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Diverse Texas beetles (Coleoptera: Elateroidea: Brachypsectridae) in mid-Cretaceous Burmese amber: sexual dimorphism and palaeoecology

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Abstract

Brachypsectridae is a species-poor elateroid family containing two extant genera with a disjunct distribution range spanning the Nearctic, Palaearctic, Oriental, and Australian regions. Here we describe a second Texas beetle from mid-Cretaceous Burmese amber, *Hongipsectra electrella* **gen. et sp. nov.** The new genus can be distinguished from all hitherto known brachypsectrids by the 11-segmented sexually dimorphic antennae with antennomeres 6–10 bilamellate in males and serrate in females, pronotum with a pair of posterolateral carinae and an M-shaped notch in the posterior margin for the reception of a cordiform scutellum. The present discovery adds a fourth genus and eleventh species to Brachypsectridae. Given that two of the known Texas beetle genera are from the Cretaceous Burmese amber, the family probably have been much more widespread and diverse in the Mesozoic than it is today. A key to the extant and fossil genera of Brachypsectridae is provided, along with a list of fossil species.

Keywords: Brachypsectridae, *Brachypsectra*, Myanmar, sexual dimorphism, palaeoecology, key, checklist

Introduction

Brachypsectridae, sometimes referred to as 'the Texas beetles', is a small elateroid family with only 10 species in 3 genera, including one extinct genus. The first representative of the family was collected by the Swedish-born entomologist Gustav Wilhelm Belfrage at the Texas-Mexico border in the late 1860s or early 1870s (LeConte, 1874; Geiser, 1933; Neck, 1993). Texas beetles strongly resemble elaterids with their pronounced and carinate hind pronotal angles, elongate prosternum, and general body shape, but differ from them in having transverse procoxae, five abdominal ventrites, and lacking a functional prothoracic 'clicking mechanism' (Young, 2002). The bizarre predaceous larvae of Brachypsectridae, that live under loose bark and in dead plant material and possess striking elongated feathery lateral lobules, have long puzzled entomologists (Barber, 1905; Ferris, 1927) and were not associated with the adults until more than half a century after the discovery of the first brachypsectrid specimen (Blair, 1930). For decades, Brachypsectridae was known only from a single genus, *Brachypsectra*, and a handful of specimens from southwestern North America.

It later became apparent that the Texas beetles are much more widely distributed than their English vernacular name suggests. *Brachypsectra fuscula* from Singapore and *B. lampyroides* from India were described almost 90 years ago (Blair, 1930). Woodruff (2002) described a new species from the Dominican Republic and further undescribed larvae have been found in Australia (Lawrence & Britton, 1994; Costa *et al.*, 2006). Only relatively recently were brachypsectrids reported from the Palaearctic region; *Brachypsectra* is now known from Cyprus, Iran, and Turkey (Hájek, 2010; Petrželková *et al.*, 2019). Kovalev & Kirejtshuk (2016) described a second brachypsectrid genus, *Asiopsectra* Kovalev & Kirejtshuk, with two species from Iran and Tajikistan.

Only two fossil brachypsectrids have been described to date (Table 1). *Brachypsectra moronei* was reported from Miocene Dominican amber by Costa *et al*. (2006). Brachypsectrid larvae have been found in Eocene Baltic amber (Klausnitzer, 2009) and we have also seen them in Burmese amber. *Vetubrachypsectra burmitica*, the first Mesozoic Texas beetle, was recently described from Burmese amber by Qu *et al*. (2019).

The systematic position of Brachypsectridae has for long represented a contentious issue. *Brachypsectra* was originally incorporated into the family Rhipiceridae

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TABLE 1. Checklist of fossil Texas beetles (Brachypsectridae) arranged stratigraphically.

Taxon	Deposit	Age	Remarks
	CRETACEOUS		
Hongipsectra electrella Tihelka, Huang & Cai **gen. et sp. nov.**	Burmese amber, northern Myanmar	Albian-Cenomanian	
Vetubrachypsectra burmitica Qu & Cai, 2019	Burmese amber, northern Myanmar	Albian-Cenomanian	
	EOCENE		
Brachypsectra **sp.**	Baltic amber	Priabonian	Undescribed larvae were mentioned by Klausnitzer (2009).
	MIOCENE		
Brachypsectra moronei Branham, 2006	Dominican amber	Burdigalian-Langhian	Known from an adult male and a larva.
Brachypsectra **sp.**	Dominican amber	Burdigalian-Langhian	Undescribed larvae and an adult specimen were mentioned by Woodruff (2002).

(LeConte, 1874) but was soon after moved to Dascillidae (Horn, 1881), before being placed into a separate family. Based on data from eight nuclear genes, McKenna *et al*. (2015) recovered Brachypsectridae as a sister group to a clade containing Cerophytidae, Eucnemidae, and Throscidae, and dated their origin to the late Jurassic. This placement is supported by morphological data (Lawrence *et al*., 2011) and fossil evidence; the presumably basal fossil genus *Vetubrachypsectra* has the pedicel attached subapically to the scape, a condition only found in Cerophytidae and Eucnemidae (Qu *et al*., 2019).

Here we describe a new brachypsectrid genus from mid-Cretaceous amber from northern Myanmar, representing the second record of the family in the Mesozoic.

Material and methods

Amber from northern Myanmar (Burma) preserves the richest Cretaceous terrestrial arthropod fauna known to science (Cai *et al*., 2017; Huang *et al*., 2018; Li *et al*., 2019). All specimens examined in this study originate from mines at the summit of the Noije Bum Hill in the Hukawng Valley, Kachin State. Volcanoclastic matrix from the amber-bearing horizon was dated radiometrically and provided a minimum age of 98.17 Ma for the deposit (Shi *et al*., 2012; Mao *et al*., 2018), while a recently discovered ammonite entombed in the amber indicates that it is at most late Albian in age (Yu *et al*., 2019). The fossilised resin was probably secreted by dawn redwood trees (Grimaldi & Ross, 2017). The Burmese amber forest palaeoenvironment was probably humid and tropical (Grimaldi *et al*., 2002). At the time the resin was secreted, the West Burma Block was an isolated island with a near-equatorial climate (Westerweel *et al*., 2019).

The amber was prepared using a handheld cutter, different grades of sandpaper, and diatomite powder. Images were taken using a Canon EOS 7D camera with a Canon MP-E 65 mm macro lens (F2.8, 1–5X) and Canon MT-24EX twin flash mounted to a WeMacro automatic focus stacking rail. Red fluorescence microphotographs were taken using the Zeiss Axio Imager 2 light microscope under the rhodamine mode. The type specimens are deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (CAS), Nanjing, China.

Systematic palaeontology

Order Coleoptera Linnaeus, 1758
Suborder Polyphaga Emery, 1886
Superfamily Elateroidea Leach, 1815
Family Brachypsectridae Horn, 1881

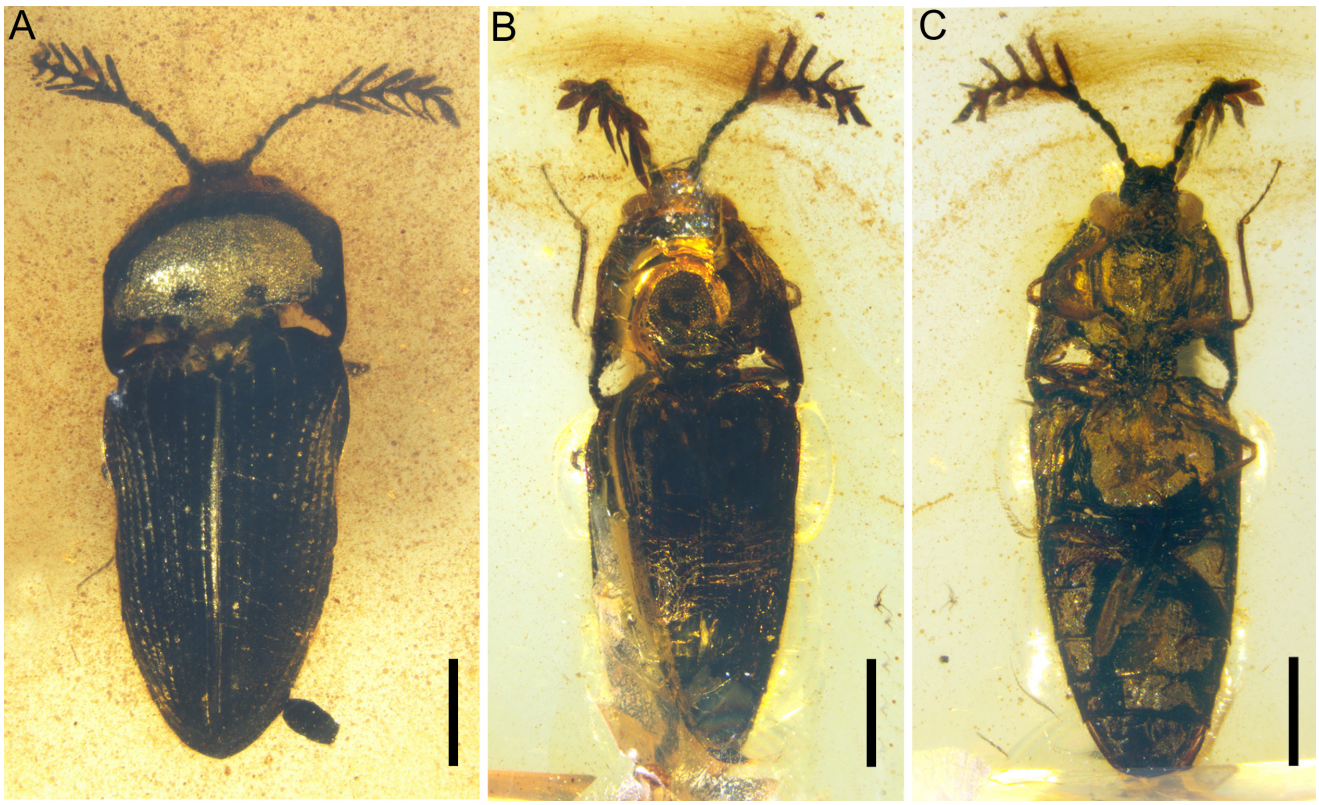

FIGURE 1. Male specimens of *Hongipsectra electrella* **gen. et sp. nov.** from mid-Cretaceous Burmese amber; under normal reflected light. **A**, Holotype (NIGP171391), dorsal view. **B**, Paratype (NIGP171392), dorsal view. **C**, Paratype (NIGP171392), ventral view. Scale bars: 1 mm.

Genus *Hongipsectra* gen. nov.

Type species. *Hongipsectra electrella* **sp. nov.**; by present designation.

Etymology. The generic name is formed from the family name of the pioneering Chinese palaeoentomologist, Prof. You-Chong Hong, and Greek "ψήκτρα" (psectra), meaning "scraper". Gender feminine.

Diagnosis. Antennae with 11 antennomeres, sexually dimorphic; antennomeres 6–10 bilamellate in males, serrate in females, always with third antennomere elongate and more than 1.5 times as long as preceding segment. Pronotum with one pair of posterolateral carinae. Pronotal base with medial M-shaped notch for reception of scutellum. Anterior margin of scutellum with medial notch. Elytra each with 10 clearly visible striae, deeply impressed throughout their length.

Hongipsectra electrella **sp. nov.**
(Figs 1–4)

Type material. Holotype: NIGP171391, a single well-preserved male in polished Burmese amber; Hukawng Valley, Myitkyina District, Kachin State, northern Myanmar; Albian-Cenomanian (Cretaceous). **Paratypes:** NIGP171392–171393, 1 male and 1 female, same locality and depository as holotype

Etymology. Derived from the Greek and Latin '*elektron*', meaning amber, in reference to the preservation medium.

Diagnosis. As for the genus, with additional characters: body length 5.54–5.70 mm; head between eyes 1.9–2.5 times as wide as the diameter of the eye; and metacoxae excavate to receive femora but not forming large plate.

Description. Body elongate, oval, slightly convex dorsoventrally. Body length 5.54–5.70 mm (♂ 5.54–5.58 mm, Fig. 1; ♀ 5.70 mm, Fig. 2), body width 2.00–2.49 mm (♂ 2.00–2.26 mm; ♀ 2.49 mm), body broadest at pronotum medially and at elytra basally. Colour uniformly black, integument glabrous.

Head visible from above, 1.93–2.7 times wider than long, slightly declined, broadest at eyes, not distinctly constricted behind eyes, deeply inserted into prothorax (Fig. 3A). Frontoclypeal region strongly declined anteriorly. Mouthparts directed ventrally. Labrum small. Mandibles slender, retracted within head capsule. Frontoclypeal suture absent. Compound eyes large, finely faceted, more or less globular, lacking interfacetal setae,

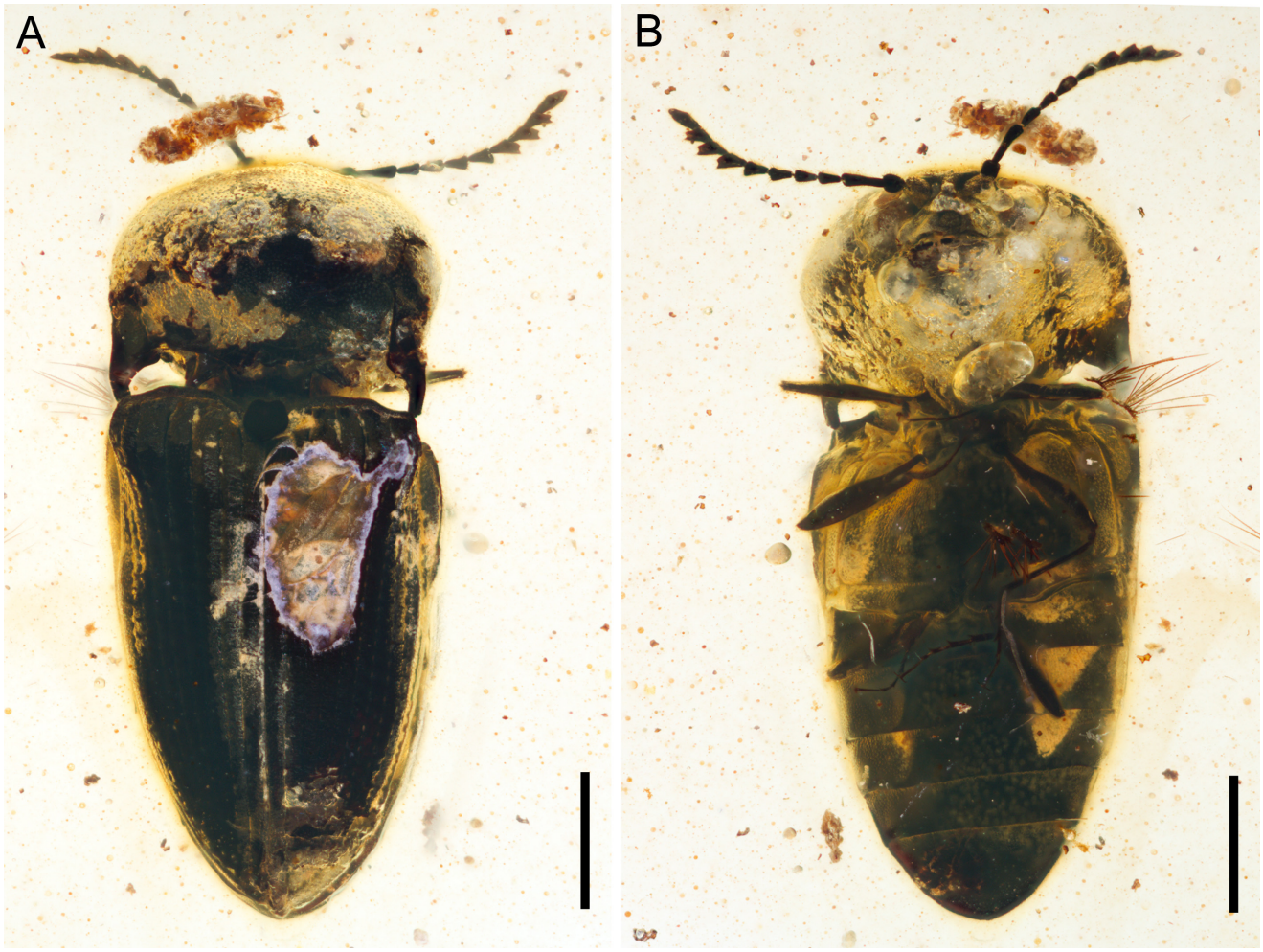

FIGURE 2. Female specimen (paratype, NIGP171393) of *Hongipsectra electrella* **gen. et sp. nov.** from mid-Cretaceous Burmese amber; under normal reflected light. **A**, Dorsal view. **B**, Ventral view. Scale bars: 1 mm.

head between eyes 1.9–2.5 times as wide as eye diameter. Antennal insertions not visible dorsally, separated from eyes by 0.5–1.0 times basal antennomere width. Antennae inserted into deep oval fossae separated by flat elevated area representing around one-quarter of fossa width. Antennae 11-segmented, sexually dimorphic (Figs 3C, D, 4A–C), reaching elytral base. Antennomere 1 barrel-shaped and wide, subequal to antennomere 2 in male, distinctly longer than antennomere 2 in female; antennomere 3 1.6–1.7 times length of preceding segment in male, 2.1 times length of preceding segment in female; antennomeres 4 and 5 subequal; antennomeres 6–10 bilamellate in male with lamellae longest basally, serrate in female with apical antennomeres most distinctly serrate; antennomere 11 with acute apex in male and somewhat more rounded apex in female.

Pronotum subtrapezoidal, 1.20–1.59 times wider than long, broadest medially. Pronotum rounded anteriorly, subparallel in posterior half, posterior margin with deep M-shaped notch medially for accommodating scutellum (Figs 3B, 4D). Anterior angles broadly rounded and not produced forward. Posterior angles acute, produced posteriorly, almost embracing elytra, bearing carinae which extend throughout their length. Pronotal disc with one pair of lateral carinae starting at base of posterior angles and extending to anterior half, subparallel with lateral margin of pronotum and with medially oriented expansion anteriorly. Disc surface densely punctate, with punctures separated by at most 3 times their diameter. Scutellum flat, with medial notch anteriorly, widest medially, and pointed apically, giving it conspicuous cordiform appearance.

Prosternum rounded anteriorly, forming short medial chinpiece. Prosternum anterior to procoxae approximately four times as long as breadth of procoxae. Prosternal process wedge-shaped and narrowing apically, apex fitting into mesoventral cavity. Mesoventrite short. Metaventrite long and flattened, with rounded anterior process reaching posterior third of mesocoxae.

Elytra elongate, 1.6–1.9 times longer than their

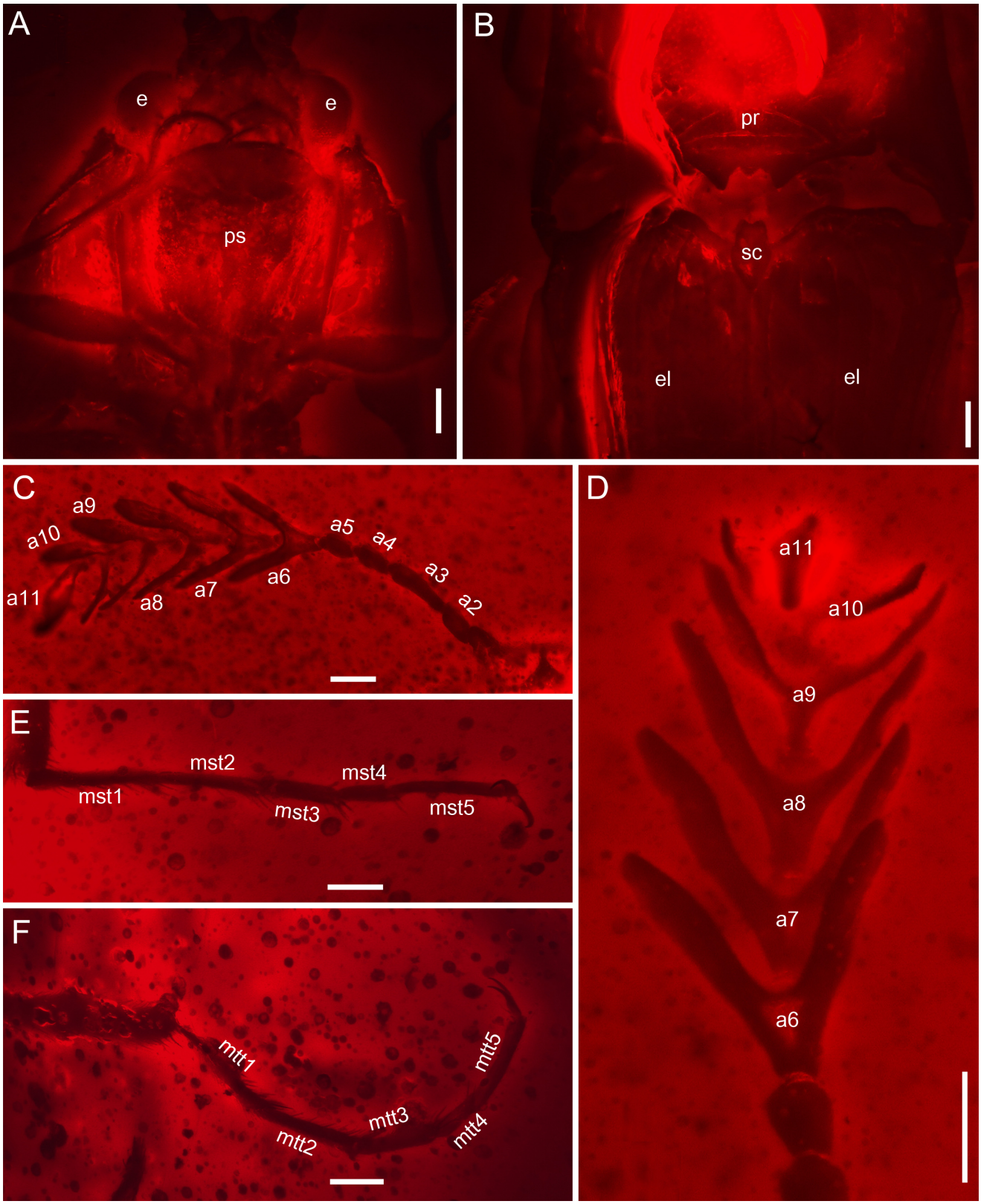

FIGURE 3. Details of *Hongipsectra electrella* **gen. et sp. nov.** from mid-Cretaceous Burmese amber; under red epifluorescence. **A** and **B**, paratype (NIGP171392); others, holotype (NIGP171391). **A**, Ventral view of prothorax. **B**, Dorsal view of prothorax and elytra. **C**, Ventral view of right antenna. D, Apical seven antennomeres of left antenna. **E**, Left mesotarsus, ventral view. **F**, Right metatarsus, ventral view. Abbreviations: a, antennomere; e, eye; el, elytron; mst, mesotarsomere; mtt, metatarsomere; pr, pronotum; ps, prosternum; sc, scutellum. Scale bars: 100 μm in **E** and **F**, 200 μm in others.

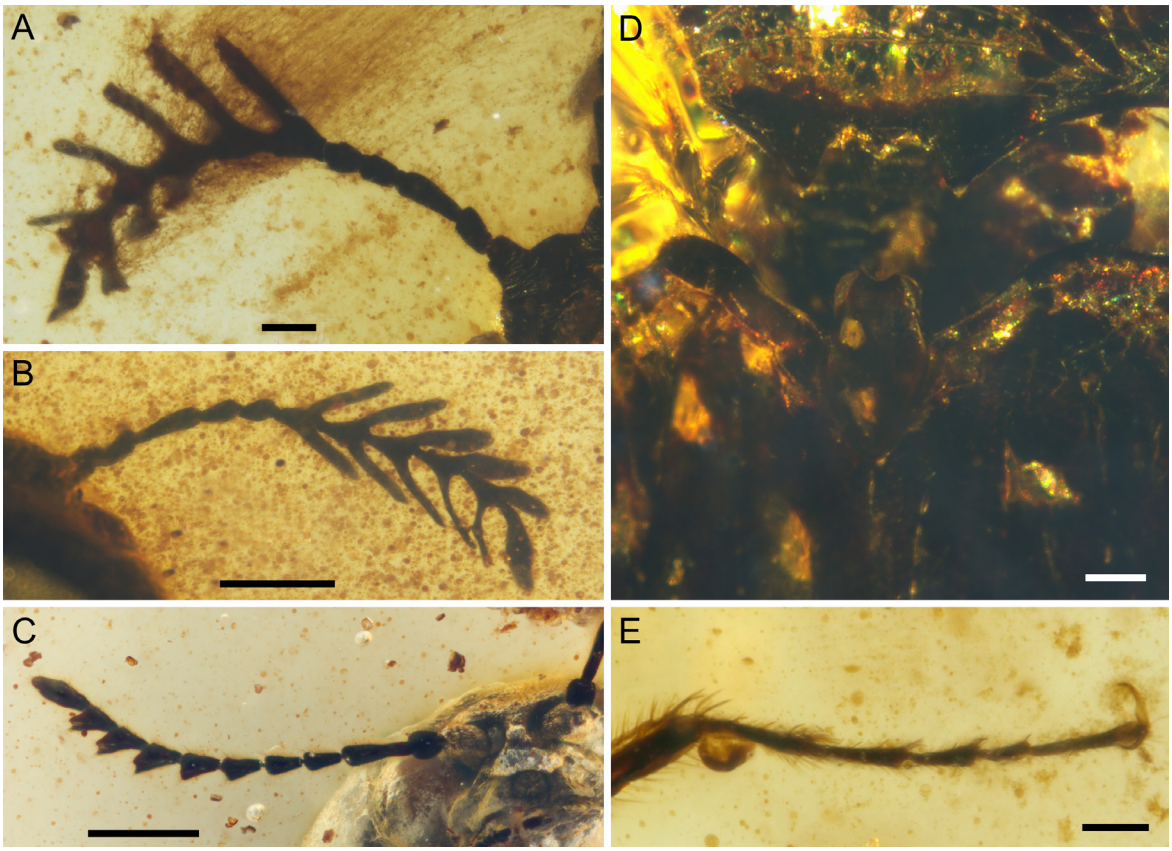

FIGURE 4. Details of *Hongipsectra electrella* **gen. et sp. nov.** from mid-Cretaceous Burmese amber; under normal reflected light. **A**, Right antenna of paratype (NIGP171392), ventral view, male. **B**, Right antenna of holotype (NIGP171391), dorsal view, male. **C**, Right antenna of paratype (NIGP171393), ventral view, female. **D**, posterior margin of pronotum and scutellum, paratype (NIGP171392). **E**, Left protarsus of paratype (NIGP171392). Scale bars: 200 μm in **A**, 500 μm in **B** and **C**, 100 μm in **D** and **E**.

combined width, subparallel basally and gradually narrowing from apical third. Elytral humeri well-developed. Elytra with 10 clearly visible and complete striae, deeply impressed throughout their length, and consisting of strongly elongate punctures. Sutural margin without distinct carina. Elytral punctation finer than on pronotum. Epipleural margin widest basally, narrowing posteriorly, terminating in mid of elytral length. Hindwings present.

Abdomen with five ventrites, broadest medially. Ventrites 1 and 3 subequal; ventrite 2 1.1–1.2 times as long as preceding segment; ventrite 4 slightly shorter than preceding segment, ventrite 5 twice as long as preceding segment. Ventrites lacking grooves for reception of legs. Legs slender. Procoxae strongly transverse, separated by more than 1.0 times procoxal width. Mesocoxae globular, cavities separated by more than 1.0 times mesocoxal width. Metacoxae excavated for reception of femora but not forming large plate. Trochanters elongate, profemora obclavate. Tarsi 5-segmented, simple (Figs 3E, F and 4E); with tarsomeres 1 and 5 subequal; tarsomere 4 shortest and representing approximately half of apical tarsomere length. Pretarsal claws simple, empodium setose.

Discussion

Systematic position

Hongipsectra **gen. nov.** can be placed into the family Brachypsectridae based on its elaterid-like habitus, somewhat flattened body, developed prosternal process, lack of a well-developed clicking mechanism, acute posterior pronotal angles, transverse prothoracic coxae, simple tarsal claws, and 5-segmented abdomen (Young, 2002; Costa *et al*., 2006, 2010).

Hongipsectra electrella **gen. et sp. nov.** combines characters present in both extant genera of Brachypsectridae. It can be distinguished from *Asiopsectra* by the 11-segmented antennae, shape of pronotum and scutellum, and the absence of irregular rows of coarse punctures on the elytra. It however shares the form of the antennal fossae, slender mandibles, and the presence of bilamellate antennomeres. *Hongipsectra* **gen. nov.** differs from *Brachypsectra* in having a pronotum with two lateral carinae aside from having carinate posterior pronotal angles, a cordiform scutellum, M-shaped posterior pronotal margin, and bilamellate antennae, but shares the number of antennomeres, and the deep and nearly adjacent antennal fossae.

Hongipsectra **gen. nov.** can be easily distinguished from *Vetubrachypsectra*, the only other Burmite brachypsectrid, by the presence of deeply impressed elytral striae, structure of the antennae, shape of the posterior pronotal margin, and pedicel not attached subapically to the scape. Among the Texas beetles, a heart-shaped scutellum is, to our knowledge, only found in *Hongipsectra* **gen. nov.** Similar scutellar shields with an incised anterior margin have convergently developed in members of the byrrhoid family Ptilodactylidae.

A key to the recent and fossil genera of Brachypsectridae is provided in Appendix 1.

Sexual dimorphism

The new brachypsectrid specimens show morphological variability that falls within the range of sexual dimorphism in extant taxa. Based on comparison with modern members of *Brachypsectra* (Costa *et al*., 2006), we conclude that one of our specimens is a female while the remaining two are males.

In Brachypsectridae, females are larger, broader, and have a more evenly rounded anterior pronotal margin than males (Costa *et al*., 2006). The same is the case in our specimens. The female is 5.70 mm long and 2.3 times as long as wide, while the males are 5.54–5.58 mm long and 2.5–2.9 times as long as wide. In *Hongipsectra electrella* **gen. et sp. nov.** the distance between the compound eyes and antennal insertions also differs between the sexes. While in the female specimen the antennal insertions are separated from the eyes by merely 0.5 times the length of the basal antennomere, it is 0.9–1.0 in the males. The female possesses a more elongate scape and a more elongate third antennomere, constituting 2.1 times the length of the second antennomere, while in males the third antennomere is always less than twice as long as the preceding segment. Most notably, the males have bilamellate antennal segments 6–10, while the female specimen has antennal segments 6–10 serrate. In extant brachypsectrids, the males likewise typically have expanded seven apical antennomeres, in contrast to the females where the expansion is less pronounced (Costa *et al.*, 2006). This may suggest that male brachypsectrids use their antennae to detect pheromones emitted by females, which would be expected to impose strong selection for a large surface area of olfactory organs.

Mathematical models predict the maintenance of sexual polymorphism over multiple generations (Le Rouzic *et al*., 2015). This is because males are likely to search for cues typical of the most common female morphs, which thus become the target of most mating attempts (Svensson *et al*., 2005; Gosden & Svensson, 2009). Evidence of sexual dimorphism is rare in the fossil record of insects, since most species of extinct terrestrial arthropods are known only from the type specimens. This has however begun to change in the recent years with growing interest in insect Konservat-Lagerstätten from the Mesozoic, such as the Burmese amber. The first cases of sexual dimorphism in Burmese amber beetles were recently reported by Jiang *et al*. (2019) in minute clubbed beetles (Monotomidae), and by Cai & Huang (2019) in silvanid flat bark beetles (Silvanidae). In both cases, the Cretaceous species show distinct sexual dimorphism similar to extant taxa. Our present discovery of *Hongipsectra* **gen. nov.** adds yet another example of sexual dimorphism in Mesozoic insects. Hopefully, as more specimens come to light, it will become possible to test the stability of sexual dimorphism and mate preference over macroevolutionary time scales.

Palaeoecology

Little has been known about the biology of the Texas beetles. Adult brachypsectrids are rarely encountered, and most specimens have been collected at UV lights during night. This, combined with their sporadic occurrence, seems to suggest that the adults are nocturnal and probably short-lived (Fleenor & Taber, 1999). It is interesting to note that the mouthparts of modern and fossil brachypsectrids are significantly reduced, implying that the beetles may not feed during their adult life. Reduced mouthparts are found in some lycid imagines, many of which also do not feed as adults and rely on metabolic reserves acquired during development (Bocák & Bocáková, 2010). This may explain the reportedly voracious behaviour of brachypsectrid larvae; they are ambush predators that prey on a range of arthropods, often much larger than themselves. They have been observed to consume many small spiders in a relatively short period of time (Crowson, 1973) and have been found associated with "notable accumulations of insect remains" (Neck, 1993).

Hongipsectra electrella **gen. et sp. nov.** possesses well-developed elytral humeri. A part of the elytron of the female specimen (NIGP171393) was polished away, exposing the basal part of the right hindwing. This indicates that the beetles could disperse by flight.

Modern brachypsectrids are apparently rare and have a highly disjunct distribution range (Hájek, 2010; Kovalev & Kirejtshuk, 2016; Petrželková *et al*., 2017). The discovery of a second brachypsectrid genus in Burmese amber suggests that the family probably has been much more diverse in the Cretaceous than today. This indicates that Texas beetles are a relictual family that may have suffered from extinctions throughout much of its original range since the Mesozoic era. It cannot however be ruled out that undescribed extant species still await discovery and have escaped the attention of entomologists due to their cryptic lifestyle.

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Appendix: Key to the genera of extant and fossil Texas beetles (Brachypsectridae)

1 Pronotum without an M-shaped medial notch on the posterior margin; scutellum without a medial notch on the anterior margin; if antennae bilamellate then 12-segmented..... 2

– Pronotum with an M-shaped medial notch on the posterior margin; scutellum with a medial notch on the anterior margin; antennae 11-segmented with segments 6–10 bilamellate in males..... †*Hongipsectra* Tihelka, Huang & Cai **gen. nov.**

2 Elytra more or less glabrous, lacking striae; pedicel attached subapically to the scape..... †*Vetubrachypsectra* Qu & Cai, 2019

– Elytra with at least faint striae or irregular rows of coarse punctures; pedicel not attached subapically to the scape.....3

3 Antennae 11-segmented, never with bilamellate segments; elytra with nine rows of weakly impressed striae ..... *Brachypsectra* LeConte, 1874

– Antennae 12-segmented, with some segments bilamellate; elytra with irregular rows of coarse punctures..... A*siopsectra* Kovalev & Kirejtshuk, 2016