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Debris-carrying camouflage among diverse lineages of Cretaceous insects

Bo Wang,^{1,2,3*} Fangyuan Xia,⁴ Michael S. Engel,⁵ Vincent Perrichot,⁶ Gongle Shi,¹ Haichun Zhang,¹ Jun Chen,^{1,7} Edmund A. Jarzembowski,^{1,8} Torsten Wappler,² Jes Rust²

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Insects have evolved diverse methods of camouflage that have played an important role in their evolutionary success. Debris-carrying, a behavior of actively harvesting and carrying exogenous materials, is among the most fascinating and complex behaviors because it requires not only an ability to recognize, collect, and carry materials but also evolutionary adaptations in related morphological characteristics. However, the fossil record of such behavior is extremely scarce, and only a single Mesozoic example from Spanish amber has been recorded; therefore, little is known about the early evolution of this complicated behavior and its underlying anatomy. We report a diverse insect assemblage of exceptionally preserved debris carriers from Cretaceous Burmese, French, and Lebanese ambers, including the earliest known chrysopoid larvae (green lacewings), myrmeleontoid larvae (split-footed lacewings and owlflies), and reduviids (assassin bugs). These ancient insects used a variety of debris material, including insect exoskeletons, sand grains, soil dust, leaf trichomes of gleicheniacean ferns, wood fibers, and other vegetal debris. They convergently evolved their debris-carrying behavior through multiple pathways, which expressed a high degree of evolutionary plasticity. We demonstrate that the behavioral repertoire, which is associated with considerable morphological adaptations, was already widespread among insects by at least the Mid-Cretaceous. Together with the previously known Spanish specimen, these fossils are the oldest direct evidence of camouflaging behavior in the fossil record. Our findings provide a novel insight into early evolution of camouflage in insects and ancient ecological associations among plants and insects.

INTRODUCTION

Some animals actively seek to hide by decorating themselves with materials, such as sand, vegetal debris, or arthropod remains from their environment, to conceal the features of their bodies and to match their backgrounds (1, 2). Such camouflaging behavior, called self-decoration or debris-carrying, occurs in some gastropods, crabs, spiders, and diverse insects (2, 3). The debris-carrying camouflage of insects is mostly confined to immatures because the weight of debris would be problematic for flying adults (3). The most famous examples are chrysopoid larvae and reduviid nymphs (4–7). The specialized behavior helps prevent these predatory insects from being detected or recognized by both predators and prey (2) and has played an important role in their diversification (2–7). Despite a high taxonomic diversity of extant insects with debris-carrying camouflage, direct evidence of such behavior has been reported mainly in Cenozoic ambers (8). To date, only a single Mesozoic example from Spanish amber has been recorded (4). Consequently, little is known about the early evolution of this complicated behavior and its underlying anatomy.

Here, we report a diverse insect assemblage of exceptionally preserved debris carriers from Cretaceous Burmese, French, and Lebanese ambers. Our study material consists of 39 immature insects belonging

to Chrysopoidea (four morphotypes), Nymphidae (one morphotype), Ascalaphidae (five morphotypes), and Reduviidae (three morphotypes). These fossils are extremely rare among more than 300,000 amber insects examined in this study. Taxonomic descriptions will be published elsewhere. Our findings are among the earliest direct evidence of camouflaging behavior in the fossil record and show unequivocal evidence of camouflage in lacewing and reduviid immatures for more than 100 million years (My). In addition, they also shed new light on the ecology and environment of the Cretaceous forest.

RESULTS

Chrysopoid larvae

More than 100 chrysopoid specimens were examined from Burmese amber, including well-preserved adults and larvae (Fig. 1 and fig. S1); however, only 12 of the larvae display camouflaging behavior or associated morphology (see the Supplementary Materials for descriptions). Two specimens (morphotype CI) exhibit modifications similar to those of the Spanish fossil *Hallucinochrysa diogenesi*, with a flat body and extremely elongate, highly setigerous tubular tubercles on the thorax and abdomen that form a dorsal basket (Figs. 1A and 2A). In addition, these specimens and *H. diogenesi* share a broad head with strongly concave frons, robust legs, and two pairs of tubular tubercles on the mesothorax and metathorax (lateral and laterodorsal pairs); however, the Burmese specimens have a larger body and lack one pair of short tubular tubercles (laterodorsal pair) on the first thoracic segment. Both the Burmese and Spanish fossils exhibit unique debris-carrying modifications, including shapes and arrangements that have not been reported in other chrysopoid taxa (4). A Burmese fossil is carrying insect exoskeletons, including a small psyllid and a large barklouse (Fig. 1A).

¹State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China. ²Steinmann Institute, University of Bonn, 53115 Bonn, Germany. ³Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China. ⁴Nanjiao Bieshu 394, Shanghai 201108, China. ⁵Division of Entomology, Natural History Museum and Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS 66045, USA. ⁶CNRS UMR 6118 Géosciences and OSUR, Université de Rennes 1, 35042 Rennes, France. ⁷Institute of Geology and Palaeontology, Linyi University, Linyi 276000, China. ⁸Department of Earth Sciences, Natural History Museum, London SW7 5BD, UK.

*Corresponding author. Email: bowang@nigpas.ac.cn

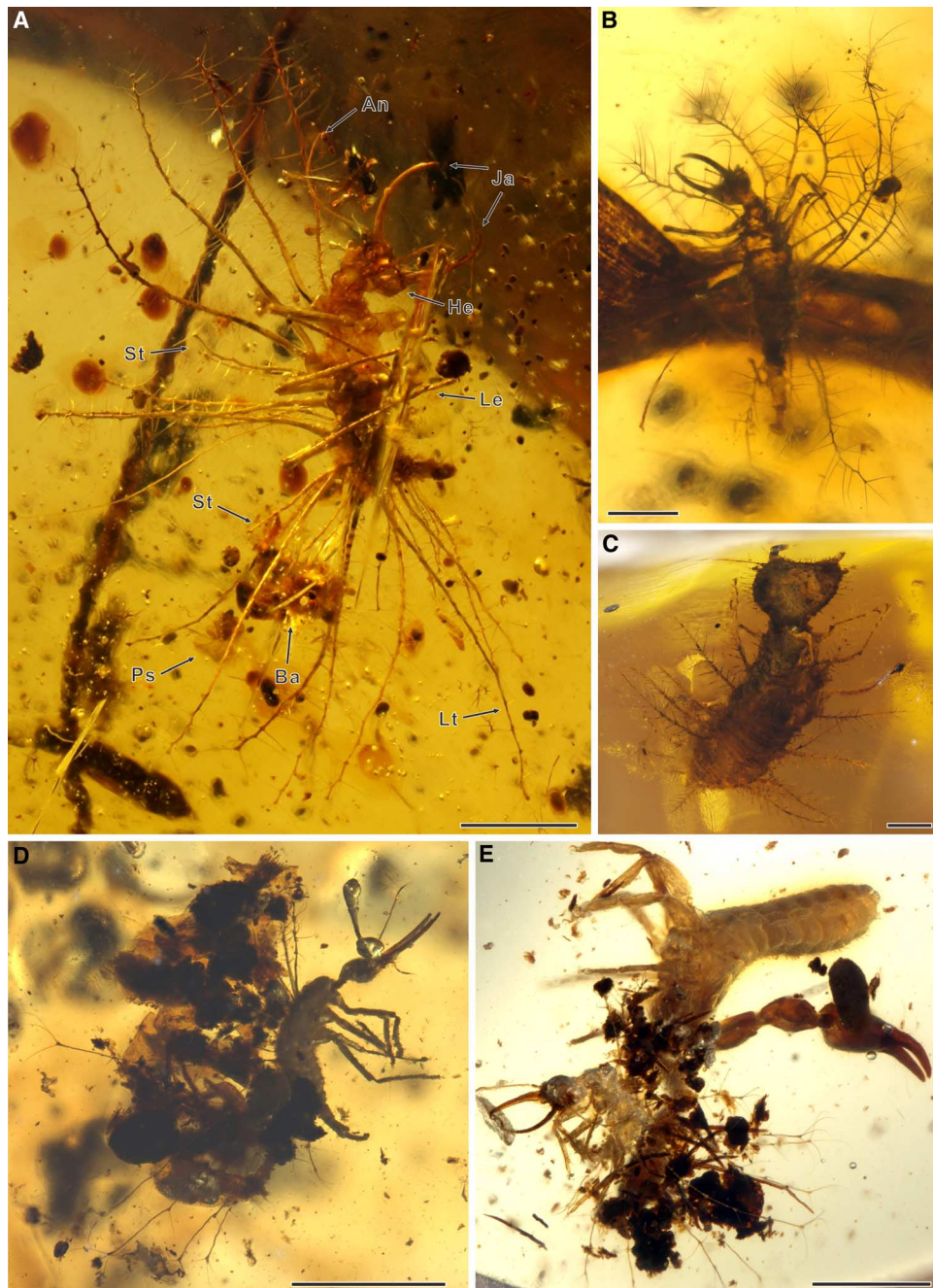


Fig. 1. Chrysopoid larvae from Mid-Cretaceous Burmese amber. (A) Morphotype CI, BA12018. An, antenna; Ba, barklouse; He, head; Ja, jaw; Ps, psyllid; Le, leg; Lt, long tubular tubercle; St, short tubular tubercle. Note the two arthropod exoskeletons (psyllid and barklouse) attached to tubular tubercles. (B) Morphotype CII, L14002, naked. (C) Morphotype CIII, BA12019, naked. (D) Morphotype CII, NIGP164061, camouflaged. (E) Morphotype CII, NIGP164054, camouflaged. Scale bars, 2 mm (A) and 1 mm (B to E).

Extant chrysopoid larvae have sucking jaws, and they inject salivary secretions and then absorb the liquefied tissues and internal fluids of their prey, resulting in an empty exoskeleton (9). The prey of extant chrysopoid larvae are usually sternorrhynchs (such as aphids, coccoids, and psyllids), thrips, and barklice (8), which are frequently found in Burmese amber (10). Some extant larvae carry discarded prey items to provide physical and/or chemical camouflage (11), which is an ex-

treme adaptation that functions as a “wolf-in-sheep’s-clothing” strategy (1); therefore, it is likely that the Burmese fossil is carrying its own prey. The elongate jaws (2.1 mm) and broadened cephalic capsule (1.5 mm) suggest specializations for feeding on large prey, supported by the debris size. Similar to its extant relatives, the larva may also have used its jaws to scoop up material and place it on its back through flexion of its front end (12).

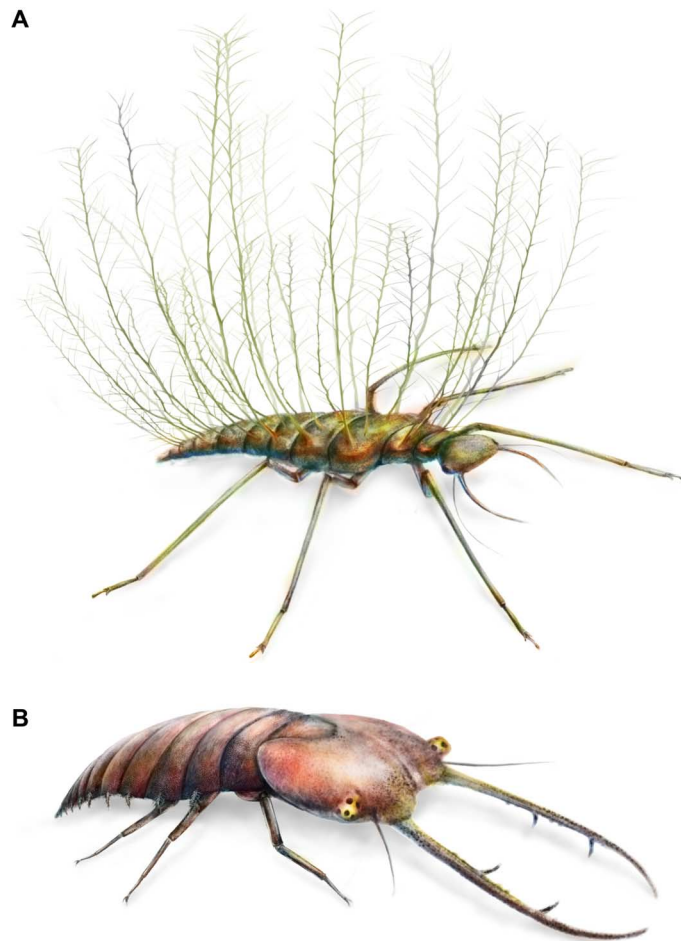


Fig. 2. Reconstructions of chrysopoid and myrmeleontoid larvae from Mid-Cretaceous Burmese amber. (A) Reconstruction of naked chrysopoid larva based on morphotype CI (specimen BA12018). (B) Reconstruction of naked ascalaphid larva based on morphotype MII (12 specimens).

Each of the other 10 Burmese specimens has a flat body and a large head with numerous small lateral spines. Morphotypes CII (nine specimens) and CIII (one specimen; Fig. 1C) have eight pairs of lateral tubular tubercles with setae, although the latter has shorter tubular tubercles. Four specimens of morphotype CII are naked (Fig. 1B), whereas the other five are carrying leaf trichomes of gleicheniacean ferns (figs. S1E and S2A) or other vegetal debris (Fig. 1, D and E), indicating that they are most likely occasional debris carriers. Their tubular tubercles are of equal length, distinctly longer than their body width, and situated on the mesothorax, metathorax, and second to seventh abdominal segments. Such patterns are morphologically divergent from extant forms: The tubular tubercles are often much more developed on the thorax than on the abdomen in extant larvae, and their lengths never exceed their body width (5). In addition to their use as a debris-carrying structure, the unusually elongate tubercles in the fossils may also serve a defensive purpose against predators with an elongate piercing or sucking proboscis, such as true bugs (4). In addition, four naked specimens (morphotype CIV; fig. S1F) from Lebanese amber show tubular tubercles similar to those of Burmese and Spanish debris carriers, revealing that this group had evolved the

camouflaging behavior at least by the Early Cretaceous [130 million years ago (Ma)].

Myrmeleontoid larvae

Twenty additional larvae (19 specimens from Burmese amber and 1 from French amber; see the Supplementary Materials for description) belong to the superfamily Myrmeleontoidea (Fig. 3 and fig. S3). They comprise six morphotypes. Morphotype MI belongs to Nymphidae, which is regarded as the most primitive group of Myrmeleontoidea (13). The other five morphotypes are attributed to Ascalaphidae. The earliest known myrmeleontoid adult is from the Middle Jurassic of China (14), and fossils of the immature stages are extremely scarce, the earliest confirmed occurrences being from the Cenozoic (15–17). The fossils reported here are the earliest record of myrmeleontoid larvae.

The myrmeleontoid larvae display a variety of debris material carried, including sand grains (Fig. 3, B and G), vegetal debris (Fig. 3, A, C, and H), and wood or bark fibers (Fig. 3D). In seven specimens of morphotype MII, debris covers the entire dorsal surface of their bodies, although different individuals vary in the amount and type of debris (table S1). Furthermore, the specimens may only be occasional debris carriers because many morphotype MII specimens in our collection are naked (Fig. 2 and figs. S3, D, G, and H). In extant myrmeleontoid larvae, all of the arboreal species and some ground-dwelling forms remain naked, and only some ground and litter dwellers (for example, *Nymphes* and *Ululodes*) carry much debris on their dorsal surface (18, 19). One camouflaged ascalaphid larva is preserved with syninclusions, including an earwig and a scorpion, which also suggests that the larva lived close to the ground (fig. S4A). Therefore, our fossil myrmeleontoid larvae are most likely ground and litter dwellers, similar to their extant relatives.

These larvae reveal that debris-carrying is an evolutionarily ancient phenomenon in myrmeleontoids, which was well established by at least the Mid-Cretaceous. In these larvae, a thick mat of filamentous and dorsal setae serves to anchor the bits of debris to the dorsal surface, and dense setae on the abdominal scoli-like processes are used to entangle camouflaging materials (fig. S2, C to E). Similar to extant ascalaphid larvae, these insects most likely gathered each particle by the tarsus of the prothoracic leg and deliberately positioned the particles at any dorsal location by virtue of the leg's capacity to rotate 180° or more around its coxal axis (18). However, tarsal or pretarsal specializations associated with this ability are not observed, and particles somehow adhere to the setose dorsal surface of the single tarsomeres (18). Features of this behavior are shared with those of the chrysopoid larvae; however, nymphid larvae used their flexible foretarsi rather than their jaws. Similar to their extant relatives, the fossil myrmeleontoid larvae have large mandibles and the ability to catch prey as large as or even larger than themselves. The dorsoventral compression of the larval body and scoli-like processes at the margins contribute to the stability of the larva during encounters with large prey (18, 19).

Reduviid nymphs

Other unexpected debris carriers in Burmese amber are three reduviid nymphs. The first morphotype is large (length, 18 mm), with a flattened body covered dorsally with vegetal debris (Fig. 4A). The dorsally inserted antennae and long postocular region reveal that this nymph belongs to the higher Reduviidae (20), which are similar to *Holotrichius* in general morphology (see the Supplementary Materials). The other two morphotypes are small (length, 2 mm) and thin nymphs covered

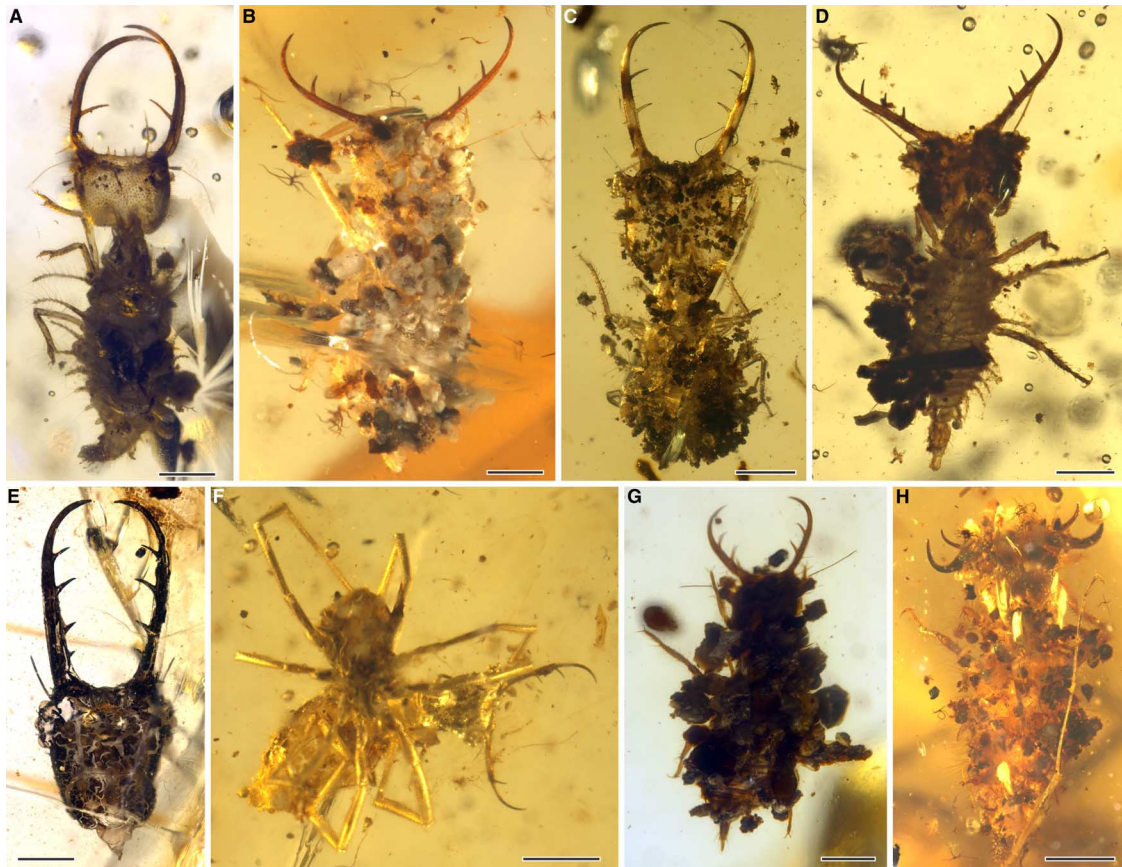


Fig. 3. Myrmeleontoid larvae from Mid-Cretaceous Burmese and French ambers. (A) Morphotype MI, BA12015, dorsal aspect. (B) Morphotype MII, NIGP164050, dorsal aspect. (C) Morphotype MII, BA12011, dorsal aspect. (D) Morphotype MIII, BA12013, dorsal aspect. (E) Morphotype MVI, IGR.ARC-236.3, head. (F) Morphotype MII, NIGP164044, dorsal aspect. Note that a spider is preying on the naked larva. (G) Morphotype MII, BA12017, dorsal aspect. (H) Morphotype MIV, BA12016, dorsal aspect. Scale bars, 0.5 mm (A, B, D, E, and G) and 1 mm (C, F, and H).

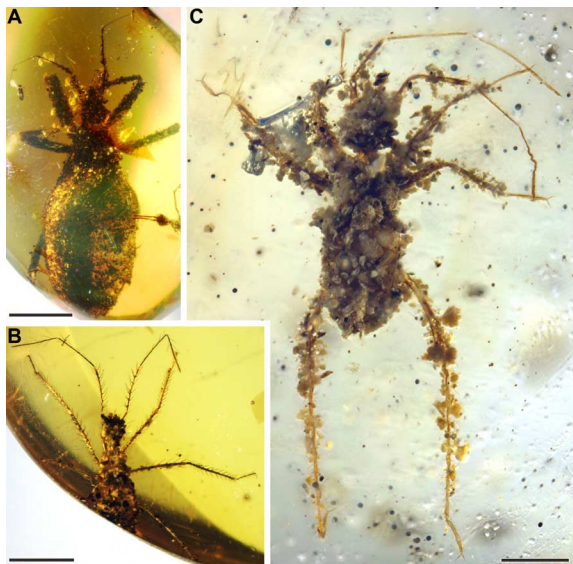


Fig. 4. Reduviid nymphs from Mid-Cretaceous Burmese amber. (A) Morphotype RI, BA12020, dorsal aspect. (B) Morphotype RII, NIGP164052, dorsal aspect. (C) Morphotype RIII, NIGP164053, dorsal aspect. Scale bars, 5 mm (A), 1 mm (B), and 0.5 mm (C).

with soil dust and vegetal debris (Fig. 4, B and C). Both of the fossil nymphs have retained primitive characters, including laterally inserted antennae and a short postocular region, suggesting that they belong to the “phymatine complex” and represent a primitive group of this family (20). Previously, the earliest unequivocal reduviid fossil was known to be from the Early Paleocene of Svalbard, Norway (21); thus, our discovery represents the earliest reduviid record, extending the geological range of this family by approximately 40 My. Moreover, the Mid-Cretaceous appearance of higher groups suggests an unexpected Early Cretaceous diversification of Reduviidae (Fig. 5B), which is much earlier than previously proposed from molecular studies (22).

Only a few extant reduviids (mainly nymphs) gather a variety of debris on their backs, which include dust, vegetal debris, or the sucked-out remains of prey (23). These insects use their hind legs as shovels to gather and load camouflaging material onto their bodies by curving the tarsal segments toward the side of their body (7). It is highly likely that fossil reduviids exhibited a similar covering behavior. Fossil reduviids used anchor setae on the dorsum to adhere dust and debris (fig. S2, G to I), which is a particle capture mechanism that independently evolved in certain reduviids and extant spiders (24–26). Debris-carrying was previously only known in extant higher Reduviidae (22, 24); however, our findings show that such an adaptation is an ancient characteristic that has repeatedly evolved (or has been lost) during the early evolution of this group (Fig. 5B).

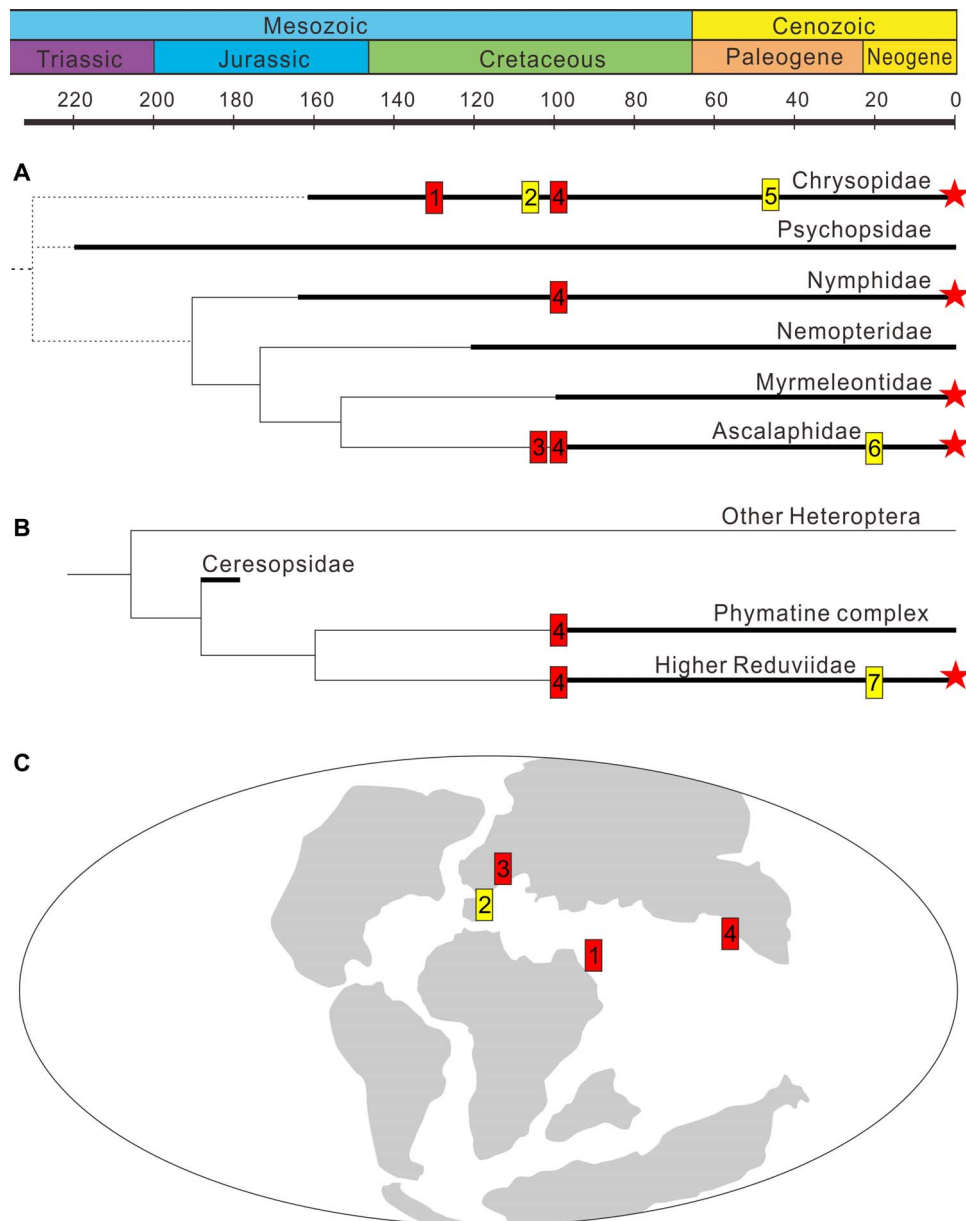


Fig. 5. Evolutionary history and paleodistribution of lacewings and reduviid bugs. (A) Simplified phylogeny of Myrmeleontoidea and related groups (13). (B) Simplified phylogeny of Reduviidae (22). (C) Paleogeographic distribution of Cretaceous camouflaged insects on a late Early Cretaceous (approximately 105 Ma) geographic map (45). Thick lines indicate the known extent of the fossil record; red stars represent extant debris-carrying insects; and red and yellow bars depict the new fossils reported here and known fossils, respectively. Fossil evidence of debris-carrying behavior has been marked with vertical bars: 1, a specimen from Early Cretaceous Lebanese amber (approximately 130 Ma); 2, a specimen from Early Cretaceous Spanish amber (approximately 105 Ma) (4); 3, a specimen from Mid-Cretaceous French amber (approximately 100 Ma); 4, specimens from Mid-Cretaceous Burmese amber (approximately 100 Ma); 5, a specimen from middle Eocene Baltic amber (approximately 45 Ma) (46); 6, a specimen from Dominican amber (approximately 20 Ma) (16); 7, specimens from early Miocene Dominican and Mexican amber (approximately 20 Ma) (8).

DISCUSSION

Our findings reveal that immature reduviids and lacewings acquired the debris-carrying behavioral suite by the Mid-Cretaceous (Fig. 5). These ancient insects have independently evolved this complex trait through multiple pathways, including different debris-anchoring structures (such as cuticular processes and filamentous or anchor setae) on the dorsal surface, as well as various organs and gathering mechanisms

(jaws, forelegs, or hind legs) for harvesting material, and each group has evolved a unique set of modifications for different anatomical plans (Fig. 6). Debris-carrying behavior and its associated morphology in insects show a high degree of evolutionary plasticity and represent a remarkable example of convergent behavioral evolution.

The costs associated with debris-carrying behavior include time spent creating and maintaining the debris pile, interference with




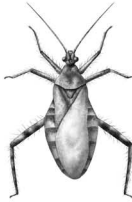
Taxonomy		Morphotype	Reconstruction
Chrysopoidea		Morphotype CI	
		Morphotypes CII	
		Morphotypes CIII	
		Morphotype CIV	
Myrmeleontoidea	Nymphidae	Morphotype MI	
	Ascalaphidae	Morphotype MII	
		Morphotype MIII	
		Morphotype MIV	
		Morphotype MV	
		Morphotype MVI	
Reduviidae		Morphotype RI	
		Morphotype RII	
		Morphotype RIII	

Fig. 6. Diversity and morphotypes of camouflaged insects in Cretaceous Burmese, French, and Lebanese ambers. Each reconstruction represents the first morphotype of each group.

feeding, and reduced movement (2, 3, 7). However, the benefits conferred are twofold: the debris provides camouflage for the nymph when stalking its prey and helps prevent predation on the nymph by acting as a camouflage and as a physical barrier during attack (5, 11). The debris provides visual camouflage (for example, improving background matching) and, possibly, olfactory camouflage (27). In addition, extant lacewing larvae and reduviids are frequently attacked by predaceous insects (28–30), and several potential predators have occurred in the Burmese amber fauna, including spiders (Fig. 3F), predaceous bugs and ants, and vertebrates, such as lizards and birds (10, 31). In one amber specimen, a spider was found preying on a naked nymph larva (Fig. 3F), thus revealing an ancient predator-prey relationship (32, 33). Considering the multitude of contemporaneous predators, it is clear that predation pressures were significant and most likely triggered the

acquisition of complex defense mechanisms. Our discoveries suggest that the immature stages of Mid-Cretaceous lacewings and reduviids were under strong selection for reducing the probability of being detected by predators and/or prey, responding to similar adaptive pressures, as did their Cenozoic counterparts. These findings establish the occurrence of a key behavior in unrelated insects by the Mid-Cretaceous and provide new insight into the development of modern insect camouflage.

Most Burmese lacewing larvae are preserved with dendritic trichomes produced by gleicheniacean ferns (figs. S1A and S4B), and two chrysopid larvae are carrying these trichomes (figs. S1, D and F, and S2A), suggesting that these fossil lacewing larvae are closely associated with the habitats of gleicheniacean ferns (4). Gleicheniaceae are important components of many Mid-Cretaceous floras worldwide and are thought to be among the earliest colonizers after fire events (34). Therefore, the frequent occurrence of gleicheniacean trichomes in our Burmese amber is indicative of fire events during the time when the amber was deposited. This supports a relationship between fire events and the high production of plant resins (4) and highlights the importance of wildfires in Mid-Cretaceous pre-angiospermous ecosystems as well (35).

In conclusion, camouflaged chrysopid larvae were found in Burmese, Spanish, and Lebanese ambers; myrmeleontid larvae in Burmese and French ambers; and camouflaged reduviid nymphs in Burmese amber. The Early Cretaceous to Mid-Cretaceous amber floras were dominated by various gymnosperms and ferns (10, 36, 37). Our findings reveal some unique morphological adaptations unknown in extant insects and suggest that complicated debris-carrying camouflage behaviors were already widespread in three groups of insects by at least the Mid-Cretaceous.

MATERIALS AND METHODS

Materials and deposits

Thirty-five insect specimens from Burmese amber, including 1 adult, 21 camouflaged, and 13 naked or decomposed specimens, are referred to in this study. Burmese amber (amber from northern Myanmar) harbors the most diverse biota in amber from the Cretaceous, and nearly 250 families of arthropods have been reported from this deposit (10). The amber under study was from an amber mine located near Noije Bum Village, Tanaing Town. The U-Pb dating of zircons from the volcanoclastic matrix of the amber gave a maximum age of 98.8 ± 0.6 My (38). However, evidence, including a high degree of roundness of the amber and bivalve borings on the surface, suggests that the amber was most likely reworked before deposition in the volcanoclastic matrix, which implies that the age of the amber should be older than that of the matrix (39). Twenty specimens (NIGP164042 to NIGP164061) are housed in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences. Specimen L14002 is in the amber collection of M. Li; two specimens, H15001 and H15002, are in the amber collection of Y. Huang; two specimens, T15001 and T15002, are in the amber collection of L. Tong; and the remaining Burmese specimens (BA12011 to BA12020) are temporarily housed at the NIGP and will eventually be deposited in the Lingpoge Amber Museum in Shanghai (specimens are available for study by contacting B.W. or F.X.).

The French specimen (IGR.ARC-236.3) is from the Upper Albian (about 100 Ma) of the Font-de-Benon quarry, near the village of Archingeay, Charente-Maritime, France (36). It is deposited in the

Geological Department and Museum of the University of Rennes 1. The Lebanese specimen is from the Sarhmoul outcrop of Caza Aley, Mount Lebanon, and its geological age is estimated to be 130 Ma (37, 40–43). It is deposited in the Natural History Museum of the Lebanese University, Faculty of Sciences II, Fanar, Lebanon.

Imaging

Photographs were taken using a Zeiss SteREO Discovery V16 microscope system and Zen software, and in most instances, incident light and transmitted light were used simultaneously. All of the images were digitally stacked photomicrographic composites of approximately 40 individual focal planes obtained using the free software CombineZP for better illustration of the three-dimensional structures. The figures were prepared with CorelDraw X4 and Adobe Photoshop CS3.

Nomenclature and measurements

The nomenclature used for the description of chrysopoid larvae follows that of Tauber *et al.* (43) and Badano and Pantaleoni (44) for the myrmeleontoid larvae. The lacewing larvae were measured according to the following protocol applied by Badano and Pantaleoni (44) to ascalaphid larvae and antlions: The body length of the larva (BL) was measured from the head (excluding mandibles) to the tip of the abdomen; the length of the head capsule (HL) was measured ventrally from the clypeolabrum to the head insertion with the thorax; the head width (HW) was measured just below the eye tubercles at the point of maximum width; and the length of the mandibles (ML) was measured from the apex to the base. To determine the respective proportions of the head and mouthparts, the head capsule width/head capsule length ratio (HW/HL) and the mandible length/head capsule length ratio (ML/HL) were calculated.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/2/6/e1501918/DC1>

Brief description of fossils

fig. S1. Chrysopoids from Cretaceous Burmese and Lebanese ambers.

fig. S2. Camouflaging structures.

fig. S3. Myrmeleontoid larvae from Mid-Cretaceous Burmese amber.

fig. S4. Myrmeleontoid larvae from Mid-Cretaceous Burmese amber.

table S1. Measurements of 20 myrmeleontoid larvae from Burmese and French ambers.

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