

ORIGINAL ARTICLE

A new genus and species of Tingidae (Heteroptera: Cimicomorpha) from Myanmar, with the analysis of the evolution of hood, carinae and paranota

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Abstract *Cucullitingis biacantha* **gen. & sp. nov.**, a new genus and species of the family Tingidae is described and established based on two fossil specimens from the mid-Cretaceous Burma amber. According to the statistical result of fossil tingids, the evolution of hood, carinae and paranota was discussed.

Key words Hemiptera, tingids, pronotal, Mesozoic.

1 Introduction

The family Tingidae was erected by Laporte (1833), belong to the infraorder Cimicomorpha and comprised 300 genera, 2500 extant species. The family was classified into three subfamilies: (1) Vianaidinae, no more than 10 species, only distributed in South America; (2) Cantacaderinae, about 135 species, spread across all Southern landmasses except Antarctica (none from North America and few from Palearctic region); (3) Tinginae (including Serenthiaia), all the remaining species, global distributed (Guilbert *et al.*, 2014). All tingids, size ranges from 2 to 8 mm, are phytophagous, prefer woody plants and are host-specific piercers and suckers, being either monophagous or oligophagous (Drake & Ruhoff, 1960). Tingids are commonly known as “lace bugs” for the lace-like pronotum and hemelytra. They are dull colored or brown, highly complex morphology, particularly the pronotum and hemelytra, such as various sizes and shapes of paranota, carinae or hemelytra, these structures can be absent, simple or exaggerated, even extending far from the body size (Guilbert *et al.*, 2014).

Currently, 36 genera and 56 species of fossil Tingidae have been described, ranging from the Lower Cretaceous to the Oligocene, with worldwide distribution in 16 countries, most from Baltic amber, secondly France. The oldest fossil record, *Sinaldocader ponomarenkoi* Golub & Popov, 2008 was from Zaza Formation (ca. 130 Ma) in Transbaikalia (Golub & Popov, 2008). Among them, only three species have been reported from Burma amber. In this paper, we report a new genus and species, *Cucullitingis biacantha* **gen. & sp. nov.**, based on two ambers. This species has some exaggerated characters similar to extant groups: four spines, two dorso-medial and two frontal; hood cover up the part of the head; median carinae emerging from the anterior of hood reaching the posterior of pronotum; paranota very broad, three row of areolae wide, apex of the paranota forming a spine, extending anteriorly to anterior margin of eyes.

The amber deposits occur about 100 km southwest of Tanai Village, in the Hukawng Valley of Kachin Province, Northern Myanmar, where has yielded many well-preserved insect fossils (Ren *et al.*, 2017, Zhang *et al.*, 2017, Lin *et al.*, 2018). Although the age of Myanmar amber is contentious (Zherikhin & Ross, 2000; Grimaldi *et al.*, 2002), it has been dated radiometrically to a maximum of 98.8 ± 0.62 Ma (Shi *et al.*, 2012), equivalent to the earliest Cenomanian (Walker *et al.*, 2012).

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2 Materials and methods

All type ambers studied herein were collected from Kachin (Hukawng Valley) of Northern Myanmar. The specimens are deposited in the Key Lab of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China (CNUB; Yunzhi Yao, Curator).

The amber specimens were examined and photographed by using a Nikon SMZ25 dissecting microscope with a Nikon DS-Ri 2 digital camera system (Nikon, Japan) and illustrated with the aid of a camera attached to the microscope. Using Adobe Illustrator CC® and Photoshop CC® graphic software drew the line drawings. Morphological terminology mainly follows Froeschner (1996). We followed and accepted the traditional systematic organization of Tingidae by Froeschner (1996), Golub (2001), Guilbert (2004) and Schuh *et al.* (2006).

Body length was measured along the midline from the head apex to the abdomen apex. Body width was measured at the maximal width of the body. The length of the fore wings was measured from the base to its apex. All measurements were given in millimeters (*mm*).

3 Systematic

Suborder Heteroptera Latreille, 1810

Infraorder Cimicomorpha Leston, Pendergrast & Southwood, 1954

Family Tingidae Laporte, 1833

Genus *Cucullitingis* gen. nov.

Type species. *Cucullitingis biacantha* sp. nov. (Fig. 1)

General description. Macropterous. Head slightly produced in front of the compound eyes, with four spines, two dorso-medial and two frontals, bucculae extended half-length of head. Antenna four-segmented, length of third segment the longest. Pronotum short, without posterior projection; Apex of the paranota forming a spine. Scutellum reduced but visible; collar three areolae wide, forming a spheroid hood, cover up the posterior of head. Hemelytra areolate, subcostal area narrower and higher than costal area and discoidal area; no stenocostal area. Legs long and slender, tarsi two-segmented.

Etymology. The generic name is a combined a Latin word “*cucull-*” (meaning hood) and the stem name of family Tingidae. The gender is feminine.

Cucullitingis biacantha sp. nov. (Fig. 1)

Diagnosis. As for the genus.

Description. Head slightly produced in front of compound eyes; eyes fully developed, globose; antennae four-segmented, first segment approximately the same length as second, third segment the longest and last segment fusiform; head armed with four long, thin and slender, very acute and very slightly curved, porrect spines, two frontal spines on each side of clypeus, two dorso-medial spines between eyes, located on both side of vertex; ocelli absent; bucculae areolate, narrow, tapering anteriorly, extending half-length of head; rostrum short, surpassing hind margin of head onto prosternum.

Pronotum short, wider than long, subequal to abdomen, slightly gibbose, without posterior projection; scutellum reduced but visible; collar three areolae wide, forming a hood, spheroid, cover up the posterior of head; pronotal disc with broad areolae, and only one median carina raised with one row of areolae; paranota very broad, three areolae wide, apex of the paranota forming a spine, extending anteriorly to anterior margin of eyes.

Hemelytra. Completely developed, extending far beyond abdomen beneath, hyaline, sharply widened at base, covered by large-subquadrate areolae, the largest being rather regular; clavus well developed; ScP strongly emerging from the base of forewing, costal area biseriate with additional areolae in the middle; subcostal area narrower than costal area, irregularly biseriate, with addition areolae in the middle; vein R+M fused with CuA at two thirds of the forewing; discoidal area slightly broader than subcostal area, with five-six rows of areolae, not separated into smaller groups; sutural area narrow, two-three areolae wide; stenocostal area absent; subcostal higher than discoidal areas and costal area. Hind wings not visible.

Legs. Long and slender, fore, mid, and hind legs of equal length; trochanters not fused with femora; tarsi two-segmented.

Abdomen (Fig. 2). Abdominal sternites II to IX visible. Female. Paratergite VIII reduce, fused with first gonocoxipodite;

posterior of paratergite VII separated, forming a subgenital plate which covers the base of ovipositor. Male. phallus not visible.

Dimensions. Body length 2.63 (♂), 2.78 (♀); maximal width of body 1.19 (♀); length of head 0.28 (♂), 0.28 (♀); length



Figure 1. Holotype of *Cucullitingis biacantha* sp. nov. A. Photograph of dorsal view. B. Photograph of labium in ventral view. C. Line drawing of dorsal view. D. Detail photograph of head. Scale bars: A, C = 500 μ m; B, D = 250 μ m.

of antennal segments I–IV: 0.10, 0.21, 1.21, 0.35 (♂), 0.09, 0.13, 1.34, 0.22 (♀); length of pronotum 0.54 (♂), 0.55 (♀), width 0.61 (♀); length of hemelytron 1.90 (♂), 1.93 (♀); length of clavus 0.70 (♂), 0.75 (♀); length of fore leg: femur 0.75 (♂), 0.87 (♀), tibia 0.54 (♂), 1.05 (♀), tarsomeres I–II: 0.02, 0.08 (♂), 0.02, 0.08 (♀); length of mid leg: femur 0.75 (♂), 0.85 (♀), tibia 0.64 (♂), 0.96 (♀), tarsomeres I–II: 0.03, 0.09 (♂), 0.02, 0.06 (♀); length of hind leg: femur 0.81 (♂), 0.69 (♀), tibia 1.10 (♀), tarsomeres I–II: 0.02, 0.07 (♀).

Material examined. Holotype ♀, Hukawng Valley, Kachin State, Northern Myanmar; lowermost Cenomanian, mid-Cretaceous, CNU-HET-MA2017001. Paratype, ♂, same data as holotype, CNU-HET-MA2017002. All deposited in CNUB.

Etymology. This species name is combined the Latin word “*bi-*” (meaning two) and “*acanthus*” (meaning spine), referring the both side of pronota forming a spine. The gender is feminine.

Remarks. The new genus and species exhibit a combination of characters of the Cantacaderinae, Tinginae (Phatnomini and Tingini). The new species shared with series of characters of Cantacaderinae: bucculae extend in front of the head; clavus fully developed; pronotum never triangularly prolonged posteriorly to obscure scutellum; posterior pronotal process absent or greatly reduced; without a cyst-like hood, just covering part of head, median cephalic spines absent. However, the new genus has the stenocostal area absent, which is typical in the Phatnomini (Tinginae). And it also has the abdominal segments I–III fused and clypeal spines absent, which specific in the Tingini (Tinginae). Therefore, we consider the new species should be closer to Tinginae.

4 Discussion

The tingids usually has highly variables in the pronotum, especially the possess hood, multiple carinae and exaggerated paranota. The characters from 29 well-preserved fossil species, including the new species, *Cucullitingis biacantha* **sp. nov.**, ranging from Upper Jurassic to Miocene were compared as in Table 1 and divided hood, carinae and paranota into four types, respectively. Statistics and analysis for the amount and time of appearance are showed in Table 2.

Hood. Before mid-Cretaceous, no fossil was recorded with hood (16 species). Afterwards, species formed a vesicula at the anterior pronotum (7 species), e.g. *Hispanocader lisae* Golub, Popov & Arillo, 2012, or a small hood to cover part of head (2 species), e.g. *Cucullitingis biacantha* **sp. nov.** The evidence suggests the hood emerged in mid-Cretaceous. Contrasting with the remarkable hood in the extant species by covering the entire head, it has a tendency to cover the head. The evolution of hood is consistent with the current point that hood absent may be a more primitive character, and vesicula and hood gradually appeared during the process of evolution (Takeya, 1962).

Carinae. There is only one longitudinal carina observed in the earliest described tingids fossil species (9 species). Up to Lower Cretaceous, more than half of 29 species were observed three longitudinal carinae (18 species). Until the Eocene, even five longitudinal carinae were reported (2 species), e.g. *Intercader uniseriatus* Golub & Popov, 2005, *Paleocader* (*Cantacader*) *avitus* Drake, 1950. The current fossil record is according with the Guilbert’s point (Guilbert, 2001) that median carina absents or only with one median carina are the primitive characters. Meanwhile, it also indicates that the amount of carinae is diversified after mid-Cretaceous.

Paranota. Before mid-Cretaceous, most tingids have simple or slightly expanding paranota. Then, the character seems to evolve in two different directions: (1) further expands, and forms lobe, spine or cysts (5 species), e.g. *Burmacader multivenosus* Heiss & Guilbert, 2013, *Cucullitingis biacantha* **sp. nov.**; (2) gradually reduced, even disappear (11 species), e.g. *Oblongomorpha lutetia* Wappler, 2003, *Vianathauma pericarti* Golub & Popov, 2003. For extant tingids, most species correspond with the first phenotype, and a handful of species retains the primitively simple or slightly expanding paranota (Drake & Ruhoff, 1965; Guilbert *et al.*, 2014).

In 2001, Guilbert proposed to divide the pronotal of Tingidae into four phenotypes, the different external morphology of hood, carina, paranota also unified into following four types: (1) without hood, only one carina or absent, paranota narrow; (2) small hood, not covering the head, multiple carinae, carinae and paranota with uniseriate areolae; (3) bigger hood, covering part of hood, lateral carinae and paranota with multiseriate areolae; (4) hood large, covering the head, multiple carinae, paranota enlarge greatly so as to form cyst. However, the evolutionary rates of the specific characters, especially hood, carinae and paranota, are apparently inconsistent from Upper Jurassic to Miocene as above. Obviously, these three characters are independently evolved. For example, *Oblongomorpha lutetia* Wappler, 2003 has a ring-like vesicular at the anterior margin of pronotum, three longitudinal carinae, but has paranota absent. So, we think it is inappropriate to regard the hood, carinae and paranota with a consistent evolutionary rate as Guilbert’s point (Guilbert, 2001).

Table 1. Morphological character on hood, carina and paranota comprised with 29 described fossil species.

Family	Species	Epoch	Country	Hood	Carina	Paranota
Tingidae	<i>Agramma tertiarium</i> Zhang, 1989	Miocene	China	Without hood	Three longitudinal carinae, median carina short, lateral carinae	No description
Tingidae	<i>Ambarcader eugenei</i> Perrichot, Nel, Guilbert & Neraudeau, 2006	Middle Cretaceous	France	Vesicula tectiform	Three longitudinal carinae, median carina with uniseriate areolae, highest	Paranota very broad, three-lobed, extending anteriorly to level of hind margin of eyes, with 5–7 rows of wide areolae
Tingidae	<i>Amberobyrsa brandti</i> Heiss, 2009	Miocene	Dominican Republic	Without hood	Only one median carina extends from larger areolae to 2/3 of the triangular posterior projection	Paranota very broad and wing-shaped reaching 1/2 of antennal segment II; a longitudinal 3–4 row of wide areolae on anterior inner margin of paranota
Tingidae	<i>Archeopovia yurii</i> Golub, 2001	Eocene	Baltic	Hood present, covering part of the head	Three low longitudinal carinae	Paranota rather narrow, in the most of length with 2 rows of rectangular or pentagonal areolae in the greater part of the length with emarginate margins
Tingidae	<i>Burmacader multivenosus</i> Heiss & Guilbert, 2013	Middle Cretaceous	Myanmar	Without hood	Without carina	Paranota broad with 4 rows of wide areolae on widest anterolateral angle
Tingidae	<i>Chorotingioites priscus</i> Wappler, 2003	Eocene	Germany	Without hood	Three parallel carinae, median carina reaching from the posterior margin to the middle of pronotum, lateral carinae nearly as long as the median carinae	Paranota broad, without projecting anterior angles but slightly rounded outer margins
Tingidae	<i>Dictyonota petrifacta</i> Golub & Popov, 2000	Oligocene-Miocene	Russia	A ring-like vesicular	Three parallel carinae	Paranota broad, without projecting anterior angles but with 2 rows of wide areolae
Ebboidae	<i>Ebboa areolata</i> Perrichot, Nel, Guilbert & Neraudeau, 2006	Middle Cretaceous	France	Without hood	Only one median carina	No description
Tingidae	<i>Eocader babyrussus</i> Golub & Popov, 2000b	Miocene	Dominican Republic	Without hood	Three longitudinal low carinae, median carina stretching from posterior margin of calloused convex area to posterior margin of pronotum	Paranota broad, with 3 rows of wide areolae narrowing backward and with 1 row of rather small areolae along most part of their length
Tingidae	<i>Exmesselensis dissipinosus</i> Wappler, 2003	Eocene	Germany	Without hood	Three longitudinal carinae, median carina stretching from a posterior margin to the middle of the pronotum, lateral carinae nearly as long as the median carinae, and weakly curved	Paranota narrow, with one row of medium size areolae of irregular and round form, getting gradually smaller to the anterior margin
Tingidae	<i>Gyaclavator kohlsi</i> Wappler, Guilbert, Labandeira, Hörschemeyer & Wedmann, 2015	Eocene	U.S.A.	Without hood	Three ridge-like carinae	Paranota narrow

Table 1 (continued)

Family	Species	Epoch	Country	Hood	Carina	Paranota
Hispanocaderidae	<i>Hispanocader lisae</i> Golub, Popov & Arillo, 2012	Middle Cretaceous	Spain	Vesicular small	Only one low medial carina with one row of small rectangular areolae	Paranota narrow, with two rows of very small areolae in there widest parts, with 1–2 areolae of the third row; outer margin of paranota seated by exclusively small tubercles
Ignotingidae	<i>Ignotingis mirifica</i> Zhang, Golub, Popov & Shcherbakov, 2005	Upper Jurassic-Lower Cretaceous	China	Without hood	Only one longitudinal carina	Paranota narrow
Tingidae	<i>Intercader uniseriatus</i> Golub & Popov, 2005	Eocene	Baltic	Vesicula finely areolate, weakly elevated, rather narrow	Five low carinae without areolae	Paranota narrow with one row of small
Tingidae	<i>Intercader velteni</i> Golub & Popov, 2002	Eocene	Baltic	Vesicula finely areolate,	Three low carinae without areolae	Paranota rather narrow with one row of small areolae
Tingidae	<i>Leptopharsa evsyunini</i> Golub & Popov, 2000a	Miocene	Dominican Republic	Vesicula tectiform	Three longitudinal carinae bearing one row of quite large, rectangular areolae; median carina highest, about 1.5 times higher than the lateral ones	Paranota broad, distinctly deflected dorsad, with weakly projecting, rounded anterior angles, rounded outer margin
Tingidae	<i>Leptopharsa tacanae</i> Coty, Garrouste & Nel, 2014	Oligocene-Miocene	Mexico	Hood high and narrow, not covering head	Three white, parallel, longitudinal carinae with one row of very low rectangular areolae; a pair of moderately long, thin, horizontally erected setae located on both sides of carinae	Paranota broad with two rows of subrectangular areolae and with marginal veins sparsely covered with minute spinules bearing short, thin and erected setae
Tingidae	<i>Leptopharsa poinari</i> Golub & Popov, 2000a	Miocene	Dominican Republic	Hood present, covering part of head	Three foliaceous, relatively low longitudinal carinae with one row of small, mostly rectangular areolae; median carina highest at the boundary of disc and posterior pronotal process	Paranota broad, without projecting anterior angles, with the outer margin slightly sinuate about midlength, along almost entire length with two rows of moderately large, mostly quadrangular or pentagonal areolae
Tingidae	<i>Oblongomorpha lutetia</i> Wappler, 2003	Eocene	Germany	A ring-like vesicular	Three longitudinal carinae, median carina extending from calli to posterior margin, lateral carinae parallel to median but only half as long	Paranota absent
Tingidae	<i>Paleocader</i> = <i>Cantacader avitus</i> Darke, 1950	Eocene	Baltic	Without hood	Five longitudinal carinae: median and lateral pairs reaching anterior pronotal margin, interrupted at calli	Paranota broad, moderately explanate

Table 1 (continued)

Family	Species	Epoch	Country	Hood	Carina	Paranota
Tingidae	<i>Parazetekella eocenica</i> Nel, Waller & De Ploeg, 2004	Eocene	France	Without hood	Three longitudinal carinae, median carinar highest	Paranota very broad, extending anteriorly to level of eyes, with 5 rows of wide areolae
Tingidae	<i>Phatnoma mattijoae</i> Jepson, Penney & Green, 2011	Miocene	Dominican Republic	Without hood	Three longitudinal carinae, each with single row of cells	Paranota broad, moderately explanate with 2–3 rows of wide areolae, each with anterior and medial projection separated by five cells
Tingidae	<i>Phymacysta stysi</i> Golub, Popov & Guilbert, 2008	Miocene	Dominican Republic	Hood present, not covering head	Three very low longitudinal carinae without distinct cells; median carina slightly higher, lateral carinae reaching vesicula and posterior margin of pronotum	Paranota very broad, reflected on pronotal disc, strongly elevated and inflated, covering lateral pronotal carinae from above, markedly projecting outwards beyond lateral angles of pronotal disc in the widest part
Tingidae	<i>Sinaldocader ponomarenkoi</i> Golub & Popov, 2008	Lower Cretaceous	Transbaikalia	No description	Three longitudinal carinae with a single row of rectangular areolae	No description
Tingidae	<i>Spinitingis ellenbergeri</i> Heiss & Guilbert, 2013	Middle Cretaceous	Myanmar	Without hood	Three ridge-like carinae, not extending anteriorly to collar	Paranota narrow, with one row of irregular areolae
Tingidae	<i>Tingiometra burmanica</i> Heiss, Golub & Popov, 2015	Middle Cretaceous	Myanmar	Without hood	Only one longitudinal median areolate carina	Paranota narrow and slightly reflexed with one row of indistinct areolae
Vianaididae	<i>Vianagramma goldmani</i> Golub & Popov, 2000c	Upper Cretaceous	U.S.A.	Without hood	Only one very long median carina	Paranota broad
Vianaididae	<i>Vianathauma pericarti</i> Golub & Popov, 2003	Upper Cretaceous	U.S.A.	Without hood	Without carina	Paranota absent
Tingidae	<i>Cucullitingis biacantha</i> sp. nov.	Middle Cretaceous	Myanmar	Hood spheroid, cover up the posterior of head	Only one median carina raised with one row of areola	Paranota very broad, three areolae wide, apex of the paranota forming a spine, extending anteriorly to anterior margin of eyes

Table.2 Different types of hood, carinae and paranota appeared in different geological.

Character		J3	K1	K2	K3	E1	E2	E3	N1	N2	Qp	Qh	Amount
29 fossil species		✱	✱	✱	✱		✱	✱	✱				29
Hood	Without hood or vesicular	▲	▲	▲	▲		▲		▲				16
	A ring-like vesicular at the anterior margin			▲			▲	▲	▲				7
	Hood small, not cover the head							▲	▲				2
	Hood larger, covering part of the head			▲			▲		▲				3
	No description		▲										1
Carina	Without or only a median carina, carina uniseriate with small areolae	●	●	●	●				●				9
	Three carinae, carina uniseriate with one row of areolae		●	●			●	●	●				18
	Three carinae, carina multiseriate												0
	More than three carinae						●						2
	No description												0
Paranota	Paranota absent				■		■						2
	Paranota narrow and uniseriate	■	■	■			■						9
	Paranota broad and multiseriate			■	■		■	■	■				10
	The paranota very broad, forming spines or lobes			■			■		■				5
	No description		■	■					■				3

Abbreviation. ▲—hood; ●—carinae; ■—paranota; J3—Upper Jurassic; K1—Lower Cretaceous; K2—Middle Cretaceous; K3—Upper Cretaceous; E1—Paleocene; E2—Eocene; E3—Oligocene; N1—Miocene; N2—Pliocene; Qp—Pleistocene; Qh—Holocene.

5 Conclusion

A new genus and new species *Cucullitingis biacantha* **gen. & sp. nov.** from Myanmar is reported. Based on the comparative morphology study of the hood, carinae and paranota in 29 well-preserved fossil species from Upper Jurassic to

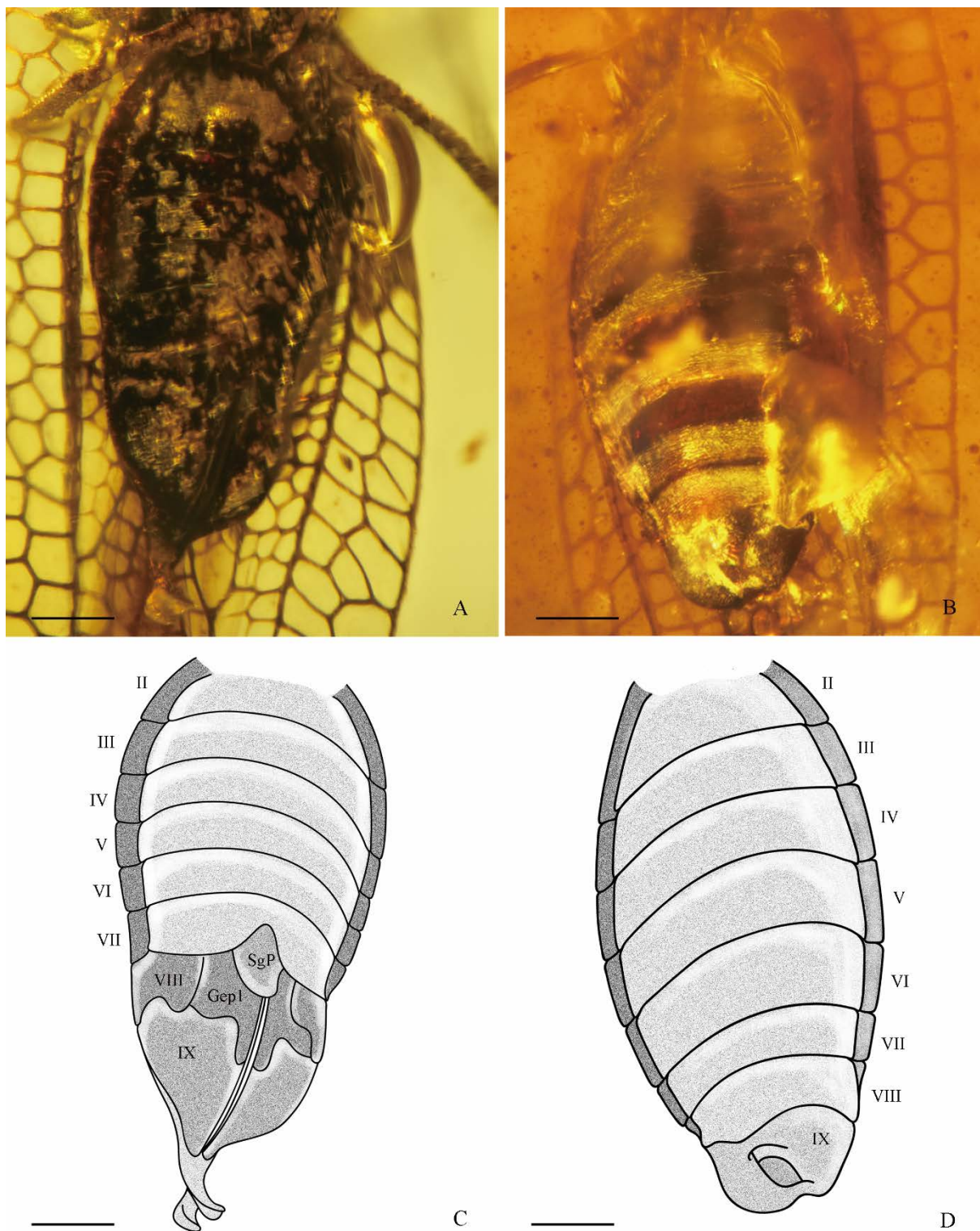


Figure 2. Abdomen of *Cucullitingis biacantha* **sp. nov.** A. Photograph of holotype, CNU-HEM-MA2017001. B. Line drawing of holotype, CNU-HEM-MA2017001. C. Photograph of paratype, CNU-HEM-MA2017002. D. Line drawing of paratype, CNU-HEM-MA2017002. Scale bars = 200 μm.

Miocene, we think the characters of hood, carinae and paranota are three independently evolutionary characters in tingids, and have different evolutionary direction during different periods of geological time.

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