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A Cretaceous bug indicates that exaggerated antennae may be a double-edged sword in evolution

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Abstract

The true bug family Coreidae is noted for its distinctive expansion of antennae and tibiae. However, the origin and early diversity of such expansions in Coreidae are unknown. Here, we describe the nymph of a new coreid species from a Cretaceous Myanmar amber. *Magnusantenna wuae* **gen. et sp. nov.** (Hemiptera: Coreidae) differs from all recorded species of coreid in its exaggerated antennae (nearly 12.3 times longer and 4.4 times wider than the head). Such antennal elaboration indicates that long-distance chemical communication behavior in Hemiptera has been already well established in the early of Upper Cretaceous. The specialized antenna maintains in adult like extant coreids, which means that antennae plays an important role in sexual display and defense behavior. Even so, the highly specialized trait would also have confronted a substantial investment and high risk, which may have facilitated the final extinction of the species.

Keywords: Mesozoic Coreidae; chemical communication; sexual display; defense behavior; extinction risk

Introduction

The emergence of individual niches facilitates the appearance of new specialized morphological features on the basis of natural selection (Kratochwil et al., 2018; Lee et al., 2011). The antennae of insects play a significant role in locating of potential host plants, suitable spawning grounds, attracting mates and escaping predation (Gao et al., 2016; Pekár and Hrušková, 2006). Expansive and delicate antennae carry more

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olfactory receptors, which facilitates the life activities of insects, especially in chemical communication and sexual selection behavior (Krogmann et al., 2013; Wappler et al., 2015). The rapid rise of angiosperms has changed the structure of terrestrial vegetation while promoting the development of plant-related insect diversity in the Cretaceous (Engel, 2015; McLoughlin and Pott, 2019). It is especially important to search and occupy survival resources quickly and efficiently in fierce competition. According to fossil evidence, long-distance chemical communication behavior occurred in numerous insect groups in the Early Cretaceous, but has not yet been found in Hemiptera (Gao et al., 2016; Krogmann et al., 2013; Wichard, 2017).

Coreids, which are commonly known as leaf-footed bugs because of their leaf-like expansive legs, vary in body form and size (Panizzi and Grazia, 2015). In addition, the similar expansion on the antennae of coreids is also an easily identifiable character (Fracker, 1919a). Coreidae is a moderately large family in the insect order Hemiptera, with nearly 500 genera and 2200 species (Hamouly et al., 2010) within four subfamilies: Coreinae Leach, 1815 (Schuh and Slater, 1995); Hydarinae Stål, 1873 (Brailovsky, 2010); Meropachyinae Stål, 1868 (Brailovsky and Barrera, 2009) and Pseudophloeinae Stål, 1868 (CoreoideaSF, 2019; Hamouly et al., 2010). The family has a worldwide distribution, particularly in the neotropics and subtropics (CoreoideaSF, 2019). Most species can be economic pests that feed on legumes, rice, fruits and other crops, usually causing the host plant to wither or die. They are identified by a combination of characteristics: antennae and rostrum four-segmented; antennal socket visible dorsally; pronotum trapezoid or hexagonal; membrane of the forewings with many parallel longitudinal veins; tarsi three-segmented; scent glands on the thorax between the middle and hind coxae; and antennae, humeral angles or hind tibiae sometimes showing expansion (Schuh and Slater, 1995). Expansion of various body parts plays a significant role in sexual selection and defense behavior (Eberhard, 1998). But we know nothing about the origin or early diversity of these exquisite expansions in Coreidae.

All the confirmed fossil records of the Coreidae during Mesozoic are preserved in China, the oldest of which is from the Upper Triassic strata (Hong, 1987; Hong, 1984; Lin, 1992). Fossil representatives are relatively common in Tertiary strata, being known from Eocene strata of the United States (Cockerell, 1909; Scudder, 1890); Oligocene rocks of France (Théobald, 1937), Germany (Heyden, 1858; Statz and Wagner, 1950); Miocene strata of China (Hong et al., 1983; Hong and Wang, 1987; Zhang, 1989; Zhang et al., 1994; Zhang and Zhang, 1990), Croatia (Heer, 1853) and Germany (Heer, 1853); and Pliocene rocks of France (Piton, 1935). *Yuripopovina magnifica* of family Yuripopovinidae is the oldest known specimen of the superfamily Coreoidea preserved in the Cretaceous Lebanese amber (Azar et al., 2011). So far, four species of the family Coreidae have been described from the Cretaceous rock impressions, all of which do not have expanded antennae (Database, 2018).

Here, we describe a coreid nymph with exaggerated, expanded antennae that lived in the area of present-day northern Myanmar during the Upper Cretaceous. During the Cretaceous, these bugs were active on gymnosperms, ferns, and early angiosperms, feeding on the nutritional material in the leaves, branches, trunks, flowers and seeds of host plants, especially in young tissue (Panizzi and Grazia, 2015). This nymph

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represents the first record of the family Coreidae preserved in amber. The characteristic foliated antennal expansion of the coreids is demonstrated to have existed approximately 99 million years ago; this improves our understanding of coreid biodiversity during the Cretaceous Period. In addition, we discuss the important role of specialized antennae in long-distance chemical communication behavior, sexual display and defense behavior, and the risk of extinction caused by exaggerated appendages.

Result

Systematic paleontology

Order Hemiptera Linnaeus, 1758

Suborder Heteroptera Latreille, 1810

Infraorder Pentatomomorpha Leston, Pendergrast and Southwood, 1955

Superfamily Coreoidea Reuter, 1815

Family Coreidae Leach, 1815

Subfamily Coreinae Leach, 1815

Genus *Magnusantenna* gen. nov.

***Magnusantenna wuae* gen. et sp. nov.**

(Figs. 1–4)

Type species. *Magnusantenna wuae* gen. et sp. nov.

Etymology. The generic name is derived from Latin prefix *margus*, meaning large, and *antenna*, meaning antenna; referring to the enlarged antennae.

Diagnosis. Body slender, length approximately 6.67 mm. Antenna extremely large, subequal to the body length, with four segments. First segment inflated; second, third and fourth segments expanded and remarkably toward the apex. Head square, compound eyes large, spherical, located at the center of each side of the head and prominently protruding. Pronotum and mesonotum trapezoidal. Legs slender.

Remarks. *Magnusantenna* gen. nov. is similar to the extant *Chariesterus* Laporte, 1832 in the following ways: body slender; lateral margins parallel; head subquadrate; compound eyes prominent and protruding; antennal socket protruding forward; antennae subequal to the length of the body; third antennal segment variously foliate; pronotum narrowed anteriorly, without collar; and hind tibiae not expanded. However, *Magnusantenna* gen. nov. can be distinguished from *Chariesterus* by several characteristics: first antennal segment slightly fusiform; second antennal segment approximately rectangular and spreading; fourth antennal segment exhibiting very large triangular spread; rostrum segments each of different length; and pronotum without spinose humeri. Conversely, *Chariesterus* exhibits several characteristics that differ from those of *Magnusantenna* gen. nov.: first antennal segment somewhat triquetral, usually bearing small denticles or acute spines, slightly curved at least in the basal area; second and fourth antennal segments not expanded; and rostrum segments subequal in length, diverging posteriorly to form prominent spinose humeri (Panizzi and Grazia, 2015; Ruckes, 1955). *Magnusantenna* gen. nov. is markedly different from all

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previously described fossil Coreidae in the scale of the antennal exaggeration.

***Magnusantenna wuae* gen. et sp. nov.**
(Figs. 1–4)

Etymology. The specific epithet, *wuae*, is in honor of Ms. Wu Lijing, who provided the specimen.
Holotype. STJS0003. Nymph, probably approach fourth instar. Deposited in the Century Amber Museum (Room 301A No.1, Songrui Road, Songgang Street, Bao'an District, Shenzhen, China). Only known specimen.
Horizon and Locality. Hukawng Village, Kachin State, northern Myanmar; Upper Cretaceous (earliest Cenomanian), 98.79 ± 0.62 Ma (Shi et al., 2012). Only known from the type locality.
Diagnosis. as for genus.
Description. Body slender, length 6.67 mm, width 0.76 mm (Figs. 1, 3, 4). Head subquadrate, length 0.55 mm, width 0.56 mm (Figs. 1, 2A, 4).

Labrum long triangle, basal area slightly broad, gradually narrowing toward apex (Fig. 2B). Compound eyes large and spherical, located on the center of the lateral margins of the head and protruding outward significantly (Figs. 1, 2A–B, 3, 4). Rostrum with four segments; first segment close to the ventral surface of the head, reaching the anterior margin of the compound eye, length 0.47 mm; second segment vertical to the body, longest rostrum segment, length 0.92 mm; third and fourth segments parallel to the body, pointing forward, length 0.79 mm and 0.42 mm, respectively, and the apex of the fourth segment sharp (Fig. 2B).

Antennae nearly 12.3 times longer than the head and 4.4 times wider than the head. Antennal socket robust, extending in front of the head. Antennae with four segments, length 6.78 mm, almost equal to body length, with significant expansion except for the first segment (Figs. 1, 2A, 4). First antennal segment inflated, 0.42 mm long and 0.20 mm wide (Figs. 1, 2C, 4). Second antennal segment approximately rectangular and expanding, with a few setae on the surface, lateral margins serrated and setaceous, distal margin of antennal axis with a sharp angle at apex, proximal margin of antennal axis thickened and cutinized, segment length 1.88 mm and width 0.29 mm (Figs. 1, 2D, 4). Third antennal segment petal-shaped, 2.17 mm long and 1.14 mm wide; basal area obtusely rounded, middle of apical area with a sharp angle, all margins bear minute setae; distal extension of antennal axis with sparse setae on the surface, proximal extension of antennal axis with dense setae on the surface, proximal margin with strong keratin thickening (Figs. 1, 2E, 4). Fourth antennal segment triangular, 3.15 mm long and 2.49 mm wide, basal area obtusely rounded, apical area a long arc, all margins with minute setae (Fig. 1, 2F); distal extension of antennal axis with sparse setae on the surface (Figs. 2G), proximal extension of the antennal axis with dense setae on the surface (Fig. 2H), proximal margin with strong keratin thickening (Fig. 2I).

Pronotum trapeziform, center with shallow longitudinal groove, length 0.65 mm and width 0.57 mm (Figs. 1, 3A, 4). Mesonotum trapeziform, center with shallow longitudinal groove, length 0.49 mm and width 0.58 mm; lateral margin bearing

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forewing bud, long ovoid, length 0.65 mm and width 0.21 mm, basal area narrow, apical area narrowly rounded, posterior margin surpassing anterior margin of the metanotum, overlapping with the basal area of the hindwing bud (Figs. 1, 3A–B, 4). Metanotum transversely wide, anterior margin nearly fused with posterior margin of mesonotum, length 0.39 mm and width 0.67 mm, lateral margin with hindwing bud, basal area wide, apical area narrowly rounded, posterior margin not reaching the anterior margin of the first abdominal tergite, length 0.34 mm and width 0.24 mm (Figs. 1, 3A–B, 4).

Fore femora cylindrical and slightly thick, length 1.98 mm. Fore tibiae narrower than the femora, length 2.03 mm. Fore tarsi with two segments, apices with two claws, length 0.71 mm (Figs. 1, 3A–C, 4). Middle femora slightly shorter than the fore femora, cylindrical, length 1.52 mm. Middle tibiae narrower than the femora, length 1.75 mm. Middle tarsi with two segments, apices with two claws, length 0.67 mm (Figs. 1, 3A–D, 4). Hind femora long and thick, cylindrical, length 1.69 mm. Hind tibiae narrower than the femora, length 2.46 mm. Hind tarsi with two segments, apices with two claws, length 0.68 mm.

Abdomen length 4.35 mm, width 0.61 mm, nine visible segments. First and second abdominal tergite transversally wide. From third to eighth segment, abdominal tergites longer than the first two tergites. Black scent gland markings visible between the third and fourth, fourth and fifth, and fifth and sixth abdominal tergites. Ninth abdominal tergite trapezoidal, basal area wide, apical area slightly narrow, no recognizable genital structure that should be present in the abdomen (Figs. 1, 2A, 3).

Remarks. *M. wuae* gen. et sp. nov. resembles the extant coreid *Chariesterus antennator* (Fabricius, 1803). In addition to the similarities and differences documented in the Remarks section for the genus, the third antennal segments of both species are obovately dilated, with a width more than one-third of the length of the segment and the apex with an obvious angle. However, *M. wuae* gen. et sp. nov. does not have a notch at the apex of the third antennal segment, and the length ratio of each antennal segment from the first to the fourth is 42:188:217:315. In contrast, *C. antennator* has a conspicuous notch at the apex of the third antennal segment, and the length ratio of each antennal segment from the first to the fourth is 105:83:60:51 (Fracker, 1919b; Ruckes, 1955). Therefore, *M. wuae* gen. et sp. nov. is sufficiently distinct from *C. antennator* to justify erection of a new genus and species.

Discussion

Taxonomic status of the nymph specimen preserved in amber

The extremely extended and oversized antennae distinguish the new coreid from all other previously known fossil and extant species, even based only on the single nymph available to us. In addition to the Coreinae, the Coreidae includes three other subfamilies. We can rule the nymph out of them by the following characteristics: The Hydarinae are recognized by possession of a third antennal segment that is more than twice as long as the second segment, anterior and posterior lobes of metathoracic peritreme that are completely separated (Brailovsky, 2010); The Meropachyinae are characterized by a distal tooth or spine on the hind tibia, a curved and usually strongly

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incrassate hind femur (Brailovsky and Barrera, 2009); The Pseudophloeinae are distinguished by a granulated surface of the pronotum, scutellum and hemelytra, with each granule bearing small adpressed setae (Hamouly et al., 2010). All previous fossil examples of Coreidae have been reported from rock impressions, and are generally poorly preserved. The coreid nymph specimen preserved in amber described in the present study most likely belongs to the subfamily Coreinae owing to the following features: third antennal segment only slightly longer than second segment; hind tibia not curved and without prominent tooth or spine distally; and pronotum smooth and not granular. This is the first report of a leaf-footed bug in amber and the second representative of the Coreoidea preserved in amber, enriching the known species diversity of the group during the Cretaceous period.

Heteropteran nymphs generally have five instars, which typically resemble adults in their morphological appearance and living environment, except that they are generally much smaller and softer than adults, they have paired scent glands located on the dorsal abdomen, and the number of tarsal segments is one less than that of adults (Panizzi and Grazia, 2015). Wing buds appear in the third instar, and external genitals and ocelli can be observed in the fifth instar (Schuh and Slater, 1995). We regard this new specimen as a nearly fourth instar nymph because of the following features: posterior margins of the hind buds not reaching the anterior margin of the first abdominal tergite; ocelli absent; scent glands located on the dorsal surface of the abdomen; tarsi two-segmented; and genitalia not developed (Schuh and Slater, 1995). Both nymphs and adults of modern *Chariesterus*, *Dalader*, and *Thasus* in Coreinae have the similar expansion on the third antennal segment, but are significantly different from the new species (Fig. 5) (Barrera and Brailovsky, 1994; Prudic et al., 2008). The first antennal segment of the nymph described here is robust (Figs. 1, 2A, C, 3A, 4); the proximal extension of the antennal axis extends from the second to fourth segment with dense setae on the surface; and the proximal margin exhibits strong keratin thickening (Figs. 1, 2A, D–I, 3–4); the fourth antennal segment is more prominent than the third segment (Figs. 1, 2A, E–F, 3–4). Therefore, the antennal expansion should have persisted in the adult stage. This discovery demonstrates that the antennal expansion of the Coreidae originated at least 99 million years ago.

Antennal expansion and long-distance chemical communication

Antennal specialization plays a vital role in the adaptive evolution of coreids. The family Coreidae have the expansive antennae, which are relatively common (uniform and slight expansion of all antennal segments or partially segment, alternatively, only obvious expansion occurs on the third antennal segment) in living insects (Fig. 5). However, there was no extension of any form in Mesozoic. The expanded antennae undoubtedly increase the superficial area of the antennae and enhance the sensory function and efficiency of the antennal sensor for potential host plants and mate locating (Krogmann et al., 2013; Liu et al., 2018a). Along with the flourishing of angiosperms, the species diversity development of coreids increased the competition for survival factors among them (Fisher and Watson, 2015). The coreids nymph owns the modified antennae, which can identify host plants more efficiently and quickly, improving

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intraspecific and interspecific competitiveness. Based on the previous analysis, the antennae are likely to still exist during adulthood. The extremely expanded antennae become a key factor in long-distance locating of the mates by sensing the sex pheromone. In many heteropteran species, single or both sexes species can release sex pheromones or aggregate pheromones (Prudic et al., 2008). The antennae sensory hairs are mainly located on the distal segment of the antennae in the Coreidae (Pekár and Hrušková, 2006). The unique expansion on the fourth antennal segment of the nymph significantly increases the sensory function of the antennae.

During the Upper Cretaceous period, the predators of the coreid nymph ranged from insects to birds and other animals (Xing et al., 2019). Aggregation behavior is an effective way for the coreids nymph to protect themselves from predators (Prudic et al., 2008). Younger instars are generally gregarious in coreids (Panizzi and Grazia, 2015). Expansive antennae enable them to receive alarm signals from other conspecifics quickly and accurately, which is beneficial to each individual. In summary, our finding indicates that the coreid has long-term chemical communication capabilities during the Cretaceous period. It is also the first discovery of long-distance chemical communication in the Cretaceous Hemiptera. The only other known hemipteran fossil with expanded antennae are lace bugs (Insecta: Heteroptera: Tingidae), which dates from the Early Eocene and deposits in the Green River Formation (Wappler et al., 2015).

Antennal expansion and sexual selection

A delicate visual display structure is a prominent signal to attract mates or defeat competitors (Warren et al., 2013). However, the specialized antennae characteristic is little known in ancient species due to the difficulty preservation in fossil. Currently, exceptional structures for sexual display found in fossils include the extremely expanded tibiae (Zheng et al., 2017), the unusually long abdominal terminal segments and sexual organs (Brucearchibald, 2010; Wang et al., 2013) and the dilated antennal segments (Wappler et al., 2015). The expanded antennae have evolved numerous times in different insect groups, especially in males (Krogmann et al., 2013). Previous studies have reported that expanded antennae are associated with sexual displays which is positively correlated with size and appearance of the trait (McCullough et al., 2016; Warren et al., 2013).

Some insect antennae reach remarkable sizes. The antennae in katydids, crickets and some longhorn beetles are often longer than the body, and the antennae in some chafers, moths and mosquitoes are relatively wide in relation to the body (but do not exceed the body width). The dilated antennal segment is known in extant coreid adults, but most of them only occur in the third segment and not wider than the head (CoreoideaSF, 2018; Fracker, 1919a; Prudic et al., 2008). In contrast, in the amber-preserved bug nymph specimen described herein, both the length and the width of the antennae are greater than the body length and width. In addition, the shape of each antennal segment of *Magnusantenna wuae* gen. et sp. nov. varies greatly, with the third and fourth segments especially significantly expanded, unlike those in other bugs, in which all segments are similar and mostly longitudinal. Such oversized and bizarre antennae (nearly 12.3 times longer than the head and 4.4 times wider than the head) are unique in the Heteroptera

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and rare in Insecta. The leaf-like expansion of the hind tibiae and the third antennal segment in modern male coreids is usually used to attract mates, and the mating success rate is closely related to male body size (McLain et al., 1993; Panizzi and Grazia, 2015). Therefore, we hypothesize that the extremely expanded antennae of *M. wuae* gen. et sp. nov. were most likely used for sexual display, and the nymph would have developed into an adult. The exaggerated antennae may have borne a large number of olfactory receptors, enabling the animal to locate females over long distances and providing a basis for sexual display behavior (Pekár and Hrušková, 2006). Interestingly, expanded antennae have been found in both ancient lace-bugs and extant leaf-footed bugs as well as in *M. wuae* gen. et sp. nov. These similarities imply the occurrence of antennal enlargement in the Hemiptera, suggesting possible behavioral convergence resulting from sexual selection (Wappler et al., 2015).

Antennal expansion and defense behavior

Camouflage is a common behavior in insects and can effectively reduce the probability of an individual being detected by a predator, and increase the chances of escape from a predator (Garrouste et al., 2016; Liu et al., 2018b; Pérez-de la Fuente et al., 2016; Wang et al., 2016; Wang et al., 2012; Wang et al., 2010). A variety of defensive mechanisms in Hemiptera have significant impacts on reducing encounters and avoiding predators, for example, species of Phloeidae can camouflage themselves as a piece of lichen on a tree (Panizzi and Grazia, 2015).

Some body parts can regenerate or are expendable. In the face of strong predation pressure, these body parts can attract a predator's attention and protect the vital parts from damage. This defense mechanism has evolved independently for multiple body parts in many animals (Maginnis, 2010). A high incidence of structure loss and regeneration in insect appendages, such as the legs, antennae and cerci, a process that increases survival opportunities, has been reported (Bely and Nyberg, 2010; Tan et al., 2013; Wu et al., 2019; Emberts, 2016). For the nymph described in this article, exaggerated antennae may have been a powerful tool to focus the attention of a predator on the antennae rather than on the head or any other part of the body, thus avoiding a deadly attack. The nymph is similar to some extant coreids, in that the leaf-like broadened antennal segments and hind tibiae may have breaked up and attracted the attention of a predator to the expendable appendages (Schuh and Slater, 1995). Molting behavior in the nymphal stage provides a greater possibility for regeneration of antennae (Leston, 1957). The exaggerated antennae of *M. wuae* gen. et sp. nov. constitute possible evidence for defensive behavior approximately 99 million years ago.

Antennal expansion and extinction risk

Extremely specialized traits have advantages in mate-finding, sexual display and defense, but the production and maintenance of these traits are associated with a corresponding cost, which could restrict the ability of individuals and populations to adapt to changing environments and accordingly increase the risk of species extinction (Tanaka, 1996). Male cytheroid ostracods with large sperm pumping and copulatory apparatuses exhibit extinction rates ten times higher than those species with the lowest

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investment in apparatuses, indicating that specialized features associated with sexual selection may be a high risk factor for species extinction (Martins et al., 2018). The damselfly *Yijenplatycnemis huangi* possessed exaggerated pod-like tibiae that probably slowed its flight speed, making it easier to prey upon and less likely to escape predators (Zheng et al., 2017). Extremely elongated abdomens and sexual organs in male mecopterans produce a large, heavy body, which causes them to move slowly when avoiding enemies and making them more visible to predators (Wang et al., 2013).

However, the spectacular antennae are more likely to have exposed the individual, increasing the chance of being discovered and preyed upon. In addition, the large appendages probably made it move slowly, which would have been a disadvantage when fleeing a predator. Moreover, exaggerated structures require more energy to produce and maintain, which increases the probability of extinction when the external environment changes drastically.

Material and Methods

The coreid nymph described herein is preserved in a piece of golden-brown Myanmar amber from an amber deposit in the Hukawng Valley of Myanmar. The age has been estimated to be ca. 99 Ma (98.8 ± 0.6 Ma; earliest Cenomanian, Upper Cretaceous) based on U-Pb dating of zircons from the volcaniclastic matrix of the amber-bearing deposit (Shi et al., 2012). The mining locality is at Noije Bum, near Tanai Village (26°21'33.41"N, 96°43'11.88"'E) (Cruickshank and Ko, 2003; Grimaldi et al., 2002). Details of the geology and stratigraphy of the deposit have been described in previous publications (Cruickshank and Ko, 2003; Shi et al., 2012).

The piece of amber was cut, ground and polished to a length × width × height of approximately 26.75 × 20.14 × 12.43 mm. The specimen was examined with a LEICA M125 C dissecting microscope.

Photographs were obtained with a LEICA MC 190 HD fitted to a LEICA M125 C stereomicroscope and a Nikon Digital Sight DS-Ri1 fitted to a Nikon AZ100M stereomicroscope. Images were stacked with Helicon Focus 6. Photographic figures were constructed in Adobe Photoshop CC.

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Figure captions:

Fig. 1 Overview of the amber. Scale bar, 5 mm.

Fig. 2 Head of *M. wuae* gen. et sp. nov. (STJS0003). A, C–I. Lateral views of the antenna: (A) Overall view. Scale bar, 1 mm. (C) First segment. Scale bar, 200 μm. (D) Second segment. Scale bar, 1 mm. (E) Third segment. Scale bar, 1 mm. (F) Fourth segment. Scale bar, 1 mm. (G) Setae on the distal extension of the fourth antennal axis. Scale bar, 100 μm. (H) Setae on the proximal extension of the fourth antennal axis. Scale bar, 100 μm. (I) Strong keratin thickening of the proximal margin of the fourth antennal axis. Scale bar, 200 μm. (B) Ven-lateral view of head. Scale bar, 500 μm.

Fig. 3 Thorax and abdomen of *M. wuae* gen. et sp. nov. (STJS0003). (A) Dorsal view of body. Scale bar, 1 mm. (B) Dorsal view of wing buds. Scale bar, 500 μm. (C) Lateral views of tibiae and tarsi of fore leg. Scale bar, 1 mm. (D) Lateral views of tibiae and tarsi of middle leg. Scale bar, 500 μm. (E) Lateral views of tibiae and tarsi of hind leg. Scale bar, 1 mm.

Fig. 4 Reconstruction of the habitus of *M. wuae* gen. et sp. nov. (STJS0003). Scale bar, 1 mm.

Fig. 5 Images of some modern coreids. (A–B) *Chariesterus antennator* (downloaded from https://www.gbif.org/occurrence/gallery). (C–D) *Chariesterus armatus* (downloaded from https://www.flickr.com/photos/brutamonte). (E–F) *Dalader* sp. (downloaded from http://www.natureloveyou.sg). (G–H) *Thasus neocalifornicus* (downloaded from http://arizonabeetlesbugsbirdsandmore.blogspot.com). A, C, E, G. Nymphs; B, D, F, H. Adults.

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Fig. 1

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Fig. 2

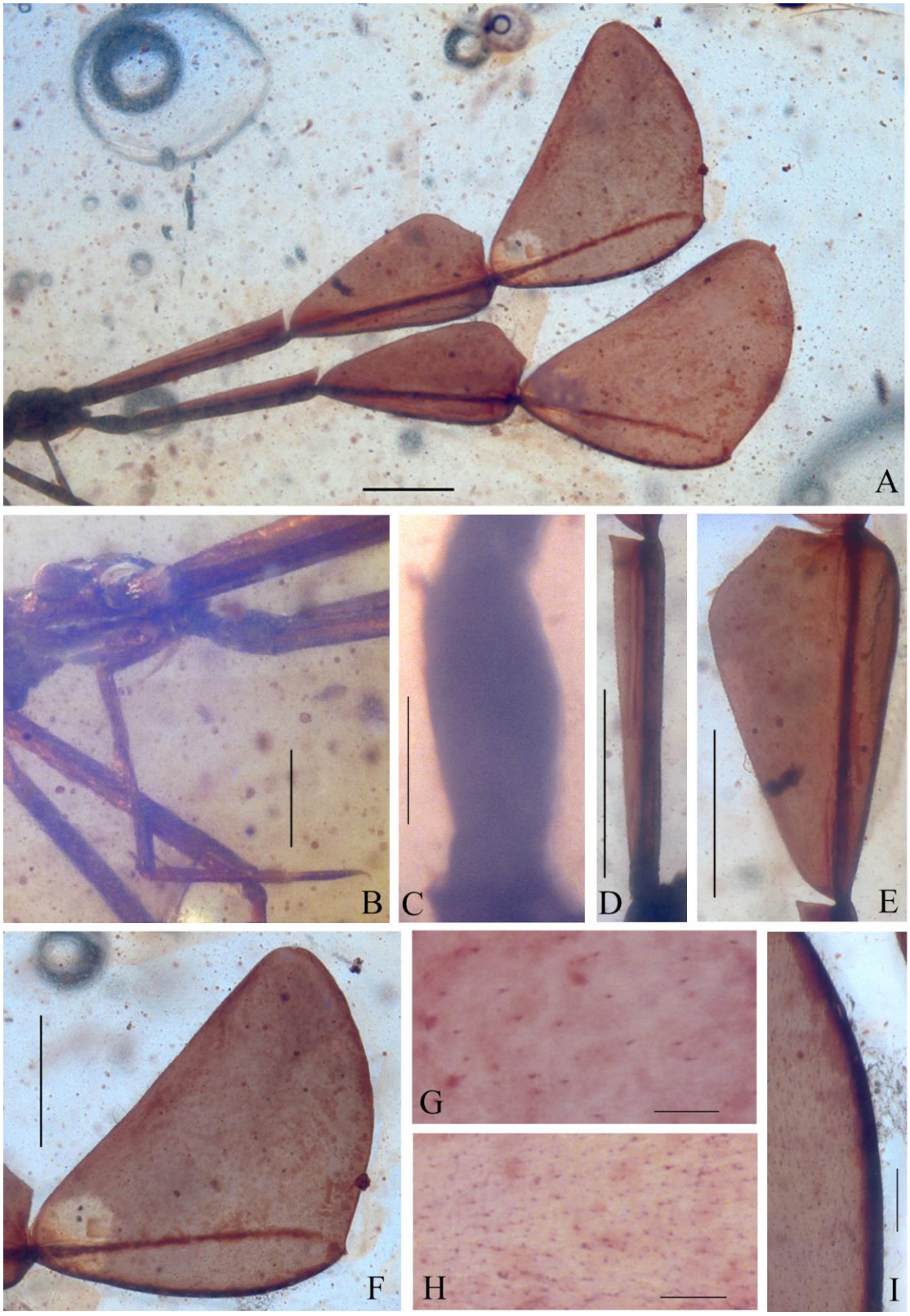

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Fig. 3

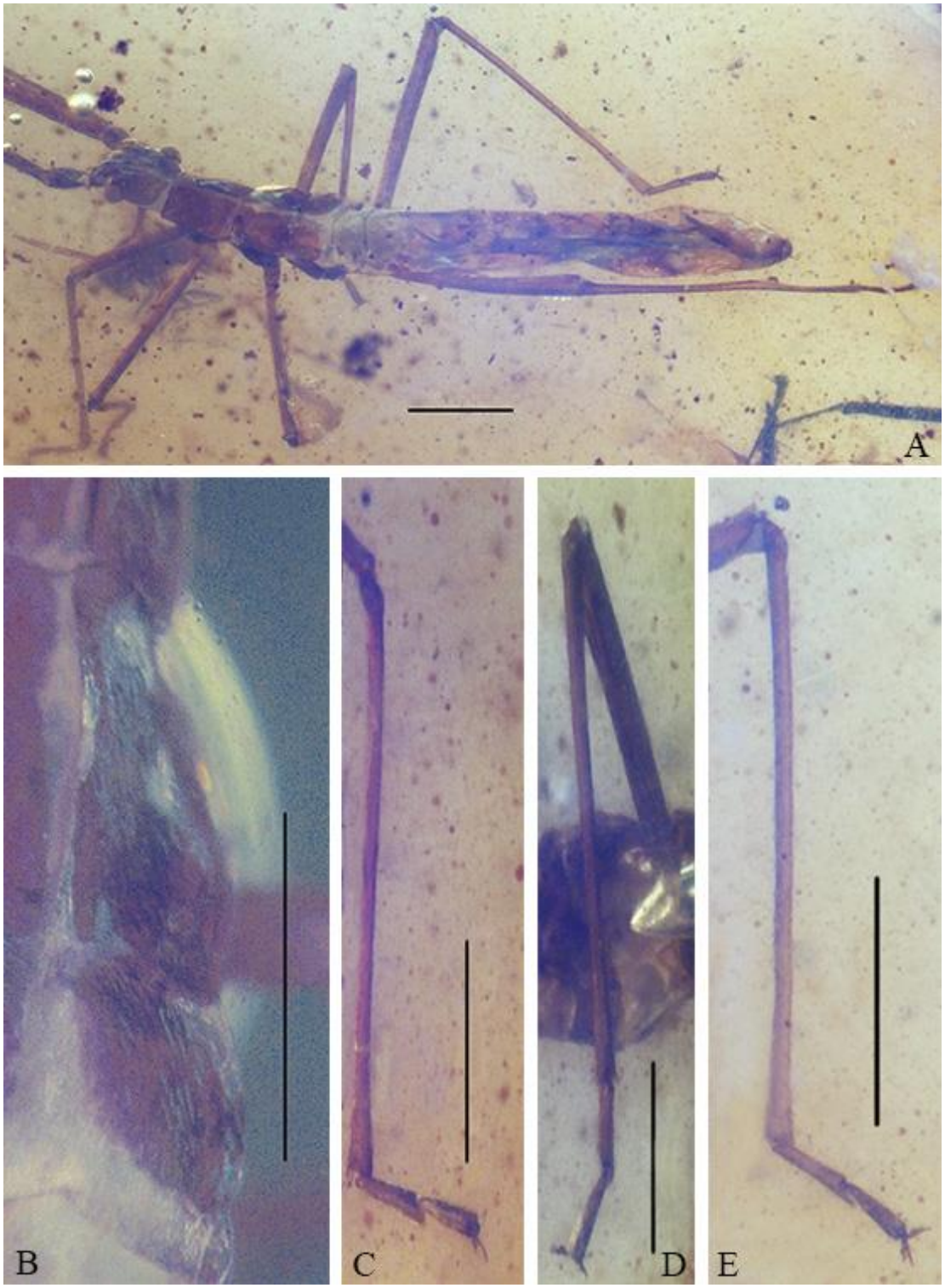

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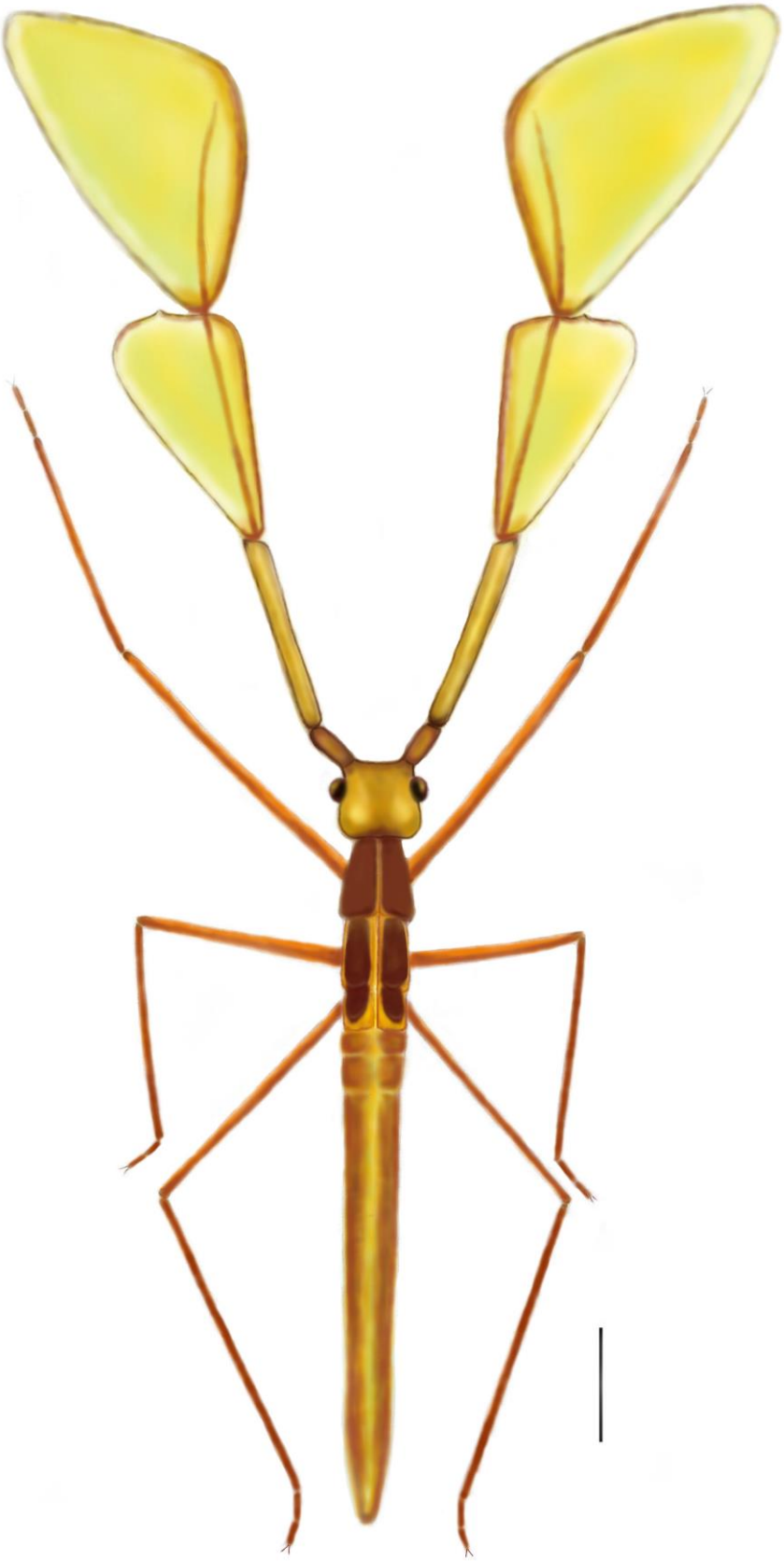
Fig. 4



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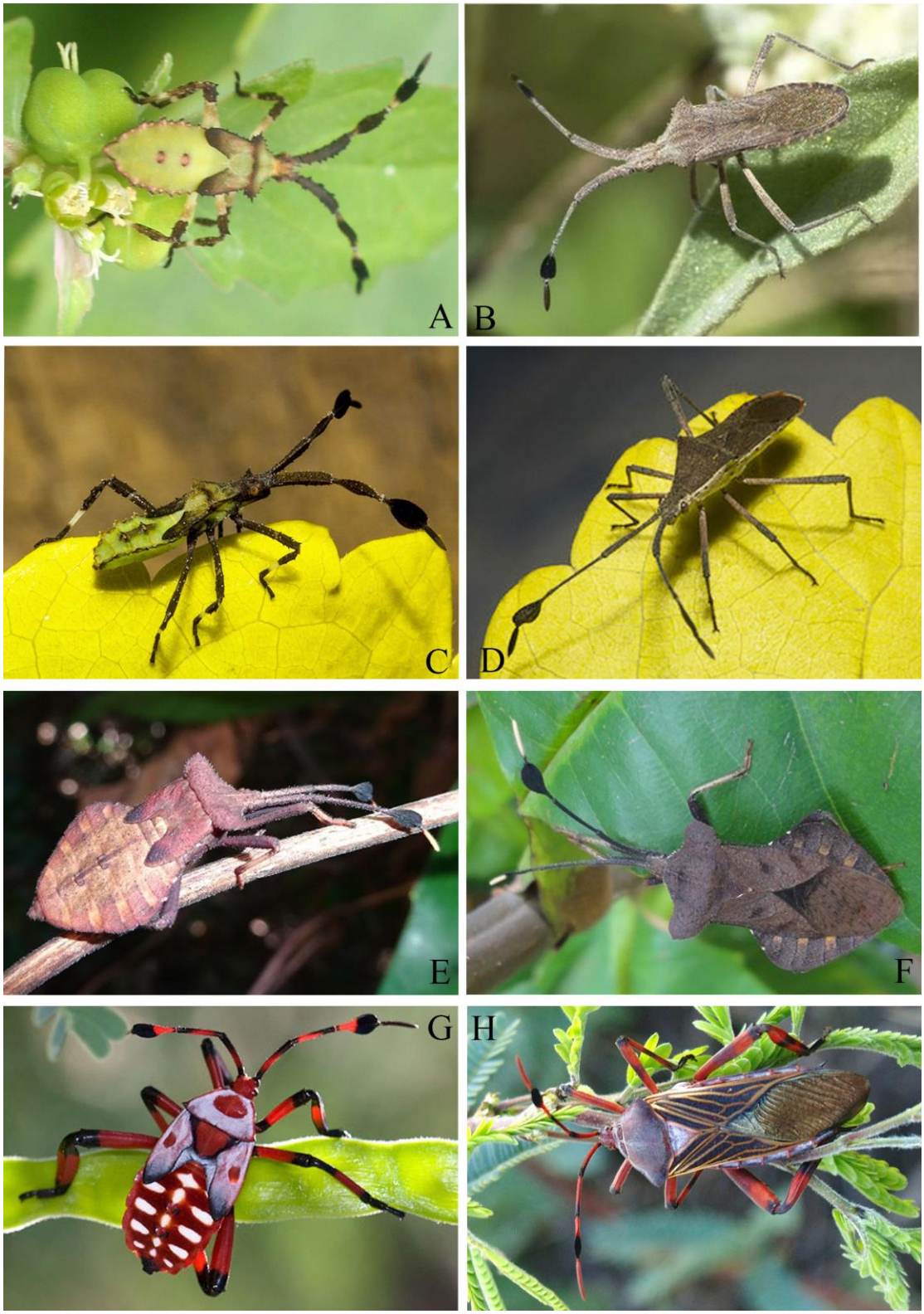
Fig. 5