# scientific reports



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# Hospesneotomae n. gen. of the Triatomini tribe presents a turnaround in the taxonomy of the Triatoma protracta species complex

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The Triatominae are of relevant public health importance because they include hematophagous species which are proven or potential vectors of Chagas disease. Currently, eighteen genera are considered valid in this subfamily. Through a comprehensive and integrative study, the description of a new genus of Triatomine, the nineteenth of the subfamily, is presented. Were generated a robust phylogeny from data deposited in Genbank, created a table comparing two genera with *Hospesneotomae*, and prepared a dichotomous key for the genus and species. To this end, several systematic pieces of evidence about this group were taken into consideration, such as morphology, genetics, ecotopes and species distribution. The new genus is proposed to include the species previously included in the *T. protracta* complex, considered now in a new taxonomic assignment. Therefore, *Hospesneotomae* n. gen. will be composed by the following seven species (in the new combination): *H. protracta*, *H. barberi*, *H. incrassata*, *H. peninsularis*, *H. sinaloensis*, *H. neotomae* and *H. nitida*, providing an innovative perspective in understanding these organisms, because the seven species grouped here in the proposed new genus are distinct from the others species of *Triatoma* and at the same time show similarities that indicates that they form a monophyletic group.

Keywords Triatomines, New combination, Reduviidae, Revised classification

The current *Triatoma protracta* complex of species belongs to the Triatominae subfamily (Hemiptera: Reduviidae), which are hematophagous insects that can transmit *Trypanosoma cruzi* (Chagas), the etiological agent of Chagas disease, by complex mechanisms involving multiple pathways<sup>1,2</sup>. Currently, 158 species, eighteen genera, and five tribes are considered valid in this group, besides the recognition of species complexes within some genera, including *Triatoma* Laporte, 1832<sup>3–7</sup>.

The grouping of species into complexes aims to reflect morphological, morphometric, molecular, and biogeographical attributes inherent to the species<sup>8</sup>. The *Triatoma protracta* complex was initially proposed by Ryckman<sup>9</sup>, in which *Triatoma protracta* (Uhler, 1894), *Triatoma incrassata* Usinger 1939, *Triatoma sinaloensis* Ryckman 1962 and, *Triatoma barberi* (Usinger, 1939) were included. Subsequently, Lent and Wygodzinsky<sup>1</sup> and Schofield and Galvão<sup>7</sup> expanded the complex to encompass additional species. This extended list includes *Triatoma peninsularis* Usinger 1940, *Triatoma neotomae* Neiva 1911, and *Triatoma nitida* Usinger 1939. All of them are found in the United States, Mexico, Guatemala, Honduras, El Salvador, Belize, Nicaragua, and Costa Rica<sup>10–12</sup>, countries with contiguous or near geographical territories.

The *Triatoma protracta* group exhibits unique morphological characteristics not shared by other species in the genus, suggesting the monophyly of the complex<sup>2,13</sup>. The synapomorphies of this group include a characteristic fusiform body; a short oval head, an anteocular region 2 to 3 times longer than postocular; short legs; ocelli not elevated in relation to the dorsal surface of head; basal host relationship with the *Neotoma* Say & Ord, 1965 (Rodentia: Cricetidae) genus of rodents<sup>2,9</sup>.

In molecular phylogenies, the  $Triatoma\ protracta$  clade is well supported <sup>14–16</sup>, but there was not a molecular phylogeny that had sampled most of the species that belong to the complex yet. This is what was done in this work.

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This study proposes the creation of a new genus, *Hospesneotomae* n. gen. belonging to Triatominae (Hemiptera: Heteroptera: Reduviidae), closer to *Triatoma* Laporte, 1832. The proposed new genus and the group of species which was chosen to be included in it are based on modern systematic approaches and aligned with integrative taxonomy, providing an innovative perspective in understanding these organisms. This categorization aims to reflect specific morphological, morphometric, molecular, and biogeographical characteristics of each species. Such an approach offers a more refined understanding of the diversity of these vectors and their evolution, providing a solid foundation for effective classification.

# Material and methods Material examined

Type specimens and respective depository collections were examined and photographed as follows: *T. protracta, T. neotomae, T. nitida*: USNM—National Entomological Collection, Smithsonian Institution, Washington, D.C.; *Triatoma incrassata, T. peninsularis, T. barberi*: CAS—California Academy of Sciences, San Francisco, USA; *T. sinaloensis*: CER—Coleção Entomológica de Referência, Faculdade de Saúde Pública, Universidade de São Paulo, São Paulo, Brazil. Additional non-type specimens studied were deposited in CTIOC—Coleção de Triatomíneos do Instituto Oswaldo Cruz, Fiocruz, Brazil, and deposited in CTJMSB—"José Maria Soares Barata" Triatominae Collection, Universidade Estadual Paulista, Unesp, Araraquara, Brazil.

# Morphological study

Characters of the head, thorax, and abdomen were examined to distinguish differences between the species and genera *Paratriatoma* Barber, *Triatoma*, and *Hospesnetomae* n. gen., as summarized in Supplementary Table 1 and in the Description in Results. The descriptions and terminology for general body parts followed Lent and Wygodzinsky² and Schuh and Weirauch¹7. Each species was not fully morphologically redescribed, because Lent and Wygodzinsky², Ryckman9, Usinger¹8, provided sufficiently detailed descriptions to confirm their specific status for our purposes.

Photographs were made using a Canon EOS D4 with 100 mm lens and Leica M205C stereomicroscope, and were processed with the software Leica LAS (version 4.9). Type specimens were examined and photographed (Figs. 1, 2, 3, 4, 5, 6, 7, and 8). Additional specimens were also listed in the Results. When describing label data, a double slash (//) separates different labels.

#### Molecular analysis

Sampling

An extensive in silico dataset was accessed that includes data from: (1) UCE (Ultraconserved Elements), (2) mtDNA genes (Cytb, COI, COII), and (3) ribosomal rRNA (16S). All the data analyzed was obtained from the GenBank. This dataset comprises 28 internal terminals and 1 external terminal (see supplementary Table 2). The selected species were chosen based on previously published phylogenies <sup>13,14</sup>, and include representatives from six genera of Triatominae (*Dipetalogaster* Usinger, *Linshcosteus* Distant, *Panstrongylus* Berg, *Paratriatoma* Barber, *Triatoma*, and *Hospesneotomae* n. gen.). The choice of genetic data was guided by the information available for the terminals under study, together with the quality of the data accessed from GenBank. The raw UCE data was accessed using the SRA-ToolKit 3.0.7 tool (https://github.com/ncbi/sra-tools). The mtDNA and rRNA sequences were accessed using a customized python script (Supplementary Table 2).

#### Data processing

The Faircloth pipeline was followed for processing UCEs with the assistance of PHYLUCE v1.7.1<sup>19</sup>. Raw UCE data was assessed using FASTQC<sup>20</sup>, and after filtering for adapters and low-quality bases with Illuminaprocessor (https://github.com/faircloth-lab/illumiprocessor), a program wrapper around Trimmomatic<sup>21</sup>. Clean reads were conducted de novo assembly using SPADES<sup>22</sup>, with default parameters. The recovered contigs were aligned using the MAFFT v7.475 E-INS-i algorithm<sup>23</sup> incorporated in PHYLUCE v1.7.1. An edge trimming was applied with phyluce\_align\_seqcap\_align and a back trimming with GBlocks 0.90b, integrated with PHYLUCE v1.7.1<sup>24</sup>. Finally, matrices with 75% completeness were generated for further analyses. mtDNA and rRNA were processed with BioEdit 7.2.5<sup>25</sup> and aligned with MAFFT v7.475<sup>23</sup>.

### Phylogenetic analyses

For phylogenetic inferences, a dataset was generated with 75% occupancy, including concatenation of UCE loci, COI, COII, Cytb, and 16S for all 29 terminals. The strategy employed to broaden the taxonomic coverage in constructing a representative phylogeny involved concatenating mitochondrial genes (mtDNA) and the ribosomal RNA gene (rRNA). This approach facilitated the inclusion of *T. nitida*, the sole species lacking available UCE data. To enhance the data matrix, the genes COI, COII, Cytb from mtDNA, and 16S rDNA were augmented from GenBank (Supplementary Table 2). The dataset underwent maximum likelihood (ML) analysis using RAxML-NG v. 1.1<sup>26</sup> and Bayesian inference with MrBayes v. 3.2.7<sup>27</sup> ML analysis involved 200 bootstrap replicates, utilizing the GTRGAMMA model for both concatenated and locus-partitioned datasets. The partitions were determined through SWSC-EN<sup>28</sup> and PartitionFinder2 v2.0.1<sup>29</sup> for UCE data. A Bayesian analysis was conducted using MrBayes v3.2.7<sup>27</sup>, incorporating partition results obtained from PartitionFinder2. Two independent runs were performed with default settings, employing one cold and three heated chains for 10 million Markov chain Monte Carlo (MCMC) generations, with sampling every 1000 generations and a 25% burn-in.

Subsequently, optimal trees were sampled every 1,000 generations to derive the final consensus tree and the respective associated probabilities. The visualization of this tree was achieved using FigTree v1.4.2 $^{30}$ .

#### Results

# Taxonomic hierarchy

Class Insecta Linnaeus, 1758, Order Hemiptera Linnaeus, 1758, Family Reduviidae Latreille, 1807, Subfamily Triatominae Jeannel, 1919, Tribe Triatomini Jeannel, 1919.

Genus Hospesneotomae n. gen. Paiva, Oliveira and Rosa 2024 (Figs. 1, 2, 3, 4, 5, 6 and 7).

[urn:lsid:zoobank.org:act:8A03CBF0-12B2-4324-BA08-F0219B9F2634]

Type species: Hospesneotomae protracta (Uhler, 1894), new combination, by original designation.

**Diagnosis:** It may be separated from *Triatoma*, which seems to be the closer genus, especially by its characteristic fusiform body; short oval head with the upper surface of the head evenly convex above; anteocular region 2–3 times longer than postocular; shorter legs; ocelli not elevated about the dorsal surface of the head, and by the combination of the characteristics presented in supplementary Table 1 and the key established in Discussion, which also include differences between *Hospesneotomae* n. gen. and *Paratriatoma*, another genus with which the new genus has similarities too (item 4.2.1).

**Description:** Coloration. General coloration brown to black. Brown to black pronotum, uniformly colored or spotted, with straight lateral edges. Pleura uniformly dark-brown. The hemelytron presents the clavus dark-brown or yellowish, the apical part may present the same color of the hemelytron or to have a dark spot over it. The corium is uniformly of the same general color of the hemelytron or has a central black spot.

Structure and Vestiture. The body surface clothed with setae, mainly on the head, pronotum and sternites. Head with integument granulose in different degrees, ovoidal in shape (similar to *Paratriatoma*), conspicuously convex. Head approximately twice as long as wide across the eyes. Anteocular region slightly less than three times as long as postocular. Maxillary plates narrowly tapered apically, not attaining level of apex of clypeus. Ocellar tubercle undeveloped. Eyes in lateral view attaining or slightly surpassing the levels of ventral but not attaining level of dorsal surfaces of the head, respectively. Antenniferous situated behind middle portion of anteocular region of head. The scape almost reaches the apex of the clypeus. The first visible segment of the labium reaches the apex of the antenniferous and the second visible exceeds the lower eye level and reaches the level of the neck. The second visible segment of the labium is longer than the others, and the last is the shortest, tapering. Labium with short setae becoming progressively longer toward apex of second visible segment. Pronotum: integument rugose; narrow anteriorly, becoming wider posteriorly. Anterolateral angles rounded apically; discal tubercles clearly defined, Anterior lobe without lateral tubercles. Humeral angles rounded. Scutellum with central portion slightly depressed, limited by sinuous carinae; apical process very short, tapering distally. Legs setose, rather short; coxae globose; femora and tibiae short and robust, most commonly uniformly colored. Abdominal sternites conspicuously setose.

Distribution: United States of America, Mexico, Guatemala, Honduras, Nicaragua, and Costa Rica.

**Etymology:** The new genus name "*Hospesneotomae*" is composed of the Latin substantival prefix "*Hospes*", meaning "the host", and *Neotoma*, the genus of rodents with which these species are strongly associated<sup>2,9,12,13</sup>.

#### Taxa included

Hospesneotomae protracta (Uhler, 1894), n. comb. (Fig. 1)

Type material examined: Holotype [female]: [printed label]: S. Diego, Cal // [handwritten and printed red label]: U.S.N.M Type no. 24713 // [handwritten label]: Conorhinus protractus Cal. Uhler // [printed label]: P R Uhler Collection// [Printed label]: USNM\_ENT UCR\_ENT 00008124 QR CODE; Additional specimen [Male]: [printed label] Triatoma protracta (Uhler, 1894) CTA 158 JMSBC UNESP/Araraquara.

Distribution: Mexico and Unites States of America.

# Remarks:

Species described from specimens from Lower and Southern California (Uhler, 1894). Its known distribution ranges from southwestern USA to northern Mexico in the Nearctic region <sup>10,12</sup>.

Uhler<sup>31</sup> detailed that the notches of the abdomen segments were marked by a pale streak, lighter brown underside, minutely wrinkled. Specimens range from black to light brown<sup>9,18</sup>. Almost 70 years later, five subspecies were described based on geographic distribution, hybridization studies, and morphological attributes, mainly the coloration of the specimens<sup>9</sup>, reflecting their polymorphic specific character. Galvão et al.<sup>32</sup> synonymized these subspecies but without a justification. Therefore, the validity (or not) of these subspecies should be studied more deeply in the future.

Hospesneotomae incrassata (Usinger, 1939), n. comb. (Fig. 2)

Type material examined: Holotype [male]: [printed and handwritten label]: California Academy of Sciences Type No. 4612 // [handwritten red label]: Holotype *Triatoma incrassata* Usinger// [handwritten label]: Dissected by Ryckman // [handwritten label]: Valley of Mexico VIII-1929// [handwritten label]: Pres. by E. C. VanDyke Collector // [handwritten label]: Mrs. Y. Mexis Collector; Additional specimen [Male]: [printed label] *Triatoma incrassata* Usinger, 1939 Macho CTIOC 5426.

Distribution: Mexico and United States of America.

#### Remarks:

According to Usinger<sup>18</sup>, this species can be recognized by its large eyes, small head, and very robust clypeus. The species has a limited range, having only been found in Sonora, Mexico (Type locality: Valle de México), and Arizona, USA<sup>9</sup>. This species has sparse data and few occurrence records. Currently, atypical forms (such as the pale-colored edge of the connexivum) of *H. protracta*, n. comb. can easily be mistaken for *H. incrassata*, n. comb., especially in unrevised popular databases like iNaturalist, highlighting the challenges in accurate species identification. The population of Southeast Arizona was known as *Triatoma incrassata apachensis* Ryckman, 1962. Later on, it was synonymized since Ryckman's differential characters were insufficient to keep it classified as subspecific<sup>2</sup>.



**Fig. 1.** The type of *Hospesneotomae protracta* comb. nov. (Uhler, 1894), deposited in U.S.N.M—National Entomological Collection, Smithsonian Institution, Washington, DC. (**A**) Dorsal view, (**B**) lateral view, (**C**) ventral view, (**D**) label of the specimen.



**Fig. 2.** The Holotype of *Hospesneotomae incrassata* comb. nov. (Uhler, 1894), deposited in CAS—California Academy of Sciences, San Francisco, USA. (**A**) Dorsal view, (**B**) lateral view, (**C**) label of the specimen. Christopher Grinter and Rachel Diaz-Bastin provided the photography. Also available at: https://monarch.calacademy.org/imagelib/search.php.

Hospesneotomae barberi (Usinger, 1939), n. comb. (Fig. 3)

Type material examined: Holotype [male]: [printed and handwritten label]: California Academy of Sciences Type No.4610 // [handwritten and printed red label]: Holotype *Triatoma barberi* Usinger// [printed label]: EPVanDuzee Collection // [handwritten label]: Cuernavaca Mex.; Additional specimens [Female]: [printed green label]: Coleção Rodolfo Carcavallo // [handwritten label]: Mexico, Guerrero, 1954 // [printed label]: CTIOC 4810; [Female]: [handwritten label]: Suporte 174 tubo 8 n°E6238// [handwritten label]: Totlan Taliso Mexico II-1973.

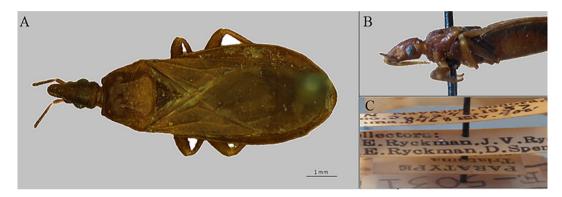
Distribution: Mexico.

#### Remarks:

It is endemic to Mexico, being found both in domestic and peridomestic habitats; has a very wide geographic distribution, a high infection rate, and is considered an important vector of Chagas disease in Mexico<sup>33</sup>. This species is very similar to *H. protracta*, n. comb., except for the reddish coloration of the connexivum<sup>18</sup>. *Hospesneotomae barberi*, n. comb. bears reddish-yellowish patterns on the connexivum and ranges in color from



**Fig. 3**. The holotype of *Hospesneotomae barberi* comb. nov. (Uhler, 1894), deposited in CAS—California Academy of Sciences, San Francisco, USA. (A) Dorsal view, (B) lateral view, (C) label of the specimen. Christopher Grinter and Rachel Diaz-Bastin provided the photography. Also available at: https://monarch.calacademy.org/imagelib/search.php.



**Fig. 4.** The *Hospesneotomae sinaloensis* comb. nov. (Uhler, 1894) (**A**) dorsal view of specimen deposited in CTIOC, (**B**) lateral view of Paratype, deposited in CER, (**C**) label of the specimen.



**Fig. 5.** The Holotype of *Hospesneotomae peninsularis* comb. nov. (Uhler, 1894), deposited in CAS—California Academy of Sciences, San Francisco, USA. (**A**) Dorsal view, (**B**) lateral view, (**C**) label of the specimen. Christopher Grinter and Rachel Diaz-Bastin provided the photography. Also available at: https://monarch.calacademy.org/imagelib/search.php.

piceous to black. The head is strongly convex. The postocular region is half as long as the anteocular region. The scape is extremely short, extending just the distance equivalent to two-thirds between the base and level of the apex of the clypeus. The pronotum is trapezoidal and entirely black.

Hospesneotomae sinaloensis (Ryckman, 1962), n. comb. (Fig. 4)

Type material examined: Paratype [male]: [printed and handwritten label]: Li.mi.N Navajoa, Sonora. Mexico. Jul. 24. 1957. Neotoma. 8468 Elv. 400// [printed label]: Collectors R.E. Ryckman, J. V. Ryckman, A. E. Ryckman, D. Spencer // [printed label]: PARATYPE *Triatoma sinaloensis* R.E.Ryckman// [printed label]: E-5031; Additional



Fig. 6. The holotype of Hospesneotomae neotomae comb. nov. (Uhler, 1894), deposited in U.S.N.M—National Entomological Collection, Smithsonian Institution, Washington, DC. (A) Dorsal view, (B) lateral view, (C) ventral view, (D) label of the specimen.



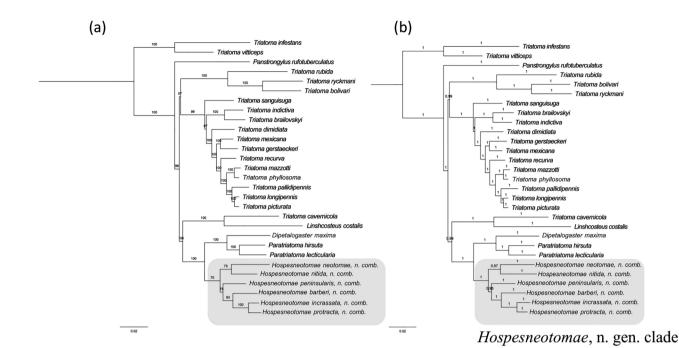
Fig. 7. The paratype of Hospesneotomae nitida comb. nov. (Uhler, 1894), deposited in U.S.N.M—National Entomological Collection, Smithsonian Institution, Washington, DC. (A) Dorsal view, (B) lateral view, (C) ventral view, (D) label of the specimen.

specimen [Male]: [handwritten label] Rodolfo Carcavallo Det. 1969 // [printed label]: Mexico, Sinaloa, Mocorito // [printed label] CTIOC 5191.

Distribution: Mexico.

#### Remarks:

Hospesneotomae sinaloensis, n. comb. occurs in the coastal belt west of the Sierra Madre Occidental mountains in the Mexican states of Sinaloa and Sonora, where the type of material was collected<sup>9,34</sup>. The holotype that was reported as being deposited in the entomological collection of the California Academy of Sciences has not been located.



**Fig. 8.** Phylogenetic trees inferred from concatenated sequences of UCE, mtDNA, and rRNA for 29 Triatominae terminals. *Hospesneotomae* gen. nov is consistently recovered as monophyletic with high support. Maximum Likelihood (ML) inference was conducted with 200 bootstrap replicates, with numbers above branches indicating bootstrap support values. Bayesian inference (BI) was performed with two independent runs using default settings, each utilizing one cold chain and three heated chains over 10 million Monte Carlo Markov Chain (MCMC) generations.

Unlike *H. protracta*, n. comb., the head is not depressed in the region of the posterior clypeal suture (Sup. Figure 1). General body color is light to dark brown, polished; It is the smallest species of the genus. Abdomen light to dark mahogany brown, without longitudinal or transverse bands on connexivum. Median ventral lamella distinctive<sup>9</sup>. Unfortunately, there is still no molecular data to characterize the species. Morphologically, it is very similar to *H. peninsularis*, n. comb., making it difficult to distinguish them in this regard. It is assumed, for all the reasons listed, that *H. sinaloensis*, n. comb. is part of the new genus.

Hospesneotomae peninsularis (Usinger, 1940), n. comb. (Fig. 5)

Type material examined: Holotype [male]: [printed and handwritten label]: California Academy of Sciences Type No.4973 // [handwritten and printed red label]: Holotype *Triatoma peninsularis* R.L.Usinger// [handwritten label]: *Triatoma peninsularis* Usinger Det. By R.L.Usinger// [printed label]: 20 mi. N.W. La Paz, L. Cal. VII-16–38// [printed label]: Michelbacher & Ross Collectors; Allotype [female]: [handwritten label]: det. Usinger 1950// [printed label]: Alotipo// [printed label]: n° 2759, Col.16/7/38. Coleção Herman Lent; Additional specimen [Male]: [printed label] Suporte 142 tubo 01 n°E5036 // [printed label]: Todos Santos T.S. Baja California. Mexico. Jul.57. [printed label]: Col. Ryckman, Spencer.

Distribution: Mexico.

#### Remarks:

Hospesneotomae peninsularis, n. comb. occurs in Baja California Sur, Mexico, and is primarily distinguished from *H. protracta*, n. comb. by the lack of a transverse arcuate groove behind the base of the clypeus and by the homogeneous dorsal surface of the head when viewed laterally. It is highly similar to *H. sinaloensis*, n. comb. corium brown. Abdomen black with indistinct transversal light markings on the posterior outer margin of connexival segments. Median ventral lamella distinctive<sup>9</sup>.

Hospesneotomae neotomae (Neiva, 1911), n. comb. (Fig. 6)

Type material examined: Holotype [male]: [printed and handwritten red label]: Type No. 04711 U.S.N.M. // [handwritten and printed label]: *Triatoma Neotomae* Neiva Det. HG Barber// [handwritten label]: Tipo // [handwritten label]: In nest of Neotoma micropus // [printed label]: HS Barber Collector// [Printed label]: Brownsville 22V04 Tex// [printed label]: Los Borregos // [printed label]: USNM\_ENT UCR\_ENT 00008119 QR CODE; Additional specimens: [Male]: [printed label] CTIOC 7094 // [handwritten label]: Las Animas. Dr. Cass N.L. Novembro 34.; [Male]: [printed label]: Suporte 140 Tubo 10 n°E5025// [handwritten label]: Texas USA. Reared R.E.Ryckman.

Distribution: Mexico and United States of America.

Remarks:

These species are distributed in the southwest of the USA and Mexico<sup>12,35</sup>. The anterior lobes of the pronotum are not very pronounced, as are the angles of the posterior portion, which are lighter in color. Middle part of pronotum crossed by two protruding, divergent striae. Scutellum with the same coloration as the pronotum. Corium yellowish, with a large dark spot in the middle and another compressed at the apex; membrane dark. Connexivum with black, median luteous spots. Legs and ventral surface of abdomen brown<sup>36</sup>.

Hospesneotomae nitida (Usinger, 1939), n. comb. (Fig. 7)

Type material examined: Paratype [male]: [printed and handwritten label]: *Triatoma nitida* Using det. HGBarber // [handwritten and printed red label]: Paratype No. 53749 USNM // [handwritten label]: 7236 // [printed label]: at light// [printed label]: FJDyer Coll // [printed label]: La Ceiba Honduras// [printed and handwritten label]: June 5-1916// [printed label]: USNMENT QR CODE 01334984; Additional specimens [Male]: CTIOC 5262, Guatemala, Coleção Rodolfo Carcavallo (4201).; [Female] CTIOC 5261, Guatemala, Coleção Rodolfo Carcavallo (4202).; [Male] Suporte 509 tubo 07 n°E12726. Paso Ancho Panamá?. 1967. Col. J. Gutierrez; [Female] Suporte 509 tubo 08 n°E12727.

Distribution: Costa Rica, Guatemala, Honduras, Mexico, and Nicaragua.

#### Remarks:

Hospesneotomae nitida, n. comb. is distributed in Central American countries and southern Mexico<sup>11,35</sup>. Rather large species, with polished surface, large eyes, short scutellum with extreme tip yellowish. Pronotum presents ochraceous lateral and anterior borders, as well as a loop on both sides of the anterior lobe disk. With an inner, smaller branch reaching to the central, deep depression, each loop extends posteriorly as a single line on a longitudinal carina to the level of transverse constriction. Additionally, a small Y-shaped mark extends from the lateral margin just behind the middle of the anterior lobe, dilating inwardly and obliquely posteriorly. Hemelytron is completely yellowish, except for the dirty, infuscate, or fumose membrane and the brown bases of the clavus, corium, and apex, except very narrowly along the border. Yellowish-colored connexivum with a noticeable, wide, black band crossing transversely across the center of each segment above and below<sup>18</sup>. When examining H. neotomae, n. comb. and H. nitida, n. comb. Lent and Wygodzinsky<sup>2</sup>, although have accepted the morphological differences described by Usinger, argued some doubt as to the validity of these species. Hospesneotomae neotomae, n. comb. differs morphologically from H. nitida, n. comb. by the disks of head and pronotum entirely brown, the venter only subflattened. The discal spot of the corium is relatively smaller in H. neotomae, n. comb. and the apical spot is not bordered with ochraceous<sup>18</sup>.

#### Comparative morphological study

The main morphological structures of *Paratriatoma*, *Triatoma* and *Hospesneotomae*, n. gen., were compared in order to show the differences between the three genera (Supplementary Table 1). The species of *Triatoma* possesses a subcylindrical head (supplementary Fig. 1); notable ventral connexival plates, though extremely small in some cases; only in micropterous females are the sides of the abdomen membranous, with a membrane joining the dorsal and ventral connexival plates. Although, the main characteristics that set *Paratriatoma* apart from species in *Triatoma*, are the ovoidal shape of the head, the absence of an arcuate interocellar sulcus, and the extremely setose body. An additional apomorphy is the separated membrane interpolated between the border of the connexival plate and the lateral edge of the urosternum. However, *Paratriatoma* shares derived characters with *Hospesneotomae*, n. gen., such as the fusiform body shape and unusually short legs, oval head, upper surface of head evenly convex above and, several species prey predominantly on wood rats of the genus *Neotoma*. The head of *H. sinaloensis*, n. comb. and *H. peninsularis*, n. comb. do not have an arcuate depression behind clypeus, differently from the other species of *Hospesneotomae*, n. gen. (supplementary Fig. 1).

#### Phylogenetics inference

In this study, 29 terminals representing six genera of Triatominae were successfully accessed, processed and analyzed using robust phylogenetic methods. The concatenated dataset, which included UCEs, mtDNA, and rRNA, resulted in a robust matrix. The matrix incorporated UCE data with 75% completeness, along with mtDNA and rRNA genes, yielding a total of 702,696 characters. The molecular phylogeny, constructed using Maximum Likelihood (ML) and Bayesian Inference (BI) methods, corroborated the hypothesis that *Hospesneotomae*, n. gen. constitutes a valid new genus within the Triatominae subfamily. Both analyses consistently revealed the monophyly of *Hospesneotomae*, n. gen. Notably, while the BI posterior probabilities (100) indicate high confidence in the monophyly of the group, the ML bootstrap values (maximum 70) are relatively low. Bootstrap values below 70 are generally considered to provide moderate support for a given clade.

Furthermore, the phylogenetic placement of *Hospesneotomae*, n. gen. in close proximity to the genus *Dipetalogaster* and *Paratriatoma* was consistently observed across both ML and BI topologies (ML 100, BPP 100), suggesting a closer evolutionary affinity between these two groups compared to other triatomine genera. This finding aligns with morphological evidence, which also points to a shared evolutionary history between *Hospesneotomae*, n. gen. *Dipetalogaster* and *Paratriatoma*. The intragenic relationships of the *Hospesneotomae*, n. gen. species show that *H. peninsularis*, n. comb., *H. barberi*, n. comb., *H. protracta*, n. comb., and *H. incrassata*, n. comb., are phylogenetically close. *Hospesneotomae nitida*, n. comb., and *H. neotomae*, n. comb., appear as close sister species from another clade.

# Dichotomous key

Key for genera

- 2. Head subcylindrical, sub-retilineous dorsoventrally, not flattened dorsoventrally, slightly less than twice as long as wide across eyes; anteocular region about 2.5 times as long as postocular; ocellar tubercle developed; maxillary plate with variable shape, which may reach or exceed the level of the apex of the clypeus; antenniferous situated at middle of anteocular portion of head; specimens with hemelytra far from reaching apex of abdomen or exceeding the apex of the abdomen; legs slender; speciose, widely distributed genus.......
- 2. Head oval, upper surface of head evenly convex above, twice as long as wide across the eyes; anteocular region slightly less than three times as long as postocular; ocellar tubercle vestigial; maxillary plate narrowly tapered apically, not attaining level of apex of clypeus; antenniferous situated behind middle of anteocular portion of head; Hemelytra almost attaining apex of abdomen, invariably; Legs short and stout; species restricted to North and Central America ........ Hospesneotomae, n. gen.

Key for species of Hospesneotomae, n. gen.

- 1'. Connexivum with more than a single color .......4
- 2. Head with arcuate depression dorsally behind clypeus, in lateral view; slightly elongate in side view, with eyes close to level of under surface of head; total length 13–23 mm. ......protracta (Fig. 1)
- 3. General color brown, found in Sinaloa and Sonora, Mexico .....sinaloensis (Fig. 4)
- 3. General color black, found in peninsula Baja California Sur, Mexico...peninsularis (Fig. 5)

- 5. Hemelytra uniformly dark colored; without dark spots on the corium...... barberi (Fig. 3)
- 5'. Corium of hemelytra with light and dark markings......6

#### Discussion

Currently, the genera Paratriatoma, Dipetalogaster and Triatoma include 84 species, approximately 40 of which are distributed in Central and North America<sup>5–7,37</sup>. The close relationship of the Hospesneotomae, n. gen. (formerly T. protracta complex) with the genera Paratriatoma, Triatoma and Dipetalogaster has been extensively investigated and evidenced<sup>2,9,14,16,38–42</sup>.

Usinger<sup>43</sup> proposed a "phylogenetic" key (elaborated based on morphological characters, which in this case does not take into account evolutionary changes) for the genera, separating *Triatoma* from *Paratriatoma* by the shape of the head, which is subcylindrical in *Triatoma* and, robustly convex above (subconical) in *Paratriatoma*, which recently included *Paratriatoma lecticularia* (Stål, 1859)<sup>44</sup>. In *Hospesneotomae*, n. gen. the head shape is oval, similar to *Paratriatoma*. However, *Paratriatoma* shares derived characters with *protracta* clade, such as the fusiform body shape and unusually short legs (see morphological characters in supplementary Table 1), as well as the host-relationship with *Neotoma*. The second hypothesis proposed by Lent and Wygodzinsky² was assumed, which postulates a sister group relationship between the *T. protracta* complex and *Paratriatoma*. Therefore, the *Hospesneotomae*, n. gen. receives a classification as a sister genus to *Paratriatoma*. It was shown through phylogenetic analyzes that the genera *Hospesneotomae*, n. gen. and *Dipetalogaster* and *Paratriatoma* form two sister clades and that the *T. rubrofasciata* (De Geer, 1773) clade (here represented by *Triatoma cavernicola* Else & Cheong, 1977 and *Linshcosteus costalis* Ghauri, 1976) is possibly closer than the *Triatoma phyllosoma* group (Fig. 8).

Were successfully accessed (Supplementary Table 2), processed and analyzed 29 terminals representing six genera of Triatominae using robust phylogenetic methods. Our results are consistent with previous studies, but there are some notable differences. While previous studies using ITS-2 and Cytb markers 40,45 revealed low support for sister group relationships within the Central and North American clade, our analysis using UCEs, mtDNA and rRNA provided stronger support for these relationships. Furthermore, our results corroborate Justi et al. 15 in identifying H. nitida, n. comb., and H. protracta, n. comb., as a sister clade to Paratriatoma, but we also observed a closer evolutionary affinity between Hospesneotomae, n. gen., Paratriatoma and Dipetalogaster in both ML and BI topologies, a finding that is in accordance with Kieran et al., 16. This consistency between different datasets and methods strengthens the case for *Hospesneotomae*, n. gen. as a distinct and valid genus. Furthermore, although previous studies<sup>41</sup> using BI and similar markers found different topologies with *Paratriatoma hirsuta* Barber, 1938 positioned more basally, our combined datasets showed the consistent placement of Hospesneotomae, n. gen. in close proximity to Dipetalogaster and Paratriatoma (Fig. 8), suggesting that the inclusion of UCEs provides a more resolved phylogeny. Intragenetic relationships of Hospesneotomae, n. gen. species show that H. peninsularis, n. comb., H. barberi, n. comb., H. protracta, n. comb., and H. incrassata, n. comb. are phylogenetically closer. An interesting finding from our study, not previously revealed by molecular studies, is the proximity between H. nitida, n. comb. and H. neotomae, n. comb. in all inferences. Although H. nitida lacks available UCE data, which may result in lower support values compared to inferences for other relationships, we analyzed widely used genes in Triatominae, with a well-described phylogenetic resolution. Hospesneotomae protracta, n. comb., H. barberi, n. comb., and H. incrassata, n. comb. form a more closely related clade, consistent with the described morphological similarities. It is relevant to note that *H. protracta*, n. comb. and *H. incrassata*, n. comb. appear as sister species, a result also supported by morphological similarities. Unfortunately, there is still no genetic data on H. sinaloensis, n. comb., but there is enough morphological evidence to classify it as a sister species of H. peninsularis n. comb.

In the context of triatomines, *Hospesneotomae protracta*, n. comb., *H. barberi*, n. comb., *H. sinaloensis*, n. comb., and *T. peninsularis*, n. comb. have the same number of diploid chromosomes in the males. The number of chromosomes of *H. neotomae*, n. comb. and *H. incrassata*, n. comb. remains unknown<sup>46</sup>. Effectively, *H. nitida* was reported to have 2n = 21 chromosomes, although a recent study erroneously indicated that *H. nitida* has the same number of chromosomes as other species in the genus<sup>47</sup>. Therefore, a new evaluation of the karyotype of *H. nitida*, n. comb. and the characterization of *H. neotomae*, n. comb. are necessary to elucidate the ancestral chromosomal conditions of this group.

The loss or gain of an X chromosome in the ancestors of the *Paratriatoma*, *Dipetalogaster* and *Hospesneotomae*, n. gen. clades may have resulted in cladogenetic events that generated *Hospesneotomae*, n. gen. through karyotypic modifications. Experimental crosses between *P. lecticularia* and *H. protracta*, *H. barberi*, *H. peninsularis* and *H. sinaloensis*, as well as between *H. barberi* and several other triatomine species (*Triatoma vitticeps* (Stål, 1859), *Triatoma sordida* (Stål, 1859), *Triatoma brasiliensis* Neiva, 1911, *Triatoma infestans* (Klug, 1834), *Triatoma eratyrusiformis* Del Ponte, 1929, *Rhodnius prolixus* (Stål, 1859), and *Panstrongylus megistus* (Burmeister, 1835)), did not produce offspring, indicating the presence of pre- or post-zygotic barriers in these experimental crosses<sup>9,34,48</sup>. On the other hand, experimental crosses between *H. protracta*, *H. barberi*, *H. sinaloensis* and *H. peninsularis* revealed reproductive compatibility, producing eggs, embryos, nymphs and sterile or fertile F1 generations. This suggests a recent common ancestor between these species<sup>13</sup>.

With the description of the new genus presented in this study, Triatominae (vectors of Chagas disease) now comprises nineteen genera. By integrative taxonomy it was verified that the species *H. barberi* n. comb., *H. incrassata*, *H. neotomae*, *H. nitida*, *H. peninsularis*, *H. protracta* and *H. sinaloensis* represent a new genus called *Hospesneotomae* n. gen., referring to the preferential sylvatic hematophagous habit of feeding on the *Neotoma* host.

### Data availability

All data required for the analysis performed in this manuscript are included in the manuscript or in the supplementary tables and figures. The holotypes are available for consultation in the collections listed in item 2.1 of the materials and methods. The molecular data was obtained from genbank and is open access, with the sequences listed in supplementary table 2.

Received: 1 October 2024; Accepted: 20 February 2025

Published online: 09 March 2025

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# Acknowledgements

Special thanks to Christopher Grinter and Rachel Diaz-Bastin of the California Academy of Sciences for providing photographs. Thanks also to Maria Anice Mureb Sallum for permission to consult specimens from the Entomological Reference Collection, USP. The authors are grateful to Talitta Guimarães Simões (Smithsonian National Museum of Natural History—NMNH) for support and provision of equipment to photograph the types, and to Dr. Thomas Henry (Smithsonian National Museum of Natural History—NMNH) for granting access to the specimens; they also thank Renan Carrenho for photographing a specimen label. Additional thanks to Dr. Patricia L. Dorn and José Manuel Ayala Landa for assistance with additional specimens.

# **Author contributions**

VFP, JO and JAR conceptualized and designed the study. VFP, TB, JO prepared materials, collected data and performed data analyses. VFP, JO prepared the first draft and revisions. TB, HRGS, CG critically reviewed the article. HRGS, CG, JAR supervised the study. All authors read and approved the final article draft.

# **Funding**

São Paulo Research Foundation – Fapesp, and National Council for Scientific and Technological Development–CNPq provided financial support to V.F. Paiva (2023/09822-5). Fapesp (23/01548-1) and CNPq (Process 317 358/2021-9) Research Productivity Grant for J.A. Rosa. Fapesp provided financial support to T. Belintani (23/15240-9). Fapesp provided financial support to J. Oliveira (19/02145-2).

# Competing interests

The authors declare no competing interests.

#### Additional information

**Supplementary Information** The online version contains supplementary material available at https://doi.org/1 0.1038/s41598-025-91399-w.

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