A new harpactorin hemipteran insect from the Miocene Dominican amber with fossula spongiosa on all three pairs of legs

PEIPEI ZHANG, YUNZHI YAO, ZHENGKUN HU, DONG REN, and YINGQI LIU

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A new genus and species of fossil harpactorin (Hemiptera: Reduviidae), *Trispongiosus hui* Zhang, Yao, & Liu gen. et sp. nov., is described from Miocene Dominican amber, representing the third fossil record of Harpactorinae. The new species is remarkable for exhibiting fossula spongiosa on all three pairs of legs, which is not only the first report in Harpactorinae but also rare within Reduviidae. This structure is considered to be related to the locomotor capabilities of assassin bugs, potentially enhancing their attachment and agility in navigating complex surfaces and vegetation. Furthermore, the present study suggests that fossula spongiosa exhibits remarkable plasticity within Reduviidae by integrating fossil and extant perspective.

Key words: Insecta, Reduviidae, Harpactorinae, assassin bug, fossula spongiosa, plasticity, Miocene, Dominican amber.

Peipei Zhang [2230801008@cnu.edu.cn; ORCID: https://orcid.org/0009-0006-7067-3464], Yunzhi Yao [yaoyz100@126.com; ORCID: https://orcid.org/0000-0003-4491-0260], Dong Ren [rendong@cnu.edu.cn; ORCID: https://orcid.org/0000-0001-8660-0901], and Yingqi Liu [yingqiliu0720@163.com; ORCID: https://orcid.org/0000-0003-0881-9670] (corresponding author), College of Life Sciences, Capital Normal University, Xisanhuanbeilu 105, Haidian District, Beijing 100048, China.

Zhengkun Hu [1428101617@qq.com; ORCID: https://orcid.org/0000-0002-7470-0830], Fanjingshan National Nature Reserve, Tongren 554400, China.

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Introduction

Reduviidae are the most diverse predatory insects among Hemiptera, having evolved a wide range of morphological characters for capturing prey. The fossula spongiosa, a hairy pad-like attachment structure located on the ventral surface of the distal part of tibia, is the most typical (Haridass and Ananthakrishnan 1980; Maldonado-Capriles 1990; Cassis and Gross 1996; Weirauch et al. 2014). Weirauch (2007) investigated the distribution of fossula spongiosa on the three pairs of legs of 171 species across 22 reduviid subfamilies. The results showed that the distribution of fossula spongiosa in extant Reduviidae can be broadly divided into four types: (i) lack of fossula spongiosa; (ii) fossula spongiosa only on the foreleg; (iii) fossula spongiosa on the foreleg and midleg; and (iv) fossula spongiosa on all three pairs of legs. Type (iv) is exceedingly uncommon among Reduviidae, occurring solely in the genera of *Microtriatoma* Prosen & Martínez, 1952, and *Parabelminus* Lent, 1943, within Triatominae (Sherlock and Guitton 1982; Lent 1943; Lent and Jurberg 1984; Weirauch 2007; Bargues et al. 2017). It is noteworthy that all investigated species of Harpactorinae in the above study had no fossula spongiosa in all three pairs of legs, and only the distal portion of the tibiae of the foreleg was more or less densely covered with setae (Weirauch 2007). In particular, Masonick et al. (2024) showed that a key diagnostic character of Harpactorinae is the lack of fossula spongiosa on the tibiae in most taxa.

Harpactorinae with more than 2250 species in over 300 genera, represents the largest subfamily within Reduviidae (Masonick et al. 2024). However, the fossil record of this subfamily is very sparse, with only two genera and two species known from the Cenozoic. *Aphelicophontes danjuddi* Swanson, Heads, Taylor & Wang, 2021, from the Eocene Green River impression fossil in the United States, has tibiae which are incompletely preserved thus the distribution of fossula spongiosa is unknown; the other species is

Apicrenus fossilis Capriles, Santiago-Blay & Poinar, 1993, from the Miocene Dominican amber, which does not have fossula spongiosa like most extant Harpactorinae species (Maldonado-Capriles et al. 1993a; Swanson et al. 2021).

This study presents a well-preserved specimen of Harpactorinae in Miocene Dominican amber, identified and described as a new genus and species. The new fossil preserves very distinct, pad-like fossula spongiosa on all three pairs of legs, being the first harpactorin species with fossula spongiosa on all three pairs of legs. This discovery not only enriches the fossil record of Harpactorinae to some extent but also broadens our understanding of the distribution pattern of this structure within Reduviidae. Furthermore, it provides valuable insights for further understanding the evolution of fossula spongiosa within both Harpactorinae and the entire Reduviidae.

Institutional abbreviations.—CNU, Capital Normal University, Beijing, China; FNNR, Fanjingshan National Nature Reserve, Tongren, China.

Nomenclatural acts.—This published work and the nomenclatural acts it contains have been registered in Zoobank: urn:lsid:zoobank.org:pub:8750ADCD-8A50-42DA-B3CD-135721EB98D4.

Material and methods

The holotype was purchased by Zhengkun Hu in the Dominican Republic in 2009 and subsequently donated to Professor Yunzhi Yao of CNU. The specimen originates from the Cordillera Septentrional, situated between Puerto Plata and Santiago in the northern Dominican Republic. Among the worldwide fossil resin occurrences, the Dominican amber deposits are considered to be one of the largest (Grimaldi 1995; Stach et al. 2021). They originated from deciduous trees of genus *Hymenaea*, which is similar to *Acacia*, but their age is still in a dispute, and is estimated as Miocene 20–15 Ma, 15.75–12.58 Ma, 25–20 Ma or Pliocene–Early Pleistocene (Stach et al. 2020, 2021; Hernández-Damián et al. 2024). These age discrepancies likely reflect limitations in dating methodologies or sample sources. Currently the more accepted view is that its geological age is Early Miocene (Schlee 1990; Grimaldi 1995; Iturralde-Vincent and Macphee 1996; Penney et al. 2010; Iturralde-Vincent and Macphee 2019; Stach et al. 2020, 2021).

This study conducted further morphological research on the materials using the Nikon SMZ25 microscope, which was connected in real-time to the Nikon DS-Ri2 digital photographic system. Sketches were drawn using the microscope's drawing arm, scanned with a printer, and then imported into drawing software to create line reconstruction drawings. The morphological terminology used in this study primarily followed Lent and Wygodzinsky (1979), Weirauch (2008), and Zhang and Weirauch (2011).

Systematic palaeontology

Order Hemiptera Linnaeus, 1758

Suborder Heteroptera Latreille, 1810

Infraorder Cimicomorpha Leston, Pendergrast & Southwood, 1954

Family Reduviidae Latreille, 1807

Subfamily Harpactorinae Amyot & Serville, 1843

Tribe Harpactorini Amyot & Serville, 1843

Genus *Trispongiosus* Zhang, Yao, & Liu nov.

Zoobank LSID: urn:lsid:zoobank.org:act:21BB5754-B477-4848-98B4-F3E5CEF35C42.

Type species: *Trispongiosus hui* Zhang, Yao, & Liu, sp. nov., monotypic; see below.

Etymology: From Latin *tri-,* three, and *spongiosus*, spongy, in refrence to having fossula spongiosa on all three pairs of legs. Gender masculine.

Diagnosis.—As for the monotypic type species.

Remarks.—According to the studies of Weirauch et al. (2014), Schuh and Weirauch (2020), and Masonick et al. (2024), *Trispongiosus* Zhang, Yao, & Liu gen. nov. should be placed in Harpactorinae because of the following characters: (i) head with postocular part cylindrical; (ii) anteocular region noticeably shorter than postocular region; (iii) sclerotized antennal basiflagellomere and distiflagellomere lacking narrow membranous rings; (iv) foretibia with a well-developed apical spur and (v) hemelytron with quadrate cell distally on corium. *Trispongiosus* Zhang, Yao, & Liu gen. nov. is placed in Harpactorini on the basis of the following characters: (i) labium curved; (ii) apex of medial posterior process of scutellum blunt; (iii) forefemur without spined; (iv) claws with basal tooth and (v) posterior cell of membrane subequal in size to anterior cell, with apex bluntly pointed and subtriangular.

Trispongiosus Zhang, Yao, & Liu gen. nov. shares the following characters with *Rocconota* Stål, 1859 (Ramírez Silva et al. 2022), a genus within Harpactorini that is primarily distributed in Panama: (i) head elongate; (ii) postocular portion of head narrowing gradually to form collum in dorsal view; (iii) antennal scape longest; (iv) pedicel shortest; (v) basiflagellomere slightly shorter than scape; (vi) distiflagellomere slightly longer than pedicel; (vii) legs elongated and slender; (viii) female with a conspicuously enlarged abdomen, maximum width of abdomen significantly greater than width across humeral angles. Nevertheless, the two can be distinguished by the following characters: *Rocconota* with (i) short conical tubercle on anterior angles of pronotum and sharp spines on humeral angles; (ii) posterior lobe with two symmetrical spines on central posterior position; *Trispongiosus* Zhang, Yao, & Liu gen. nov. with (i) blunt, rounded, anterior and humeral angles; (ii) posterior lobe without two symmetrical spines. Hemelytron of *Rocconota* in addition is uniformly dark brown, without pterostigmata, and the coloration of corium and membrane

Fig. 1. Harpactorin reduviid bug *Trispongiosus hui* Zhang, Yao, & Liu gen. et sp. nov., holotype, CNU-HET-DM2024011 from Burdigalian, Lower Miocene; Cordillera Septentrional, Dominican Republic. Dorsal (A_1) and ventral (A_2) views.

of *Trispongiosus* Zhang, Yao, & Liu gen. nov. is uneven, with dark pterostigmata.

Trispongiosus Zhang, Yao, & Liu gen. nov. shares the following characters with *Parahiranetis* Gil-Santana, 2015, which belongs to the wasp-mimicking Harpactorini in the Neotropical Region: (i) head elongate; (ii) postocular portion of head narrowing gradually to form collum in dorsal view, without postantennal spines; (iii) visible segment I of labium subequal to length of visible segment II; (iv) visible segment III shortest and (v) fore femur subequally longer than head and pronotum together. Nevertheless, the two can be distinguished by the following characters: *Parahiranetis* with (i) pubescence of long hairs on postocular portion; females of *Parahiranetis* with (ii) narrower abdomen and (iii) maximum width of abdomen subequal to width across humeral angles; (iv) hemelytron of *Parahiranetis* dark brown overall with bright yellow pterostigmata in specific positions. While in *Trispongiosus* Zhang, Yao, & Liu gen. nov., (i) the whole head is covered with hairs; (ii) the abdomen is conspicuously enlarged and (iii) maximum width of abdomen is significantly greater than width across humeral angles; (iv) hemelytron of retains pterostigmata in same positions but with color noticeably darker than surrounding wing surface. It is of particular significance that *Trispongiosus* Zhang, Yao, & Liu gen. nov. exhibits distinct fossula spongiosa on all three pairs of legs, which is quite unique within Harpactorinae. Therefore, a new genus was finally established based on the fossil specimen.

Stratigraphic and geographic range.—In the northern mountain range (Cordillera Septentrional) of the Dominican Republic between the cities of Puerto Plata and Santiago. Burdigalian, Lower Miocene.

Trispongiosus hui Zhang, Yao, & Liu sp. nov.

Figs. 1–3.

Zoobank LSID: urn:lsid:zoobank.org:act:6147E673-2167-4720-82EE-82FD9AD2B014.

Etymology: Dedicated to Zhengkun Hu of the Fanjingshan National Nature Reserve (Tongren, China) for his donation of this amber specimen.

Holotype: CNU-HET-DM2024011, an adult female.

Type locality: The northern mountain range (Cordillera Septentrional) of the Dominican Republic between the cities of Puerto Plata and Santiago. Details unknown.

Type horizon: Burdigalian, Lower Miocene.

Diagnosis.—Body medium-sized; head oval, length of head slightly shorter than length of pronotum; posterior lobe of pronotum with parentheses-shaped indentations on both sides, humeral angles blunt; pronotum and each leg densely covered with short, decumbent to suberect, curly setae; membrane with external cell longer and narrower than internal cell; basal teeth of tarsi of foreleg and midleg rounded.

Description.—Macropterous female. Body medium-sized.

Vestiture: Head with dense, short, suberect to erect, curly setae on dorsal and lateral surfaces; antennae densely covered with very short, decumbent to suberect setae; labium with short, suberect to erect setae; pronotum and legs densely covered with short, decumbent to suberect, curly setae.

Structure: Body oval. Head elongate, with dorsum weakly inflated and venter flattened; postocular part 1.2 times as long as anteocular part; eyes slightly protruding anterolaterally; ocelli small, slightly elevated. Antennal scape longest, 2.0 times as long as length of head, base of scape notched, pedicel shortest, 0.7 times as long as length of

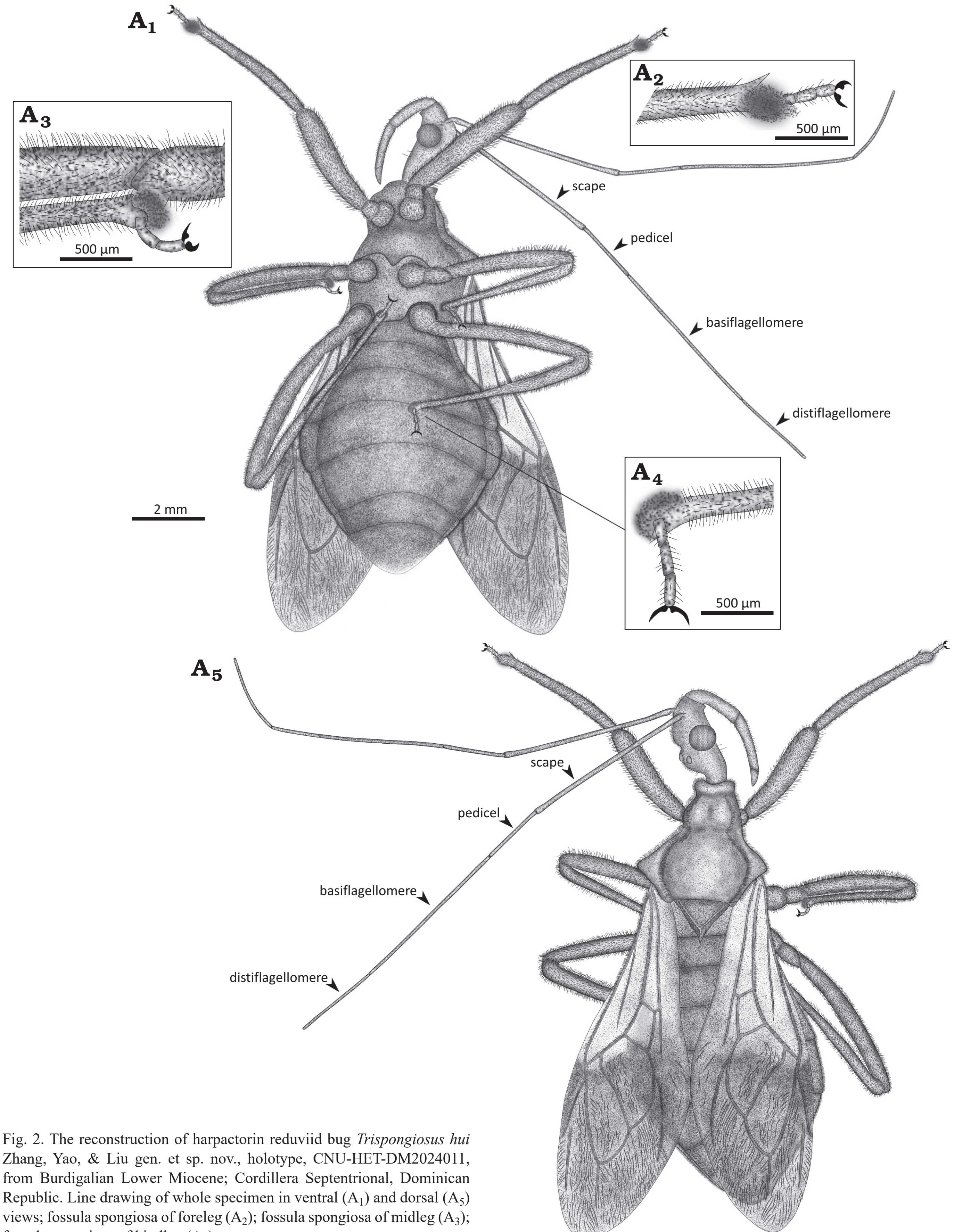


Fig. 2. The reconstruction of harpactorin reduviid bug *Trispongiosus hui* Zhang, Yao, & Liu gen. et sp. nov., holotype, CNU-HET-DM2024011, from Burdigalian Lower Miocene; Cordillera Septentrional, Dominican Republic. Line drawing of whole specimen in ventral (A_1) and dorsal (A_5) views; fossula spongiosa of foreleg (A_2); fossula spongiosa of midleg (A_3); fossula spongiosa of hindleg (A_4).

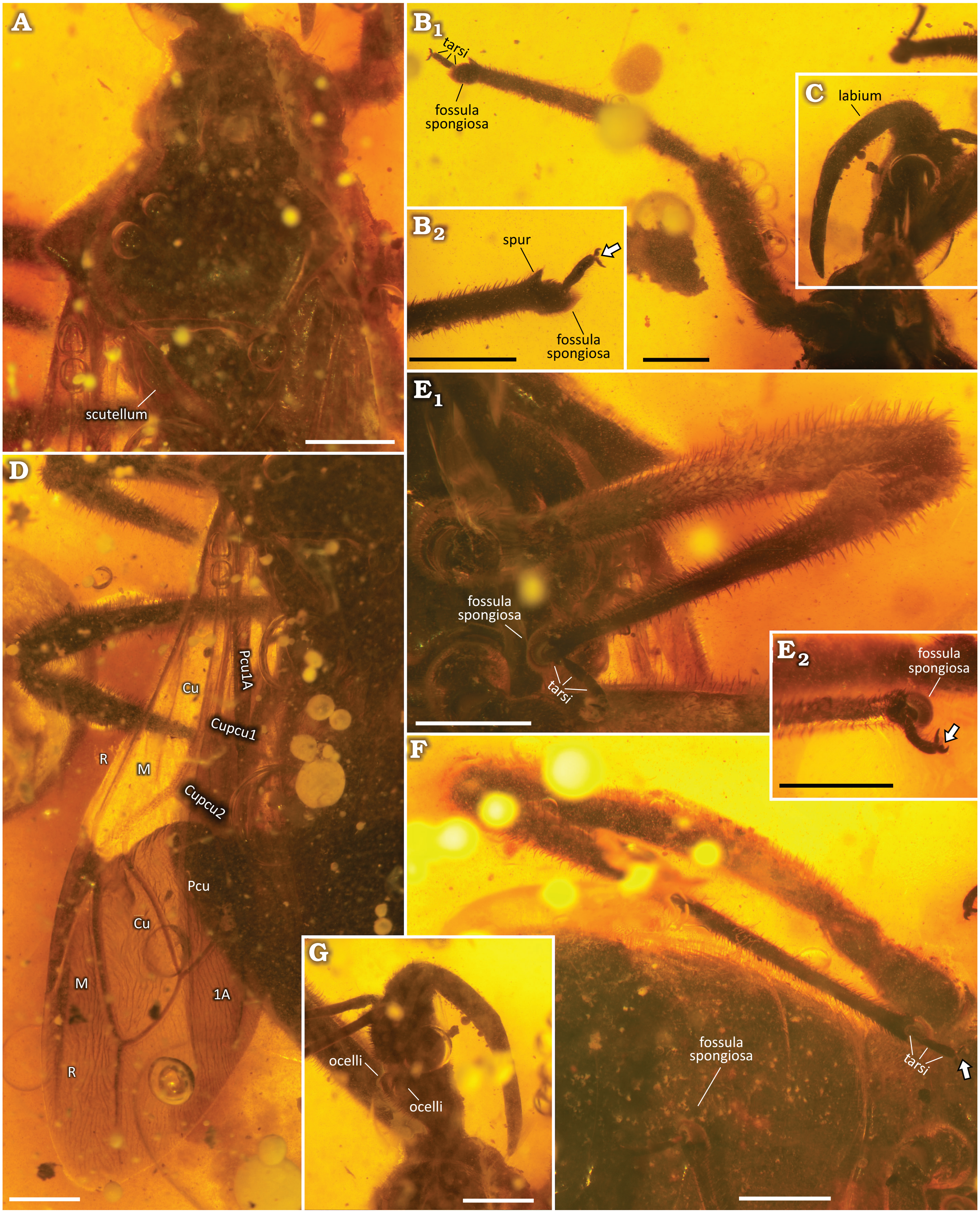
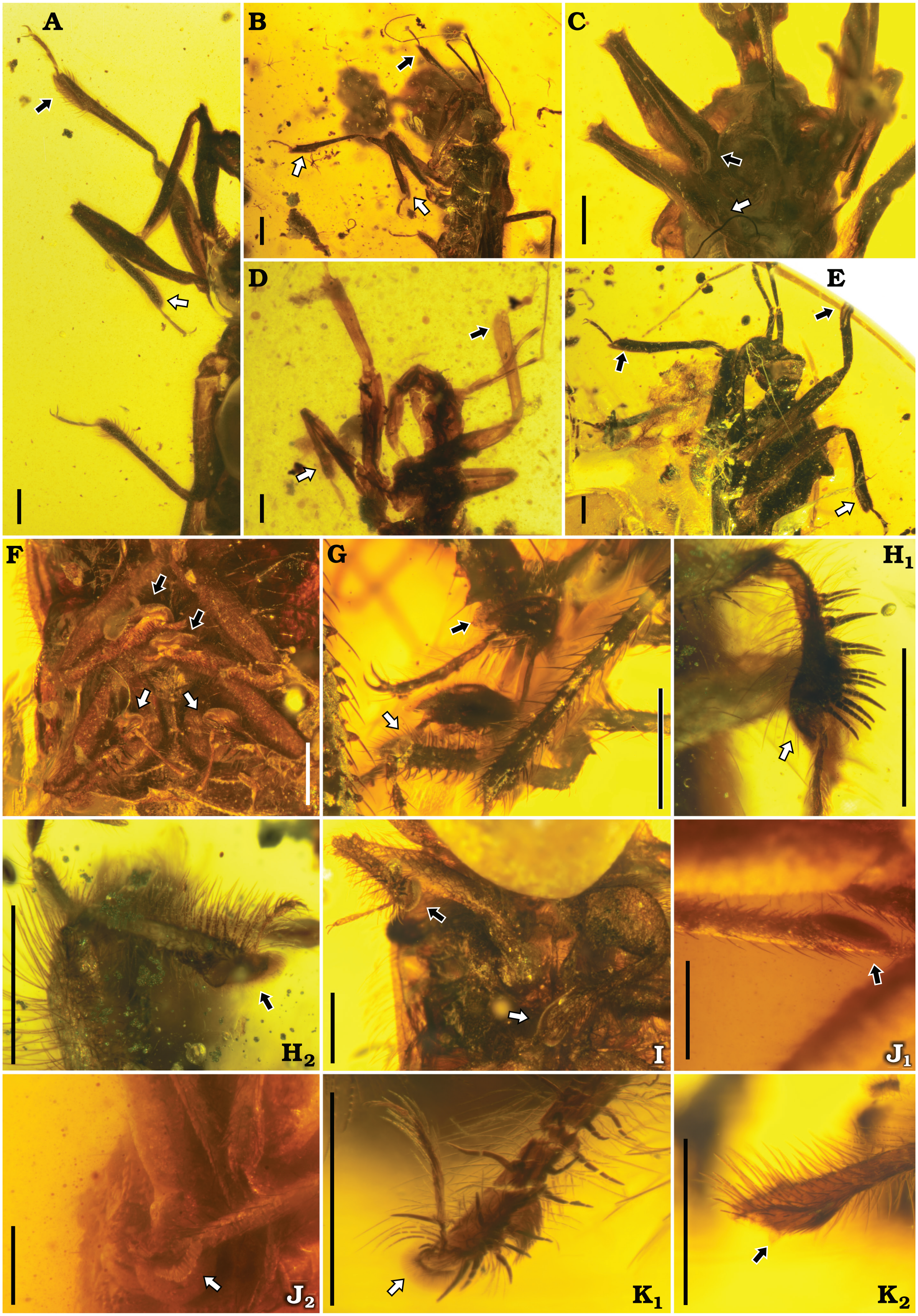


Fig. 3. The detailed partial view of harpactorin reduviid bug *Trispongiosus hui* Zhang, Yao, & Liu gen. et sp. nov., holotype, CNU-HET-DM2024011 from Burdigalian, Lower Miocene; Cordillera Septentrional, Dominican Republic. **A**. Pronotum and scutellum. **B**. Foreleg. **C**. Labium. **D**. Hemelytron. **E**. Midleg. **F**. Hindleg. **G**. Ocelli. Arrows in B_2 and E_2 indicates the basal tooth of claw, arrow in F points to the blunt tooth on the hind tarsal claw. Scale bars 1 mm. Abbreviations: Cu, cubitus; Cupcu1, Cupcu2, first and second vein formed by the fusion of the cubitus and postcubitus; M, media; Pcu, postcubitus; Pcu1A, fusion of the postcubitus and the first anal vein; R: radius; 1A: first anal vein.


A
B
C
D
E
F
G
H1
H2
I
J1
J2
K1
K2

← Fig. 4. Fossula spongiosa on the forelegs and midlegs of 11 yet undescribed species of fossil reduviids from Upper Cretaceous Burmese amber. **A**. CNU-HET-MA2025003, sp. 1. **B**. CNU-HET-MA2025004, sp. 2. **C**. CNU-HET-MA2025005, sp. 3. **D**. CNU-HET-MA2025006, sp. 4. **E**. CNU-HET-MA2025007, sp. 5. **F**. CNU-HET-MA2025008, sp. 6. **G**. CNU-HET-MA2025009, sp. 7. **H**. CNU-HET-MA2025010, sp. 8. **I**. CNU-HET-MA2025011, sp. 9. **J**. CNU-HET-MA2025012, sp. 10. **K**. CNU-HET-MA2025013, sp. 11. H_1, J_1, K_1, forelegs; H_2, J_2, K_2, midlegs. Black arrows indicate the fossula spongiosa on the forelegs, while white arrows indicate those on the midlegs. Scale bars 250 µm.

head, basiflagellomere slightly shorter than scape, 1.9 times as long as length of head, distiflagellomere as long as length of head; labium curved, slightly surpassing anterior margin of prosternum, visible segment I subequal to length of visible segment II, visible segment III shortest, conical, 0.3 times as long as visible segment I.

Collar processes obtuse horn-shaped, produced laterally; length of pronotum along midline just as long as width across humeral angles, 1.5 times as long as length of head; anterior margin slightly concave, anterior lobe round and bulged, 0.5 times as long as posterior lobe, with deep median longitudinal sulcus; posterior lobe separated from anterior lobe by faint transverse sulcus; posterior lobe with parentheses-shaped indentations on both sides, anterior region of posterior lobe with shallow median longitudinal groove, humeral angles blunt, posterior margin nearly straight, lateral margin finely concave. Scutellum partially exposed, Y-shaped ridges narrow, scutellar process rounded.

Fore coxa spherical, fore femur thickened, somewhat flattened laterally, fore tibia slender, slightly curved, 1.2 times as long as fore femur, fore tarsus three-segmented, with a pair of tiny claws at apex; mid and hind coxae widely separated from each other; mid and hind femora moderately and strongly thickened, mid tibia 1.1 times as long as mid femur, hind tibia 1.2 times as long as hind femur, mid and hind tarsi three-segmented, with a pair of small claws at apices, base of claw with a relatively rounded and blunt tooth. Each tibia with fossula spongiosa approximately 0.1 times as long as of total length of each tibia.

Hemelytron slightly extending beyond abdominal tip, corium with quadrate cubitalcell, membrane with external cell longer and narrower than internal cell.

Abdomen broad oval, length 1.6 times as long as its maximum width, connexivum clearly extended outwards on both sides.

Dimensions.—Table 1.

Stratigraphic and geographic range.—In the northern mountain range (Cordillera Septentrional) of the Dominican Republic between the cities of Puerto Plata and Santiago. Burdigalian, Lower Miocene.

Table 1. Measurements (in mm) of *Trispongiosus hui* (CNU-HET-DM2024011).

Body part	Measurement	
body	length	14.27
head	length	2.43
anteocular part	length	0.84
postocular part	length	0.98
antennal segments I–IV	length	4.94; 1.57; 4.68; 2.51
visible labial segments I–III	length	1.61; 1.63; 0.55
anterior lobe of pronotum	length	1.23
	width	1.70
posterior lobe of pronotum	length	2.32
	width	3.50
scutellum	length	1.17
	width	1.74
hemelytron	length	10.05
abdomen	length	8.60
	width	5.24
fore: femur; tibia; tarsus	length	3.37; 4.16; 0.41
mid: femur; tibia; tarsus	length	3.59; 4.05; 0.78
hind: femur; tibia; tarsus	length	4.93; 6.12; 1.01

Discussion

Evolutionary plasticity of fossula spongiosa in Reduviidae.—The fossula spongiosa, a cushion-like expanded area on the tibia that is composed of thousands of minute hairs, and represents a key morphological character of Cimicomorpha (Weirauch 2007; Schuh et al. 2009). This structure is often conspicuous within Reduviidae, and is thought to be associated primarily with predatory behavior and sometimes with mating and locomotor functions (Haridass and Ananthakrishnan 1980; Weirauch 2007; Zhang et al. 2016). This study surveys the distribution of fossula spongiosa with hairy pad-like attachment structure on each leg of previously reported reduviid fossils, a newly described fossil within this paper, and 11 unpublished reduviid fossils from Burmese amber (Fig. 4, Table 2). The results show that the majority of currently known Cretaceous Reduviidae have fossula spongiosa on both the forelegs and midlegs (Fig. 5). A phylogenetic analysis of the evolution of raptorial leg in Reduviidae by Zhang et al. (2016) suggests that fossula spongiosa is a plesiomorphy of Reduviidae. Zhang et al. (2022) described the oldest fossils of Reduviidae, concluded that the presence of fossula spongiosa on both the foreleg and the midleg was the ancestral state of fossula spongiosa of Reduviidae. The statistical results of the present study further verify the above conclusions.

In addition, the results show that these fossils encompass all types of fossula spongiosa observed in extant Reduviidae: total lack of fossula spongiosa; only foreleg with fossula spongiosa; foreleg and midleg with fossula spongiosa; foreleg, midleg and hindleg with fossula spongiosa (Table 2). Excluding fossils with both undetermined subfamily and fossula spongiosa type, the types of fossula spongiosa in Reduviidae show a gradual trend of diversification over geological time (Fig. 5). During the Cretaceous, fossula spongiosa was relatively uniform in type, present only on

Table 2. Distribution of fossula spongiosa on each leg in Reduviidae fossils. + presence; – absence; ? unknown.

Epoch	Subfamily	Species	Foreleg	Midleg	Hindleg	Reference
Miocene	Reduviinae	*Reduvius diatomus*	?	?	?	Zhang and Zhang 1990
		Reduvius shandongianus	?	?	?	Zhang and Zhang 1990
	Triatominae	*Triatoma dominicana*	?	?	?	Poinar 2005
		Panstrongylus hispaniolae	+	+	–	Poinar 2013
	Holoptilinae	*Praecoris dominicana*	–	–	–	Poinar 1991
	Emesinae	*Emesites voigti*	?	?	?	Popov and Weitschat 2005
		Empicoris copal	–	–	–	Popov 1987a
		Malacopus wygodzinskyi	–	–	–	Popov 1987b
		Alumeda antilliana	–	–	–	Popov 1989
		Alumeda dominicana	–	–	–	Popov 1989
		Alumeda nigricans	–	–	–	Popov 1989
		Paleoploiariola venosa	–	–	–	Maldonado-Capriles et al. 1993b
		Empiploiariola inermis	–	–	–	Popov 1993
	Phimophorinae	*Phimophorus chiodii*	?	?	?	Boderau et al. 2024
	Harpactorinae	*Apicrenus fossilis*	–	–	–	Maldonado-Capriles et al. 1993a
		Trispongiosus hui	+	+	+	this paper
		Harpactor chomeraciensis	?	?	?	Riou 1999
		Arilus faujasi	?	?	?	Riou 1999
	Ectrichodiinae	*Ectrichodiella electrina*	–	–	–	Bush et al. 2024
	unknown	*Oncocephalus astutus*	?	?	?	Zhang et al. 1994
		Reduvius immitus	?	?	?	Zhang et al. 1994
		Reduvius nicus	?	?	?	Zhang et al. 1994
		Reduvius piceus	?	?	?	Zhang et al. 1994
Oligo-Miocene	Emesinae	*Empicoris electricus*	–	–	–	Thomas 1992
Oligocene	unknown	*Rhinocoris michalki*	?	?	?	Statz and Wagner 1950
Eocene	Reduviinae	*Platymeris insignis*	?	?	?	Germar and Berendt 1856
	Centrocnemidinae	*Redubitus centrocnemarius*	+	+	–	Putshkov and Popov 1993
		Redubinotus liedtke	+	+	–	Putshkov and Popov 1998
	Holoptilinae	*Proptilocerus dolosus*	–	–	–	Wasmann 1932
		Proptilocnemus longispinis	–	–	–	Heiss 2009
	Emesinae	*Collarhamphus mixtus*	?	?	?	Putshkov and Popov 1995
		Amphibolus disponsi	–	–	–	Kinzelbach 1970
		Danzigia christelae	–	–	–	Popov 2003
		Emesopsis putshkovi	–	–	–	Popov and Chłond 2015
		Emesopsis similis	–	–	–	Popov and Chłond 2015
	Phimophorinae	*Koenigsbergia herczeki*	+	–	–	Ramirez et al. 2024
	Harpactorinae	*Aphelicophontes danjuddi*	?	?	?	Swanson et al. 2021
	unknown	*Tagalodes inermis*	?	?	?	Swanson et al. 2021
		Poliosphageus psychrus	?	?	?	Kirkaldy 1910
Paleocene	unknown	*Hymenopterites deperditus*	?	?	?	Heer 1870
Cretaceous	Reduviinae	*Simplicivenius rectidorsius*	?	?	?	Zhang et al. 2022
		Simplicivenius tuberculosus	+	+	–	Zhang et al. 2022
	Triatominae	*Paleotriatoma metaxytaxa*	+	+	–	Poinar 2019
	Centrocnemidinae	*Acutiangulus densus*	?	?	?	Zhang et al. 2024
	unknown	sp. 1	+	+	–	unpublished
		sp. 2	+	+	–	unpublished
		sp. 3	+	+	–	unpublished
		sp. 4	+	+	–	unpublished
		sp. 5	+	+	–	unpublished
		sp. 6	+	+	–	unpublished
		sp. 7	+	+	–	unpublished
		sp. 8	+	+	–	unpublished
		sp. 9	+	+	–	unpublished
		sp. 10	+	+	–	unpublished
		sp. 11	+	+	–	unpublished

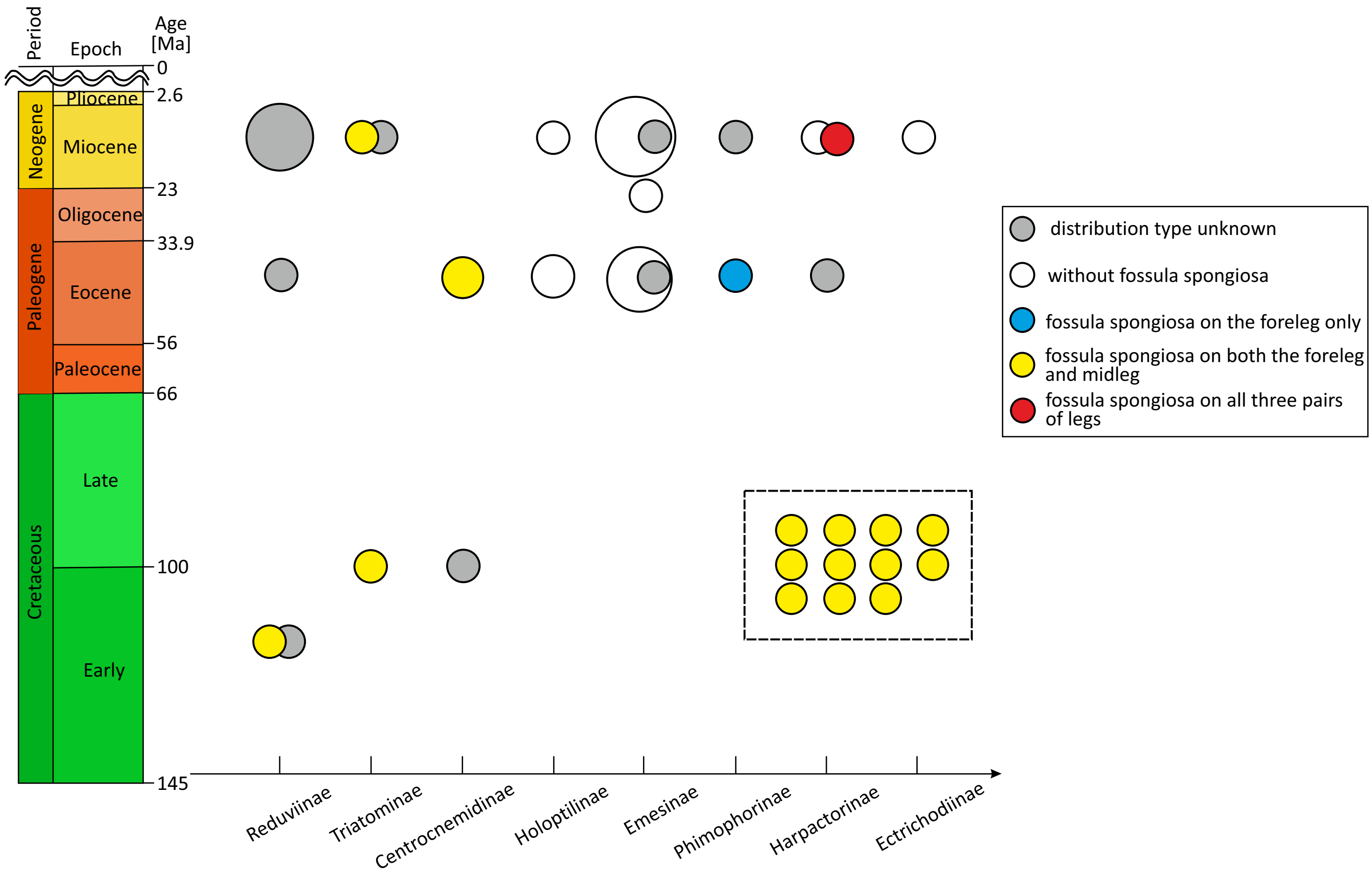


Fig. 5. Distribution pattern of fossula spongiosa in fossil reduviids. Circle size reflects the number of fossils discovered, with larger circles indicating more fossils. The dashed box indicate the distribution patterns of fossula spongiosa in 11 unpublished fossil reduviids. Fossils of which the subfamilies and fossula spongiosa type are both unknown were excluded from statistical analyses.

the fore- and midlegs. However, since the Eocene, various types of fossula spongiosa began to appear in the fossil record, including the lack of fossula spongiosa, with fossula spongiosa only on the forelegs, and fossula spongiosa on both the foreleg and midleg. By the Miocene, the types of fossula spongiosa in Reduviidae became even more diverse, encompassing all types seen in extant species, ranging from no fossula spongiosa to fossula spongiosa on all three pairs of legs.

There are significant differences in the type of fossula spongiosa in extant Reduviidae, even within the same subfamily, e.g., the majority of species in Peiratinae have fossula spongiosa on the foreleg and midleg, whereas the genus *Sirthenea* Spinola, 1837, has fossula spongiosa on the foreleg only, with the exception of *S. laevicollis* Horváth, 1909, which occurs in Australia, possessing fossula spongiosa on both the foreleg and midleg (Weirauch 2007; Chłond et al. 2019). Additionally, the present study identifies a fossil within Harpactorinae that exhibits pad-like fossula spongiosa on all three pairs of legs, a feature that is traditionally absent in this subfamily. These observations suggest the significant diversity and plasticity of fossula spongiosa within Reduviidae. Consequently, the present study proposes that the evolution of fossula spongiosa within the Reduviidae was not following a linear direction by integrating fossil and extant perspectives. Zhang et al. (2016) suggested that the evolution of fossula spongiosa may be related to complex interrelated factors associated with prey type, predatory behavior, salivary toxicity, and morphological adaptation. Building on their work, this study further hypothesize that the plasticity of fossula spongiosa evolution in Reduviidae likely represents a flexible adaptation to varying ecological conditions and predatory needs.

Exploration of the adaptive functions of fossula spongiosa on all three pairs of legs.—It has been shown that fossula spongiosa enhances the gripping efficiency of the legs and is sexually dimorphic in some bedbugs (Haridass and Ananthakrishnan 1980; Reinhardt et al. 2019). Fossula spongiosa in some male bedbugs possess a higher density of setae compared to females, which results in greater adhesive strength (Reinhardt et al. 2019). This adaptation likely aids males in securely grasping females during traumatic insemination (Jung et al. 2023). Chłond et al. (2019) suggested that the distribution of fossula spongiosa in Peiratinae is closely related to their ecological environments, with the reduction of fossula spongiosa to only the forelegs in *Sirthenea* possibly being an adaptation to warm and humid ecological niches with abundant prey species and lower levels of competition.

The most remarkable character of *Trispongiosus hui* Zhang, Yao, & Liu gen. et sp. nov. is the presence of distinct and roughly uniformly-sized fossula spongiosa on all three pairs of legs, which is for the first time recorded in Harpactorinae. Currently, the presence of fossula spongiosa in all three pairs of legs within Reduviidae is also very rare, with similar phenomena observed only in species of two genera of Triatominae, i.e., *Parabelminus* and *Microtriatoma* (Lent 1943; Weirauch 2007; Bargues et al. 2017).

Parabelminus occurs in southeastern Brazil, while *Microtriatoma* species have a wider distribution, covering Central America (such as Costa Rica and Panama) and South America (such as Trinidad, Peru, Bolivia, as well as northern and southeastern Brazil) (Lent 1943; Sherlock and Guitton 1982; De la Riva et al. 2001; Abad-Franch and Monteiro 2007; Bargues et al. 2017; Dos Santos Souza et al. 2019; Hylton et al. 2020; Gil-Santana et al. 2021; Kieran et al. 2021; Galvão et al. 2024). It seems that Reduviidae with fossula spongiosa on all three pairs of legs are known to be distributed in tropical and subtropical regions. However, this is consistent with the ecological niche of Reduviidae with underdeveloped fossula spongiosa as indicated by Chłond et al. (2019). It should be noted that the study of Chłond et al. (2019) focused on Peiratinae, which is predominantly ground-dwelling (Weirauch et al. 2014). Given their habitat, Peiratinae may not rely heavily on fossula spongiosa to enhance grip on rough ground surfaces. The primary role of fossula spongiosa of Peiratinae is more likely to aid in predation. Nevertheless, most members of Harpactorinae are arboreal, living on plant surfaces (Weirauch et al. 2014). Many extant species within this subfamily lack fossula spongiosa, which may suggest a reduced reliance on fossula spongiosa for predation in Harpactorinae. Additionally, some lineages have evolved sticky predation strategies, which may have partially supplanted the predatory function of fossula spongiosa (Zhang and Weirauch 2013; Weirauch et al. 2014; Masonick et al. 2024). Triatominae members with fossula spongiosa on all three pairs of legs have been primarily found on smooth plant surfaces, such as *Microtriatoma borbai* Lent & Wygodzinsky, 1979, collected from a hybrid eucalyptus crop, and *Microtriatoma trinidadensis* Lent, 1951, found on palm leaves (Dos Santos Souza et al. 2019; Gil-Santana et al. 2021). As hematophagous insects, Triatominae rely less on their legs for capturing prey, but instead use their labium to feed on the blood of their prey (Weirauch et al. 2014; Masonick et al. 2024). These implies that fossula spongiosa may have a different major function in these two subfamilies compared to Peiratinae. Furthermore, the study by Haridass and Ananthakrishnan (1980) demonstrated that fossula spongiosa of some reduviids generate greater static tension on smooth surfaces. In conclusion, this study hypothesizes that *Trispongiosus hui* Zhang, Yao, & Liu gen. et sp. nov. with fossula spongiosa on all three pairs of legs is more likely to be arboreal. The presence of fossula spongiosa on all legs may be associated with locomotor functions, such as enhanced adhesion and movement. In tropical and subtropical regions which are characterized by warm and humid climates and a high diversity of plant species, assassin bugs may need to adapt to various plant surfaces, some of which can be relatively smooth, such as the leaves of certain palm species. The fossula spongiosa on all three pairs of legs can enhance the attachment ability of assassin bugs on these smooth surfaces, thereby increasing their flexibility in complex ecological niches and effectively aiding in prey pursuit and predator evasion. In addition, extant predatory Reduviidae usually immobilize their prey using the foreleg and midleg, and the fossula spongiosa of foreleg is generally slightly larger than the midleg (Weirauch 2007; Zhang et al. 2022). However, in *Trispongiosus hui* Zhang, Yao, & Liu gen. et sp. nov., and species of *Parabelminus*, and *Microtriatoma*, the hind legs, which are not involved in predation, also possess fossula spongiosa that are comparable in size to those on the forelegs and midlegs. This phenomenon further implies that fossula spongiosa present on all three pairs of legs may play a major role in locomotion. However, direct evidence for its locomotor function is still unavailable. Future research should incorporate extensive fossil records and experimental approaches to elucidate its precise role and evolutionary importance.

Conclusions

This study describes a new genus and species of Harpactorinae, *Trispongiosus hui* Zhang, Yao, & Liu gen. et sp. nov., discovered in Miocene Dominican amber. The new species is remarkable for possessing distinct fossula spongiosa on all three pairs of legs, a character recorded for the first time in Harpactorinae and also rare within Reduviidae. This study proposes that the structure could contribute to the locomotor abilities of assassin bugs, enhancing their grip and maneuverability on challenging surfaces and dense vegetation. Additionally, the research highlights the significant plasticity of the fossula spongiosa within Reduviidae, as demonstrated through the integration of fossil and extant perspectives. This discovery not only expands the fossil record of Harpactorinae but also provides new perspectives and evidence for understanding the evolution of fossula spongiosa within Reduviidae.

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