

## Short communication

# A primitive triatomine bug, *Paleotriatoma metaxytaxa* gen. et sp. nov. (Hemiptera: Reduviidae: Triatominae), in mid-Cretaceous amber from northern Myanmar

George Poinar Jr.

Department of Integrative Biology, Oregon State University, Corvallis, OR 97331, USA

## ARTICLE INFO

## Article history:

Received 10 March 2018

Received in revised form

22 August 2018

Accepted in revised form 4 September 2018

Available online 7 September 2018

## Keywords:

Triatominae

Mid-Cretaceous

Burmese amber

*Paleotriatoma metaxytaxa* gen. et sp. nov.

Gondwana

## ABSTRACT

The present study describes a primitive kissing bug (Hemiptera: Reduviidae: Triatominae) in mid-Cretaceous amber from northern Myanmar. The fossil, which is described as *Paleotriatoma metaxytaxa* gen. et sp. nov., contains a predominance of features of the Triatominae as well as some characters of the Reduviinae and is considered an intermediate fossil representing an early progenitor of the Triatominae. Based on the present distribution of the Triatominae and recent studies indicating that Burmese amber fossils could have originated in Gondwana, it is proposed that *Paleotriatoma metaxytaxa* is a Gondwanan lineage that evolved in the mid-Cretaceous. The specimen contains developing trypanosome flagellates in its hindgut, suggesting that early triatomines could have been vectoring pathogenic protozoa to vertebrates some 100 Ma.

© 2018 Elsevier Ltd. All rights reserved.

## 1. Introduction

The family Reduviidae (Hemiptera: Heteroptera), commonly called assassin bugs, is one of the most diverse groups of true bugs. While the members of most subfamilies attack only invertebrates, those of the subfamily Triatominae, often called kissing bugs, are notorious vertebrate feeders and many of the 147 known species vector pathogenic trypanosomes (Lent and Wygodzinsky, 1979; Galvão et al., 2003; Patterson and Guhl, 2010; Otálora-Luna et al., 2015; Galvão and Justi, 2018).

The hosts of triatomines are quite diverse and include mammals, birds, amphibians, reptiles and insects (Rabinovich et al., 2011). Since the Triatominae probably evolved from the Reduviinae, feeding on insects can be considered a primitive feature and the early triatomines probably fed on both insect and vertebrates (Weirauch and Munro, 2009). Likewise, the early vertebrate feeders would have been transitory forms that possessed morphological features of both the Triatominae and Reduviinae.

The present study describes an adult kissing bug in Burmese amber that possesses features of extant members of the Triatominae as well as some features of the Reduviinae. The specimen

is considered an intermediate fossil representing an early progenitor of the Triatominae. The only previous triatomine fossils are species of *Triatoma* Laporte and *Panstrongylus* Burg in mid-Tertiary amber from the Dominican Republic (Poinar, 2005, 2013).

Most of the five tribes of the Triatominae (Alberproseniini, Bolboderini, Cavernicolini, Rhodniini and Triatomini) are mainly American in origin with only a few endemic species occurring in Africa, India and Australia. Diversification of the subfamily in South America was considered to have been due to changes resulting from the Andean uplift and variations in sea levels in North America (Justi et al., 2016). Based on evidence that Burmese amber fossils originated in Gondwana and rafted to SE Asia in the Cretaceous (Poinar, 2018), it is proposed that triatomines evolved in Gondwana. This scenario is congruent with the present distribution of the subfamily with representatives in South America, Africa, India and Australia.

## 2. Materials and methods

The specimen originated from the Noije Bum 2001 Summit Site mine excavated in the Hukawng Valley and located southwest of Maingkhwan in Kachin State (26°20'N, 96°36'E) in Myanmar (Cruickshank and Ko, 2003, figs. 1–3). Based on paleontological evidence, this site was dated to the late Albian of the Early

E-mail address: [poinarg@science.oregonstate.edu](mailto:poinarg@science.oregonstate.edu).

Cretaceous (Cruikshank and Ko, 2003), placing the age at 97 to 110 Ma. A more recent study using U-Pb zircon dating determined the age to be  $98.79 \pm 0.62$  Ma or at the Albian/Cenomanian boundary (Shi et al., 2012). Nuclear magnetic resonance (NMR) spectra and the presence of araucaroid wood fibers in amber samples from the Noije Bum 2001 Summit Site indicate an araucarian tree source for the amber (Poinar et al., 2007). Observations and photographs were made with a Nikon SMZ-10 R stereoscopic microscope and Nikon Optiphot compound microscope with magnifications up to 800 $\times$ . Helicon Focus Pro X64 was used to stack photos for better depth of field.

### 3. Systematic paleontology

Characters presented by Schuh and Slater (1995), Weirauch et al. (2014) and Lent and Wygodzinsky (1979) were used to align the fossil with the Triatominae. These characters include: head lacking a transverse constriction behind the eyes, presence of ocelli on oblique cephalic elevations, antennae inserted on tubercles on lateral side of head, antennal segments 3 and 4 inserted on the apex of 2 and 3, respectively, antennal segment 2 with trichobothria, non-raptorial forelegs, membrane with closed cells and the presence of a simple cubitus.

A size greater than 5 mm with the ocelli positioned on the postocular portion of a subcylindrical head that is longer than wide, labium extending to stridulatory groove (sulcus) on the prosternum, and the second (first visible) labial (rostral) segment shorter than the third (second visible), would place the specimen in the Tribe Triatomini (Lent and Wygodzinsky, 1979). The fossil resembles extant triatomines possessing a comparatively short head with antenniferous tubercles positioned close to the eyes and the body bearing conspicuous long hairs (Lent and Wygodzinsky, 1979). Since the fossil cannot be assigned to an extant genus, it is described below in a new genus.

Reduviidae Latreille, 1807

Triatominae Jeannel, 1919

*Paleotriatoma* gen. nov.

LSID: 89G29B9C-51A9-4E85-8EDE-541E35C9324A

*Etymology.* The generic name is from the Greek “paleo” = old and the extant genus name, *Triatoma*.

*Type species.* *Paleotriatoma metaxytaxa* gen. et sp. n.

*Diagnosis.* short body; elongate head lacking constriction behind eyes; ocelli elevated on protuberances; long slender labium (rostrum); long straight body hairs; antenniferous tubercles located close to eyes; short first antennomere; lateral insertion of antennae close to apex of head; pedicel lacking pseudosegments, with trichobothria; head with four (three visible) labial segments, the first visible straight, shorter than the second visible segment, second visible segment with slight curve near tip, third visible straight, shortest of the three visible segments; pronotum constricted cephalad of middle with posterior lobe longer than anterior lobe, scutellum with short posterior process; fossula spongiosa on fore and mid tibia; fore tibia with comb; membrane with 2 closed cells, vein R+M separate from Sc.

*Paleotriatoma metaxytaxa* gen. et sp. n.

(Figs. 1–4)

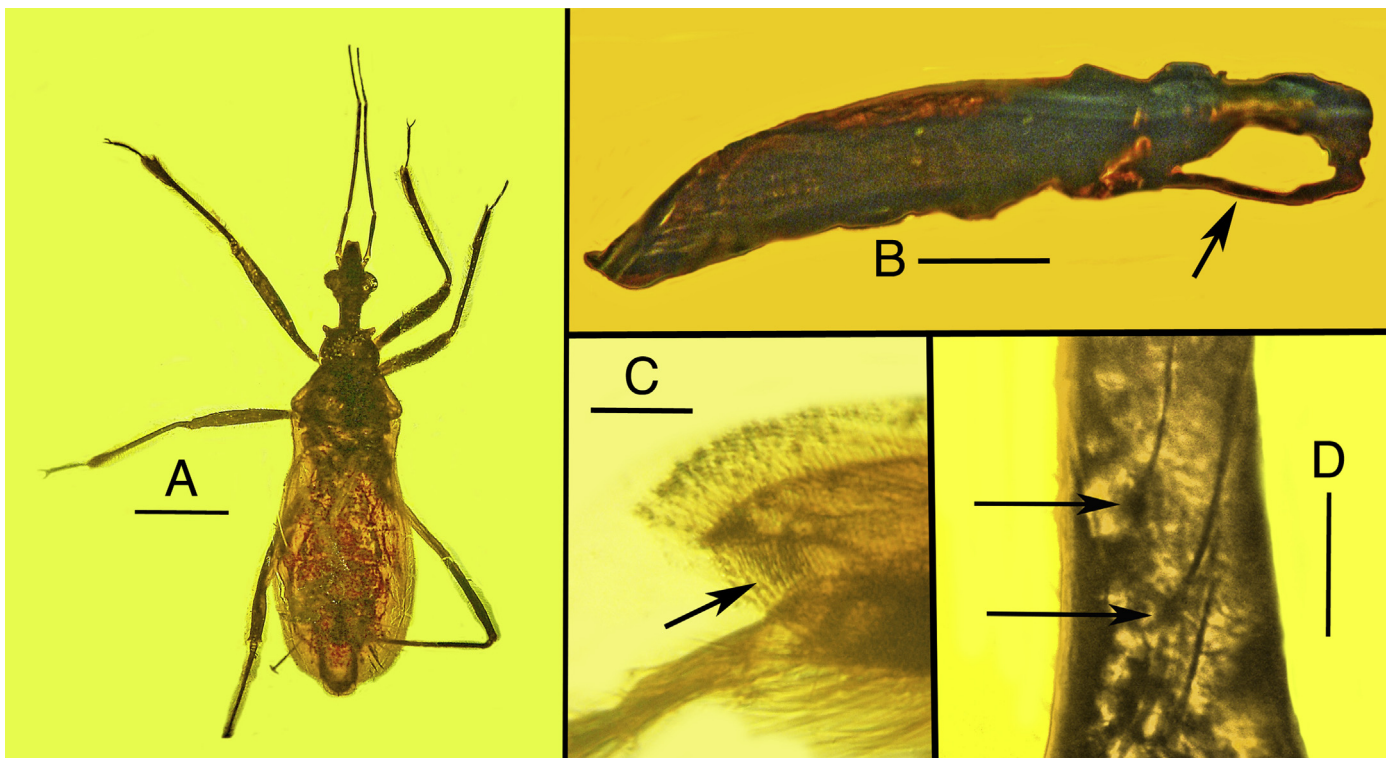
LSID: 2BC806B5-060E-47F5-B0AF-46F329DB93A4

*Included species.* Type species only.

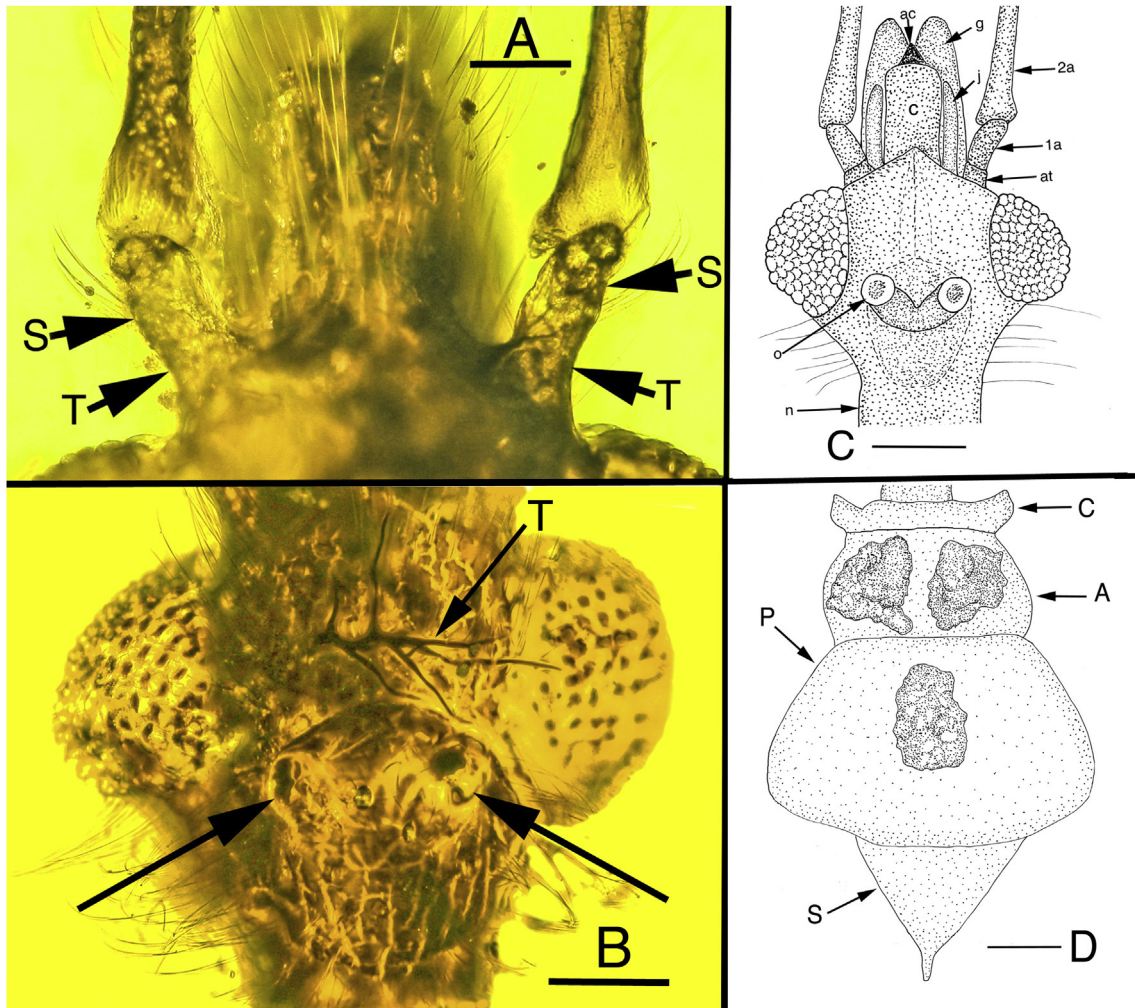
*Etymology.* The specific epithet is taken from the Greek “metxy” = between and the Greek “tasso” = arrange in reference to the intermediate state of the fossil.

*Type material.* Holotype male deposited in the Poinar amber collection (accession # B-He-28) maintained at Oregon State University.

*Type locality.* Hukawng Valley southwest of Maingkhwan in Kachin State (26°20'N, 96°36'E), Myanmar.



**Fig. 1.** *Paleotriatoma metaxytaxa* gen. et sp. nov. in Burmese amber. A. Holotype specimen. Scale bar = 1.6 mm. B. Lateral outline of body with appendages and antennae removed. Arrow shows rostrum. Scale bar = 1.3 mm. C. Protibial comb (arrow). Scale bar = 70  $\mu$ m. D. Pedicellar trichobothria (arrows). Scale bar = 37  $\mu$ m.



**Fig. 2.** *Paleotriatoma metaxytaxa* gen. et sp. nov. in Burmese amber. A. Dorsal view of anterior portion of head showing antenniferous tubercles (T) and first antennal segment (S). B. Dorsal view of posterior portion of head. Arrows show ocelli on elevation. T = plant trichome. Scale bar = 0.1 mm. C. Illustration of head. Ac = anteclypeus; at = antenniferous tubercle; 1a = first antennomere; 2a = second antennomere; c = clypeus; g = gena; j = jugum; o = ocellus; n = neck. Scale bar = 0.25 mm. D. Pronotum and scutellum of *Paleotriatoma metaxytaxa* gen. et sp. nov. in Burmese amber. A = anterior lobe with two callosities; C = collar; P = posterior lobe with single callosity; S = scutellum. Scale bar = 0.3 mm.

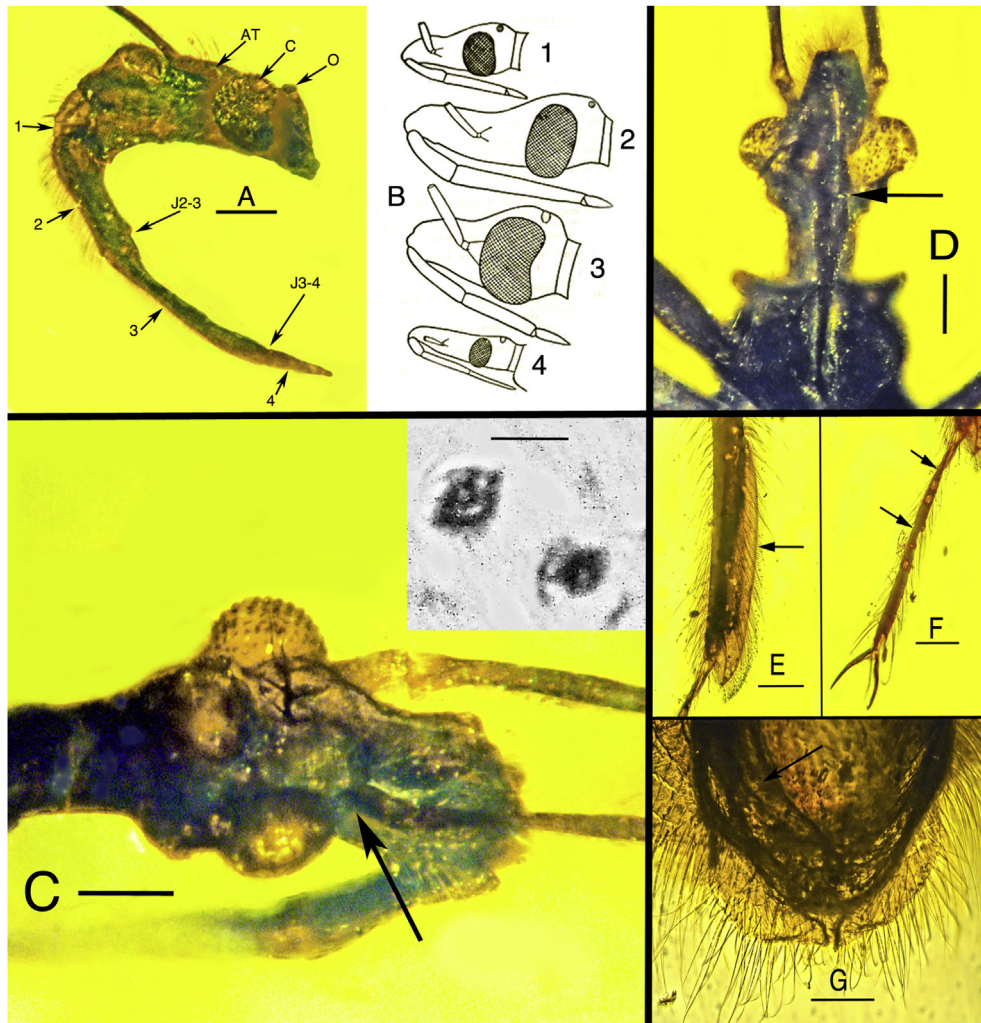
**Holotype male.** Body elongate, well-preserved and nearly complete, with only the tips of the 4th antennomeres and the claw on the right middle leg missing; length, 7.8 mm, broadest behind middle of abdomen; head, thorax and legs dark brown to black; abdomen reddish, body bearing erect hairs.

**Head.** (Figs. 1–3) brown, 1.5 as long as wide across eyes, length, 1.12 mm; width, 0.8 mm; antelocular region three times as long as postocular; clypeus 0.3 mm long, with flattened triangular anteclypeus; genae wide, extending beyond anteclypeus; jugae narrow, cylindrical, extending anterior of first antennomere; eyes large, semi-globular, diameter, 0.3 mm; interocular sulcus obsolete; callosities behind eyes lacking; ocelli large (diameter, 0.1 mm), elevated, situated on protuberances on oval elevated area of disc; antennae inserted laterally on short antenniferous tubercles positioned close to anterior border of eyes (Figs. 2 and 3); first antennomere very short (0.1 mm), not surpassing apex of clypeus; antennomere 2 simple, 0.7 mm long, lacking pseudosegments, with trichobothria; antennomeres three (1.8 mm long) and four (1.0 mm long but broken off at tip) filiform; labium (rostrum) elongate, slender (Figs. 1 and 3), tip extending to stridulatory groove on prosternum, with 4 segments: first segment reduced so only 3 are visible; first visible labial segment 0.6 mm long; second visible

labial segment 1.0 mm long, slightly curved at apex; third visible labial segment 0.3 mm long.

**Thorax.** (Figs. 1–3) Pronotum length, 1.6 mm, constricted cephalad of middle, with posterior lobe longer than anterior lobe, sides carinate, anterior lobe with 2 large rugose discal callosities, posterior lobe with central rugose callosity; humeri angulate, anterolateral angles obliquely directed forward; scutellum triangular with single short posterior process. Stridulatory sulcus present, length, 0.5 mm; anterolateral angles of collar prominent, width collar, 0.8 mm, length collar, 0.1 mm; legs slender, anterior coxae only slightly longer than wide, fore femur subapically with 2 small denticles on lower surface, foretibial comb present. Tarsi 3-segmented; claws paired, simple, without basal tooth; pretarsus bearing two bristle-like parempodia; length foreleg segments: profemur 2.3 mm; protibia 2.0 mm; protarsus, 0.3 mm; length midleg segments: mesofemur, 2.3 mm; mesotibia, 2.4 mm; mesotarsus, 0.3 mm; length hind leg segments: metafemur, 3.8 mm; metatibia, 2.3 mm; metatarsus, 0.3 mm; all femora, tibiae and tarsi setaceous. Fore and mid tibia with fossula spongiosa approximately 1/3 as long as tibia, with free apex shorter than first tarsal segment. Hemelytra (length, 5.1 mm) attaining apex of abdomen; membrane with 2 closed cells, vein R+M separate from Sc.





**Fig. 3.** *Paleotriatoma metaxytaxa* gen. et sp. nov. in Burmese amber. A. Lateral view of head. Arrows with numbers refer to labial segments 1–4. AT = antenniferous tubercle; C = compound eye; O = ocellus; J2-3 = joint between second and third labial segments; J3-4 = joint between 3rd and 4th labial segments. Scale bar = 0.3 mm. B. Variation in male head shapes of extant species of triatomines: **1** = *Triatoma rubrofasciata* (De Geer) **2** = *Triatoma tibiamaculata* Pinto; **3** = *Panstrongylus megistus* (Burmeister); **4** = *Triatoma nigromaculata* (Stål). Images modified from Pinto (1931). C. Dorsal-lateral view of head showing lateral attachment of antennae. Arrow shows attachment point of right antenna on side of head. Scale bar = 0.23 mm. Insert shows 2 partial integument glands of the fossil. Scale bar = 7  $\mu$ m. D. Ventral view of head showing labium (arrow) Scale bar = 0.27 mm. E. Fossula spongiosa (arrow) at base of fore tibia. Scale bar = 0.1 mm. F. Foretarsus. Arrows show joints separating segments. Scale bar = 0.1 mm. G. Lower portion of pygophore with parameres. Arrow shows possible phallus inside pygophore. Scale bar = 150  $\mu$ m.

**Abdomen.** (Figs. 1 and 3). Ovoid, reddish, length, 4.8 mm, with faint dorsal connexival segments. Venter bearing long erect setae; eighth urotergite widely rounded behind; pygophore distinct, with paired terminal parameres.

**Comments.** Several of characters of *Paleotriatoma metaxytaxa* gen. et sp. nov. are synapomorphic for the Triatominae, including the elongate head lacking a constriction behind the eyes, ocelli elevated on protuberances, long slender labium, pedicel lacking pseudo-segments, pronotum constricted cephalad of middle with posterior lobe longer than anterior lobe, scutellum with short posterior process, wing membrane with 2 closed cells, vein R+M separated from Sc and the presence of fossula spongiosa on the fore and mid tibia (Lent and Wygodzinsky, 1979; Schuh and Slater, 1995; Weirauch et al., 2014). Long straight body hairs similar to those of the fossil occur on members of the genus *Paratriatoma* Barber. Antenniferous tubercles positioned close to the eyes occur in members of the genera *Panstrongylus* Berg, *Cavernicola* Barber, *Paratriatoma* Barber and *Triatoma* Laporte. Other features of *Cavernicola* that resemble those of the fossil are the small size (under 13 mm in length), the head barely twice as long as wide and a short

first antennomere (Lent and Wygodzinsky, 1979). The fossil also shares its small size, reduced first antennomere, position of antenniferous tubercles and fossula spongiosa with members of *Microtriatoma* Prosen and Martínez.

Some “flower-shaped” pores occur on the integument of the fossil (Fig. 3C, insert). These pores resemble those of the dermal glands on the extant *Eratyus mucronatus* (Weirauch, 2008). According to this author, ornamented pores are a synapomorphy of the Triatominae.

While extant triatomines normally have a straight labium, the rostrum of *Paleotriatoma metaxytaxa* has a slight bend. While this is likely a feature carried over from its Reduviinae ancestors, some triatomines, such as *Panstrongylus rufotuberculatus* (Champion) and *Triatoma circummaculata* (Stål) 1859 do have a slight bend of the rostrum (Lent and Wygodzinsky, 1979). The shape and length of the head and labium of triatomines vary considerably (Fig. 3B).

Several characters, such as the very short first antennomere, head shape and wing venation, are diagnostic for *Paleotriatoma*. While adult male triatomines normally have fossula spongiosa on

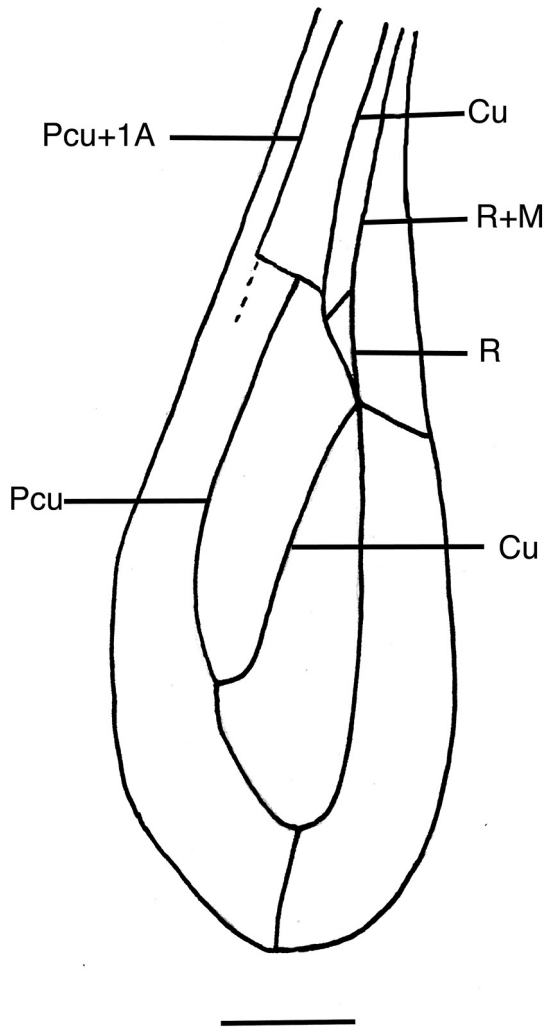


Fig. 4. Hemelytra of *Paleotriatoma metaxytaxa* gen. et sp. nov. in Burmese amber. Scale bar = 0.7 mm.

the fore and middle tibia (Usinger, 1943), they are usually not as extended as in the present fossil. This feature, along with the head declivity and slight bend at the tip of the second visible labial segment are symplesiomorphic characters that the fossil shares with members of the Reduviinae and show the intermediate status of *Paleotriatoma* (Lent and Wygodzinsky, 1979; Schuh and Slater, 1995; Weirauch et al., 2014).

**Trypanosomes.** Areas within the hindgut lumen of *Paleotriatoma* are occupied by flagellates considered to represent primitive trypanosomatids (Fig. 5). Different morphological types were present with the most elongate ones reaching 25  $\mu\text{m}$  in length. These elongate forms with a centrally located nucleus and a single, anteriorly directed flagellum correspond to trypomastigote stages illustrated in Vickerman (2000). The length of the trypomastigotes falls within the range of extant species of the subgenus *Schizotrypanum* Chagas (17–24  $\mu\text{m}$ ) of the genus *Trypanosoma* Gruby (Hoare, 1972). It is not known if these are monogenetic trypanosomes that are known to occur in the gut of some Reduviinae and were carried over from the ancestor of *Paleotriatoma* or if the trypanosomes are digenetic forms that are found today in triatomines and are transferred to vertebrate hosts (Wallace, 1966; Cerisola et al., 1971; Vickerman, 2000). Aside from the presence of *Trypanosoma cruzi* in Mexican and South and Central American

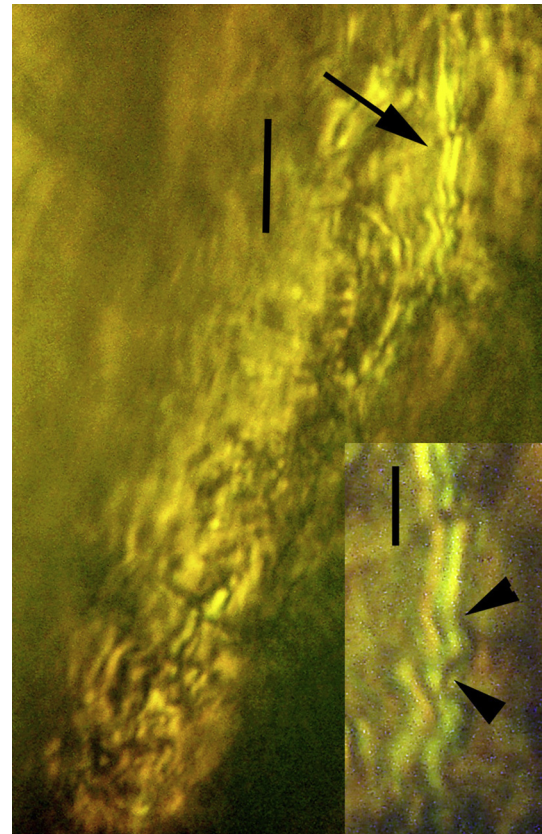


Fig. 5. Trypanosomes in the hindgut of *Paleotriatoma metaxytaxa* gen. et sp. nov., in Burmese amber. Arrow shows elongate flagellates in situ. Scale bar = 850  $\mu\text{m}$ . Insert shows detail of several flagellates. Upper arrowhead shows darker nuclear area. Lower arrowhead shows attenuated terminus. Scale bar = 11  $\mu\text{m}$ .

populations of *Triatoma*, *Dipetalogaster*, *Rhodnius*, *Panstrongylus* and *Meccus* (Patterson and Guhl, 2010), trypanosomatid flagellates with epimastigotes and small metacyclic trypomastigotes have also been found in representatives of the Indian triatomine, *Linshcosteus* sp. (Patterson et al., 2001A). While no flagellates have been reported from the Australian *T. leopoldi* (Schouteden), an isolate from an Australian kangaroo was aligned with the “*T. cruzi*” clade (Stevens and Gibson, 1999). This suggests that *T. leopoldi* or still undiscovered Australian triatomines are transmitting trypanosomes to mammals.

#### 4. Discussion

*Paleotriatoma metaxytaxa* gen. et sp. nov. is regarded as an intermediate fossil bridging the gap between the invertebrate predatory Reduviinae and the vertebrate feeding Triatominae. Intermediate fossils normally contain both plesiomorphic and derived features. An example is the Burmese amber bee, *Melittosphex burmensis* Poinar and Danforth, 2006, which has some bee characters, but also two ancestral wasp features (Danforth and Poinar, 2011). The presence of ocelli, 3-segmented tarsi, 2 closed cells on the forewing membrane, slight bend in the labium and fossula spongiosa on the fore and mid tibiae suggest that *Paleotriatoma* evolved from a lineage of the subfamily Reduviinae. This scenario was proposed earlier by Ryckman (1986) and Wygodzinsky and Usinger (1964).

As a group, the fossil record of the Reduviidae date back to the Jurassic/Cretaceous boundary (Rasnitsyn and Quicke, 2002) when



they were evolving as efficient invertebrate predators. Using a fossil-calibrated molecular tree, Hwang and Weirauch (2012) concluded that the Reduviidae originated in the Middle Jurassic, with further lineage diversification occurring around the mid-Cretaceous (ca. 97 Ma). This latter date agrees with earlier molecular clock studies indicating that the Triatominae evolved between 93.5 and 109 Ma (Gaunt and Miles, 2002; Patterson and Gaunt, 2010). These dates are congruent with the age of the amber containing *Paleotriatoma*.

Both Hwang and Weirauch (2012) and Justi et al. (2016) postulated that the Triatominae evolved in South America in the Oligocene or Eocene when that continent was essentially isolated from the other Gondwana continents (Smith et al., 2004). However this scenario would not explain the presence of endemic triatomines in Australia, Africa and India.

While the subfamily has a basic Gondwanan distribution (Fig. 6), the center of diversity of the Triatominae is in tropical-subtropical South America, with some species having entered southwestern United States through Mexico, the Caribbean and Central America. Localities in North America, Mexico and Central America indicate migration points from ancestral sites in South America (Usinger et al., 1966). An example of the latter is *Dipetalonema maximum* (Uhler) (Fig. 7A) that lives in a restricted dry habitat at the southern tip of Baja California where it feeds mainly on lizards. This lineage probably was carried to this site on the feet of seabirds since the Chilean species, *Triatoma spinolai* Porter, has been observed to feed on the legs and feet of guano birds nesting on coastal cliffs (Lent and Wygodzinsky, 1979).

The Australian *Triatoma leopoldi* (Fig. 7B) is endemic to refugia in Queensland, New Guinea, Sulawesi and Biak (Monteith, 2015) and members of the genus *Linshcosteus* Distant occur on the Indian subcontinent (Lent and Wygodzinsky, 1979; Galvão et al., 2002, 2003). *Triatoma africana* Neiva, 1911 and *Triatoma howardi* Neiva, 1911 were described as endemic species native to tropical Africa that were collected during the Emin Pascha expedition (Neiva, 1911). While both species were later transferred to the genus *Panstrongylus* Berg by Pinto (1931), their African status was recognized by Hussey (1922), Pinto (1931) and Usinger (1944). *Triatoma rubrofasciata* (De Geer) is tropicopolitan, presumably as a result of human transportation (Ryckman and Archbold, 1981). Analyses of this species as well as seven other Old World related forms indicate that they have a New World ancestry and the dissemination of this group of related species in the Old World was deduced to have occurred within the past 350 years (Patterson

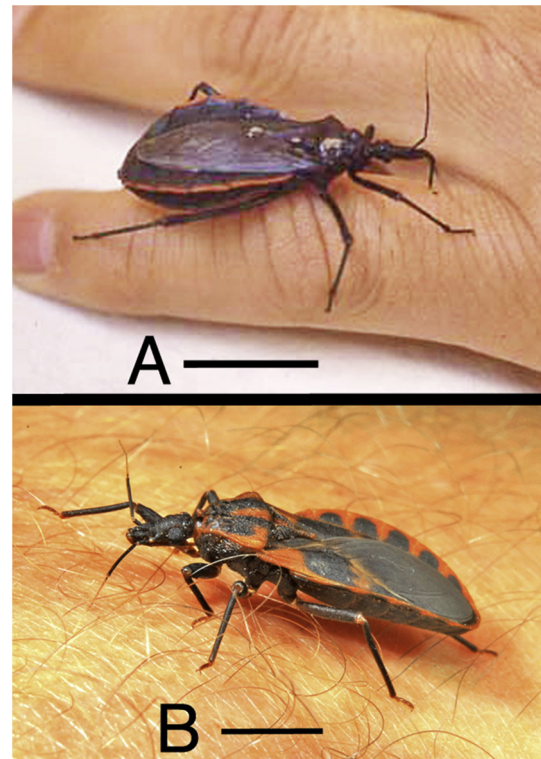


Fig. 7. A. Restricted to the southern tip of Baja California, *Dipetalogaster maximum* represents a species arriving at its present location by dispersal events. Scale bar = 18 mm. B. *Triatoma leopoldi* from Queensland, Australia, is also endemic to refugia in New Guinea, Sulawesi and Biak. Photo by Eric Vanderduys, courtesy of Geoff Monteith. Scale bar = 7.5 mm.

et al., 2001B). No endemic species of triatomines have been reported from Myanmar.

Evidence has been presented that the Burmese amber mines are located on the West Burma Block that rafted from Australia to SE Asia in the Early to mid-Cretaceous (Poinar, 2018). Based on these premises and the present distribution of the Triatominae, it is proposed that *Paleotriatoma* originated in Gondwana. Triatomine lineages in Gondwana may have been widely distributed on that supercontinent, explaining how many species now occur in South America. Some could have occupied the Greater India Plate when it



Fig. 6. Map showing worldwide distributions of extant members of the Triatominae (stars). Taxa that occur outside regions of Gondwana origins, such as North and Central America, Mexico and the Antilles, are depicted by outlined markers and their presence is attributed to dispersal events from Gondwana regions.

departed from Gondwana in the Early to mid-Cretaceous. The Greater Indian Plate was never completely submerged (Funnell, 1990; White, 1994; Smith et al., 2004) and could have carried early lineages of triatomines. This would explain the disjunct distribution between the endemic Indian genus *Linshcosteus* and the South American triatomines. It would also explain why *Linshcosteus* has a New World ancestry (Patterson et al., 2001A) and why the *Linshcosteus* clade is considered to be a basal-most lineage of the Triatomini (Hypsa et al., 2002).

The presence of trichomes in the amber adjacent to the fossil (Fig. 2B) suggests that *Paleotriatoma* had arboreal habits. It may have had a life style similar to *Triatoma sanguisuga* (Leconte) that rests under loose bark and feeds on tree frogs. *Belminus herreri* Lent and Wygodzinsky is another arboreal triatomine that lives under the bark of trees and feeds on lizards (Ryckman, 1986). In Brazil, *Triatoma sordida* (Stål) occurs in bromeliads and hollow trees and *T. pseudomaculata* Corrêa and Espínola is found under tree bark (Galvão and Justi, 2018).

Since extant triatomines feed on amphibians, reptiles, birds, mammals and insects (Schofield, 1979; Schofield and Galvão, 2009; Otálora-Luna et al., 2015), the host or hosts of *Paleotriatoma* could have been any number of vertebrates, including avian and non-avian dinosaurs. There is a good possibility that *Paleotriatoma*, in its intermediate state, fed on both invertebrates and vertebrates, similar to some extant species of *Triatoma* (Schofield and Galvão, 2009).

If the trypanosomes in the hindgut of *Paleotriatoma* were digested forms, it would support the proposal that this transitory fossil was a vertebrate feeder and could have been vectoring flagellates to its hosts, much in the same manner as South American triatomines vector *Trypanosoma cruzi*. It is interesting that a *Trypanosoma* sp. obtained from an Australian kangaroo was aligned with the “*T. cruzi*” clade (Stevens and Gibson, 1999), indicating that not only the Triatominae but also this clade of trypanosomes had their origin on Gondwana.

## 5. Conclusions

Evidence is provided why *Paleotriatoma metaxytaxa* gen. et sp. nov. is considered to be an intermediate fossil between the Triatominae and the Reduviinae. While containing some features of the Reduviinae, many characters of *Paleotriatoma metaxytaxa* gen. et sp. nov. occur in members of the subfamily Triatominae (Lent and Wygodzinsky, 1979; Schuh and Slater, 1995; Weirauch et al., 2014). Based on the fossil and present distribution of the Triatominae, it is proposed that this subfamily evolved in Gondwana in the Early Cretaceous with *Paleotriatoma* representing one of the progenitors. Members of the subfamily were then carried to SE Asia on the Greater Indian Plate, thus explaining the presence of triatomines almost exclusively limited to the Gondwanan lands of Australia, Africa, India and South America.

## Acknowledgments

The author thanks Alex Brown for donating the specimen to the Poinar amber collection, Eric Vanderduys for taking the photograph in Fig. 7B, Geoff Monteith for supplying the photograph and literature on *Triatoma leopoldi*, and Roberta Poinar for reviewing earlier drafts of the manuscript. Thanks are also extended to the reviewers whose comments greatly improved the paper.

## References

Cerisola, J.A., Del Prado, C.E., Rohwedder, R., Bozzini, J.P., 1971. *Blastocrithidia triatomae* n. sp. found in *Triatoma infectans* from Argentina. *Journal of Protozoology* 18, 503–506.

- Cruickshank, R.D., Ko, K., 2003. Geology of an amber locality in the Hukawng Valley, northern Myanmar. *Journal of Asian Earth Sciences* 21, 441–455.
- Danforth, B.D., Poinar Jr., G.O., 2011. Morphology, classification, and antiquity of *Melittospheex burmensis* (Apoidea: Melittosphecidae) and implications for early bee evolution. *Journal of Paleontology* 85, 882–891.
- Funnell, B.M., 1990. Global and European Cretaceous shorelines, stage by stage. In: Ginsburg, R.N., Beaudoin, B. (Eds.), *Cretaceous Resources, Events and Rhythms*. Kluwer Academic Publishers, The Netherlands, pp. 221–235.
- Galvão, C., Justi, S.A., 2018. An overview on the ecology of Triatominae (Hemiptera: Reduviidae). *Acta Tropica* 151, 116–125.
- Galvão, C., Patterson, J.S., da Silva Rocha, D., Jurberg, J., Carcavallo, R., Rajen, K., Ambrose, D.P., Miles, M.A., 2002. A new species of Triatominae from Tamil Nadu, India. *Medical and Veterinary Entomology* 16, 75–82.
- Galvão, C., Carcavallo, R., da Silva Rocha, D., Jurberg, J., 2003. A checklist of the current valid species of the subfamily Triatominae Jeannel, 1919 (Hemiptera, Reduviidae) and their geographical distribution, with nomenclatorial and taxonomic notes. *Zootaxa* 202, 1–36.
- Gaunt, M., Miles, M., 2002. An insect molecular clock dates the origin of the insects and accords with palaeontological and biogeographic landmarks. *Molecular and Biological Evolution* 19, 748–761.
- Hoare, C., 1972. *The Trypanosomes of Mammals*. Blackwell Scientific Publications, Oxford, p. 749.
- Hussey, R.F., 1922. A bibliographical notice on the reduviid genus *Triatoma* (Hemip.). *Psyche* 29, 109–123.
- Hwang, W.S., Weirauch, C., 2012. Evolutionary history of assassin Bugs (Insecta: Hemiptera: Reduviidae): insights from divergence dating and ancestral state reconstruction. *PLoS One* 7 (9), e45523. <https://doi.org/10.1371/journal.pone.0045523>.
- Hypsa, V., Tietz, D.F., Zrzavy, J., Rego, R.O.M., Galvão, C., Jurberg, J., 2002. Phylogeny and biogeography of Triatominae (Hemiptera: Reduviidae): molecular evidence of a New World origin of the Asiatic clade. *Molecular Phylogenetics and Evolution* 23, 447–457.
- Justi, S.A., Galvão, C., Schrago, C.G., 2016. Geological changes of the Americas and their influence on the diversification of the Neotropical Kissing Bugs (Hemiptera: Reduviidae: Triatominae). *PLoS Neglected Tropical Diseases* 10, e0004527. <https://doi.org/10.1371/journal.pntd.0004527>.
- Lent, H., Wygodzinsky, P., 1979. Revision of the Triatominae (Hemiptera, Reduviidae), and their significance as vectors of Chagas' Disease. *Bulletin of the American Museum of Natural History* 163, 123–520.
- Monteith, G.B., 2015. Two new records of Australian *Triatoma* Laporte (Hemiptera: Reduviidae: Triatominae). *Australian Entomologist* 42, 105–106.
- Neiva, A., 1911. Zwei neue Afrikanische Arten des genus *Triatoma* (Oder Conorhinus) Laporte. *Proceedings of the Entomological Society of Washington* 13, 239–240.
- Otálora-Luna, F., Pérez-Sánchez, A.J., Sandoval, C., Aldana, E., 2015. Evolution of hematopharous habit in Triatominae (Heteroptera: Reduviidae). *Revista Chilena de Historia Natural* 88, 4. <https://doi.org/10.1186/s40693-014-0032-0>.
- Patterson, J.S., Gaunt, M.W., 2010. Phylogenetic multi-locus codon models and molecular clocks reveal the monophyly of haematophagous reduviid bugs and their evolution at the formation of South America. *Molecular Phylogenetics and Evolution* 56, 608–621.
- Patterson, J.S., Guhl, F., 2010. Geographical distribution of Chagas Disease. *American Trypanosomiasis Chagas Disease*. Elsevier Inc, pp. 83–114. <https://doi.org/10.1016/B978-0-12-384876-5.00005-8>.
- Patterson, J.S., Rajen, K., Ambrose, D.P., Miles, M.A., 2001a. First record of trypanosomes from the endemic Indian genus of Triatominae, *Linshcosteus* sp. nov. *Transactions of the Royal Society of Tropical Medicine and Hygiene* 95, 248–249.
- Patterson, J.S., Schofield, C.J., Dujardin, J.P., Miles, M.A., 2001b. Population morphometric analysis of the tropicopolitan bug *Triatoma rubrofasciata* and relationships with Old World species of *Triatoma*: evidence of New World ancestry. *Medical and Veterinary Entomology* 15, 443–451.
- Pinto, C., 1931. Valor do rostró e antenas na caracterização dos generos de Triatomídeos, Hemiptera, Reduvidóidea. *Boletim Biológico* 19, 44–136.
- Poinar Jr., G.O., 2005. *Triatoma dominicana* sp. n. (Hemiptera: Reduviidae: Triatominae), and *Trypanosoma antiquus* sp. n. (Stercoraria: Trypanosomatidae), the first fossil evidence of a Triatomine-Trypanosomatid Vector Association. *Vector-Borne and Zoonotic Diseases* 5, 72–81.
- Poinar Jr., G.O., 2013. *Panstrongylus hispaniolae* sp. n. (Hemiptera: Reduviidae: Triatominae), a new fossil triatomine in Dominican amber, with evidence of gut flagellates. *Palaeodiversity* 6, 1–8.
- Poinar Jr., G.O., 2018. Burmese amber: evidence of Gondwanan origin and Cretaceous dispersion. *Historical Biology*. <https://doi.org/10.1080/08912963.2018.1446531>.
- Poinar Jr., G.O., Lambert, J.B., Wu, Y., 2007. Araucarian source of fossiliferous Burmese amber: spectroscopic and anatomical evidence. *Journal of the Botanical Research Institute of Texas* 1, 449–455.
- Rabinovich, J.E., Kitron, U.D., Obed, Y., Yoshioka, M., Gottdenker, N., Chaves, L.F., 2011. Ecological patterns of blood-feeding by kissing-bugs (Hemiptera: Reduviidae: Triatominae). *Memórias do Instituto Oswaldo Cruz* 106, 479–494.
- Rasnitsyn, A.P., Quicke, D.L.J., 2002. *History of Insects*. Kluwer Academic Publishers, Dordrecht, p. 517.
- Ryckman, R.E., 1986. The vertebrate hosts of the Triatominae of North and Central America and the West Indies (Hemiptera: Reduviidae: Triatominae). *Bulletin of the Society for Vector Ecology* 11, 221–241.
- Ryckman, R.E., Archbold, E.F., 1981. The Triatominae and Triatominae-borne trypanosomes of Asia, Africa, Australia and the East Indies. *Bulletin of the Society of Vector Ecologists* 6, 143–166.

- Schofield, C.J., 1979. The behaviour of Triatominae (Hemiptera: Reduviidae): a review. *Bulletin of Entomological Research* 69, 363–379.
- Schofield, C.J., Galvão, C., 2009. Classification, evolution, and species groups within the Triatominae. *Acta Tropica* 110, 88–100.
- Schuh, R.T., Slater, J.A., 1995. *True Bugs of the World (Hemiptera: Heteroptera). Classification and Natural History*. Cornell University Press, Ithaca, New York, p. 336.
- Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yand, M., Lei, W., Li, Q., Li, X., 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretaceous Research* 37, 155–163.
- Smith, A.G., Smith, D.G., Funnel, B.M., 2004. *Atlas of Mesozoic and Cenozoic Coastlines*. Cambridge University Press, Cambridge, p. 99.
- Stevens, J.R., Gibson, W.C., 1999. The evolution of pathogenic trypanosomes. *Cadernos de Saúde Pública* 15, 673–684.
- Usinger, R.L., 1943. A revised classification of the Reduvidae with a new subfamily from South America (Hemiptera). *Annals of the Entomological Society of America* 36, 602–618.
- Usinger, R.L., 1944. The Triatominae of North and Central America and the West Indies and their public health significance. *Public Health Bulletin* 288, 1–81.
- Usinger, R.L., Wygodzinsky, P., Ryckman, R.E., 1966. The biosystematics of Triatominae. *Annual Review of Entomology* 11, 309–330.
- Vickerman, K., 2000. Order Kinetoplastea Honigberg. In: Lee, J.J., Leidale, G.F., Bradbury, P. (Eds.), *An Illustrated Guide to the Protozoa*, second ed. Society of Protozoologists, Lawrence, pp. 1159–1180.
- Wallace, F.G., 1966. The Trypanosomatid parasites of insects and arachnids. *Experimental Parasitology* 18, 124–193.
- Weirauch, C., 2008. Cladistic analysis of Reduviidae (Heteroptera: Cimicomorpha) based on morphological characters. *Systematic Entomology* 33, 229–274.
- Weirauch, C., Munro, 2009. Molecular phylogeny of the assassin bugs (Hemiptera: Reduviidae), based on mitochondrial and nuclear ribosomal genes. *Molecular Phylogenetics and Evolution* 53, 287–299.
- Weirauch, C., et al., 2014. An illustrated identification key to assassin bug subfamilies and tribes (Hemiptera: Reduviidae). *Canadian Journal of Arthropod Identification* 26, 1–115.
- White, M.E., 1994. *After the Greening*. Kangaroo Press, Kenthurst, Australia, p. 288.
- Wygodzinsky, P., Usinger, R.L., 1964. The genus *Reduvius* Fabricus in Western North America (Reduviidae, Hemiptera, Insecta). *American Museum Novitates* 2175, 1–15.