A Cretaceous bug with exaggerated antennae might be a double-edged sword in evolution

Bao-Jie Du, Rui Chen, Wen-Tao Tao, ..., Fan-Li Kong, Jin-Hua Xiao, Da-Wei Huang

xiaojh@nankai.edu.cn (J.-H.X.)
huangdw@ioz.ac.cn (D.-W.H.)

Highlights

A new coreid is described from Cretaceous Burmese amber

This is the oldest bug with exaggerated leaf-like expanded antennae in Coreidae

The bizarre antennae may be associated with sexual selection and defense behavior

Coexisting with the advantages of the antennae is the huge costs of survival

Du et al., iScience 24, 101932
January 22, 2021 © 2020 The Authors.
https://doi.org/10.1016/j.isci.2020.101932
A Cretaceous bug with exaggerated antennae might be a double-edged sword in evolution

Bao-Jie Du,1,7 Rui Chen,2,7 Wen-Tao Tao,1 Hong-Liang Shi,3 Wen-Jun Bu,1 Ye Liu,4,5 Shuai Ma,4,5 Meng-Ya Ni,4 Fan-Li Kong,6 Jin-Hua Xiao,1,* and Da-Wei Huang1,2,8,*

Summary
Sexual selection can favor production of exaggerated features, but the high cost of such features in terms of energy consumption and enemy avoidance makes them go to extinction under the influence of natural selection. However, fossils preserved with specialized features are very rare. Here, we report a new nymph from Burmese amber, Magnusantena wuae Du & Chen gen. et sp. nov., which has exaggerated leaf-like expanded antennae. Such bizarre antennae indicate that sensitive and delicate sensory system and magnificent appearance in Hemiptera have been already established in mid-Cretaceous. Our findings may provide evidence for Darwin’s view that sensory organs play an important role in sexual selection. This nymph with the leaf-like antennae may also represent a new camouflage pattern. However, the oversized antennae are costly to develop and maintain, increasing the risks from predators. Such unparalleled expanded antennae might be the key factor for the evolutionary fate of the coreid.

Introduction
Luxurious and decorative structures are usually regarded as weapons or ornaments and are vital features in sexual selection, including feathers, antlers, pebbles, horns, jaws, etc (Jay and Borgia, 2000; Melnycky et al., 2013; Emlen, 2008; Emlen et al., 2007; McCullough et al., 2014). Female mate choice and male-male competition further complicate and beautify male specialized characters (Johnson et al., 2017). Just as Darwin once proposed, the success rate of animal mating depends not only on the above two widely accepted mechanisms of sexual selection but also on the efficient locating to the mate, that is, the sense organ plays an important role in sexual selection (Darwin, 1871). Chemical and acoustic signals seem to be most commonly used to locate mates, especially in long distances (Holwell et al., 2007). However, Darwin’s idea has been more or less ignored (Johnson et al., 2017; Elgar et al., 2019). At present, most studies attribute the mate’s positioning to communication behavior rather than sexual selection behavior (Nakano et al., 2019; Wang et al., 2018). There are only a few cases where sensory organs are associated with sexual selection: the size of thoracic spiracles in katydids (Gwynne and Bailey, 1999), the length of antennae in moths (Yan et al., 2014; Johnson et al., 2017), and the number of sensory structures of antennae in false garden mantids (Jayaweera and Barry, 2017). The research studies on sensory organs mainly focus on the morphology of antennae, expansive and delicate antennae carry more olfactory receptors, which facilitates the location of mate (Krogmann et al., 2013; Jayaweera and Barry, 2017). Once an individual enters the process of short distance courtship, visual signals play a significant role; surprisingly, the importance of antennae as an important display function in sexual selection has been greatly overlooked. Fossil materials have provided evidence for the origin and evolution of important characters of many species, as well as related behavioral information (Bao et al., 2019; Labandeira et al., 2016; Yang et al., 2019; Chen et al., 2018), but the materials related to the functional morphology of specialized antennae are rare. Some insects with ramified antennae exhibited chemical communication in the Early Cretaceous but do not show the sexual display behavior (Krogmann et al., 2013; Gao et al., 2016; Wichard, 2017; Liu et al., 2018a). So far, the only fossil species of Hemiptera with leaf-like dilated antennae are Reticulatitergum hui Du et al. (2018) (Yuripopovinidae) from the Cretaceous and Gyaclavator kohlsi Wappler et al. (2015) (Tingidae) from the Eocene, and the expansion of their antennae occurs in the fourth antennal segment (Du et al., 2018; Wappler et al., 2015). A few of extant coreids have the similar antennae (Barrera and Brailovsky, 2018).
1994). However, there is no evidence that the antennae of Cretaceous insects play an important role in both mate positioning and sexual display.

Coreidae is a moderately large family in Hemiptera, with nearly 500 genera and 2200 species (Hamouly et al., 2010). Coreids are hemimetabolous herbivore insects, commonly known for their leaf-like expansive antennae and legs (Fernandes et al., 2015). Expansion of various body parts plays a significant role in sexual selection and defensive behavior (Fernandes et al., 2015; Wappler et al., 2015; Eberhard, 1998; Schuh and Slater, 1995). So far, only four species of the family Coreidae have been described from the Cretaceous rock impressions, all of which do not have expanded antennae. Therefore, the origin, evolutionary diversity, and corresponding functions of these early exquisite expansions in Coreidae remain poorly understood.

Here, we report a coreid nymph with exaggerated, expanded antennae from mid-Cretaceous Burmese amber. Magnusantenna wuae Du & Chen gen. et sp. nov. represents the first record of the family Coreidae preserved in amber. The leaf-like antennal expansion of coreids is demonstrated to have existed approximately 99 million years ago. This discovery improves our understanding of coreid biodiversity during the Cretaceous and provides evidence for the prominent role of sensory organs in sexual selection. We then discuss the role of the specialized antennae in defensive behavior, as well as the negative effects on survival.

**Results**

**Systematic paleontology**

Order Hemiptera Linnaeus, 1758

Family Coreidae Leach, 1815

Subfamily Coreinae Leach, 1815

Genus Magnusantenna Du & Chen gen. nov (Figures 1, 2, 3, and S1).

**Type species**

Magnusantenna wuae Du & Chen gen. et sp. nov.

**Diagnosis**

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

**Etymology**

The generic name is derived from Latin prefix margus, meaning large, and antenna, meaning antenna: referring to the enlarged antennae. The specific epithet, wuae, is in honor of Ms. Wu Lijing, who discovered the specimen.

**Type locality and horizon**

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.

**Remarks**

Magnusantenna Du & Chen gen. nov. is similar to the extant Charisterus 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 Charisterus 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, Charisterus 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 (Fernandes et al., 2015; Ruckes, 1955). Magnusantenna gen. nov. is markedly different from all previously described fossil Coreidae in the scale of the antennal exaggeration.

**Magnusantenna wuae Du & Chen gen. et sp. nov.**

(Figures 1, 2, 3, and S1)

The new taxon is registered in ZooBank under the publication LSID. urn:lsid:zoobank.org:pub:D14C87DF-5440-4BE1-A214-20E1071D262F.

**Diagnosis**

As for genus.

**Description**

STJS0003. Nymph, probably approach fourth instar. Gender undeterminable.

Body slender, length 6.67 mm, width 0.76 mm. Head subquadrate, length 0.55 mm, width 0.56 mm.

Labrum long triangle, basal area slightly broad, gradually narrowing toward apex. Compound eyes large and spherical, located at the center of the lateral margins of the head and protruding outward significantly. Rostrum with four segments; first segment close to the ventral surface of the head, reaching the anterior margin of the compound eyes, length 0.47 mm; second segment longest, 0.92 mm in length, vertical to the body; 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.

Figure 1. Holotype of *M. wuae* gen. et sp. nov

(A) Line drawing habitus in dorsal view. (B) Photograph habitus in dorsal view. Scale bar, 5 mm. See also Figures S1 and S2.
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, slight longer than body length, with significant expansion except for the first segment. First antennal segment inflated, 0.42 mm long and 0.20 mm wide. 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. 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 expansion of antennal axis with sparse setae on the surface, proximal expansion of antennal axis with dense setae on the surface, proximal margin with strong keratin thickening. 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; distal expansion of antennal axis with sparse setae on the surface, proximal expansion of the antennal axis with dense setae on the surface, proximal margin with strong keratin thickening.

Pronotum trapeziform, center with shallow longitudinal groove, length 0.65 mm and width 0.57 mm. Mesonotum trapeziform, center with shallow longitudinal groove, length 0.49 mm and width 0.58 mm; lateral margin bearing forewing bud, long ovoid, length 0.65 mm and width 0.21 mm, basal area narrow, apical

Figure 2. Head of *M. wuae* gen. et sp. nov

(A) Lateral view of antenna. Scale bar, 1 mm.
(B) Ventral view of head. Scale bar, 500 μm.
(C) First segment of antenna. Scale bar, 200 μm.
(D) Second segment of antenna. Scale bar, 1 mm.
(E) Third segment of antenna. Scale bar, 1 mm.
(F) Fourth segment of antenna. Scale bar, 1 mm.
(G) Setae on the distal expansion of the fourth antennal axis. Scale bar, 100 μm.
(H) Setae on the proximal expansion 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. See also Figures S1 and S2.
area narrowly rounded, posterior margin surpassing anterior margin of the metanotum, overlapping with the basal area of the hindwing bud. 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

Figure 3. The thorax and abdomen of M. wuae gen. et sp. nov

(A) Dorsal view of the body. Scale bar, 1 mm.
(B) Dorsal view of wing buds. Scale bar, 500 µm.
(C) Lateral views of tibiae and tarsi of the fore leg. Scale bar, 1 mm.
(D) Lateral views of tibiae and tarsi of the middle leg. Scale bar, 500 µm.
(E) Lateral views of tibiae and tarsi of the hind leg. Scale bar, 1 mm. See also Figure S1.
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.

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. 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. 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 transversely wide. From third to eighth segment, abdominal tergites longer than the first two tergites. Ninth abdominal tergite trapezoidal, basal area wide, apical area slightly narrow, no recognizable genital structure that should be present in the abdomen.

Remarks
M. wuae gen. et sp. nov. resembles the extant coreid Charisterus 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 (Fracher, 1919; Ruckes, 1955). Therefore, M. wuae gen. et sp. nov. is sufficiently distinct from C. antennator to justify the erection of a new genus and species.

Discussion
Taxonomic status of the nymph specimen
The extremely expanded and oversized antennae distinguish the new coreid from all other previously known fossil and extant species. The coreid nymph specimen preserved in amber described in the present study most likely belongs to the subfamily Coreinae (Coreidae) owing to the combination of following features: bucculae extending posteriorly beyond antennal insertion; the base of the first segment of the antennae slightly contracted; the second, third and fourth segments of the antennae expanded to varying degrees, especially the fourth segment, and the third antennal segment only slightly longer than second segment; pronotum smooth and not granular; hind femora straight; hind tibia not curved and without prominent tooth or spine distally. In addition to Coreinae, Coreidae includes three other subfamilies. We can rule the nymph out of them by the following characteristics: Hydarinae is 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); Meropachyinae is characterized by a distal tooth or spine on the hind tibia, a curved and usually strongly incrassate hind femur (Brailovsky and Barrera, 2009); Pseudophloeinae is 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 (please refer to the Supplemental Information) and are generally poorly preserved. This is the first report of Coreidae species in amber.

Yuripopovina magnifica (Yuripopovinidae), preserved in the Cretaceous Lebanese amber, is the first definitive Mesozoic record in Coreoidea (Azar et al., 2011). Retigulatitergum Hui, a member of Yuripopovinidae, has an expanded fourth antennal segment similar to the nymph (Du et al., 2018). However, we cannot attribute the nymph to this family owing to the combination of the following characters: compound eyes small sphere; second, third and fourth antennal segments significantly expanded; without collar; pronotum nearly trapeziform and compressed; hind tibiae terete. On the contrary, Yuripopovinidae has the following important diagnosis characteristics: large spherical compound eyes slightly “pedunculate”; all antennal segments cylindrical; collar well developed; circular, not depressed dorso-ventrally; wide pronotum with sinuous flank; callus well developed; tibiae fusiform (Du et al., 2018; Azar et al., 2011).
Antennal expansion maintained in adults

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 (Fernandes et al., 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 characters (Figures 1, 2, 3, and S1): 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).

The family Coreidae has the expanded antennae, which are relatively common in living insects and likely to still exist during adulthood (Figure S2). Both nymphs and adults of modern Charisterus, Dalader, and Thasus in Coreinae have the similar expansion on the third antennal segment (Barrera and Brailovsky, 1994; Prudic et al., 2008) but are significantly different from the new species with more exaggerated expansion (Figures 1, 2, 3, and S1). The first antennal segment of the nymph described here is robust; 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; the fourth antennal segment is more prominent than the third segment. Combining the developmental stage of the nymph and the specialized form of the antennae, we speculate that expanded antennae should continue throughout the adult stage. In addition, we cannot rule out the possibility that adults with larger antennae were not preserved due to the lack of amber’s ability to preserve larger inclusions. The multiple segments expansion antennae represent a new type of insect antennae. This discovery demonstrates that the antennal expansion of Coreidae originated at least 99 million years ago.

Antennal expansion and sexual selection

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 these antennae cannot be longer and wider than the body at the same time. The antennal length and width of M. wuae gen. et sp. nov. preserved in the amber described herein are greater than the body length and width (about 12.3 times of the head length and 4.4 times of the head width), which is unique in Heteroptera and rare in insects. The presence of nymph suggests that if we find an adult in the future, the antennae may be larger and expansion of the third and fourth segments of the antennae may be more remarkable. The similar large, exquisite lamellate antennae and pectinate antennae significantly increase the surface area of the antennae and enhance the interaction between odors and receptors (Ramsey et al., 2015). When the recognition of certain odors becomes an important factor in reproductive fitness, the evolution of olfactory receptors tends to maximize the surface area of antennae (Mankin and Mayer, 1984). The antennae sensilla capable of obtaining information are mainly located on the distal end and lateral extension of the flagellum (Pekár and Hrušková, 2006; Elgar et al., 2018). The exaggerated antennae may have borne a large number of olfactory receptors, enabling the coreids to locate mates even when they release relatively low concentrations of pheromones and providing a strong basis for sexual display behavior, improving intraspecific and interspecific competitiveness (Pekár and Hrušková, 2006; Krogmann et al., 2013; Liu et al., 2018a). The leaf-like expansion of the antennae in modern male coreids is usually used to courtship, and the mating success rate is closely related to male body size (Fernandes et al., 2015; McLain et al., 1993; Wappler et al., 2013). The special antennae provide a significant visual signal for females to find high-quality males. Normally, only a strong male can support such a large antenna. Therefore, we suspect that the extremely expanded antennae of M. wuae gen. et sp. nov. may be used for sexual selection in adult, which is reflected in the locating and attracting to the mates.

In summary, our finding provides the possibility that the coreid has high-efficiency mates positioning and sexual display capabilities during the Cretaceous period. The occurrence of the extremely expanded antennae is a powerful and effective survival strategy. It is the result of natural selection and sexual selection (Figure 4) and may be strongly influenced by sexual selection (Darwin, 1871). This may be a case of the emergence of sexual selection characters caused by positive feedback (Figure 4). If so, it provides evidence for the idea that sexual selection may also act on “organs of sense” suggested by Darwin. Other known Hemiptera fossils with expanded antennae are species from Yuripopovinidae and Tingidae (Wappler et al., 2015; Du et al., 2018). These similar expansions of antennae found in Hemiptera suggest possible behavioral convergence.
Antennal expansion and defensive behavior

Camouflage is a common behavior in insects and can effectively reduce the probability of an individual being preyed upon by predators. Leaf-like expansion is usually related to the leaves of mimic plants; however, the beneficial behavior in fossils is extremely rare (Wang et al., 2010, 2012; Liu et al., 2018b). Insects have evolved various ways of avoiding predators but most have focused on the adaptive evolution of their wings (Wang et al., 2010).

For the nymph described here, it is probably simulating a branch with leaves in stationary, which is more complex than simply imitating a leaf or a branch. This is a unique and effective defense pattern evolved in response to the numerous cotemporaneous predators, such as reptiles, mammals, birds and other vertebrates, as well as spiders and other insectivorous invertebrates. It provides evidence for the evolution of insect behavior diversity under natural selection (Figure 4).

Unlike the previous leaf-like mimicry that present on the imaginal wing and the larval thorax and abdomen, then nymph’s leaf-like expansion on the antennae is a new evolutionary innovation. This discovery may represent a new mimicry pattern. It is the earliest record of camouflage behavior in Hemiptera.

Antennal expansion and possible costs

The balance between the considerable benefits and the enormous costs brought by special features is one of the most exciting and under-researched topics in sexual selection studies (Martins et al., 2018). Although in some cases, the presence of sexual selection makes adaptation more effective, the experiments on wild populations have found that sexual selection could restrict the ability of individuals and populations to adapt to changed environments and accordingly increase the risk of species extinction (Doherty et al., 2003; Bro-Jørgensen, 2014; Morrow and Fricke, 2004).

Since the Cretaceous, the rise of herbivorous and carnivorous insects, birds, and other animals improved the diversity and number of competitors and predators of the nymph (Xing et al., 2019; Schachat et al., 2019). Therefore, the survival pressure of the nymph increased dramatically. As far as the exaggerated antenna is concerned, it requires a lot of energy to produce and maintain, which may need to put more efforts when the competitive pressure increases. Moreover, 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. The combination of these factors may increase the cost caused by the specialized character in an all-round way (Figure 4). Similar examples are the exaggerated pod-like tibiae of the dancing dragonfly and the extremely elongated abdomens and sexual organs of the mecopterans (Zheng et al., 2017; Wang et al., 2013).

Limitations of the study

The fossil is a nymph, and its sex cannot be accurately predicted, so the relationship between its expanded antennae and sexual selection behavior is highly speculative. Currently, only this specimen with expanded antennae has been reported in Coreidae. Therefore, a lot of work is needed in the future to further verify these hypotheses about the origin of this specialized feature and its related functions.
Resource availability
Lead contact
Further information and requests for resources should be directed to and will be fulfilled by the Lead Con-
tact, Dawei Huang (huangdw@ioz.ac.cn).

Materials availability
This study did not generate new unique reagents.

Data and code availability
This study did not generate/analyze data sets/code.

Methods
All methods can be found in the accompanying Transparent Methods supplemental file.

Supplemental information
Supplemental information can be found online at https://doi.org/10.1016/j.isci.2020.101932.

Acknowledgments
We thank two anonymous reviewers for their valuable comments on improving the quality of the article. We are grateful to Century Amber Museum for depositing the specimen. We sincerely thank Max Barclay (Nat-
ural History Museum, UK), Paula L. Mitchell (Winthrop University, USA), Richard Packauskas (Fort Hays State
University, USA), Torsten Wappler (Senckenberg Forschungsinstitut und Naturmuseum Frankfurt, Ger-
many) for their valuable comments on our article. We would like to express our gratitude to Ms. Melanie
Schuchart, Mr. Steve Kerr, Mr. Branco, Kwan, and Dr. Margarethe Brummermann for providing us with
photos. This work was supported by the National Natural Science Foundation of China, China
(31830084, 31672336), and also supported by the Construction Funds for “Double First-Class” Initiative
for Nankai University, China (96172158, 96173250 and 91822294).

Author contributions
D.W.H., R.C., J.H.X., and B.J.D. designed the project. B.J.D., R.C., W.T.T., H.L.S., W.J.B., Y.L., S.M., and
F.L.K., contributed to the new taxon descriptions. J.H.X. gave important guidance in behavioral analysis.
M.Y.N. participated in the drawing. B.J.D. and R.C. wrote the paper. B.J.D. and R.C. contributed equally
to this work. All authors discussed and confirmed the final manuscript.

Declaration of interests
The authors declare no competing interests.

Received: September 29, 2020
Revised: November 4, 2020
Accepted: December 7, 2020
Published: January 22, 2021

References
Azar, D., Nel, A., Engel, M., Garrouste, R., and Matocq, A. (2011). A new family of Coreoidea
from the lower cretaceous Lebanese amber (Hemiptera: pentatomomorpha). Pol. J. Entomol. 80, 627–644.

Bao, T., Wang, B., Li, J., and Dilcher, D. (2019). Pollination of cretaceous flowers. Proc. Natl.
Acad. Sci. U S A 116, 24707–24711.

Barrera, E., and Brailovsky, H. (1994). Descripcion de cuatro especies y una subspecie nuevas de la
tribu Anisoscelidini (Hemiptera-Heteroptera-Coreidae). Ser. Zool. 65, 45–62.

Brailovsky, H. (2010). New genus and new species of Hydarini (Hemiptera, Heteroptera, Coreidae)
from south America. Dtsch. Entomol. Z. 57, 85–88.

Brailovsky, H., and Barrera, E. (2009). New species of merocoris (merocoris) perty from Brazil, with
keys to known subgenera and species of the tribe merocorini (Hemiptera: Heteroptera: Coreidae: Meropachyinae). Fl. Entomol. 92, 134–138.

Bro-Jorgensen, J. (2014). Will their armaments be their downfall? Large horn size increases
extinction risk in bovid. Anim. Conserv. 17, 80–87.

Chen, S., Yin, X.C., Lin, X.D., Shih, C.K., Zhang, R.Z., Gao, T.P., and Ren, D. (2018). Stick insect in
Burmese amber reveals an early evolution of lateral lamellae in the Mesozoic. Proc. R. Soc. B
Biol. Sci. 285, 20180425.

Darwin, C. (1871). The Descent of Man, and Selection in Relation to Sex (William Clowes and
Sons Press).

Doherty, P.F., Sorci, G., Royle, J.A., Hines, J.E., Nichols, J.D., and Boulinder, T. (2003). Sexual
selection affects local extinction and turnover in bird communities. Proc. Natl. Acad. Sci. U S A
100, 5858–5862.
Du, S., Hu, Z., Yao, Y., and Ren, D. (2018). New genus and species of the Yurupavoninae (Pentatomomorpha: Coreidae) from mid-Cretaceous Burmese amber. Cret. Res. 94, 141–146.

Eberhard, W.G. (1998). Sexual behavior of Acanthocephala declivis guatemalanum (Hemiptera: Coreidae) and the allometric scaling of their modified hind legs. Ann. Entomol. Soc. Am. 91, 863–871.

Elgar, M., Zhang, D., Wang, Q., Wittwer, B., Pham, H., Johnson, T., Freelance, C., and Coquilleau, M. (2018). Insect antennal morphology: the evolution of diverse solutions to odorant perception. Yale J. Biol. Med. 91, 457–469.

Elgar, M., Johnson, T.L., and Symonds, M.R.E. (2019). Sexual selection and organs of sense: odorant perception. Yale J. Biol. Med. 92, 457–469.

Fabricius, J.C. (1803). Systema Rhyngotorum: Synonymis, Locis, Observationibus, Descriptionibus (C. Reichard Press).

Fernandes, J.A.M., Mitchell, P.L., Livermore, L., and Nikunlassi, M. (2015). True Bugs and Nikunlassi. Netherlands Press).

Fracher, S.B. (1919). Chariestus and its neotropical relatives (Coreidae Heteroptera). Ann. Entomol. Soc. Am. 12, 227–230.

Gao, T., Shih, C., Labandeira, C.C., Santiagoblay, J.A., Yao, Y., and Ren, D. (2016). Convergent evolution of ramified antennae in insect lineages from the Early Cretaceous of Northeastern China. Proc. R. Soc. B Biol. Sci. 283, 20161448.

Gwynne, D.T., and Bailey, W.J. (1999). Female-female competition in katydids: sexual selection for increased sensitivity to male signals? Evolution 53, 546–551.

Hamoully, H.E., Sawab, R.F., and Fadd, H.H. (2010). Taxonomic review of the subfamily Pseudophlebinae (Hemiptera: Coreidae) from Egypt. J. Egypt. J. Biol. 12, 108–124.

Hovol, G.I., Barry, K.L., and Herberstein, M.E. (2007). Male location, antennal morphology, and ecology in two praying mantids (Insecta: Mantodea). Biol. J. Linn. Soc. 91, 307–313.

Jayaweera, A., and Barry, K.L. (2017). Male antenna morphology and its effect on scramble competition in false garden mantis. Sci. Nat. 104, 75.

Johnson, T.L., Symonds, M.R.E., and Elgar, M.A. (2017). Sexual selection on receptor organ traits: younger females attract males with longer antennae. Sci. Nat. 104, 44.

Krogmann, L., Engel, M.S., Bechly, G., and Nel, A. (2013). Lower Cretaceous origin of long-distance mate finding behaviour in Hymenoptera (Insecta). J. Syst. Palaeontol. 11, 83–89.

Labandeira, C.C., Yang, Q., Santiago-Blay, J.A., Hotton, C.L., Monteiro, A., Wang, Y.J., Goreva, Y., Shih, C., Siljestrom, S., Rose, T.R., et al. (2016). The evolutionary convergence of mid-Mesozoic lacewings and Cenozoic butterflies. Proc. R. Soc. B Biol. Sci. 283, 2152893.

Liu, Q., Lu, X., Zhang, Q., Chen, J., Zheng, X., Zhang, W., Liu, X., and Wang, B. (2018a). High niche diversity in Mesozoic pollinating lacewings. Nat. Commun. 9, 3793.

Liu, Y.X., Shi, G.L., Xia, F.Y., Lu, X.M., Wang, B., and Engel, M.S. (2018b). Liverwort mimesis in a Cretaceous lacewing larva. Curt. Biol. 28, 1–7.

Mankin, R., and Mayer, M. (1984). The insect antenna is not a molecular sieve. Experientia 40, 1251–1252.

Martins, M.J.F., Puckett, T.M., Lockwood, R., Swadde, J.P., and Hunt, G. (2018). Male sexual investment as a driver of extinction in fossil scarabacids. Nature 556, 366–369.

McCullough, E.L., Tolbatske, B.W., and Enlen, D.J. (2014). Structural adaptations to diverse fighting styles in sexually selected weapons. Proc. Natl. Acad. Sci. U S A 111, 14484–14488.

McLain, D.K., Burnette, L.B., and Deeds, D.A. (1993). Within season variation in the intensity of sexual selection on body size in the bug Margus obcurator (Hemiptera Coreidae). Ethol. Ecol. Evol. 5, 75–86.

Melnick, N.A., Waldaji, R.B., Holand, O., and Nieminen, M. (2013). Scaling of antler size in reindeer (Rangifer tarandus). sex and variability in resource allocation. J. Mammal. Evol. 20141448.

Morrow, E., and Fricke, C. (2004). Sexual selection and variability in resource allocation. J. Mammal. Evol. 20141448.

Nieminen, M. (2013). Scaling of antler size in reindeer (Rangifer tarandus). sex and variability in resource allocation. J. Mammal. Evol. 20141448.

Niu, J., Ying, Q., Liu, B., and Payne, J.L. (2019). A Cretaceous peak in family-level insect diversity estimated with mark-recapture methodology. Proc. R. Soc. B Biol. Sci. 286, 20192054.

Schachat, S.R., Labandeira, C.C., Clapham, M.E., and Payne, J.L. (2019). A Cretaceous peak in family-level insect diversity estimated with mark-recapture methodology. Proc. R. Soc. B Biol. Sci. 286, 20192054.

Shu, C., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q., and Li, X. (2012). Age constraint on Burmese amber based on U-Pb dating of zircons. Cretaceous Res. 37, 155–163.

Uy, J.A.C., and Borgia, G. (2000). Sexual selection drives rapid divergence in bowerbird display traits. Evolution 54, 273–278.

Wang, Y., Liu, Z., Wang, X., Shih, C., Zhao, Y., Engel, M.S., and Ren, D. (2010). Ancient pine needle mimics among lacewings. Proc. Natl. Acad. Sci. U S A 107, 16212–16215.

Wang, Y., Labandeira, C.C., Shih, C., Ding, Q., Wang, C., Zhao, Y., and Ren, D. (2012). Jurassic mimicry between a hangingfly and a ginkgo from China. Proc. Natl. Acad. Sci. U S A 109, 20514–20519.

Wang, Q., Shih, C., and Ren, D. (2013). The earliest case of extreme sexual display with exaggerated male organs by two middle Jurassic Mecopterans. PLoS ONE 8, e71378.

Wang, Q.K., Hong, D.S., Inthavong, K., Zhang, D., and Elgar, M.A. (2018). Antennal scales improve signal detection efficiency in moths. Proc. R. Soc. B Biol. Sci. 285, 20172832.

Wappler, T., Guilbert, E., Labandeira, C.C., Hörnschemeyer, T., and Wedmann, S. (2015). Morphological and behavioral convergence in extinct and extant bugs: the systematics and biology of a new unusual fossil lace bug from the Eocene. PLoS ONE 10, e0133330.

Wichard, W. (2017). A remarkable caddisfly with beinite antennae in Cretaceous Burmese amber (Insecta, Trichoptera). Cre. Res. 69, 198–203.

Xing, L., Niu, K., and Evans, S.E. (2019). Inter-amphibian predation in the early cretaceous of China. Sci. Rep. 9, 7751.

Yan, X.Z., Deng, C.P., Sun, X.J., and Hao, C. (2014). Effects of various degrees of antennal ablation on mating and oviposition preferences of the diamondback moth, Plutella xylostella L. J. Integr. Agric. 13, 1311–1319.

Yang, H., Yin, X., Lin, X., Wang, C., Shih, C., Zhang, W., Ren, D., and Gao, T. (2019). Cretaceous winged stick insects clarify the early evolution of Phasmatodea. Proc. R. Soc. B Biol. Sci. 286, 20191085.

Zheng, D., Niel, A., Jarzembowski, E.A., Chang, S.-C., Zhang, H., Xia, F., Liu, H., and Wang, B. (2017). Extreme adaptations for probable visual courtship behaviour in a Cretaceous dancing damselfly. Sci. Rep. 7, 44932.
Supplemental Information

A Cretaceous bug with exaggerated antennae might be a double-edged sword in evolution

Bao-Jie Du, Rui Chen, Wen-Tao Tao, Hong-Liang Shi, Wen-Jun Bu, Ye Liu, Shuai Ma, Meng-Ya Ni, Fan-Li Kong, Jin-Hua Xiao, and Da-Wei Huang
Supplemental Information

Figure S1. Reconstruction of the habitus of *M. wuae* gen. et sp. nov., related to Figures 1–3. Scale bar, 1 mm.
Figure S2. Images of some modern coreids, related to Figures 1–2. (A–B) *Chariesterus antennator* (A. Courtesy of Ms. Melanie Schuchart, downloaded from https://www.inaturalist.org/photos/20221697; B. Courtesy of Mr. Steve Kerr, downloaded from http://www.inaturalist.org/photos/1758620). (C–D) *Chariesterus armatus* (Courtesy of Mr. Branco, downloaded from https://www.flickr.com/photos/brutamonte). (E–F) *Dalader* sp. (Courtesy of Kwan downloaded from http://www.natureloveyou.sg). (G–H) *Thasus neocalifornicus* (Dr. Margarethe Brummermann, downloaded from http://arizonabeetlesbugsbirdsandmore.blogspot.com). A, C, E, G. Nymphs; B, D, F, H. Adults.
**Transparent 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 volcanioclastic 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 type material is deposited in the Century Amber Museum (Room 301A No.1, Songru Road, Songgang Street, Bao’an District, Shenzhen, China). The new taxon is registered in ZooBank under the publication LSID. urn:lsid:zoobank.org:pub:D14C87DF-5440-4BE1-A214-20E1071D262F.

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.

**Fossil Records of Coreidae.**

All the confirmed and named fossil records of Coreidae during the Mesozoic are preserved in China, the oldest of which is from the Upper Triassic strata (Lin, 1992, Hong, 1984, Hong, 1987). Fossil representatives are relatively common in Tertiary strata, being known from Eocene strata of the United States (Scudder, 1890, Cockerell, 1909); Oligocene rocks of Germany (Heyden, 1858, Statz and Wagner, 1950); Miocene strata of China (Hong et al., 1983, Hong and Wang, 1987, Zhang, 1989, Zhang and Zhang, 1990, Zhang et al., 1994), Croatia (Heer, 1853) and Germany (Heer, 1853); and Pliocene rocks of France (Piton, 1935).

**Supplemental References**

Azar, D., Nel, A., Engel, M., Garrouste, R., and Matocq, A. (2011). A new family of Coreoidea from the Lower Cretaceous Lebanese Amber (Hemiptera: Pentatomomorpha). Polish Journal of Entomology 80, 627–644.

Brailovsky, H. (2010). New genus and new species of Hydarini (Hemiptera, Heteroptera, Coreidae) from South America. Dtsch. Entomol. Z. 57, 85–88.

Brailovsky, H., and Barrera, E. (2009). New species of *Merocoris* (*Merocoris*) Perty from Brazil, with keys to known subgenera and species of the tribe Merocorini (Hemiptera: Heteroptera: Coreidae: Meropachyinae). Fla. Entomol. 92, 134–138.

Cockerell, T.D.A. (1909). Fossil insects from Colorado. The Entomologist 42, 170–174.

Cruickshank, R.D., and Ko, K. (2003). Geology of an amber locality in the Hukawng Valley, Northern Myanmar. J. Asian Earth Sci. 21, 441–455.
Grimaldi, D.A., Engel, M.S., and Nascimbene, P.C. (2002). Fossiliferous Cretaceous amber from Myanmar (Burma): Its rediscovery, biotic diversity, and paleontological significance. Am. Mus. Novit. 62, 1–71.

Hamouly, H.E., Sawaby, R.F., and Fadl, H.H. (2010). Taxonomic review of the subfamily Pseudophloeinae (Hemiptera: Coreidae) from Egypt. Egypt J. Biol. 12, 108–124.

Heer, O. (1853). Die Insektenfauna der Tertiärgebilde von Oeningen und von Radoboj in Croatien. Dritte Theil: Rhynchoten (Neue Denkschriften der allgemeinen Schweizerischen Gesellschaft für die gesammten Naturwissenschaften Zürich Press).

Heyden, C.v. (1858). Fossile Insekten aus der Braunkohle von Salzhausen. Palaeontographica 5, 115–120.

Hong, Y. (1987). The study of Early Cretaceous insects of Kezuo, west Liaoning. Professional Papers of Stratigraphy & Palaeontology 18, 76–87.

Hong, Y.C. (1984). Insecta. Palaeontological Atlas of North China, II, Mesozoic, 128–185.

Hong, Y.C., Cora, J., and Johnson, N. (1983). Fossil insects in the diatoms of Shanwang. Bulletin of the Tianjin Institute of Geology and Mineral Resources 8, 1–15.

Hong, Y.C., and Wang, W.L. (1987). Miocene Heteroptera and Coleoptera (Insecta) from Shanwang of Shandong Province, China. Journal of the Lanzhou University of Natural Science 33, 116–124.

Lin, Q.B. (1992). Late Triassic insect fauna from Toksun, Xinjiang. Acta Palaeontol. Sin. 31, 313–335.

Piton, L.E. (1935). La faune entomologique des gisements mio-pliocenes du Massif Central. Revue des Sciences Naturelles d'Auvergne (N. S.) I, 65–104.

Scudder, S.H. (1890). The Tertiary insects of North America. (Washington George Mason University Press).

Shi, G., Grimaldi, D.A., Harlow, G.E., Wang, J., Wang, J., Yang, M., Lei, W., Li, Q., and Li, X. (2012). Age constraint on Burmese amber based on U-Pb dating of zircons. Cretaceous Res. 37, 155–163.

Statz, G., and Wagner, E. (1950). Geocorisae (Landwanzen) aus den Oberoligocäner Ablagerungen von Rott. Journal of Differential Equations 34, 496–522.

Zhang, J.F. (1989). Miocene insects from Shanwang of Shandong, China and their bearing on palaeoenvironment. Proceedings of International Symposium on Pacific Neogene Continental and Marine Events, 149–156.
Zhang, J.F., Sun, B., and Zhang, X.Y. (1994). Miocene insects and spiders from Shanwang, Shandong (Science Press).

Zhang, J.F., and Zhang, X.Y. (1990). Fossil insects of cicada (Homoptera) and true bugs (Heteroptera) from Shanwang, Shandong. Acta Palaeontol. Sin. 29, 337–348.