galvão, 2009), which has been proposed to include the species—*T. lecticularia, T. sanguisuga, T. gerstaeckeri, T. indictiva, T. recurva*, and *T. rubida*. Nevertheless, by reconciling morphological, molecular, and cytogenetic data, it was possible to propose a new combination of *Paratriatoma lecticularia*, putting the complex in doubt (de Paiva et al., 2021). The most recent analyzes include *P. lecticularia* in the *Triatoma protracta* complex (Kieran et al., 2021; Monteiro et al., 2018) and our results corroborate the data (Table 3).

Triatoma protacta group includes the *T. rubida* and *T. protracta* complexes. The *T. protracta* complex was proposed by Lent and Wygodzinsky (1979) and endorsed by Schofield & Galvão (2009) and Monteiro et al., (2018), however we show the complete *T. protracta* complex for the first time with the species: *T. protracta, T. incrassata, T. peninsularis, T. sinaloensis, T. barberi, P. lecticularia, P. hirsuta,* and *D. maxima.* The similarity of the fusiform body and short legs of *Paratriatoma* and the *T. protracta* complex (or enlargement of abdominal capacity like in *D. maxima*) may be due to convergence, but as we have seen, we can assign a sister-group relationship between the *T. protracta* complex and *Paratriatoma* (Lent and Wygodzinsky, 1979).

Morphologically *T. neotomae* and *T. nitida* are very similar and, the validity of *T. nitida* has been questioned (Lent and Wygodzinsky, 1979). Therefore, with the study of male genitalia, it was possible to obtain characters that theoretically differentiate them (Lent and Jurberg, 1992). The first signs of the existence of the *T. nitida/T. rubida* complex were shown by Bargues et al., (2008). The *T. rubida* complex was initially proposed with the species *T. nitida, T. rubida, T. ryckmani, and T. bolivari* (de la Rúa et al., 2014). Years later Monteiro et al., (2018) kept the species in the complex, so it changed the name to *T. nitida.* The conformation of the species was maintained by Kieran et al., (2021). We contributed to the complex including *T. neotomae,* which even increased the support of clades.

The *T. phyllosoma* group currently includes *T. dimidiata, T. recurva*, *T. phyllosoma* complexes and 17 species. The phylogeny of this group is well understood, but a complete tree of the species has not yet been presented (de la Rúa et al., 2014; Dorn et al., 2018;

Espinoza et al., 2013; Justi et al., 2014; Kieran et al., 2021; Rengifo-Correa et al., 2021, 2020). The *T. phyllosoma* complex is composed of the six species that belonged to the genus *Meccus*, which are *T. bassolsae, T. longipennis, T. mazzottii, T. pallidipennis, T. phyllosoma,* and *T. picturata*.

The *Triatoma recurva* complex was initially postulated by Lent & Wygodzinsky (1979), due to the similarity between *T. recurva* and *T. gerstaeckeri*. Molecular phylogenies retrieved a sister relationship between *T. gerstaeckeri* and *T. mexicana* (Bargues et al., 2008; Espinoza et al., 2013; de la Rúa et al., 2014), and the dark phenotype of *T. gerstaeckeri* morphologically resembles *T. indictiva* (Rengifo-Correa et al., 2021)*. Triatoma indictiva* was once considered a subspecies of *Triatoma sanguisuga*, due to the morphological similarity found in some specimens (de Paiva et al., 2022). Therefore, we support the reestablishment of the *Triatoma recurva* complex composed of the five species: *T. indictiva, T. mexicana, T. sanguisuga, T. gerstaeckeri, T. recurva*.

Triatoma dimidiata complex was approached by Schofield and Galvão (2009), with the species *T. dimidiata, T. hegneri, T. brailovskyi,* and *T. gomeznunezi. Triatoma hegneri* is an insular form of *Triatoma dimidiata*, with valid species status (Bargues et al., 2008; Rengifo-Correa et al., 2021). *T. gomeznunesi* is close to *T. brailovsky, and T. dimidiata* sp. aff. (Carcavallo et al., 2000; Rengifo-Correa et al., 2021).

Triatoma mopan and *T. huehuetenanguensis* were recently described from populations formerly considered *T. dimidiata,* clearly belonging to this complex (Dorn et al., 2018; Lima-Cordón et al., 2019; Rengifo-Correa et al., 2021).

Conclusions

Through a phylogenetic analysis using molecular and morphological data we studied the relationship of three groups and six complexes of several North Central American species, mainly from *Triatoma*. In this work we allocated three groups and six complexes, including 35 species in their respective arrangements. We confirmed the *T. dispar, T. protracta,* and *T. phyllosoma* groups by checking the respective complexes. We also reinforced the maintenance of the *T.nitida/T.rubida* complex and the reestablishment of the *T. recurva* complex.

Supporting Information Appendix 1.

Esse apêndice contém informações referentes ao número de espécies utilizadas, ao número de caracteres da matriz morfológica e molecular combinadas, quais caracteres morfológicos foram utilizados e por fim os 4248 nucleotídeos dos seis genes analisados. O arquivo original é escrito em formato ‘bloco de notas’ (.txt), (uma diagramação diferente é visualizada quando copiamos para o editor de texto .doc, formato da tese).

#NEXUS

BEGIN DATA;

DIMENSIONS NTAX=23 NCHAR=4321;

FORMAT DATATYPE = MIXED (STANDARD:1-73, DNA:74-4321) GAP = - MISSING = ?;

CHARSTATELABELS

1. General Integument of the Head: Smooth (0), grainy/rough (1).
2. General hairiness of the head: Low hairiness (0); sharp hairiness (1).
3. Head shape, dorsal view: ovoid (0), subconical (1), subcylindrical (2)
4. Dorsally convex head, side view: absent (0), present
5. Length of head (excluding neck) is twice or more than width including eyes, (0); less than twice as long as wide (1).
6. Length of the head (excluding the neck) in relation to the length of the pronotum: Shorter (0); equal or longer (1).
7. Head, arched depression behind the clypeus: Absent (0); Present (1)
8. Length of the ante-ocular region in relation to the post-ocular region: greater (0), smaller (1).
9. Post-ocular region, callosity between eye and ocellus: (0) Absent; (1) Present
10. Sides of the postocular region of the head: Subparallel, slightly converging backwards (0); with the edges converging sharply backwards (1); distinctly rounded on the sides (2)
11. Dorsal interocular distance from Eye Width: less or even equal (0); up to approximately double (1); more than double (2)
12. Shape of the posterior margin of the eye, lateral view: concave (0), linear (1).
13. Length of the eye in dorsal view, in relation to the length of the head, is: less than or equal to 1/5 (0); 1/5 to 1/3 (1).
14. Ocelli: not elevated, situated close to the integument level (0); situated on evident

protrusions (1).

15. Ocellus Shape: juxtaposed, forming a circle (0); in “V or U” shape (1); linear (2).
16. Ocellus located close to the interocular sulcus: absent (0); present (1)
17: Rostrum: Robust and curved (0); Slender and straight (1)
18. Clypeus, lateral view: protruding posteriorly, upper surface convex (0); not protruding (1).
19. Maxillary plate: rounded apical tip (0); maxillary plate with a sharp or pointed tip (1).
20. Maxillary plate: not elongating beyond the clypeus (0); maxillary plates extending beyond the clypeus (1).
21. Second Visible segment of the lip, in lateral view: shorter or its tip reaching the anterior border of the eye (0); its tip exceeds the level of the anterior border of the eye (1).
22. Third visible segment of the lip, length in relation to the second: Shorter (0); equal (1)
23. Last visible segment of labium, shape of apex: Tapered/Conical (0); Truncated (1).
24. Anteniferous tubercle: without spiniform projection or lateral protrusion (0); with lateral spiniform projection present (1).
25. Anteniferous tubercle, insertion location in the anteocular region: Proximal, close to the eyes (0); proximal, between the eyes and the median region (1); Median (2).
26. Antenna insertion point: lateral (0), dorsal (1).
27. Antenna, segment I, length in relation to the apex of the clypeus: Short, not exceeding it (0); Long, being able to reach or surpass it (1).
28. Antenna, third segment, length relative to second: Shorter (0); equal (1); longer (2).
29. General integument of the pronotum: Smooth (0), granular/rough (1).
30. Pronotum coloration: unicolor (0); with more than one shade/color (1).
31. Pronotum, humeral angles with different coloration: Absent (0); Present (1)
32. Pronotum with spiniform projections: absent (0); a pair (1).
33. Pronotum, visible bristles: Absent (0); Present (1).
34. Pronotum, anterior lobe, developed basal disc tubercles: absent (0); Present (1)
35. Pronotum, anterior lobe, lateral tubercles developed: Absent (0); Present (1)
36. Pronotum, posterior lobe, lateral margins in relation to the anterior lobe: Straight, almost continuous (0); sinuous, with angulation (1).
37. Pronotum, humeral angles: rounded (0); sharp or pointed (1)
38. Pronotum, posterior lobe, direction of humeral angles: Not elevated (0); curved up (1).
39. Scutellum has more than one coloration: absent (0); present (1).
40. Scutellum – median process: present (0); absent (1).
41. Scutellum, median longitudinal groove in the posterior process: absent (0); Present (1).

42. Scutellum, posterior process with the “base” shorter than the process length (0); “base” greater than length (1).
43. Scutellum, apex of the posterior process, shape in dorsal view: Cylindrical (0); Conical (1); Spoon shape (2); bifurcated (3).
44. Scutellum, lateral processes: absent (0); present (1)
45. Prosternum, prosternal sulcus (estridulatory): Absent (0); straight, parallel lateral margins, narrowing in the apical third (1); convergent from the base, narrowing continuously from the base to the apex (2).
46. Mesosternum continuous with Metasternum: Absent (0); Present (1)
47. Mesosternum, with a central depression: Present (0); Absent (1)
48. Metasternum with a central depression: Present (0); Absent (1)
49. Pleuron with a single color (0); pleura with more than one color (1).
50. Leg coloration: Unicolor (0); more than one color (1).
51. Femur has ring-shaped coloration: Absent (0); Present (1)
52. Femurs compared to tibias: swollen / thick (0); similar (1).
53. Anterior femurs: with spines / denticles (0); no spines / denticles (1).
54. Medium femurs: with spines / denticles (0); no spines / denticles (1).
55. posterior femurs: with spine / denticles (0); no thorn / denticles (1).
56. Anterior tibiae: without fossula spongiosa (0); with fossula spongiosa (1).
57. anterior tibiae: with spines/ denticles (0); no spines/ denticles (1).
58. Medium tibiae: without fossula spongiosa (0); with fossula spongiosa (1).
59. Corium: multicolor (0); single color (1).
60. Corium of the hemelytra: no colored spots (0); with spots on the base (1); subapical/apical spot (2); spots at base and subapical/apical (3) markings that extends over the entire subcostal part of the corium (4) Spots near the clavus (5) Irregular spot distributed over the corium (6)
61. Corium with similar staining to membrane (0); Corium darker than membrane (1).
62. Clavus of hemelytra: single color (0); multicolor (1)
63. Clavus with same color as the corium: absent (0); present (1)
64. Veins of the hemelytra lighter than the Membrane (0); veins similar in color to the membrane (1); veins darker than the membrane (2).
65. Hemelytra, length in relation to the apex of the abdomen: Short, leaving a considerable dorsal portion uncovered, including the abdominal tergites VI and/or VII (0); long, covering the entire abdomen, but not exceeding the apex (1); Hemelytra that go beyond the apex of the abdomen (2).

66. Corium extension in the hemelytra: corium surrounding the subcostal part of the hemelytra (0); well-developed corium, in the area between the clavus and the median membrane (1).

67. General hairiness of the abdomen, ventrally: apparent hairiness (0); not apparent (1).

68. Abdomen, ventral view, color pattern of sternites: Unicolor (0); more than one color (1).

69. Abdomen shape, ventral view: longitudinally flat (0); evenly rounded (1).

70. Connexivum, pleated membrane connecting the dorsal plates to the sternites: Absent (0); Present (1).

71. Connexivum, dorsal plate spotting pattern: Single color / no spot (0); Dark and light spots not covering the intersegmental sutures (1); Dark spots on the anterior and/or posterior portions, covering the intersegmental sutures (2); Dark spots on the inner portion and light spots on the outer portion, covering the intersegmental sutures (3); dark spot on the outside and light on the inside (4)

72. Longitudinally well-delimited sternites: absent (0); Present (1).

73. Respiratory estigmas: Distant from the connexivum suture (0); Next to the connexivum suture (1);

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GGGGAGTCATTGCAATAGTCTCATCAATTGCAATTATTTTAATCCTCCCATTCACTAATAAAAGAAAATTTCA
AGGCCTCCCATTTTACCCAAT

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11200110021101101100100020001110010000100000111100000111010030001110100111GTCCTTTTGTTTATTTATT
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CCTCCCAAGACTTCACATTCTATATCTAATAGATGAAATAAATAACCCTGCAGTAACAATTAAATCCATTGGA
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TGACCTAGAAATAGGAGATTTTCGACTTCTAGATGTAGATAACCGAGCTGTTTTACCTATAAATACACAAATC
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TTATCTTAATTCTCCCAATCACCAATAAAAGAAAATTTCAAGGACTTGCCTTTTATCCAAT

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CTAACCTGCCCAATGAGGAGTTCAATGGCCGCAGTATTTTAACTGTGCTAAGGTAGCATAATCATTTGTCTTT

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TAATTGAGGGCTAGTATGAAAGGTTGGACGAGGTATTAACTTTCTTTAACTTAATTAAATGAATTTAATTTTT
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TAGAGATTAT-TTTATTTAAAGCAAAAGAATTATTTTGTTGGGGTGACCATAGAATTTAAAAAACTTCTATT-
AATAATATCATTCATTTATGTTTTTTTGATCCATAT-TTTATGAT------------------------------------------------------------------------
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CCCGTAATCGGAATGAGTACACTTTAAATCCTTTAACAAGGATCCATTGGAGGGCAAGTCTGGTGCCAGCA
GCCGCGGTAATTCCAGCTCCAATAGCGTATATTAAAGTTGTTGCGGTTAAAAAGCTCGTAGTTGGTTCTGCG
TGCCGCGCTGTCGGTTCGCCGCCTGTCGGTGTAACTGGCATGTCGCGGCATGTCCTGTCGGTGGTGAACGG
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CCTTTAATGACTCGGCGGGGAGCTTCCACCCGGGAAACCAAAGCTTTTGGGTTCCGGGGGAAGTATGGTTG
CAAAGCTGAAACTTAAAGGA?????????????????????????????????????????????????????????????????????????????????????????
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11200100021101101100100020 1?1000110100100111101000001011100300111101001 01GTCCTTTTGTTTATTTATT
TAAGGTCTGACCTGCCCAATGAGGAATTCAATGGCCGCAGTATTTTAACTGTGCTAAGGTAGCATAATCATT
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AATTTCAAGGACTTACCTTTTACCCAAT

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AAACGATGCCAGCCAGCGATCCGCCAATGTTCCTTTAATGACTCGGCGGGGAGCTTCCACCCGGGAAACCA
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AAGAGTACGTGAAACCGCTCAGGGGTAAACGGAAAAGACCTGAATATCCGAAAGGGGAGATTCACGTCTT
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CTGTTGGTAAACTGTTCCTTGGACAGTGCTTATAACACCGGTCGGCAGCGATTCAGGTTCAGGCTCTTATCC
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TGACCACACCTTAATAATTCTTACCATAATTACCATTCTAGTAGGATACATGATAGGAACAGTCCTAACAAAC
AAACTTTCCAACCGTTACTTACTCGAAGGCCAGACCATTGAATTAATCTGAACCATCTTACCGGCAATTACT
TTAGTATTCATCGCTCTCCCCAGATTACGGATCCTGTACTTGATAGATGAAATTAATGAACCACT----------------
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CTGGAATATTAGGAACATCATTAAGCTGATTAATTCGAATTGAACTAGGACAACCAGGACCTTTCATTGGAG
ACGACCAAATTTATAATGTTGTAGTTACAGCCCATGCCTTTGTTATAATTTCTTTATAGTAATACCAATTATAA
TTGGAGGATTCGGAAATTGACTTGTACCTTTAATGATTGGGGCTCCAGATATAGCATTCCCCCGAATAAATAA
TATAAGATTTTGATTATTGCCCCCTTCCCTCACCCTTTTATTAATAAGAATATTAGTAGAAGGAGGGGCAGGG
ACTGGATGAACTGTTTACCCCCCATTATCAAGAAATATCGCCCACAGAGGTGCATCTGTAGATTTAGCAATC
TTCTCATTACATTTAGCCGGAGTATCCTCAATTCTAGGAGCAGTTAATTTTATTTCAACAATTATTAACATGCG
ACCAGAAGGTATAACTCCTGAACGTATTCCATTATTTGTATGATCAGTTGGAATTACTGCTCTACTATTATTAC
TTAGACTTCCTGTTCTTGCAGGAGCCATTACTATACTTTTAACAGATCGGAATTTTAATACTTCATTTTTTGAC
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begin mrbayes;
charset morphology= 1-73;
charset 16S= 74-582;
charset 18S= 583-1317;
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charset 28S= 1318-1894;
charset COX1= 1895-3078;
charset COX2= 3079-3680;
charset CYTB= 3681-4321;
partition locus = 7: morphology, 16S, 18S, 28S, COX1, COX2, CYTB;
set partition = locus;
 lset applyto=(1) nst=1 rates=invgamma;
 lset applyto=(2) nst=6 rates=gamma;
 lset applyto=(3) nst=2 rates=gamma;
 lset applyto=(4) nst=6 rates=gamma;
 lset applyto=(5) nst=6 rates=invgamma;
 lset applyto=(6) nst=6 rates=invgamma;
 lset applyto=(7) nst=2 rates=invgamma;
prset topologypr=uniform;
prset applyto=(all) statefreqpr=fixed(equal) shapepr=uniform(0.1,50) pinvarpr=uniform(0,1);
  mcmc nruns=2 ngen=1000000 printfreq=1000 samplefreq=500 diagnfreq=5000 nchains=4;


END;
```

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5. Considerações finais

Na tese explicamos o papel dos triatomíneos na transmissão da doença de Chagas, exploramos os aspectos taxonômicos desses vetores e, finalmente, discutimos brevemente todas as espécies que são alvo do trabalho. Os resultados do Capítulo 1, publicados na revista Parasitological Research, envolvem taxonomicamente todas as subespécies dos gêneros *Panstrongylus, Paratriatoma* e *Triatoma*. Neste artigo, múltiplos táxons negligenciados são considerados e, portanto, demonstramos que critérios mais confiáveis são necessários para inferir o "status" dos táxons. A partir das informações apresentadas, pode-se concluir que são necessárias melhores inferências para validar subespécies para todos os táxons. Portanto, mais pesquisas sobre a taxonomia, evolução, filogenia, biogeografia, ecologia, fisiologia e comportamento das espécies são necessárias para estabelecer ou invalidar o status das subespécies na subfamília, um passo essencial em qualquer programa de controle.

No Capítulo 2, apresentamos um artigo no qual publicamos a nova combinação *Paratriatoma lecticularia*. O gênero *Paratriatoma* está intimamente relacionado ao gênero *Triatoma*, que é o mais relevante na epidemiologia da doença de Chagas. O exame preliminar de *Triatoma lecticularia* revelou hirsutismo, cobrindo todo o corpo - uma marca registrada dos membros do gênero *Paratriatoma* - e estudos sistemáticos revelaram várias outras características morfológicas compatíveis com o *Paratriatoma*. O processamento filogenético molecular trata consistentemente a espécie *Triatoma lecticularia* como irmã do gênero *Paratriatoma.* Para determinar sua correta atribuição taxonômica, examinamos a morfologia de vários espécimes, incluindo os espécimes-tipo e dados citogenéticos para ambos os taxa. As observações apoiam claramente a transferência oficial de *Triatoma lecticularia* para o gênero *Paratriatoma* e a criação de uma nova combinação: *Paratriatoma lecticularia* (Stål, 1859) comb. nov. (Hemiptera: Reduviidae: Triatominae).

No Capítulo 3, por meio de análise filogenética usando dados moleculares (CytB, COX1, COX2, 16S, 18S e 28S) e morfológicos, investigamos a relação de três grupos e seis complexos de várias espécies norte-americanas, principalmente *Triatoma*. Neste trabalho, atribuímos três grupos e seis complexos, incluindo 35 espécies em seus respectivos arranjos. Confirmamos os grupos *T. dispar, T. protracta* e *T. phyllosoma* examinando seus respectivos complexos. Também mantivemos o complexo *T. nitida/T. rubida* e o restabelecimento do complexo *Triatoma recurva*.

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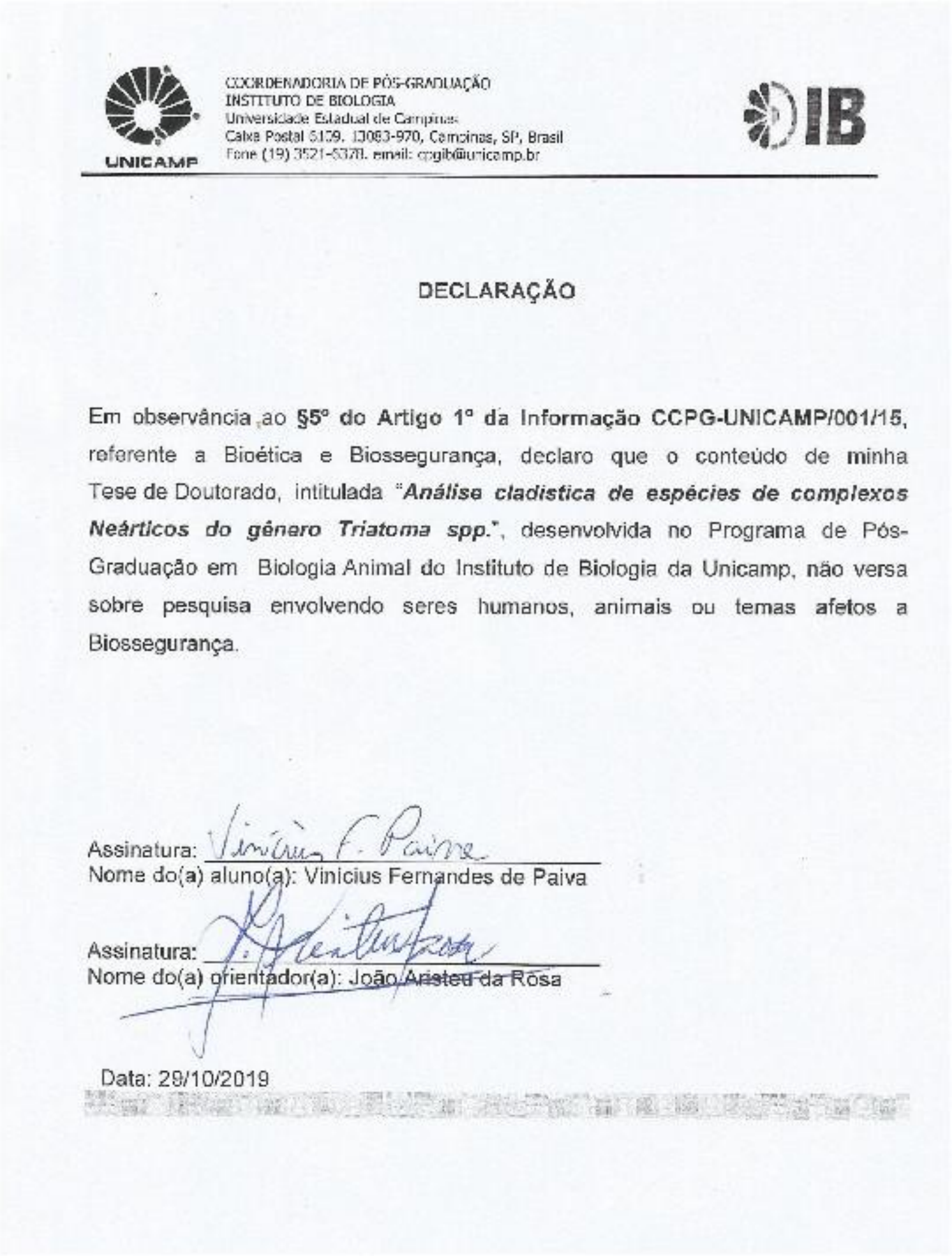
7. Anexos

7.1 Declaração de Biossegurança



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DECLARAÇÃO

Em observância ao **§5º do Artigo 1º da Informação CCPG-UNICAMP/001/15**, referente a Bioética e Biossegurança, declaro que o conteúdo de minha Tese de Doutorado, intitulada ***"Análise cladistica de espécies de complexos Neárticos do gênero Triatoma spp."***, desenvolvida no Programa de Pós-Graduação em Biologia Animal do Instituto de Biologia da Unicamp, não versa sobre pesquisa envolvendo seres humanos, animais ou temas afetos a Biossegurança.

Assinatura: Vinicius F. Paiva
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Data: 29/10/2019

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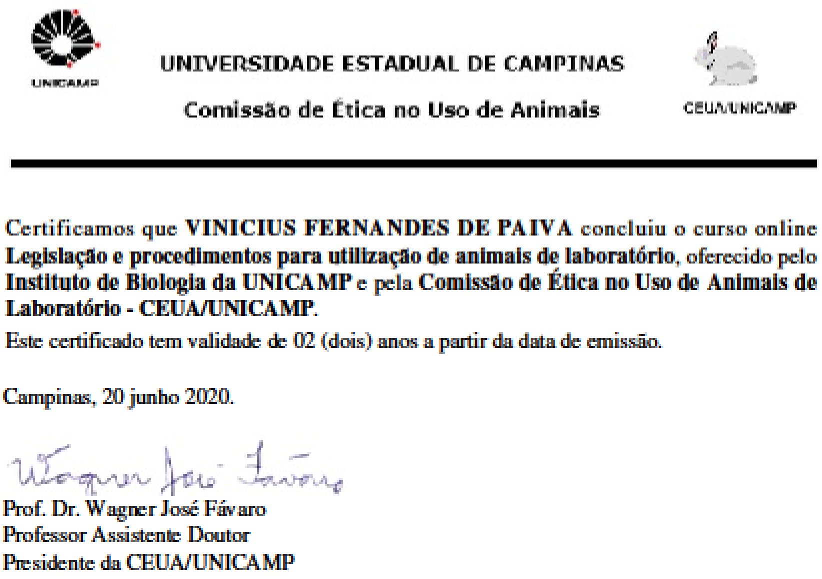
7.2 Curso de Ética no uso de Animais



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Comissão de Ética no Uso de Animais

Certificamos que **VINICIUS FERNANDES DE PAIVA** concluiu o curso online **Legislação e procedimentos para utilização de animais de laboratório**, oferecido pelo **Instituto de Biologia da UNICAMP** e pela **Comissão de Ética no Uso de Animais de Laboratório - CEUA/UNICAMP**.

Este certificado tem validade de 02 (dois) anos a partir da data de emissão.

Campinas, 20 junho 2020.

Wagner José Fávaro

Prof. Dr. Wagner José Fávaro
Professor Assistente Doutor
Presidente da CEUA/UNICAMP

7.3 Direitos autorais

Declaração

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