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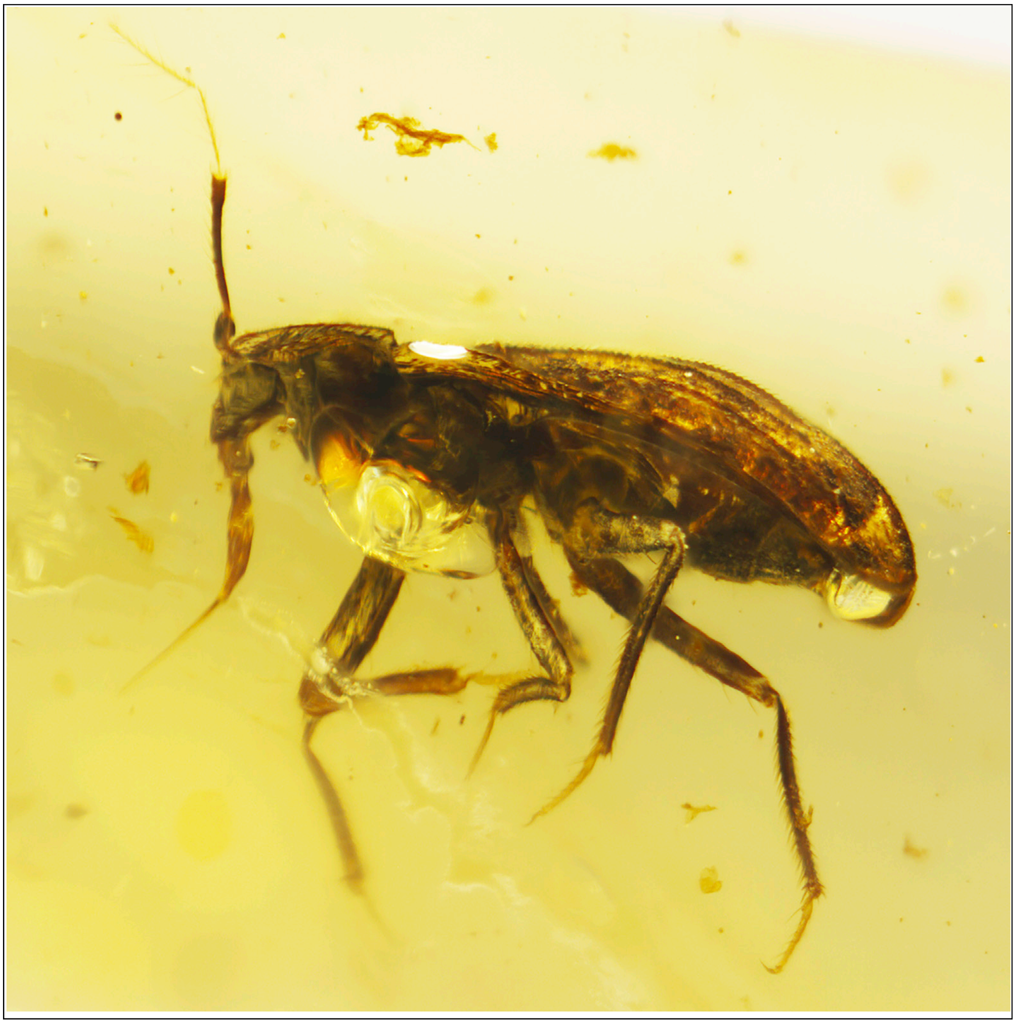

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HIGHLIGHTS

A new family of beetle-mimicking bugs is described from Cretaceous amber

Berstidae were aggressive or defensive mimics of polyphagan beetles

They are one of the earliest mimics in the fossil record of insects

The discovery points at a high ecological complexity in mid-Cretaceous rainforests

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Mimicry in Cretaceous Bugs

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SUMMARY

Mimicry is ubiquitous in nature, yet understanding its origin and evolution is complicated by the scarcity of exceptional fossils that enable behavioral inferences about extinct animals. Here we report bizarre true bugs (Hemiptera) that closely resemble beetles (Coleoptera) from mid-Cretaceous amber. The unusual fossil bugs are described as *Bersta vampirica* gen. et sp. nov. and *Bersta coleopteromorpha* gen. et sp. nov. and are placed into a new family, Berstidae fam. nov. The specialized mouthparts of berstids indicate that they were predaceous on small arthropods. Their striking beetle-like appearance implies that they were either involved in defensive mimicry or mimicked beetles to attack unsuspecting prey. The latter would represent the first case of aggressive mimicry in the invertebrate fossil record. These findings enrich our understanding of the paleoecological associations and extinct behavioral strategies of Mesozoic insects.

INTRODUCTION

Mimicry, whereby organisms resemble living or inanimate objects, is a keystone concept in evolutionary biology and has received considerable interdisciplinary attention as one of the most vivid illustrations of Darwinian natural selection (Casewell et al., 2017). Mimics deploy a range of elaborate methods, including morphological, physiological, and behavioral adaptations, to avoid recognition by predators, prey, or conspecifics (Pfennig, 2012). Defensive mimicry (e.g., Batesian or Müllerian mimicry) involves species that conceal their true identities to avoid predation. Defensive Batesian mimicry is widespread in some animals such as in some groups of butterflies that resemble toxic species despite being harmless themselves (Barber and Conner, 2007; Pinheiro, 1996). On the other end of the spectrum of mimetic associations in nature, aggressive mimicry (Peckhamian mimicry, Peckham, 1889) involves predators that imitate, often in intricate ways involving visual and chemical deceit, their own prey to avoid being detected (Jamie, 2017). Some of the most striking examples of aggressive mimicry include humpback anglerfish that use their bioluminescent dorsal spine to lure and capture prey, parasitic trematodes that gain entry into their unsuspecting hosts by mimicking their food, and predaceous spiders that, like true "wolfs in sheep's clothing," mimic harmless species by releasing a cocktail of deceitful chemical cues (Nelson and Jackson, 2012; Pietsch and Grobecker, 1978). However, the fossil record of complex ecological interactions such as mimicry is very sparse, disclosing little about their evolution (Boucot, 1990).

Few reliable examples of mimicry have been described from the fossil record to date (Boucot and Poinar, 2010; Kácha and Petr, 1996; Topper et al., 2015; Vinther et al., 2016), mostly because incomplete preservation of isolated fossils makes paleoecological interpretations difficult (Wang et al., 2012). Among extinct vertebrates, defensive mimicry was hypothesized, among others, in ankylosaurid dinosaurs that may have used their enlarged tail clubs to divert predator attacks from their heads to this well-defended region (Thulborn, 1993). The earliest putative case of aggressive mimicry in vertebrates has been recognized in a Late Jurassic piranha-like pycnodontiform fish that likely used its close resemblance of harmless species to approach prey unnoticed (Kölbl-Ebert et al., 2018). Cases of defensive mimicry in Mesozoic arthropods are rare (Hinkelman, 2020; Vršanský et al., 2018) and no cases of aggressive mimicry have so far been demonstrated in fossil invertebrates (Kácha and Petr, 1996, 1997).

Here we report a new group of beetle-mimicking Cretaceous bugs based on exceptionally preserved fossils in mid-Cretaceous amber from northern Myanmar, one of the most biodiverse insect Lagerstätten from the Mesozoic (Cai et al., 2019; Ross, 2019). These beetle-mimicking bugs are exceptionally rare, only three specimens belonging to two species were found after examining more than 40,000 inclusions. The lifelike fidelity of our fossils reveals morphological characters that identify them as predaceous visual mimics of beetles. Based on their striking beetle-like morphology, the bugs are placed into a new family, Berstidae

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fam. nov. These extinct Cretaceous bugs belong to the order Cimicomorpha, which includes modern bed bugs and kissing bugs, providing a new insight into the early evolution of this economically important group of insects, as well as a rare window into the ecological complexity of Cretaceous tropical rainforests at the heart of the Cretaceous terrestrial revolution.

RESULTS

Systematic Paleontology

Order Hemiptera Linnaeus, 1758, suborder Heteroptera Latreille, 1810.

Infraorder Cimicomorpha Leston, Pendergrast et Southwood, 1954.

Family Berstidae fam. nov.

Diagnosis

Body elongate to subelliptical, glabrous, not covered with layers of setae, coleopteroid (Figure 1). Size rather small, when compared with the remainder of Hemiptera; length ranging from 2.0 to 2.6 mm. Head hypognathous, more or less pentagonal in dorsal view, without a constriction posterior to compound eyes; collar present. Labium four-segmented, tapering apically, inserted on ventral head surface. Antenna with four articles; prepedicellite absent; antennomere II (pedicel) longer than antennomere III (basiflagellomere), antennomeres III and IV (distiflagellomere) filiform, much narrower than preceding antennomeres, with erect setae. Compound eyes well developed, but not surpassing collar posteriorly. Ocelli absent. Thoracic labial groove present; pronotum trapezoidal. Pronotum almost butterfly shaped, with anterior margin sinuate, anterior angles smoothly curved, and posterior angles approximately right angled. Pronotal and hemelytral margins pronouncedly expanded, clearly overlapping sides of thorax and abdominal base. Legs slender and setose, of cursorial type. Prolegs lack any specialist raptorial adaptations. Tarsi trimerous, pretarsal parempodia absent.

Comparison

Berstids differ from other hemipteran families with a coleopteroid appearance, such as Omaniidae, Schizopteridae, and Tingidae, in having their forewings coriaceous, sclerotized throughout their posterior margins, parallel, and connate (apices not overlapping), each with simple longitudinal veins and lacking a costal fracture. They can be assigned to Cimicomorpha based on the presence of cephalic trichobothria; body not covered with a short hair pile and lacking marginal laminae; head not transversely constricted or divided into two distinct lobes; eyes small; antennae not concealed below head in grooves under compound eyes, longer than head, antennomere 2 longer than antennomere 1; forewings modified into coleopteroid hemelytra with longitudinal carinae; abdominal sterna without trichobothria placed sublaterally or submedially; protibiae not flattened; tarsi three-segmented, claws lacking pulvilli. Within Cimicomorpha, the fully coriaceous, parallel, and non-overlapping hemelytra represent an apomorphy of Berstidae.

Type Genus

Bersta gen. nov.

Genus *Bersta* gen. nov.

Type Species

Bersta vampirica sp. nov.

Other Species Included

Bersta coleopteromorpha sp. nov.

Diagnosis

As for the family with the following additional characters, abdominal trichobothria absent, abdominal spiracles on unified sternal plates, each hemelytron with three longitudinal veins, body length $\leq$ 2.6 mm.

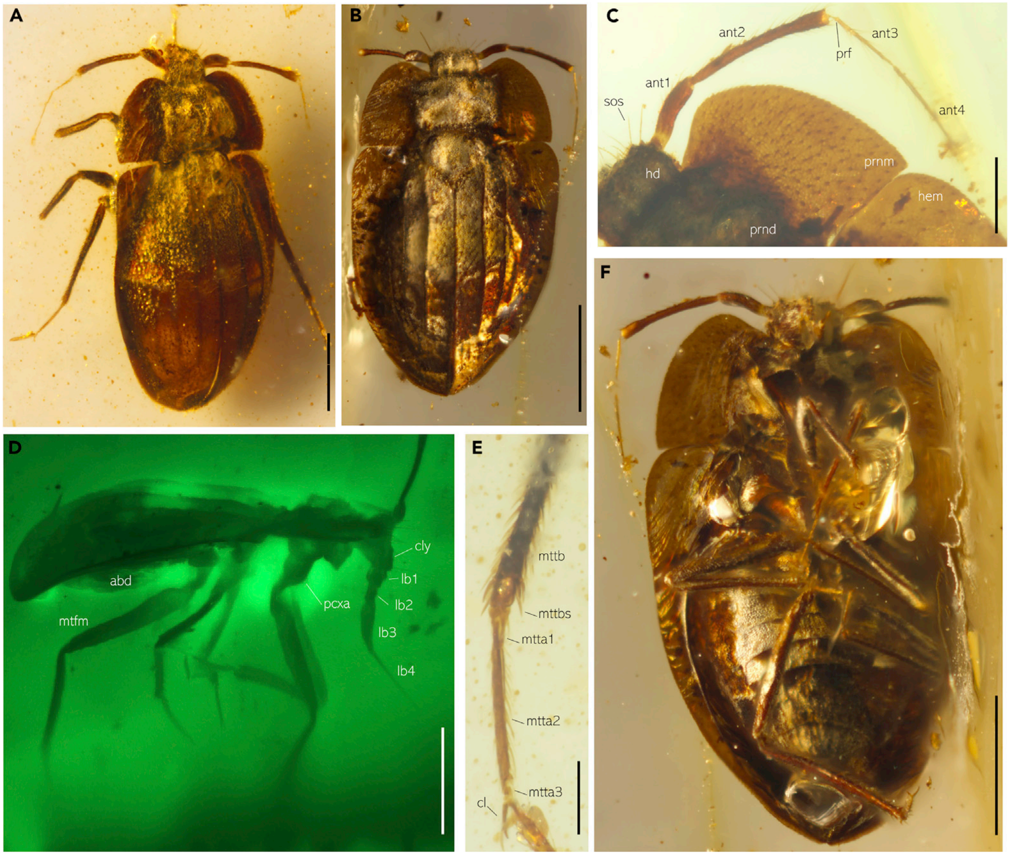

Figure 1. Berstidae fam. nov.: Photographs of Specimens Entombed in Mid-Cretaceous Amber

(A) Habitus of *Bersta coleopteromorpha* gen. et sp. nov. under reflected light.

(B) Habitus of *Bersta vampirica* gen. et sp. nov. under reflected light.

(C) Antenna of *Bersta vampirica* gen. et sp. nov. under reflected light.

(D) Lateral view of *Bersta vampirica* gen. et sp. nov. under green fluorescence.

(E) Metatarsus of *Bersta coleopteromorpha* gen. et sp. nov. under green fluorescence.

(F) Ventral view of *Bersta vampirica* gen. et sp. nov. under reflected light.

Scale bars: 500 µm in (A–F) and 200 µm in (C and E). abd, abdomen; ant1–4, antennomere 1–4; cl, claw; cly, clypeus; hd, head; hem, hemelytron; lb 1–4, labial segments 1–4; mtfm, metafemur; mtta1–3, metatarsi 1–3; mttb, metatibia; mttbs, metatibial spine; pcxa, procoxa; prf, preflagelloid; prnd, pronotal disc; prnm, pronotal margin; sos, supraocular seta. See also Figures S1–S3.

Etymology

The new generic name is an euphonious combination of letters inspired by "Berstuk" a deity of the Wendic Slavs and Sorbs that, according to myth, inhabited deep forests and had the ability to morph into different animals, and refers to the likely paleoenvironment and paleoecology of the bugs. The name is considered of feminine gender.

Type Locality and Horizon

Amber mine in the Hukawng Valley, Myitkyina District, Kachin State, Myanmar; Albian/Cenomanian boundary to late Albian (mid-Cretaceous).

Bersta coleopteromorpha sp. nov.

Distinguished from *B. vampirica* by hemelytral vein 1 not connected to the sutural margin and veins 2 and 3 fading posteriorly, not joining, with the posterior part of vein 1 directed laterally and the posterior part of vein 3 directed medially. Moreover, the pronotum has four clearly defined longitudinal ridges connected to an anterior latitudinal ridge. Unlike its sister species, *B. coleopteromorpha* lacks elevated keels to the side of eyes.

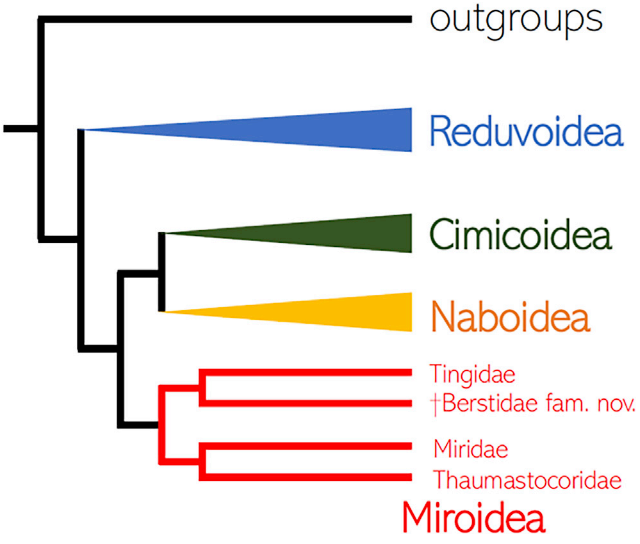

Figure 2. Phylogenetic Hypothesis on the Placement of Berstidae fam. nov.
Based on an analysis of mitogenomes and morphological data (Figures S4 and S5).

Bersta vampirica *sp. nov.*

The species can be differentiated from *B. coleopteromorpha* by the hemelytral vein 1 abruptly curving medially in its posterior part and joining the sutural margin and veins 2 and 3 fused posteriorly. Moreover, it differs by the anterior pronotal angles reaching to the posterior part of the antennal insertions, and by pronotum with an indistinct longitudinal and latitudinal ridge forming a raised cross-like structure with four depressions. In addition, it can be distinguished from *B. coleopteromorpha* gen. et sp. nov. by the presence of supraocular ridges, each with a single seta.

Description

For a full description of *Bersta vampirica* sp. nov. and *B. coleopteromorpha* sp. nov., please refer to the Supplemental Information. All new taxonomic acts are registered in ZooBank under the publication LSID urn:lsid:zoobank.org:pub:F2D47B4A-0F3A-43AB-814B-3D92A7A9506D.

DISCUSSION

Paleoecology of Berstidae

To determine the systematic position of Berstidae fam. nov., we have conducted a total evidence phylogenetic analysis including morphological data for all extinct and extant families of Cimicomopha. We used 13 mitochondrial protein-coding genes and two mitochondrial rRNA for 9 families to reconstruct the backbone phylogeny of the infraorder, which has so far proven difficult to resolve with morphological data alone (Yang et al., 2018). Berstids have been recovered as a sister group to the family Tingidae based on a maximum parsimony analysis of 81 morphological characters (Figure 2). This affinity is supported by the shared coleopterous structure of the hemelytra. Extant tingids are phytophagous, whereas some members of Miroidea are known to be predaceous (Dolling and Palmer, 1991; Schuh and Slater, 1995).

Even among extant bugs, making behavioral inferences from morphological data alone is difficult (Yao et al., 2014). Nonetheless, morphological evidence from our fossils provides important information that can help approximate the diet of Berstidae. Berstids have a labium that is widest proximally and tapers apically (Figure 1). This condition is present in all predaceous and blood-sucking true bugs, but never occurs in phytophagous species (Cohen, 1990; Yao et al., 2014). The presence of filiform antennae with the apical two antennomeres thinner than the second antennomere appears to be associated with predaceous and hematophagous lifestyles (Yao et al., 2014) and living in dead plant material (Jung and Lee, 2012), although there understandably are exceptions. The presence of this antennal morphotype in Cretaceous amber berstids would be consistent with the notion that pre-Paleogene cimicomorphs lived in dead plant matter (Jung et al., 2010; Jung and Lee, 2012).

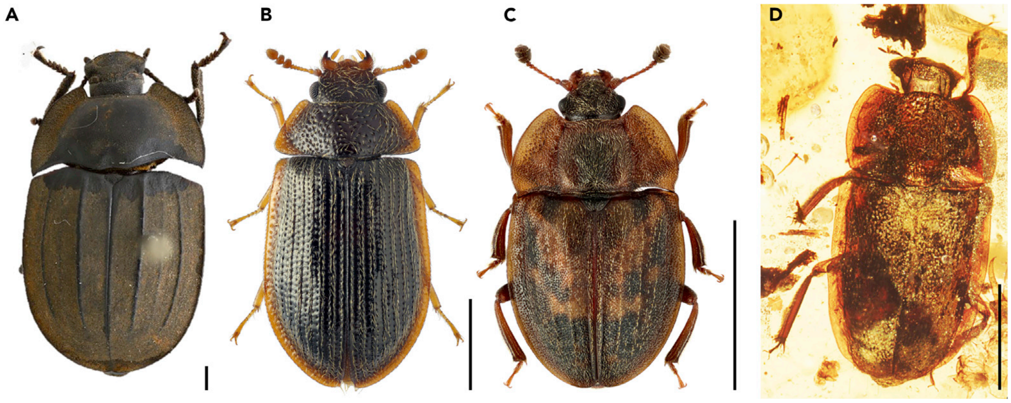

Figure 3. Recent and Fossil Beetles with a Body Plan Similar to Berstidae fam. nov.
(A) Recent *Boreosaragus* sp. (Tenebrionidae). Image courtesy of L. Gibson.
(B) Recent *Ancyrona japonica* (Trogossitidae). Image courtesy of K.V. Makarov.
(C) Recent *Omosita depressa* (Nitidulidae). Image courtesy of M.E. Smirnov.
(D) Fossil *Sorodites angustipes* (Nitidulidae) from Burmese amber. Image courtesy of A.G. Kirejtshuk.
Scale bars: 1 mm.

A predatory, as opposed to a hematophagous, lifestyle is supported by the presence the bug's completely coriaceous forewings and sclerotized abdominal ventrites that would not allow for large abdominal expansion following a blood meal (Schuh and Slater, 1995). A flexible abdomen is necessary for facilitating hematophagy because in extant bedbugs a single blood meal may represent between 130% and 200% of the body weight of an unfed individual (Reinhardt and Siva-Jothy, 2007; Wattal and Kalra, 1961).

Defensive or Aggressive Mimicry?

Perhaps the most striking feature of Berstidae is their remarkable resemblance to beetles. They possess a beetle-like body form with coriaceous forewings sclerotized throughout their entire length, longitudinal hemelytral striae, and a pronotum that is anteriorly much wider than the head. In particular, the beetle-like hemelytra are highly atypical of true bugs. While some hemipteran families have a coleopterid body form, the complete sclerotization of the forewings and their parallel arrangement is an unusual feature. This was probably not the result of convergent evolution due to selection by predators such as arachnids (Huang et al., 2018) or ants (Tihelka et al., 2020), as the berstid hemelytral margin is still much smaller than in some myrmecophilous beetles where it confers protection from arthropod predators (Hölldobler and Kwapich, 2017; Olberg, 2015). In addition, this interpretation cannot explain other similarities with beetles such as the presence of subparallel hemelytral veins and the beetle-like head shape, neither of which are directly related to anti-predatory defense.

In particular, berstids resemble some beetle taxa belonging to the diverse polyphagan families Trogossitidae (bark-gnawing beetles), Nitidulidae (sap beetles), and Tenebrionidae (darkling beetle, namely the extant Australian pie-dish beetles), some of which occur under bark or in dead wood where they feed on fungi, organic remains, or are predaceous (Figure 3). All the three aforementioned families are recorded from or believed to have occurred in the same Cretaceous amber fauna (Kirejtshuk and Chetverikov, 2018; Peris et al., 2014; Ross, 2019). Recently, an interesting sap beetle has been documented from this same amber deposit that exhibits striking superficial similarities to *Bersta* (Kirejtshuk and Chetverikov, 2018). Given the marked similarity between berstids and polyphagan beetles and the likely co-occurrence of the two, it is reasonable to assume that the former mimicked the latter.

But why may have berstids mimicked beetles? There appear to be two plausible explanations: defensive or aggressive mimicry. In the former case, the mimic signals either genuine or false unprofitability to the predator, usually in terms of unpalatability or toxicity. The majority of the beetles that berstids resemble are not known to be aposematic, noxious, or otherwise harmful (Schmidt, 1990), although the existence of toxic or distasteful species in the Cretaceous cannot be ruled out. It seems more probable that the tough exoskeleton of most beetles may make them less palatable than soft-bodied insects to some predators. Some extant true bug families such as Scutelleridae have a remarkably coleopteran-like body plan, although it is not known whether it contributes to defensive mimicry (Schuh and Slater, 1995).

Figure 4. A "Wolf in Sheep's Clothing"?

Paleoecological reconstruction of *Bersta vampirica* gen. et sp. nov. showing one scenario of beetle mimicry in Berstidae. The berstid bug, herein depicted as an aggressive mimic, is praying on a sap beetle (Nitidulidae) in the Cretaceous amber forest, ~99 Ma. Artwork by Mr. Jie Sun.

Aggressive mimicry, whereby a predator tries to "fool" a prey species by looking like the prey itself or another species that is beneficial or harmless to the prey (Ruxton et al., 2019), has been reported from several groups of extant true bugs that feed on ants (McIver and Stonedahl, 1993) and spiders (Wignall and Taylor, 2011, 2010). By resembling harmless beetles, species of *Bersta* could have approached their prey without eliciting an escape response. Just like some modern predaceous bugs, berstids may have fed on nymphs and adults of small insects (Schuh and Slater, 1995). Given that some bark-gnawing and darkling beetles are predaceous themselves, the bugs may have targeted these model beetles, as other insects would most likely avoid a potential predator (Snyder and Wise, 2000). Aggressive mimicry between bugs and beetles has been hypothesized in at least one extant species; the coloration and gross morphology of the predaceous nymphs *Afrius purpureus* (Pentatomidae) appear remarkably similar to the leaf beetle *Mesoplatys cincta* (Chrysomelidae). Both species frequently co-occur on riverhemp (*Sesbania* spp.) in Senegal, and it has been indicated that the striking similarity may enable the *Afrius* to approach the beetles without eliciting an escape response close enough to allow for capture (Bourdouxhe and Jolivet, 1981). In either way, it is possible that berstid mimicry was neither exclusively defensive nor aggressive, and that the bugs preyed on other species aside from the beetles they mimicked. A hypothetical reconstruction of berstids as aggressive mimics of beetles is depicted in Figure 4.

Although the similarity between berstids and polyphagan beetles is not perfect, many cases of imperfect resemblance between mimics and their models are known (Kikuchi and Pfennig, 2013; Pfennig, 2012). Mimicry is always dependent on the sensory abilities of the organism being deceived, and so, for example, although many hoverflies may be easily distinguished by the trained human eye from the bees and wasps they mimic, they are sufficiently similar to deceive their predators (Kikuchi and Pfennig, 2013; Kraemer and Adams, 2014; Penney et al., 2012). With reference to the presence of metathoracic scent glands in *Bersta*, it is possible that the bugs also employed chemical mimicry to further conceal themselves from their prey. Although admittedly traces of chemicals in amber are difficult to detect (McCoy et al., 2019), it is likely that chemical mimicry did exist in some Cretaceous insects, such as in termitophilous beetles that may have used chemical camouflage to infiltrate termite nests (Cai et al., 2017).

The Fossil Record of Insect Mimicry

To our knowledge, berstids represent the earliest potential example of aggressive mimicry in the invertebrate fossil record. Mimicry is difficult to recognize even in extant faunas, so it should not be surprising that its detection is even more problematic in the fossil record. Insects with leaf-mimicking wings, a form of camouflage, have existed since at least the Permian (Garrouste et al., 2016; Wang et al., 2012). Among Mesozoic insects, liverwort-mimicking larvae from the Cretaceous mimicked their surroundings to prevent predation, thus qualifying as mimesis or masquerade, as contrasted to true aggressive mimicry in berstids, which involved resemblance between predators and their prey with the aim of deceiving the latter (Liu et al., 2018). Further examples of camouflage are documented from Cretaceous amber lacewings (Liu et al., 2018; Pérez-de la Fuente et al., 2018; Wang et al., 2016) and planthoppers (Jiang et al., 2019), but these cases again involve mimesis of inanimate objects and not resemblance of prey species as is the case in berstids. Moreover, mimesis in these lacewings is based on a constructed concealment rather than morphological modifications (i.e., physical mimicry) of the body as is documented here.

The earliest occurrence of Batesian mimicry has been inferred in alienopterid cockroaches from the Early Cretaceous Crato Formation in Brazil; this group of cockroaches also occurs in Burmese amber (Bai et al., 2016; Hinkelman, 2020; Vršanský et al., 2018). Other cases of defensive mimicry in Burmese amber include a wasp-mimicking zhangsolvid fly (Grimaldi, 2016) and coleopterans possibly mimicking noxious net-winged beetles (Lycidae) (Bocák et al., 2019; Poinar and Fanti, 2016).

Although warning coloration and crypsis have been inferred in Carboniferous insects (Jarzembowski, 2005), no convincing examples of aggressive mimicry are known from Paleozoic arthropods. Only the extinct giant Lower Paleozoic sea scorpions (Eurypterida) have been suggested as possible aggressive mimics in the past. Lamont (1969) hypothesized that the apparently ''scaly'' cuticle of *Parastylonurus* could have been used to conceal the predator from its fish prey. However, this claim is problematic on several accounts. First, eurypterids are rather large ''scorpion-like'' creatures that share little with fish in terms of their gross morphology. Second, the scaly cuticular ornament is only present in some parts of the body, whereas the rest was apparently unornamented, and the scales display great variability in different body parts (Waterston, 1979). In the absence of comparative studies of eurypterid and fish scales, in terms of their structure and paleocolour, it is most parsimonious to consider this superficial resemblance as a case of convergence, and consequently the hypothesis is not generally accepted (Kácha and Petr, 1996, 1997).

Despite their extreme rarity, it is reasonable to assume that as the number of known mimetic interactions from localities with exceptional fossil preservation grows, we will be better equipped to address the macroevolutionary implications of this ecological phenomenon. Although studies of mimicry in animals made significant progress for decades with very little input from paleontological lines of evidence (Boucot, 1990), the fossil record can provide important insights into the origin and evolution of this complex behavior. Do mimics suffer a higher extinction rate as predicted by their low population sizes, constantly pruned by frequency-dependent selection (Finkbeiner et al., 2018; Lindström et al., 1997; Pfennig et al., 2001), or do mimics represent chronically rare, low-density specialists that are able to persist in low numbers (Vermeij and Grosberg, 2018)? If yes, how? Mimics that parade energetically costly signals are the least likely to be detected (Johnstone and Grafen, 1993), but as the models learn to recognize their mimics (Cheney and Côté, 2005) these will be forced to invest in even costlier signals. How often must mimics innovate to keep pace with their models and can the models outcompete their mimics by forcing them to invest more than they can afford to lose? The expanding wealth of data from cases of fossil mimicry open up new questions with important implications for behavioral ecology and evolutionary biology that can be answered by combining insights from extant species, fossils, and mathematical modeling.

Limitations of the Study

The fossil record of mimicry in insects, and invertebrates more generally, is at present far too sparse to be used to test hypotheses about the origin of this behavior. More work will be required before fossils can be used to answer macroevolutionary questions about the emergence of mimicry.

Resource Availability

Lead Contact

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Chenyang Cai (cycai@nigpas.ac.cn).

Materials Availability

This study did not generate new unique reagents.

Data and Code Availability

Original data have been deposited to Mendeley Data: https://data.mendeley.com/datasets/6vk54mggfg/2 and in the Supplemental Information.

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.2020.101280.

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AUTHOR CONTRIBUTIONS

E.T. and C.C. conceived and designed the study. All authors contributed to the taxon descriptions. E.T. drafted the manuscript to which C.C., D.H., and M.S.E. contributed. E.T. and C.C. conducted the phylogenetic analyses.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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Supplemental Information

Mimicry in Cretaceous Bugs

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Figure S1. Morphological details of *Bersta vampirica* gen. et sp. nov. (NIGP171324, holotype), related to Figure 1.

(A) Dorsal view under reflected light.

(B) Ventral view under reflected light.

(C) Hemelytra in dorsal view under reflected light.

(D) Head and pronotum in dorsal view under green fluorescence.

Scale bars (A, B) 500 μm; (C, D) 200 μm. Abbreviations: 1–3, hemelytral veins 1–3; mscu, mesoscutum; pd, pronotal depression; scu, scutellum; sor, supraocular ridges; sutural margin.

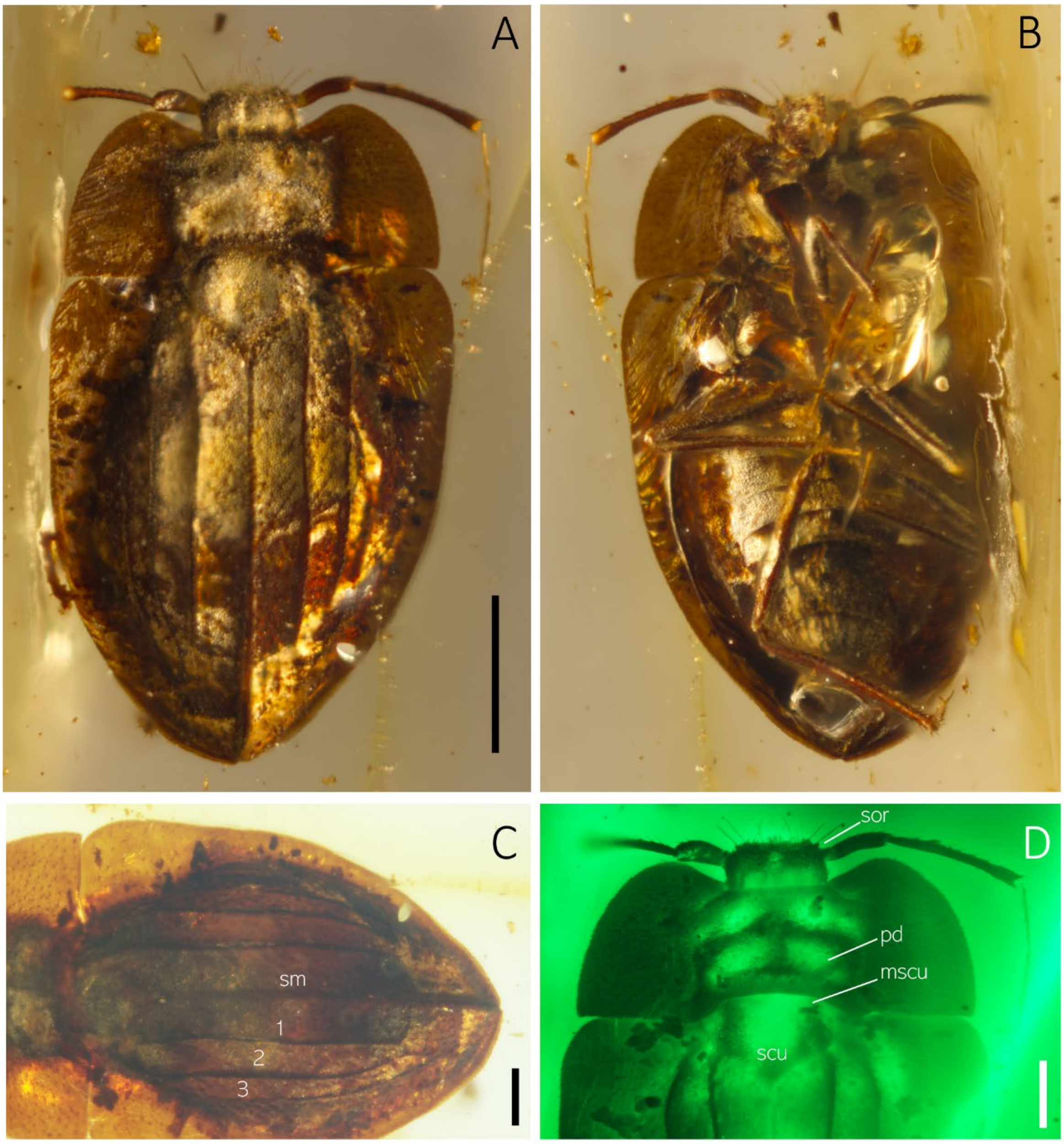

Figure S2. Morphological details of *Bersta vampirica* gen. et sp. nov. (NIGP171324, holotype; NIGP171325, paratype), related to Figure 1.

(A) Dorsal view of paratype under reflected light.

(B) Lateral view of holotype under reflected light.

Scale bars (A, B) 500 μm. Abbreviations: abd, abdomen; cly, clypeus; lb 1–4, labial segments 1–4; mtfm, metafemur.

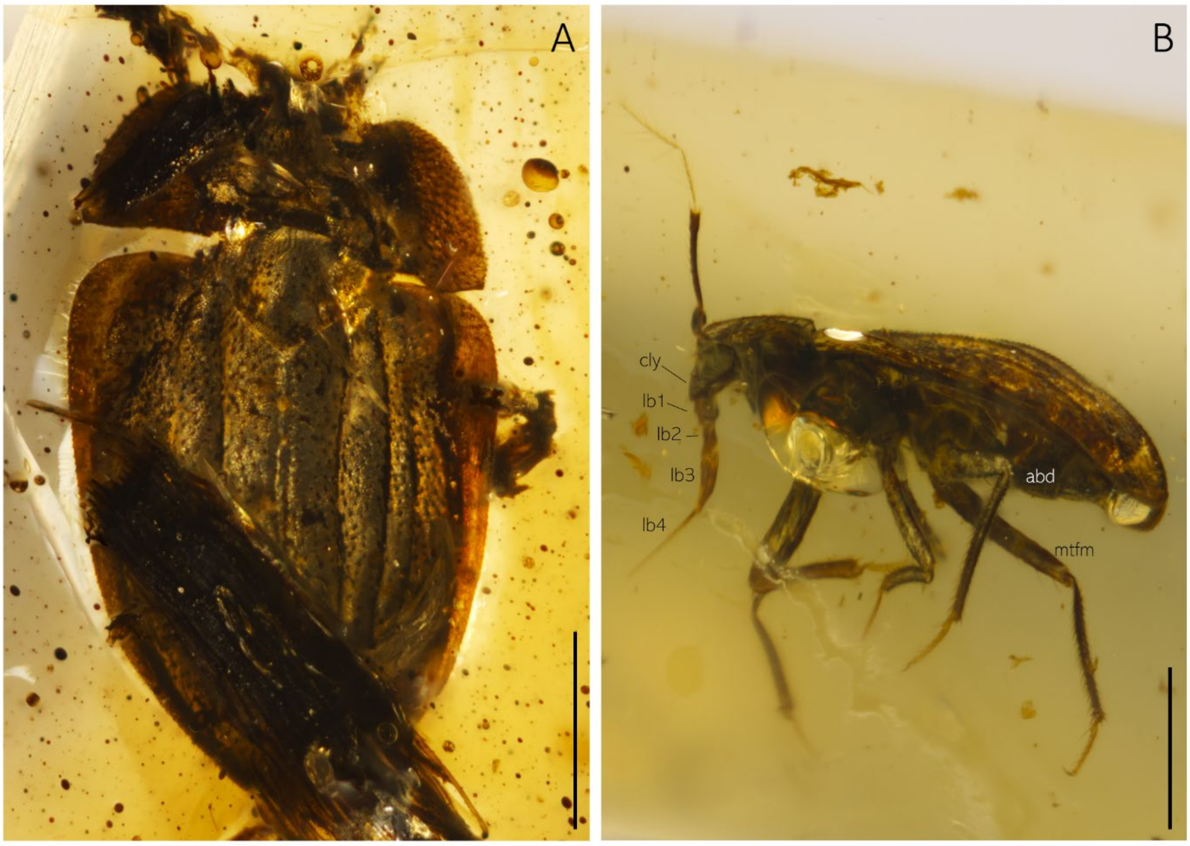

Figure S3. Morphological details of *Bersta coleopteromorpha* gen. et sp. nov. (NIGP171323), related to Figure 1.

(A) Dorsal view under green fluorescence.

(B) Ventral view under reflected light.

(C) Head and pronotum in dorsal view under reflected light.

(D) Prothoracic leg under reflected light.

(E) Hemelytra in dorsal view under reflected light.

Scale bars (A, B, E) 500 μm; (C, D) 200 μm. Abbreviations: 1–3, hemelytral veins 1–3; lar, latitudinal pronotal ridges 1–2; lor, longitudinal pronotal ridges 1 –4; pfm, profemur; prnm, pronotal margin; ptb, protibia; ptbc, protibial cushion; scu, scutellum; sm, sutural margin; sos, supraocular setae.

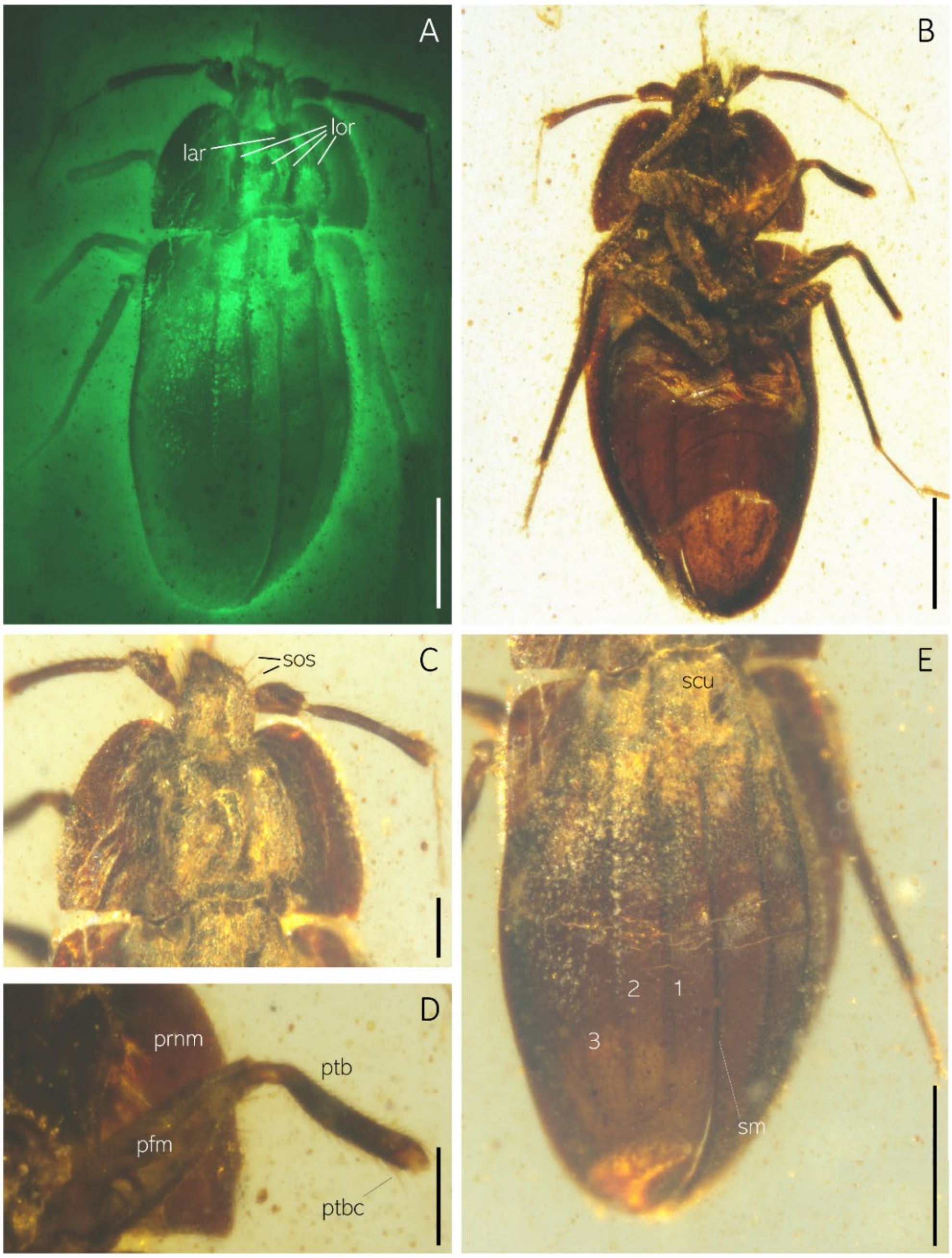

Figure S4. Phylogeny of Cimicomorpha inferred from a CAT-GTR analysis of mitogenomes (P123RNA), related to Figure 2.

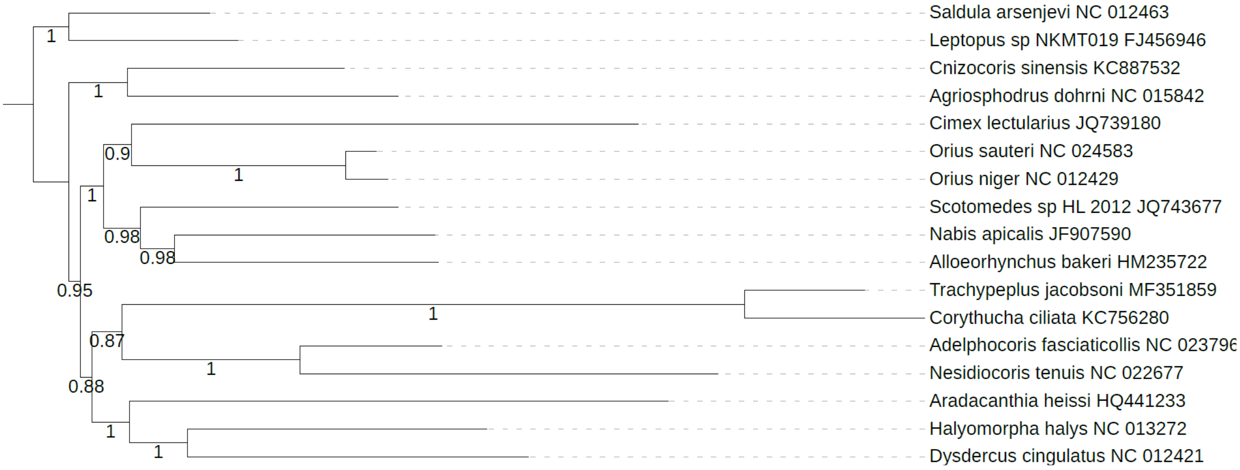

Figure S5. A majority-rule consensus cladogram of four most parsimonious trees (tree length = 297 steps; consistency index = 0.391; retention index = 0.749) showing the systematic position of *Bersta vampirica* gen. et sp. nov., with mapped character states, related to Figure 2. Characters are numbered starting from 0, such as that the first character in the matrix is displayed as character 0.

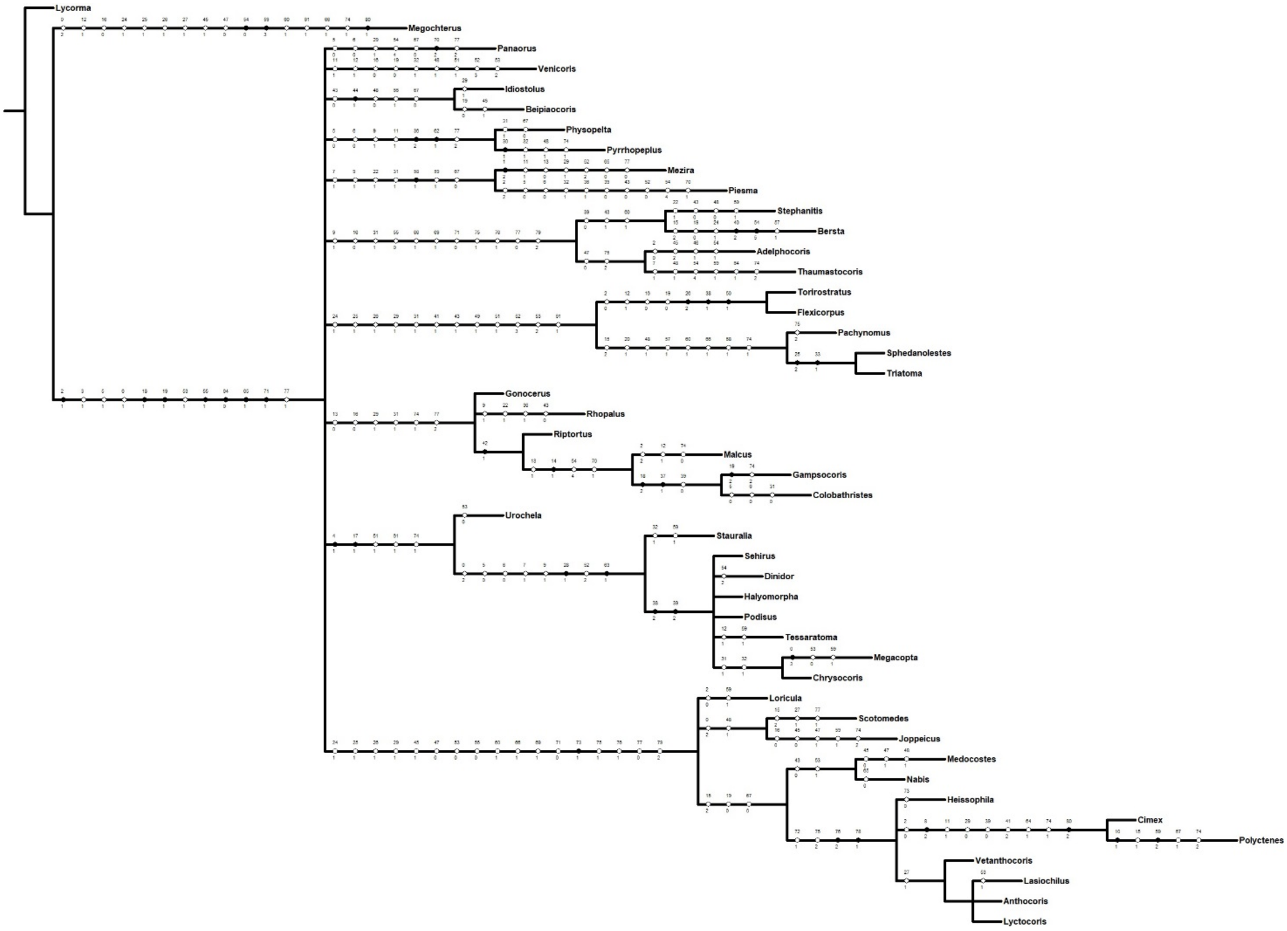

Table S1. GenBank accession numbers for taxa used in the mitogenome analysis, related to Figures 2, S5, and S6.. Systematics follow Schuh and Weirauch (2020).

Taxon	mtDNA
CIMICOMORPHA	
REDUVIOIDEA	
Reduviidae	
Agriosphodrus dohrni	NC_015842
Cnizocoris sinensis	KC887532
NABOIDEA	
Nabidae	
Alloeorhynchus sp.	HM235722
Nabis apicalis	JF907590
Velocipedidae	
Scotomedes sp.	JQ743677
CIMICOIDEA	
Anthocoridae	
Orius sauteri	NC_024583
Orius niger	NC_012429
Cimicidae	
Cimex lectularius	JQ739180
MIROIDEA	
Miridae	
Nesidiocoris tenuis	NC_022677
Adelphocoris suturalis	NC_023796
Tingidae	
Corythucha ciliata	KC756280
Trachypeplus jacobsoni	MF351859
PENTATOMOMORPHA	
PENTATOMOIDEA	
Pentatomidae	
Halyomorpha halys	NC_013272
PYRRHOCOROIDEA	
Pyrrhocoridae	
Dysdercus cingulatus	NC_012421

Transparent methods

Fossil preparation

The amber inclusions originate from a mine at the slope of the Noije Bum hill in the Hukawng Valley, Kachin State, northern Myanmar. The amber piece was polished using sandpapers of gradually finer grits and finally with diatomite mud prior to photography. The type material is deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China. All new taxonomic acts are registered in ZooBank under the publication LSID urn:lsid:zoobank.org:pub:F2D47B4A-0F3A-43AB-814B-3D92A7A9506D.

Photographs under reflected light were taken using a Canon EOS 5D Mark III digital camera, equipped with a Canon MP-E 65 mm macro lens (F2.8, 1–5X), and with an attached Canon MT-24EX twin flash. Fluorescence images with a green background were taken using a Zeiss Axio Imager 2 microscope equipped with a mercury lamp and using the eGFP filter. Helicon Remote 3.9.9 and Helicon Focus 3.10 were used to capture and stack images to increase the depth of field.

Phylogenetic analysis

A total evidence phylogenetic analysis combining both molecular and morphological data was performed to determine the systematic position of Berstidae fam. nov. To reconstruct deep relationships within Cimicomorpha, which have been traditionally difficult to resolve based on morphological data alone, we used published mitochondrial genome sequences (P123RNA for 12 ingroup taxa). To determine the position of Berstidae fam. nov., we used the character matrix of Yao et al. (2014) (81 characters for 46 taxa). We did not use the more recent character matrix of Weirauch et al. (2019), since it uses many characters that are difficult to score in fossil taxa. Taxa belonging to Pentatomorpha, Fulgoromorpha, and Nepomorpha were used as outgroups.

GenBank accessions for the analysed mitogenomes are provided in Table S1. The mitochondrial genomes were downloaded from GenBank using PhyloSuite v 1.2.1 (Zhang et al., 2020). Protein-encoding genes were aligned using the G-INS-i algorithm implemented in the MAFFT v 7.313 plugin within PhyloSuite (Katoh and Standley, 2013), while the ribosomal RNAs were aligned using the E-INS-I algorithm, and the aligned genes were concatenated using PhyloSuite. Concatenation was carried out in PhyloSuite. The decisive matrix was analysed using the site-heterogeneous CAT-GTR+G model in PhyloBayes MPI 1.7 (Lartillot et al., 2013); two independent Markov chain Monte Carlo (MCMC) chains were run until convergence (maxdiff < 0.3).

We tried to separately analyze data for four genes (16S, 18S, 28S, and COI) to shed light on the systematic position of more cimicomorph families, but the recovered tree was poorly supported. Evidently, a small four gene dataset is not sufficient for resolving family-level relationships within Cimicomorpha.

For the morphological data, maximum parsimony analyses were performed in TNT v 1.5 (Goloboff and Catalano, 2016) using the New Technology Search and implied weighting. The recommended value of k = 12 was used (Goloboff et al., 2018). Collapsing rules were set to 'none'. The analysis was run using default settings in 'New Technology Search'. A majority-rule consensus tree was calculated, and a nonparametric bootstrap analysis run with 1,000 replicates. Character states were mapped using ASADO v. 1.61 (Nixon, 2004). The original dataset provided by Yao et al. (2014) was used, which was designed specifically for testing the systematic position of extinct families. In total, 50 out of the total 81 available characters could be scored for *B. vampirica* gen. et sp. nov. The following three new character states were introduced to describe morphological structures observed in Berstidae fam. nov. but not present in the other taxa: character 41 (2: forewings held flat over the abdomen, adjacent to each other, coriaceous throughout their length), character 42 (3: forewing completely coriaceous) and character 55 (5: hemelytral membrane not present). All characters were unordered and equally weighted. All characters were unordered and equally weighted.

The two phylogenetic analyses were run separately, and their results are displayed in Figs. S5–6. A phylogenetic hypothesis on the placement of Berstidae, using mitogenome data to inform deeper nodes, morphological data to infer shallower nodes, and enforcing the monophyly of Miroidea strongly supported by molecular analyses after accounting for compositional heterogeneity (Yang et al., 2018), is presented in Fig. 3. Datasets, analysis files, and output files are available at Mendeley Data https://data.mendeley.com/datasets/6vk54mggfg/2 (DOI: 10.17632/6vk54mggfg.2).

Supplemental description and taxonomic treatment

Berstidae fam. nov.

Type genus. *Bersta* gen. nov.

Diagnosis. Body elongate to subelliptical, glabrous, not covered with layers of setae, coleopteroid. Size rather small, when compared to the remainder of Hemiptera, length ranging from 2.0 to 2.6 mm. Head hypognathous, more or less pentagonal in dorsal view, without a constriction posterior to compound eyes, collar present. Labium 4-segmented, tapering apically, inserted on ventral head surface. Antenna with four articles; prepedicellite absent; antennomere II (pedicel,) longer than antennomere III (basiflagellomere), antennomeres III and IV (distiflagellomere) filiform, much narrower than preceding antennomeres, with erect setae. Compound eyes well-developed, but not surpassing collar posteriorly. Ocelli absent. Thoracic labial groove present; pronotum trapezoidal. Pronotum almost butterfly-shaped, with anterior margin sinuate, anterior angles smoothly curved, and posterior angles approximately right-angled. Pronotal and hemelytral margins pronouncedly expanded, clearly overlapping sides of thorax and abdominal base. Legs slender and setose, of cursorial type. Prolegs lack any specialist raptorial adaptations apart from the presence of a minute setose cushion-like structure at the apex. Tarsi trimerous, pretarsal parempodia absent.

Berstids differ from other hemipteran families with a coleopteroid appearance, such as Omaniidae, Schizopteridae, and Tingidae, in having their forewings coriaceous, sclerotized throughout their posterior margins, parallel, and connate (apices not overlapping), each with simple longitudinal veins, and lacking a costal fracture. They can be assigned to Cimicomorpha based on the presence of cephalic trichobothria, and setose cushion on the forelegs, body not covered with a short hair pile and lacking marginal laminae; head not transversely constricted or divided into two distinct lobes; eyes small; antennae not concealed below head in grooves under compound eyes, longer than head, antennomere 2 longer than antennomere 1; forewings modified into coleopteroid hemelytra with longitudinal carinae; abdominal sterna without trichobothria placed sublaterally or submedially; protibiae not flattened; tarsi 3-segmented, claws lacking pulvilli. Within Cimicomorpha, the fully coriaceous, parallel and non-overlapping hemelytra represent an apomorphy of Berstidae.

Included taxa. A single genus, *Bersta* gen. nov., containing two species.

Bersta gen. nov.

Type species. Bersta vampirica sp. nov.

Diagnosis. As for the family with additional characters: abdominal trichobothria absent, abdominal spiracles on unified sternal plates, each hemelytron with three longitudinal veins, body length ≤ 2.6 mm.

Etymology. The new generic name is a euphonious combination of letters inspired by "Berstuk" a deity of the Wendic Slavs and Sorbs that, according to myth, inhabited deep forests and had the ability to morph into different animals, and refers to the likely paleoenvironment of the bugs and their mimetic association with beetles. The name is considered of feminine gender.

Included species. Two new species: *Bersta vampirica* sp. nov. and *B. coleopteromorpha* sp. nov.

Description. Body elongate to subelliptical, dorsal surface somewhat convex, more or less glabrous. Body length 2.0 to 2.6 mm from clypeus to hemelytral apices, body width 1.0 to 1.2 mm at widest point at the base of the hemelytra. Colour light to dark brown, darker towards the midline, sometimes with a reddish to orange tinge on the pronotal and hemelytral margins.

Head hypognathous, more or less pentagonal in dorsal view, not forming a distinct neck. Clypeus sparsely setate and strongly declivent from the base of the antennae. Mandibular plates short, not reaching to the clypeal apex. Bucculae long, extending over two thirds of the head length. Labium inserted distally on the head, four-segmented, tapering apically, and reaching approximately to the metacoxae. Compound eyes finely faceted and oval, not protruding, and not visible in dorsal view. Ocelli apparently absent. Three pairs of thick and elongate cephalic macrosetae present, each on a raised carina. Antennae inserted anteroventrally to the compound eyes, antenniferous tubercles absent. Antennae 4-segmented, reaching to the base of forewings. Antennal segment 1 (scape) broad and barrel-shaped, longer than half of head width, sparsely setate towards the apex. Antennal segment 2 (pedicel) 1.8 – 2.0 times longer than scape and narrower, slightly expanding apically, with rows of setae. Preflagelloid present, spherical. Antennal segment 3 (basiflagellum) shorter and distinctly thinner than the preceding two segments, transparent, with rows of erect setae. Antennal segment 4 (distiflagellum) also narrow and transparent, with rows of setae, 1.6 – 1.8 times longer than the preceding segment.

Pronotum 0.36 – 0.46 times as long as wide, widest in its second third, slightly narrower basally, and gradually curving inwards anteriorly, forming a distinct collar such that the anterior apices project to the basal quarter of the head. Posterior angles approximately right-angled, directed posteriorly, not overlapping hemelytral apices. Pronotal surface with sparse, equally spaced, dark setae. Pronotal disc with a raised medial and various lateral ridges. Pronotal margin expanded, up to 2.3 times wider than thorax. Labial groove accommodating no more than two thirds of the labium length. Metathoracic scent glands diastomian. Mesoscutum narrowly exposed. Scutellum 0.27 – 0.28 mm long, pentagonal, depressed medially, with a pointed apex. Scutellum small, representing approximately 1/5 of hemelytron length.

Hemelytra elongate, 1.3 – 1.6 times longer than wide, broadest in the basal quarter and tapering in the posterior half, flattened anteriorly and concave in the apical half. Hemelytra sclerotized throughout their length, membranous apical region absent. Hemelytral apices not overlapping. Each coriaceous hemelytron with three longitudinal raised veins. Vein 1 starting at the scutellum, almost straight. Veins 2 and 3 starting in the basal ninth of the hemelytron, bending medially in the posterior third. Veins never reaching the hemelytral apex, all terminating in the apical ninth of the hemelytra. Distances between veins decreasing laterally. Sutural margin raised or not. Cuneus and costal fracture absent. Hindwings not visible.

Legs slender, with rows of setae. Procoxal lamellae triangular, widest anteriorly and tapering posteriorly, forming a labial groove. Mesocoxae directed posteriorly, metacoxae directed laterally. Profemur clavate, as long as protibia, without spines. Mesofemur obclavate, not shorter than mesotarsi. Metafemur slightly expanded distally, approximately half as long as mesotibia. Tibiae terminating with groups of large thick setae or spines and/or tuft of setae. Tarsi elongate, slender, 3-segmented. Claws simple, gradually curving and tapering towards the apex. Pulvilli absent.

Abdomen broadest medially. Tergites apparently sclerotized, each with spiracles located laterally, borders between tergites most apparent medially. No pores or scars of abdominal glands visible. Ventral laterotergites not visible.

Bersta coleopteromorpha sp. nov.

Figs. 1, S3

Etymology. Derived from 'Coleoptera' (beetle) and the Greek '-morphus' in reference to the species' striking beetle-like appearance.

Diagnosis. Distinguished from *B. vampirica* gen. et sp. nov. by hemelytral vein 1 not connected to the sutural margin and veins 2 and 3 fading posteriorly, not joining, with the posterior part of vein 1 directed laterally and the posterior part of vein 3 directed medially. Moreover, the pronotum has four clearly defined longitudinal ridges connected an anterior latitudinal ridge. Unlike its sister species, *B. B. coleopteromorpha* lacks elevated keels to the side of eyes.

Holotype. NIGP171323, sex undetermined.

Type locality and horizon. Amber mine in the Hukawng Valley, Myitkyina District, Kachin State, Myanmar; Albian/Cenomanian boundary to late Albian (mid-Cretaceous).

Description. Body length 2.52 mm, body width 1.09 mm, 2.3 times as long as wide. Head, pronotal disc, hemelytra along midline, and appendages black to dark brown; two apical antennomeres transparent; rest of body brown.

Head 1.1 times as long as wide. Supraocular setae not positioned on ridges. Ratio of antennal segment lengths (in mm): 0.19 : 0.39 : 0.18 : 0.35. Antennal segment 1 representing 0.7 times of head width. Labium not clearly visible.

Pronotum 0.46 mm long along the medial line, 0.99 mm wide across the broadest point, 3.9 times wider than head. Anterior margin incurved medially, anterior angles not reaching to the posterior part of the antennal insertions. Pronotal disc with three medial longitudinal ridges, the middle one being the shortest and the lateral two connected to each by one latitudinal ridge. A fourth additional lateral ridge is present on the right side and is connected to the complex by an anterior latitudinal ridge. Scutellum with distinctly raised lateral ridges.

Hemelytra 1.73 mm long along medial suture, 1.10 mm wide across the broadest point. Vein 1 distinctly raised, straight throughout its length, gradually fainting posteriorly, with posterior part slightly curved laterally, not fused to the sutural margin. Vein 2 raised and more or less straight, gradually fainting posteriorly, shortest of the three veins. Vein 3 more or less straight, gradually fainting posteriorly, with posterior part slightly curved medially. All veins terminating in the posterior ninth of the hemelytron. Sutural margin raised.

Pro- and mesotibia lacking spines. Protibial apex with a cushion of hairs located ventrally. Protibia 1.4 times longer than protarsi. Mesofemur 1.3 times longer than mesotibia. Mesotibia 1.2 times longer than mesotarsi. Metafemur 1.4 times longer than metatibia. Metatibia with four apical spines arranged in two rows. Metatibia 2.9 times longer than metatarsi.

Abdominal tergites subequal, two abdominal tergites missing, revealing a part of the hollow body cavity, hindwings not visible.

Bersta vampirica sp. nov.
Figs. 1, S1, S2

Etymology. Derived from the Slavic '*vampir*', in reference to the species' likely predaceous habits and its piercing and sucking mouthparts.

Diagnosis. The species can be differentiated from *B. coleopteromorpha* gen. et sp. nov. by the hemelytral vein 1 abruptly curving medially in its posterior part and joining the sutural margin, and veins 2 and 3 fused posteriorly. Moreover, it differs from by the anterior pronotal angles reaching to the posterior part of the antennal insertions, and by pronotum with an indistinct longitudinal and latitudinal ridge forming a raised cross-like structure with four depressions. Additionally, it can be distinguished from *B. coleopteromorpha* gen. et sp. nov. by the presence of supraocular ridges, each with a single seta.

Holotype. NIGP171324, sex undetermined.

Paratype. NIGP171325, sex undetermined.

Type locality and horizon. Amber mine in the Hukawng Valley, Myitkyina District, Kachin State, Myanmar; Albian/Cenomanian boundary to late Albian (mid-Cretaceous).

Description. Body length 2.00 mm (2.37 mm in paratype), body width 1.20 mm (1.34 mm in paratype), 1.7 times as long as wide (1.8 times in paratype). Head, pronotal disc, hemelytra along midline, and appendages black to dark brown; two apical antennomeres transparent; expanded pronotal and hemelytral margins distinctly bright brown.

Head 1.1 times as long as wide. Supraocular setae positioned on short ridges. Ratio of antennal segment lengths (in mm): 0.20 : 0.37 : 0.19 : 0.34. Antennal segment 1 representing 0.8 times of head width. Labial segment 1 stout and almost as long as wide, labial segment 2 slightly longer and equally wide throughout, labial segment 3 tapering in the distal quarter, labial segment 4 tapering throughout its length and subequal to the preceding segment.

Pronotum 0.38 mm long along the medial line (0.37 in paratype), 1.06 mm wide across the broadest point (1.26 mm in paratype), 3.8 times wider than head (4.1 in paratype). Anterior margin strongly incurved medially, anterior angles reaching to the posterior parts of the antennal insertions. Pronotal disc with indistinctly raised longitudinal and latitudinal ridges intersecting and forming a cross-like structure surrounded by four oval depressions. Scutellum slightly raised laterally.

Hemelytra 1.50 mm long along medial suture (1.74 mm in paratype), 1.16 mm wide across the broadest point (1.34 mm in paratype). Vein 1 distinctly raised, abruptly curving medially in its posteriormost part and joining the sutural margin. Vein 2 raised, curved in the posterior third, straight in the posterior ninth, fusing with vein 2. Vein 3 indistinct, not easily visible in its basal half, curved medially in its posterior third. Sutural margin raised.

Tibiae terminating with a tuft of large setae or spines. Protibial apex with a patch of setae. Protibia 1.8 times longer than protarsi. Mesofemur 1.2 times longer than mesotibia. Mesotibia 2.4 times longer than mesotarsi. Metafemur as long as metatibia.

Abdominal tergites subequal, two apical tergites each approximately twice the width of the preceding segments.

Systematic position

The present fossils can be placed into the infraorder Cimicomorpha on the basis of the combination of the following characters: body not covered with a short hair pile and lacking marginal laminae; head not transversely constricted or divided into two distinct lobes, with trichobothria; eyes small; antennae not concealed below head in grooves under compound eyes, longer than head, antennomere 2 longer than antennomere 1; forewings modified into coleopteroid hemelytra with longitudinal carinae; abdominal sterna without trichobothria placed sublaterally or submedially; protibiae not flattened; tarsi 3-segmented, claws lacking pulvilli (Schuh and Slater, 1995). Moreover, the foretibia of *B. coleopteromorpha* gen. et sp. nov. and *B. vampirica* gen. et sp. nov. possess small cushion-like structures, variably preserved in our specimens. These cushion-like structure preserved ventrally at the apex of the tibiae are structurally dissimilar to the fossula spongiosa traditionally considered to be unique to Cimicomorpha (Kerzhner, 1981). The fossula spongiosa is in fact apparently absent in the extinct family Vetanthocoridae (Tang et al., 2017; Yao et al., 2014) and phylogenetic studies suggest that it likely emerged independently multiple times in predatory and hematophagous cimicomorphs (Schuh et al., 2009).

To ascertain the systematic position of the beetle-mimicking bugs, a phylogenetic analysis was performed. The morphological analyses resulted into four most parsimonious trees. The majority consensus tree (tree length = 297 steps; consistency index = 0.391; retention index = 0.749) recovered *B. vampirica* gen. et sp. nov. as a sister group to the lace bug genus *Stephanitis* (Tingidae) (Fig. 3, S4). Berstidae fam. nov. is united with the recent Tingidae by the presence of long and narrow bucculae, absence of armature on the scutellum, and corium size. Indeed, some modern members of Tingidae share with *Bersta* gen. nov. the presence of highly sclerotized forewings with raised veins (e.g. genus *Physatocheila*), giving them a highly superficial beetle-like appearance. The new family Berstidae can be easily distinguished from all other cimicomorph families including Tingidae by the hemelytron thickened throughout its length and lacking a membranous apical region. The loss of the costal fracture is reminiscent of some Joppeicidae and taxa with staphylinoid hemelytra (Schuh et al., 2009). Berstidae fam. nov. can also be distinguished from all other cimicomorph families by the apparent absence of parempodia (Schuh et al., 2009). It is also notable that *Bersta* has a longer scape than other fossils such as *Beipiaocoris* that have been sampled in the study. Another unusual characteristic of the beetle-mimicking bugs is their small size, they are significantly smaller than most heteropterans; the smallest adult hemipterans reach around 2 mm in length (Schuh et al., 2008). The new family can also be easily distinguished from all fossil taxa; Berstids are also the only Mesozoic true bugs without a trapezoidal pronotum (Yao et al., 2014).

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