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Behaviors and Interactions
of Insects in Ecosystems
of Mid-Mesozoic
Northeastern China

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Keyword

Yanliao Entomofauna, Jehol Entomofauna, coevolution, fossil insects, paleoentomology

Abstract

During the past 20 years, more than 1,600 species of well-preserved fossil insects, including members of over 270 families within 24 orders, have been described from the Middle Jurassic Yanliao Entomofauna and Early Cretaceous Jehol Entomofauna in Northeastern China. Diversified fossil insects not only document the origin, systematics, and early evolution of many lineages, but also reveal these lineages' behaviors and interactions with coexisting plants, vertebrates, and other insects in their ecosystems. For example, fossil evidence has been documented, for example, regarding insects' feeding and pollination mutualism with gymnosperms; ectoparasitic feeding on blood of vertebrates; camouflage, mimicry of gymnosperm plants, and eyespot warning; sound stridulation for attracting potential mates; and sexual display, mating, egg-laying, and parental care. In this article, we review the diverse taxonomy of mid-Mesozoic insects of Northeastern China and elucidate their behaviors and interactions within their ecosystems, which have impacted their early evolution and development into extant insects.

1. INTRODUCTION

Insects, which make up the largest class of extant animals, have a very long evolutionary history, with the earliest known fossil insects being from the Early Devonian before 400 million years ago (Mya) (20, 60) (see the sidebars titled Geological Periods and Devonian and Carboniferous). *Rybniognatha hirsti* Tillyard from the Middle Devonian of Scotland, first discovered in 1928, is commonly considered to be the earliest record of a winged insect, making members of this species the earliest fliers within the animal kingdom (8). Holometabolous insects appeared during the Late Carboniferous (53). The Mesozoic is considered to be an important era for the evolution of insects (40) in which major lineages of insects first occurred and diversified (see the sidebar titled Triassic, Jurassic, and Cretaceous). Many vertebrates such as birds, dinosaurs, pterosaurs, mammals, reptiles, and fish appeared in the mid-Mesozoic, resulting in new ecosystems and environments with abundant and diverse predators feeding on insects or hosts for insect ectoparasites (101). The origin and rise of angiosperms in the Early Cretaceous undoubtedly created new and different ecosystems that not only offered diverse and rich food sources, but also changed the body structures and habitats of insects (41). In addition, that warm and moist climate worldwide in the Mesozoic made these ecosystems suitable for rapid diversification of insects and resulted in the development of clades of mid-Mesozoic insects similar to early members of extant insect orders.

As a key focus in studying paleoentomology about the origins of major clades of living insects, many localities around the world with well-preserved Mesozoic insect fossils have been studied and

GEOLOGICAL PERIODS

Geological periods, also called geologic time scales, were demarcated by the International Commission of Stratigraphy to mark important boundary times of evolution for creatures and have been adopted by geologists and paleontologists. The Earth's history is divided into eras and further subdivided into geological periods, such as the Jurassic and Cretaceous.

DEVONIAN AND CARBONIFEROUS

The Devonian and Carboniferous are two adjacent geological periods. According to the latest version of the geological periods published by the International Commission on Stratigraphy, the Devonian consists of the Early Devonian (419.2 Mya to 393.3 Mya), Middle Devonian (393.3 Mya to 382.7 Mya), and Late Devonian (382.7 Mya to 358.9 Mya); the Carboniferous lasted from 358.9 Mya to 298.9 Mya.

TRIASSIC, JURASSIC, AND CRETACEOUS

The Triassic, Jurassic, and Cretaceous are the three geological periods that constitute the Mesozoic Era. In geological time, the Triassic covers the period from 251.9 Mya to 201.3 Mya, the Jurassic covers that from 201.3 Mya to 145.0 Mya, and the Cretaceous covers that from 145.0 Mya to 66.0 Mya. The Jurassic is further divided into the Early Jurassic (201.3 Mya to 174.1 Mya), Middle Jurassic (174.1 Mya to 163.5 Mya), and Late Jurassic (163.5 Mya to 145.0 Mya), while the Cretaceous is divided into the Early Cretaceous (145.0 Mya to 100.5 Mya) and Late Cretaceous (100.5 Mya to 66.0 Mya). These are rough boundary times of these periods; the most accurate times are always updated on the website of the International Commission on Stratigraphy (<https://stratigraphy.org/>).

PALEOENTOMOLOGY

Paleoentomology, as an entomological and paleontological discipline, focuses on all aspects of fossil insects, especially their phylogeny and evolution, based on fossil materials discovered from different geological times.

STRATIGRAPHY

Stratigraphy, in geology, refers to the rock layers that are gradually formed by sedimentary or volcanic rocks during the changes of geological activities. Stratigraphy is always associated with geological time via accurate dating.

reported (20, 52, 60) (see the sidebar titled Paleoentomology). The insect-bearing stratigraphic occurrence in the mid-Mesozoic of Northeastern China, as a part of the Asian Continent, was formed in the Late Triassic and has yielded abundant insect fossils, especially in the numerous horizons of the Jurassic and Cretaceous (see the sidebar titled Stratigraphy). Studies of the diverse fossil insects from the Yanliao area of China, including Beijing, northern Hebei province, western Liaoning province, southeastern Inner Mongolia, and the Laiyang Basin of Shandong province, have been more comprehensive and with greater depth (see 26, 64, 97). Many works have documented the Mesozoic terrestrial sediments in Northeastern China (see 10, 63, 101). In the different fossil assemblages and geological periods, most or nearly all of the described fossil organisms are mainly from two major ecosystems: the Yanliao Biota of the Middle Jurassic (approximately 165 Mya) (91) and the Jehol Biota of the Early Cretaceous (approximately 125 Mya) (103). The most important locality of the Yanliao Biota, the Daohugou area of Inner Mongolia, might have been a shallow lacustrine basin consisting of several different microenvironments with a humid and warm climate (79), yielding abundant and diverse vegetation (76). In contrast, the Jehol Biota of the Early Cretaceous experienced a relatively cool and humid climate, as suggested by the fossil evidence (103), even though many studies have shown that the Early Cretaceous was, on the whole, an extremely warm period with higher atmospheric CO₂ levels around the world. In this article, we review important findings of fossil insects from the Yanliao Biota and the Jehol Biota to highlight the diverse systematics and early evolution of insects; their behaviors; and their interactions with plants, vertebrates, and other insects in these two ecosystems. For convenience, we used Yanliao Entomofauna and Jehol Entomofauna to refer to the insect faunas from the Yanliao Biota and the Jehol Biota, respectively.

2. HISTORY OF PALEOENTOMOLOGY IN CHINA

Dr. Amadeus Grabau, who graduated from Harvard University and later worked as a Professor in Peking University, described four fossil insects in 1923 (19) in the first paper on Chinese paleoentomology, and he named the Jehol Biota for the Early Cretaceous fossils from Northeastern China. Dr. Chi Ping, the first Chinese scholar to study insect fossils, received a Ph.D. in entomology from Cornell University in 1918. From 1928 to 1935, Dr. Ping reported 35 species in 32 genera of fossil insects from China (56), initiating an increase in paleoentomological research in China. After a long gap, Dr. Youchong Hong began to specialize in fossil insects in 1958, publishing 152 papers and 6 monographs and collaborating on 17 additional monographs (see 31), including the book *Amber Insects of China* (23), summarizing the amber research in China. From

1960 to the present, Dr. Qibin Lin has reported fossil insects from southern China in over 60 papers and an important monograph titled *Early Mesozoic Fossil Insect from South China* (48). Dr. Hong and Dr. Lin, besides conducting systematics studies for insect fossils from many localities in China, have guided and trained many subsequent Chinese paleoentomologists, including Junfeng Zhang, Dong Ren, Haichun Zhang, and Di-ying Huang. Since 2005, Chinese researchers have carried out many important and detailed studies on fossil insects from Northeastern China and published many peer-reviewed academic papers and several books (see 26, 64, 65, 97).

3. FOSSIL INSECTS FROM THE YANLIAO AND JEHO ENTOMOFAUNAS OF CHINA

3.1. Coexisting Animals and Plants

The Yanliao and Jehol Biotas are renowned for yielding abundant fossil vertebrates (102), insects (64), and plants (75); these coexisting organisms supported and maintained well-balanced ecosystems from 165 to 125 Mya. Various plants, such as mosses, ferns, cycads, ginkgos, conifers, and the basal forms of the angiosperm plants *Archaeoartocarya liaoningensis* (73) and *Archaeoartocarya sinensis* (74), provided the main food sources and living environments for insects. Carnivorous vertebrates, the top predators of the food chain; spiders (68); and some other insects fed on insects. Examples of carnivorous vertebrates included feathered dinosaurs such as *Sinosauropteryx prima*, the first dinosaur reported with dense primitive protofeathers (35); *Microraptor gui*, the first dinosaur reported to possess feathers on its forelimbs, hind limbs, and tail (92); pterosaurs such as *Jeholopterus ningchengensis*, which had a skull shape similar to that of a frog and hair-like structures on its body (83); birds such as *Confuciusornis sanctus* (25) and *Dingavis longimaxilla* (54); mammals such as *Jeholodens jenkinsi* (36) and *Juramaia sinensis* (50); and reptiles such as *Monjurosuchus splendens* (11). Insects evolved several strategies to avoid predation, such as camouflage with patches, markings, spots, or stripes on the wings; mimicry of pinnate leaves or ginkgo leaves; and eyespot warning. In addition, ectoparasitic basal fleas and blood-feeding true bugs have been documented to feed on host feathered or haired vertebrates.

3.2. Diversity of Insects in Mid-Mesozoic Northeastern China

To date, more than 1,600 species of well-preserved fossil insects, including members of over 270 families within 24 orders, have been described from the Middle Jurassic Yanliao Entomofauna and the Early Cretaceous Jehol Entomofauna of Northeastern China; these discoveries have enhanced our understanding of the morphology, taxonomy, systematics, and evolution of insects. Although adult mayflies with fully developed wings are very rare in fossils, there is a high number of Ephemeroptera (mayfly) fossil nymph specimens in the Jehol Entomofauna. The larva and imago of the mayfly *Ephemeroptera trisetalis*, the conchostracan *Eosetheria middendorffii*, and the fish *Lycoptera jobolensis* have been considered the three representative species of the Jehol Biota (22). However, in 2007, Huang et al. (32) examined imago specimens, previously classified as *E. trisetalis*, from the Jehol Entomofauna and described them as *Epicharmeropsis hexavenulosus* and *Epicharmeropsis quadrivenulosus*; they argue that these species should be the new representative insects for the Jehol Biota.

The orders with the highest numbers of species represented in the fossil record are Coleoptera (beetles), Hymenoptera (sawflies and wasps), Diptera (flies), Hemiptera (cicadas, hoppers, and true bugs), and Neuroptera (lacewings) (**Figure 1**). Among extant insects, the first four of these are still among the most species-diverse orders. In contrast, only 18 species of Lepidoptera have been reported from the Mesozoic of Northeastern China (29, 99); Lepidoptera diversified significantly

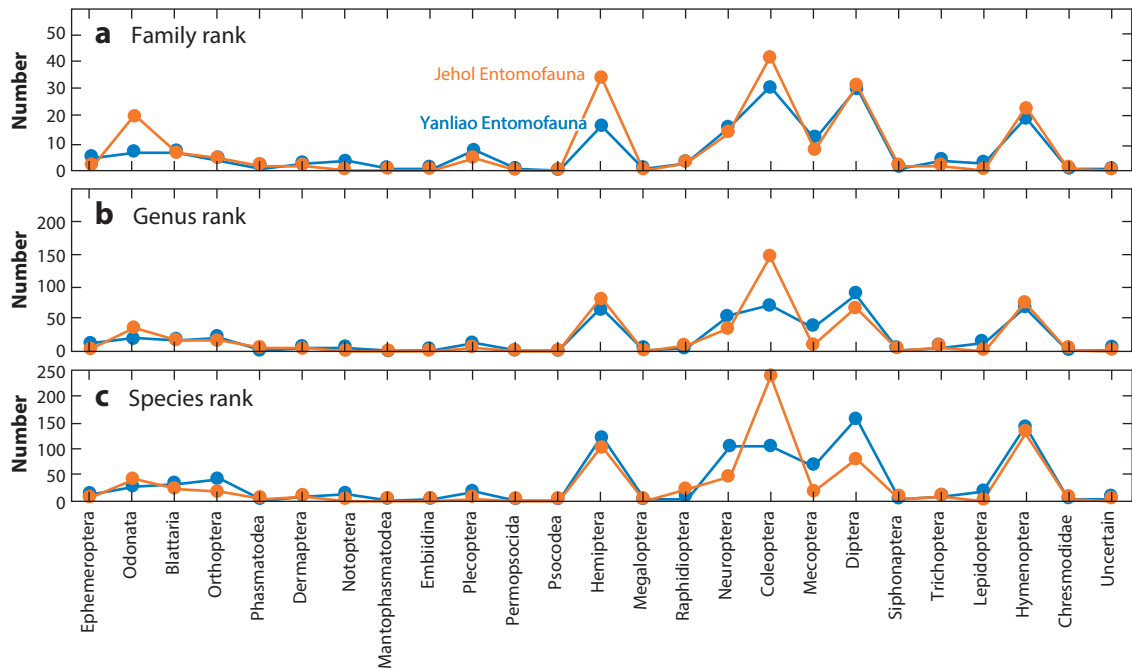


Figure 1

Quantity variance of the known fossil insect groups from the Yanliao Entomofauna and the Jehol Entomofauna in number of (a) families, (b) genera, and (c) species.

after the Cretaceous, likely because of the rapid expansion of flowering plants in the Late Cretaceous. The clades of Hymenoptera from the Mesozoic of China showed rich species diversity. The largest fossil sawfly is an example of *Hoplityloda duolunica* (Praesiricidae) from the Jehol Entomofauna, with an estimated body length of >55 mm and a wingspan of >92 mm (15). The largest fossil wasp is *Megapelecinus changi*, with a body length of 50.9 mm, similar to those of the extant female peleciniids (71). Wang et al. (80) proposed that the number of forewing nygmata gradually decreased during evolution of sawflies. In addition, Li et al. (45) identified three typical but different propodeal-metasomal articulations (wasp waist) within Ephialtitidae and suggested three different pathways of the transformation to the propodeal-metasomal articulations in basal Apocrita. Over 260 species of fossil Diptera have been described from the Mesozoic in China; Huang et al. (28) analyzed 10 specimens of Strashilidae from the Yanliao Entomofauna and confirmed that strashilids are highly specialized flies and relict members of the aquatic fly family Nymphomyiidae (59). To understand the systematic positions of known extinct groups of Neuroptera, Yang et al. (93) conducted a phylogenetic analysis to reconstruct the phylogeny of Neuroptera, covering 30 extant and extinct families based on both morphological and molecular data.

Five orders, Odonata (dragonflies and damselflies), Blattaria (cockroaches), Orthoptera (grasshoppers and katyids), Plecoptera (stoneflies), and Mecoptera (scorpionflies), have moderately high numbers of described species (**Figure 1**). A member of an extinct group of Odonata, *Hsiufua chaoi*, from the Yanliao Entomofauna was considered to be the largest known fossil dragonfly in China; it has a forewing length of 107.6 mm (98). Some clades of living cockroaches, such as the oldest-known representative of Blattidae, have been reported from the Jehol Entomofauna (19). Fuziidae is an indigenous Chinese family including six species within four genera that can

be distinguished by the male's elongated body and forceps of earwig-like cerci (89). The diverse mecopterans from Mesozoic China not only included some relict families such as Eomeropidae and Choristopsychidae, but also demonstrated the significance of antennal (14) and mouthpart modifications (62) and even of foliaceous mimicry (85).

Four orders, Isoptera (termites), Mantophasmatodea (rock crawlers), Embiodea (webspinners), and Psocoptera (barklice and booklice), are extremely rare in the fossil record (**Figure 1**). Seven species of termites in six genera, reported from the Cretaceous Fuxin Entomofauna, represent the earliest documented termites in China (63). The earliest known rock crawler (Mantophasmatodea), from the Yanliao Entomofauna, shares apomorphic characters with Cenozoic and extant Mantophasmatodea (30). Although only two living apterous ice crawlers (Grylloblattodea), *Gal-loisiana sinensis* and *Grylloblattella cheni*, have been described in China (1), 12 fossil species in five extinct families of Grylloblattodea, with two pairs of fully developed wings, have been reported from the Yanliao Entomofauna (4).

As shown in **Figure 1**, Grylloblattodea, Mantophasmatodea, Embiodea, Psocoptera, Megaloptera, and Lepidoptera have to date only been found in the Yanliao Entomofauna, and not in the Jehol Entomofauna. Specimens of *Jurochauliodes* and *Eochauliodes* (Megaloptera) described from the Yanliao Entomofauna are the oldest evidence of Corydalidae (49). In contrast, Isoptera have been found in the Jehol Entomofauna, but not in the Yanliao Entomofauna. Comparing the quantities between the Yanliao Entomofauna to the Jehol Entomofauna, the species counts of Odonata, Hemiptera, Raphidioptera, Coleoptera, and Hymenoptera have apparently increased at the levels of families (**Figure 1a**), genera (**Figure 1b**), and species (**Figure 1c**). However, the taxonomic varieties of Ephemeroptera, Blattaria, Orthoptera, Plecoptera, Neuroptera, and Mecoptera have distinctly decreased from the Yanliao Entomofauna to the Jehol Entomofauna. The differences might have been caused by changes in climates and environments from the Middle Jurassic to the Early Cretaceous in Northeastern China. Morphological changes and evolutionary developments within insect groups were other important influencing factors. It is worth mentioning that extant earwigs have robust cercal forceps for defending, feeding, mating, and folding the hind wings. However, all described earwigs from the Jurassic possessed very long and multisegmented cerci, rather than forceps (7), including *Perissoderma triangulum* of Archidermaptera from the Yanliao Entomofauna; in contrast, *Cylindropygia falcate* of Neodermaptera from the Jehol Entomofauna had a clearly curved forceps. These findings suggest that the long and segmented cerci in the Middle Jurassic earwigs might have evolved to the stout terminal forceps without segmentation in extant groups (90). In addition, a clade of enigmatic and extinct insects, Chresmodidae, found in both the Yanliao and Jehol Entomofaunas, are theorized to have been capable of walking on the water surface by using their extremely long legs with dense and short setae, similar to water striders, although the phylogenetic position of this clade is still contentious (100).

4. INSECT BEHAVIORS AND INTERACTIONS WITH COEXISTING CREATURES FROM THE YANLIAO AND JEHOL ENTOMOFAUNAS

4.1. Insect Feeding

Due to lack of fossil evidence, behaviors and modes of insects feeding in deep time are poorly known. Based on the well-preserved fossil materials from the mid-Mesozoic of China, we now understand more about the various modes of insect feeding during that time.

4.1.1. Herbivores: feeding on plants. It is difficult to obtain direct fossil evidence of insects' feeding behaviors; however, their feeding modes or food intakes can sometimes be identified

by their mouthpart types or abdominal contents. Many fossil cicadas, hoppers, and true bugs (Hemiptera) (**Figure 2a**), possessing a long rostrum used to suck plant fluid or juice (3, 84), have been described from the Yanliao and Jehol Entomofaunas. Fossil species of Xyelidae (**Figure 2b**) from the mid-Mesozoic in China are believed to have fed on pollens or leaves of deciduous trees (12). Moreover, fossil plants preserve different damage caused by the feeding or egg-laying of various insects (**Figure 2c**), and such damage types (DTs) are categorized using the shape, size, and structures of damage described in detail, facilitating identifying and searching (42) (see the sidebar titled Damage Types). Herbivorous insect behaviors can be inferred by observing DTs on fossil plants. Wang et al. (85) reported piercing and sucking damage (DT48) and margin feeding (DT12) on Ginkgoite leaves of *Yimaia capituliformis* from the Yanliao Biota. Ding et al. (5, 6) examined more than 1,000 specimens of plants from the Yanliao and Jehol Biotas and documented 23 distinctive DTs. These DTs were assigned to five functional feeding groups of external foliage feedings possibly caused by grasshoppers with chewing mandibles (**Figure 2d**) and piercing and sucking possibly caused by cicadas and hoppers.

4.1.2. Pollinators: feeding on pollination drops before angiosperms. The relationships among extant flowers and insect pollinators have been well-documented (57). Based on several flower-associated Brachycera fossils from the Jehol Entomofauna, Ren (61) proposed that angiosperms occurred in the Early Cretaceous of the Jehol Biota (**Figure 2b,i**), which was confirmed later by the direct evidence of angiosperm plant fossils from the same stratum (73). Furthermore, three clades of siphon-bearing, fluid-feeding scorpionflies in the Yanliao Entomofauna revealed a probable pollination mode before angiosperms (62). These fossil scorpionflies (**Figure 2e-g**) of Aneuretopsychnina have elongate siphonate (tubular) proboscides bearing hairy and obliquely ridged surfaces correlating with the hidden pollen-receptive areas on the ovulate organs of coexisting seed ferns and/or conifers. These scorpionflies might have fed on gymnosperm pollination drops or ovular secretions and likely engaged in pollination mutualisms with extinct gymnosperms during the mid-Mesozoic. This pollination mode adopted by scorpionflies is clearly 65 to 25 million years ahead of the pollination by nectar-feeding insects, such as flies, moths, and bees, of angiosperms. In addition, four major clades (**Figure 2j**) of Kalligrammatidae of Neuroptera from the Yanliao and Jehol Entomofaunas also convergently evolved elongate tubular proboscides derived from an ancestral chewing mandibulate state, which might be suitable to probe the larger, sturdier reproductive structures of contemporaneous Bennettitales and cycad-like plants (43).

4.1.3. Predators: preying on other insects. Mantispidae, also known as mantidflies or mantisflies, are characterized by their raptorial forelegs and elongate pronotum. Four species within three genera of an extinct clade of Mantispidae have been described from the Jehol and Yanliao Entomofaunas; these are the first representatives of mantisflies with specialized raptorial forelegs (**Figure 2m**) (34). Makarkin et al. (51) reported a neuropteran (**Figure 2n**) in Dipteromantispidae from the Jehol Entomofauna with well-developed forewings but reduced hind wings. This specimen also had raptorial forelegs, which might have been used for preying on other insects. Other insects from the Yanliao and Jehol Entomofaunas are also considered to be predators, e.g., dragonflies (**Figure 2k**), Raphidiomimidae (**Figure 2l**), the extinct clade of Blattaria (47), and hangingflies including Bittacidae and Cimbrophlebiidae (95).

4.1.4. Ectoparasites: feeding on blood. In 2012, several giant basal fleas assigned to Pseudopulicidae were reported from the Middle Jurassic and Early Cretaceous of Northeastern China (18, 27). Pseudopulicids (**Figure 2o**) share several characteristics with living fleas, e.g., setae and scattered ctenidia on the body, particularly on the metatibiae; a small wingless thorax; a long and

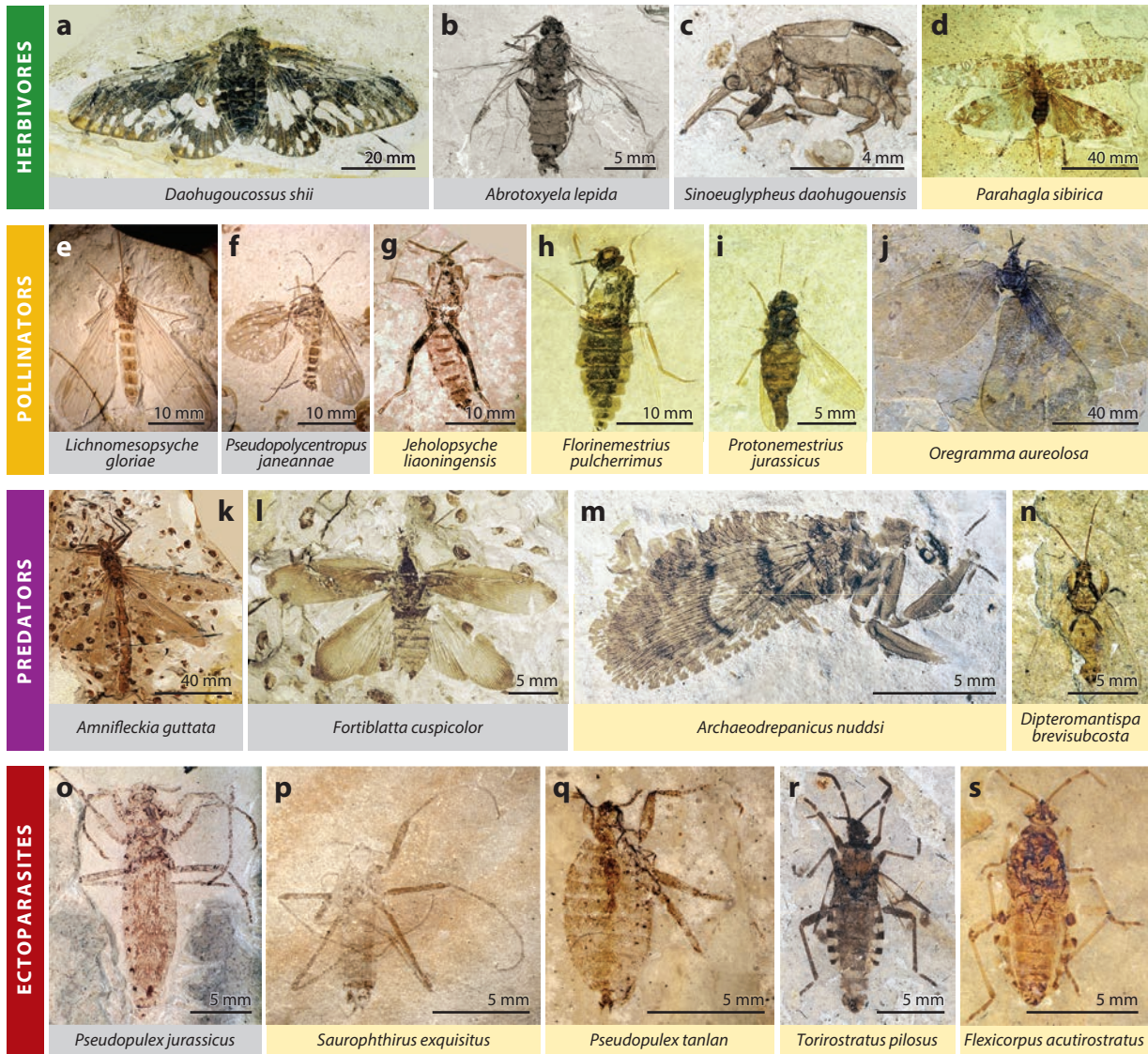


Figure 2

Diverse feeding behaviors in the mid-Mesozoic insects from Northeastern China. Representative species of (a–d) herbivores, (e–j) pollinators, (k–n) predators, and (o–s) ectoparasites from the Yanliao Entomofauna (gray background) and Jehol Entomofauna (yellow background). (a) *Daobugoucossus shii* (Homoptera). (b) *Abrotoxyela lepida* (Hymenoptera). (c) *Sinoeuglypheus daobugouensis* (Coleoptera). (d) *Parahagla sibirica* (Orthoptera). (e) *Lichnomesopsyche gloriae* (Mecoptera). (f) *Pseudopolycentropus janeanae* (Mecoptera). (g) *Jeholopsyche liaoningensis* (Mecoptera). (h) *Florinemestrius pulcherrimus* (Diptera). (i) *Protonemestrius jurassicus* (Diptera). (j) *Oregramma aureolosa* (Neuroptera). (k) *Amnifleckia guttata* (Odonata). (l) *Fortibratta cuspicolor* (Blattaria). (m) *Archaeodrepanicus nuddsi* (Neuroptera). (n) *Dipteromantispia brevisubcosta* (Neuroptera). (o) *Pseudopulex jurassicus* (Siphonaptera). (p) *Saurophthirus exquisitus* (Siphonaptera). (q) *Pseudopulex tanlan* (Siphonaptera). (r) *Torirostratus pilosus* (Heteroptera). (s) *Flexicorpus acutirostratus* (Heteroptera).

DAMAGE TYPES

Damage types (DTs) were proposed by Dr. Conrad Labandeira and his colleagues for describing and defining the shapes and types of damage on a plant caused by insects' chewing, sucking, egg-laying, etc. Each cause of plant damage creates unique shapes and structures and is named and described by a number, e.g., DT1, DT2, etc. Over 350 plant DTs have been described and collected in an updated list (42).

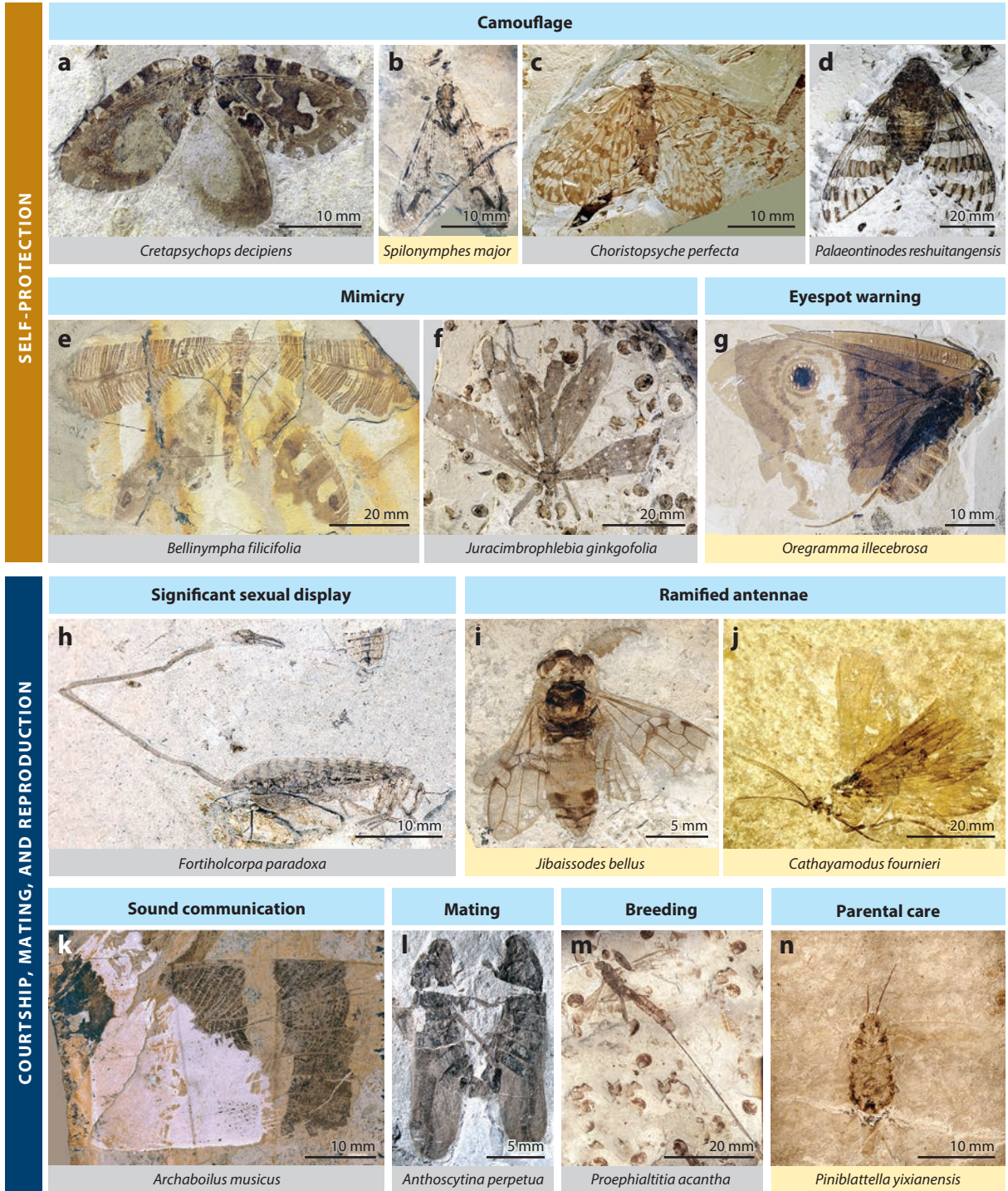
serrate piercing-suctorial siphon; and a pygidium with sensilla. It is thought that pseudopulicids might have lived on and sucked the blood of contemporaneous feathered dinosaurs, pterosaurs, or mammals. Gao et al. (16) described *Saurophthirus exquisitus* (**Figure 2p**) of Saurophthiridae in Siphonaptera from the Jehol Entomofauna. Saurophthirids possessed rows of short and stiff bristles on the thorax, partly retracted male external genitals, small body size, and short piercing-sucking stylet mouthparts and are supposed to have made up a transitional clade closer to crown fleas than to Pseudopulicidae (16). A specimen of *Pseudopulex tanlan* (**Figure 2q**) from the Jehol Entomofauna has an extremely distended abdomen, suggesting that it might have consumed a last blood meal before demise (17).

Yao et al. (96) reported two true bugs, *Torirostratus pilosus* (**Figure 2r**) and *Flexicorpus acutirostratus* (**Figure 2s**) of Torirostratidae in Hemiptera, based on 397 specimens from the Jehol Entomofauna; these bugs possess stout rostra with the basal segment swollen and in a laterally stretched orientation or extended anteriorly, suggesting predaceous or hematophagous lifestyles. For blood-feeding insects, iron (Fe) is incorporated into their tissues and might be preserved during the fossilization process. Analyzing the geochemical composition of Fe, Yao et al. found that *T. pilosus* and *F. acutirostratus* had distinctly higher Fe concentrations than those of control groups, further suggesting that these new torirostratids might have fed on the blood of coexisting mammals, birds, or feathered dinosaurs.

4.2. Self-Protection: Camouflage, Mimicry, or Eyespot Warning

Many mid-Mesozoic fossil insects from China adopted different strategies to avoid predation by potential predators, including camouflage, mimicry, and eyespot warning, which are still widespread in extant insects.

4.2.1. Camouflage. Camouflage appeared very early in some insect groups, such as cockroaches or archaeorthopterans, back to the Carboniferous to avoid predation (33). There are many fossil insects of Odonata, Orthoptera, Hemiptera, Neuroptera, and Mecoptera from the Yanliao and Jehol Entomofaunas possessing various markings on their wings for camouflage. For example, *Cretapsychops decipiens* (**Figure 3a**) of Neuroptera (55) and *Daobugoucosus shii* (84) of Hemiptera from the Yanliao Entomofauna have irregular splotches and markings on their entire wings to imitate the unordered patterns on surrounding tree bark or branches. There are three other types of camouflage for displaying irregular and dispersed dark or light markings: distributing on part of the margin and/or center of the wing (70) (**Figure 3b**), forming dispersed large or small dark spots, and exhibiting dispersed small or large light spots surrounded by small dark spots (58) (**Figure 3c**). Two other types of disruptive camouflage are regular transverse stripes of light and dark bands, which have been found in some extinct lacewings in Grammolingiidae (69) and extinct cicadas in Palaeontinidae (**Figure 3d**), and longitudinal stripes of light and dark bands, which have been found in extinct lacewings in Osmylidae (38).



(Caption appears on following page)

Figure 3 (Figure appears on preceding page)

Insect behaviors and interactions with other creatures in the mid-Mesozoic of Northeastern China. Representative species demonstrating self-protection, courtship, mating, and reproduction from the Yanliao Entomofauna (gray background) and Jehol Entomofauna (yellow background) are shown. (a) *Cretapsychops decipiens* (Neuroptera). (b) *Spilonymphes major* (Neuroptera). (c) *Cboristopsyche perfecta* (Mecoptera). (d) *Palaeontinodes reshuitangensis* (Homoptera). (e) *Bellinympha filicifolia* (Neuroptera). (f) *Juracimbrophebia ginkgofolia* (Mecoptera). (g) *Oregramma illecebrosa* (Neuroptera). (h) *Fortiholcorpa paradoxa* (Mecoptera). (i) *Jibaissodes bellus* (Hymenoptera). (j) *Cathayamodus fourneri* (Trichoptera). (k) *Archaboilus musicus* (Orthoptera). (l) *Anthoscytina perpetua* (Homoptera). (m) *Proepihaltitia acantha* (Hymenoptera). (n) *Piniblattella yixianensis* (Blattaria).

4.2.2. Mimicry. Bates (see 9) proposed the concept of mimicry in 1862, and it was considered to be the most important evidence of natural selection since Darwin. Many insects have developed mimicry of the leaves of angiosperms, but the origins of leaf mimicry are unclear due to sparse fossil evidence. Wedmann et al. (88) described the oldest known leaf insect, *Eophyllum messeleensis*, from 47 Mya Eocene of Germany, which has a clear foliaceous appearance similar to extant male leaf insects (Phasmatodea). Since mimicry of angiosperms by insects should have developed after the radiation of flowering plants, it was generally accepted that the appearance of leaf mimesis within insects did not appear earlier than the Early Cretaceous. However, *Bellinympha filicifolia* (Figure 3e) and *Bellinympha dancei*, large lacewings from the Yanliao Entomofauna, show an almost perfect imitation of pinnate leaves of Jurassic Cycadales and Bennettitales (86) and push the origin of leaf mimicry by insects back to the Middle Jurassic of 165 Mya. Wang et al. (85) reported another case of leaf mimicry and mutualism between hangingflies and multilobed leaves of the ginkgo plant. *Juracimbrophebia ginkgofolia* (Figure 3f) (Cimbrophebiidae) possessed significant wing and body structures mimicking leaves of *Y. capituliformis* to avoid predation; these insects preyed on phytophagous insects and provided antiherbivore functions for their ginkgo plant hosts. More interestingly, the associations between Cimbrophebiidae and ginkgoaleans lasted from the Middle Jurassic to the Early Eocene, according to a phylogenetic analysis (85). These two cases of leaf mimesis by lacewings and hangingflies from the Yanliao Entomofauna shed new lights on insect behaviors and predation avoidance before the origins of angiosperm plants.

4.2.3. Eyespot warning. Extant lepidopterans possess the most dramatic and highest varieties of eyespots on their wings of all insects; however, Mesozoic moths lack any eyespot structures. Although there are no conclusions about their exact function, eyespots on the wing of insects are generally considered to be a mechanism of antipredation. Kalligrammatids, an extinct family of Neuroptera documented from the Middle Jurassic to Early Cretaceous, have clear eyespot structures (94) (Figure 3g). Labandeira et al. (43) described six different types of forewing eyespots or spots found on most species of four derived kalligrammatid clades. Based on comparative analyses of these eyespot features and phylogenetic relationships among kalligrammatids, Labandeira et al. proposed that butterflies evolved convergently with these kalligrammatid lacewings, as demonstrated by several common morphological characters, such as wing eyespots, wing scales, elongate tubular proboscides, and similar feeding styles.

4.3. Courtship, Mating, and Reproduction by Insects

Several studies based on the morphological characteristics of well-preserved fossil insects from mid-Mesozoic China shed new light on the evolutionary development of courtship, mating, and reproduction by insects.

4.3.1. Significant sexual display. Many studies have documented sexual display, sexual competition, and sexual selection of living insects. However, it is difficult to elucidate the early

evolution of insects due to sparse records of well-preserved fossils. Three male mecopterans reported from the Yanliao Entomofauna, two assigned to the family of *Incertae sedis* and one of Holcorpidae, have extremely long sixth, seventh, and eighth abdominal segments and enlarged robust genitalia (44, 82) (**Figure 3h**). Such exaggerated male genital organs were supposed to enhance sexual display and sexual selection, since the females possessed an abdomen similar to those of other mecopterans (78). Similar male characteristics are present in some extant *Leptopanorpa* of Panorpidae, which suggests that the advantages to sexual display and/or sexual selection of having extremely elongated male organs outweigh the negative impact of bulky body and poor mobility in the evolutionary process of some clades of Mecoptera.

4.3.2. Ramified antennae. Most insects detect environmental cues and/or communicate with other insects via sensory organs on their antennae (77). Although ramified (multibranching) antennae are common in extant insects and considered to have evolved many times within several groups of insects, they were documented rarely during or before the Early Cretaceous. Three fossil insects, attributed to three orders [Trichoptera (**Figure 3j**), Mecoptera, and Hymenoptera], were described as possessing multibranching antennae from the Jehol Entomofauna (14). All extant scorpionflies and caddisflies have filiform antennae, and multibranching antennae have been reported for these two orders of insects. Although some extant sawflies (Hymenoptera) have pectinate antennae, there are at least three types of multibranching antennae for fossil sawflies, i.e., bilabellate in *Atefia rasnitsyni* (39), feathery in *Jibaissodes bellus* (**Figure 3i**) (14), and pectinate in *Jibaissodes peichenae* (87). Multibranching antennae are important for insect communication; nevertheless, such multibranching antennae never became common features for all insects and are only found in some clades of Lepidoptera, Coleoptera, Diptera, and Hymenoptera.

4.3.3. Sound communication for mate searching. Reconstructions of the acoustic communication of extinct organisms are challenging, since sound-producing organs of vertebrates or insects are rarely preserved in fossils. Some extant insects use stridulation, rubbing a row of finely ridged structures against a plectrum on the other wing, to produce species-specific calling sounds. Gu et al. (21) described a nocturnal katydid fossil from the Yanliao Entomofauna, *Archaboilus musicus* (**Figure 3k**), with well-preserved stridulatory structures on its wings. Based on these structures, Gu et al. reconstructed the song that *A. musicus* produced. The musical pure-tone calls, at a low frequency of 6.4 kHz, were well-adapted to long-distance communication in sparse forest vegetation dominated by coniferous trees and giant ferns. This reconstruction of paleontological enunciation based on accurate physical structure and rigorous mathematical calculations is undoubtedly an important step in paleontological studies, adding accurate acoustic information to our knowledge about the fauna of the Middle Jurassic (37) and pushing us to find more fossil insects to better understand the evolution of insect communications (67).

4.3.4. Mating. Although male or female genitalia have been described in detail for some compression fossil insects of mid-Mesozoic China (4), only one indication of insect mating behaviors, a pair of well-preserved copulating froghoppers, *Anthoscytina perpetua* (**Figure 3l**) of Procercopidae from the Yanliao Entomofauna, has been documented (46). The preserved specimen of *A. perpetua* shows a belly-to-belly mating position, with the male's aedeagus inserting into the female's bursa copulatrix, indicating symmetric structures of genitalia. The belly-to-belly position is different from the side-by-side position of extant froghoppers, but the possibility of twisting during the taphonomic and fossilization processes cannot be ruled out.

4.3.5. Breeding: oviposition, gall, and leaf mining. Insects have various methods of oviposition. Palaeopterans like mayflies and dragonflies lay eggs in the water, and major orders of pteropterans arrange their eggs neatly in a specific pattern on the surface of potential food for their nymphs. Numerous holometabolic insects evolve oviparous ways to protect eggs from being eaten, most commonly oviposition into the trunks of trees or onto leaves. Many fossil sawflies and wasps with a wide variety of ovipositors in different lengths have been reported from the Yanliao Entomofauna (72, 81). For example, *Proepialtitia acantha* (Figure 3m), assigned to Ephialtitidae of Hymenoptera, has a body length of 23.7 mm with an ovipositor length of 38.3 mm; this wasp might put her eggs into a tree via this long ovipositor, assisted by a wasp waist formed by a narrow propodeal-metasomal articulation (45). In addition, the DTs on fossil leaves or stalks caused by insect feeding or oviposition have been used to study and understand the coevolution of plants and insects (42). Ding et al. (5) reported several insect-mediated DTs caused by oviposition and gall- and leaf-mining from the Jehol Biota. The statistical results suggest that the damage caused by endophytic interactions such as oviposition and leaf mining was becoming in the Jehol Biota, replacing the insect piercing and sucking in the Yanliao Biota (5).

4.3.6. Parental care. In species with parental care, one or both parents devote certain types of care to their offspring to increase their fitness and survivability (66), e.g., insects protect their young via hiding or guarding eggs after oviposition or provisioning food for immature offspring. Fossil evidence of parental care by insects is rare for the mid-Mesozoic. Cai et al. (2) documented several burying beetles from the Yanliao and Jehol Entomofaunas displaying three distinct types of antennae, a pair of stridulatory files on the abdominal tergite, and Y-shaped gular sutures similar to those found in extant burying beetles, which suggest that elaborate biparental care by true burying beetles might have occurred before the Cretaceous. Most extant cockroaches produce capsular structures called oothecae to enclose eggs for protection; however, the oothecae are rarely preserved in the fossil records. Six cockroaches of *Pimiblattella yixianensis* (Figure 3n) with clear oothecae have been documented from the Jehol Entomofauna (13), which predated by 10 million years the previous reported oothecate cockroaches from the Lower Cretaceous Crato Formation in Brazil (approximately 115 Mya) (24). *P. yixianensis* has an oviparity B reproduction mode of oothecal structures, as do extant cockroaches, highlighting the fact that oothecal carriage and egg protection until hatching as forms of maternal care developed during or before the Early Cretaceous.

5. CONCLUSIONS

Accompanied by the decline of gymnosperms and rise of angiosperms in the mid-Mesozoic, the group diversity and morphological characters of insects changed and evolved. Numerous fossil insects reported from the Yanliao and Jehol Entomofaunas have provided a window into the diverse and sophisticated ecosystems of the mid-Mesozoic. The insects from these two Entomofaunas show not only taxonomic diversity, but also complicated behaviors and interactions with coexisting plants, vertebrates, and other insects. They fed on plants or pollination drops, preyed on other insects, or sucked blood from feathered or haired vertebrates. They protected themselves via wing modifications displaying camouflage, mimicry, or eyespot warning. Some insects could create pure-tone calls for attracting potential mates, and some developed ramified antennae to detect environmental cues for food or for potential mates. Some insects deposited eggs deeply into tree trunks with long ovipositors, and some embraced and protected eggs in carrying capsules. Pending discoveries of new fossils and more in-depth studies with advanced new technologies, we expect that more new insect taxa will be identified, and more evidence of the ways in which insects fed, escaped being fed on, and passed on their genes will be reported.

FUTURE ISSUES

1. More fossils are needed to clarify the origin, early evolutionary development, and eusociality of termites and to elucidate the phylogenetic relationships among termites and cockroaches.
2. It is necessary to find more fossils of Notoptera and Embiodea from the Yanliao Entomofauna to understand the early evolution of these insects and their possible mechanisms of wing reduction.
3. Phylogenetic studies are needed for the genera Mecoptera, Diptera, and Siphonaptera to understand the relationships among these three orders.
4. Fossil wasps from the Jehol Entomofauna should be investigated more deeply to understand the origin of ant eusociality.
5. More studies about potential flower-visiting insects from the Jehol Entomofauna are needed to provide more information about the early evolution of pollination behaviors and relationships between insects and basal angiosperms.
6. It is necessary to carry out studies of systematics and morphological characteristics for abundant fossil larvae from the mid-Mesozoic of China to expand and reconstruct the ecosystems of the Yanliao and Jehol Entomofaunas.

DISCLOSURE STATEMENT

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