

# Ancient pinnate leaf mimicry among lacewings

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**Insects have evolved diverse methods of predator avoidance, many of which implicate complex adaptations of their wings (e.g., Phylliidae, Nymphalidae, Notodontidae). Among these, angiosperm leaf mimicry is one of the most dramatic, although the historical origins of such modifications are unclear owing to a dearth of paleontological records. Here, we report evidence of pinnate leaf mimicry in two lacewings (Neuroptera): *Bellinympha filicifolia* Y. Wang, Ren, Liu & Engel gen. et sp. nov. and *Bellinympha dancei* Y. Wang, Ren, Shih & Engel, sp. nov., from the Middle Jurassic, representing a 165-million-year-old specialization between insects and contemporaneous gymnosperms of the Cycadales or Bennettitales. Furthermore, such lacewings demonstrate a preangiosperm origin for leaf mimicry, revealing a lost evolutionary scenario of interactions between insects and gymnosperms. The current fossil record suggests that this enigmatic lineage became extinct during the Early Cretaceous, apparently closely correlated with the decline of Cycadales and Bennettitales at that time, and perhaps owing to the changing floral environment resulted from the rise of flowering plants.**

mimicry | Neuroptera | Jurassic | Inner Mongolia | gymnosperm

Crypsis, or the ability to avoid detection, is a pervasive and effective method of defense used by insects against potential predators. In particular, mimicry of other species in morphology or signals (behavioral or chemical) represents a significant theme in arthropod evolution. On the other hand, mimicry, whereby the dupe is indifferent to the model, is less common (1, 2). Mimicry is most readily known through the evolution of plant mimics that have appeared in various orders of insects, ranging from the stick and leaf insects of the Phasmatodea, to flower- and leaf-mimicking mantises (Mantodea), to the famous thorn-mimicking treehoppers of the membracoid Hemiptera, among others (1). Within this diversity of mimics, leaf specializations are the most elaborately developed among angiosperm-mimicking species of the family Phylliidae (Phasmatodea), the leaf katydids (Orthoptera), the mantises (Mantodea) of the genera *Gongylus* and *Deroplatys*, and some butterflies of the Nymphalidae and moths of the Notodontidae (Lepidoptera). All of these lineages have wings and/or body parts that vividly imitate live or dry angiosperm leaves, including the nature of leaf veins, splotches, and even markings of damage. Given the phylogenetic placement of these families and genera among their respective orders (1), such mimicry of angiosperm models likely appeared subsequent to (rather than along with) the radiation of flowering plants. Accordingly, it has been considered that leaf mimicry is a mid-Cretaceous or younger phenomenon.

Despite the diversity of leaf mimicry among living insects, evidence of this unique evolutionary adaptation in the fossil record is exceptionally rare (1). Early researchers considered the resemblance between Carboniferous roachoid wings and fern pinnae a case of early mimetic evolution (3); however, more recent studies have concluded that such alleged mimicry was due to functional convergence in laminar organs (4). More recently, an Eocene (47 million years old) fossil leaf insect, *Eophyllum messelensis*, was described as the earliest evidence of such unique adaptations among insects (5). Living neuropterans are themselves typically generalist predators with few specialized relationships with particular plant lineages. Although some lacewings have moder-

ately leaf-like wings, such as *Drepanopteryx phalaenoides* (6) in which they loosely resemble dried angiosperm leaves in shape and coloration, the most dramatic examples of mimicry among the order are the various mimics of social wasps. Such mimicry can be so precise that color polymorphism in a single mimic species corresponds to a diversity of wasp models (7). However, neither modern neuropterans nor insects as a whole exhibit pinnate leaf mimicry. The trait is seemingly confined to the mimicking of angiosperm leaf morphologies among previously known insect mimics.

Two extraordinary fossil lacewings, *Bellinympha filicifolia* Y. Wang, Ren, Liu & Engel gen. et sp. nov. and *Bellinympha dancei* Y. Wang, Ren, Shih & Engel sp. nov. (Neuroptera), from the Jiulongshan Formation in northeastern China, preserve wings that are dramatically modified to resemble pinnate leaves (Fig. 1). These are the earliest evidence of leaf mimicry and predation *Eophyllum* by nearly 120 million years. *Bellinympha* demonstrates that lacewings of the late Middle Jurassic (165 million years ago) already had evolved highly specialized mimicry of pinnate leaves as a strategy for avoiding predators such as contemporaneous mammals, pterosaurs, dinosaurs, birds, spiders, and other predacious insects, suggesting a much richer biotic world in the Mesozoic Era.

## Systematic Paleontology

Insecta Linnaeus, 1758; Neuroptera Linnaeus, 1758; Saucrosymylinae Ren & Yin, 2003; *Bellinympha* Y. Wang, Ren, Liu, Shih & Engel gen. nov.; *Bellinympha filicifolia* Y. Wang, Ren, Liu & Engel gen. et sp. nov. (type species of genus, here designated); *Bellinympha dancei* Y. Wang, Ren, Shih & Engel sp. nov.

## Etymology

The generic name is a combination of *belli* (Latin, meaning beautiful) and *nympha* (Latin, meaning girl) and is of feminine gender. The specific epithet *filicifolia* (Latin) is derived from the pinnate leaf-like forewing. The specific name *dancei* is a patronym honoring Mr. Tom Dance, an excellent business leader and mentor providing guidance, motivation, and inspiration to C.S.

## Diagnosis

Antenna filiform, shorter than forewing. Forewing extremely broadened, with undulating postero-apical margin, apex somewhat falcate. Membrane with distinct pinna-like markings (Fig. 1A and C and Figs. S1 and S2). Nygma present in center of wing. Costal veinlets forked distally, with numerous interconnecting veinlets (Figs. S3 and S4). Rs region with two to five rows of cells; Rs arching anteriorly in apical quarter of wing; first fork of Rs near origin of Rs; in forewing distal branches of Rs apically curving

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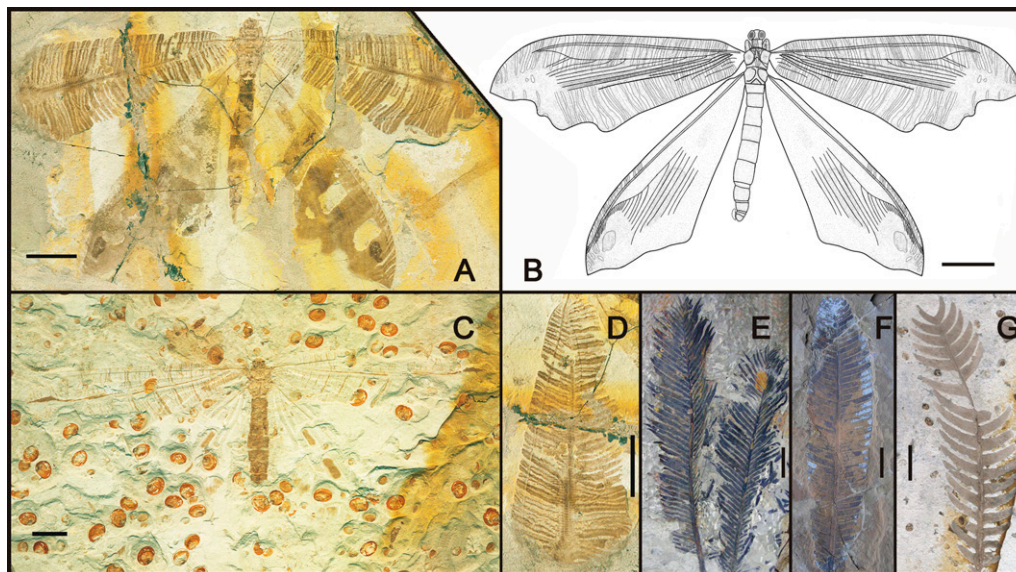
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**Fig. 1.** Species of *Bellinympha* and potential model plants from the Middle Jurassic of China. (A) Specimen CNU-NEU-NN2010240-1 of *B. filicifolia* sp. nov., exhibiting outstretched wings, apices of forewings not preserved [for photo of counterpart (CNU-NEU-NN2010240-2) refer to Fig. S1]. (B) reconstruction of *B. filicifolia*. (C) Specimen CNU-NEU-NN2010241-1 of *B. dancei* sp. nov., exhibiting similar wing position to *B. filicifolia* although the coloration preservation is poorer [for photo of counterpart (CNU-NEU-NN2010241-2) refer to Fig. S2]. (D) Forewing of specimen CNU-NEU-NN2010241-1, depicting distinct pinnate leaf markings. (E–G) Potential models of pinnate-leaved plants. (E) *Holozamites* (Cycadales) (30). (F) Unnamed leaf of a cycadophyte. (G) *Nilssonia* (Cycadales). (Scale bars, 10 mm in A–D, 20 mm in E–G.)

toward posterior margin.  $MP_2$  with many pectinate branches. CuA forked at midwing, forming complicated pectinate branches.

#### ***B. filicifolia* Y. Wang, Ren, Liu & Engel gen. et sp. nov**

**Holotype.** CNU-NEU-NN2010240-1 and -2, part and counterpart. A well-preserved almost complete body with most of four wings but missing wing apices and part of antennae (Fig. 1A and Fig. S1). Deposited in the Key Laboratory of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China.

**Locality and Age.** Collected from the Jiulongshan Formation, the late Middle Jurassic (Bathonian-Callovia boundary interval) of Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China. Daohugou strata are well known for yielding diverse lacewings and belong to a lacustrine deposit, representing a humid and warm-temperate climate (8, 9).

**Diagnosis.** Forewing CuP long, extending beyond midlength of CuA; hind wing costal cross-veins forked distally; wings broader and shorter, with more tightly spaced markings, pinna-like markings prominent.

**Description and Comparisons.** Body, fairly well preserved, is 39.8 mm long. Compound eyes protrudent, antennae filiform and incompletely preserved. Thorax distinctly differentiated; prothorax narrow; sclerite in meso- and metathorax well developed. Forelegs only with femora preserved, not crassate, with small, fine setae. Abdomen with 10 segments and with an appendix close to caudal segment. The appendix resembles the *gonapophysis lateralis* of Osmyidae, which represents a primitive character of Neuroptera (10).

Forewing 54.4 mm long and 19.7 mm wide, with numerous pinna-like markings (Fig. 1A and B). Trichosors and nygmata present. Outer margin with conspicuous undulating projections, similar to those in *Kempynus* (a genus of Osmyidae: Kempyninae). Costal cross-veins forked distally, interlinked by numerous veinlets (Fig. S3). Rs expanded in middle and bent anteriorly sharply toward R1. Space between Rs and R1 broad, forming two to five rows of cells. Rs with 19 branches, each with complicated distal forks and angled

toward posterior apical margin. Cross-veins in radial sector numerous, arranged irregularly. MA coalescent with Rs.  $MP$  forked close to wing base,  $MP_2$  with eight to nine distal pectinate branches. Cu forked at wing base. CuA with numerous oblique pectinate branches medially, forming a large triangular region; CuP deeply dark; long, extending beyond midlength of CuA. Anal region incompletely preserved. Two rows of cells between A1 and A2.

Hind wing, poorly preserved, is 53.8 mm long and 19.2 mm wide. Membrane with numerous oblique stripes close to apex, resembling the pinna-like forewings. Trichosors well spread across outer margin and part of anterior margin. Venation is similar to that of the forewing: costal cross-veins forked distally, interconnected by veinlets; Rs bent anteriorly toward R1 distally, forming a large space between R1 and Rs; cross-veins in radial sector numerous, arranged irregularly.

#### ***B. dancei* Y. Wang, Ren, Shih & Engel sp. nov**

**Holotype.** CNU-NEU-NN2010241-1 and -2, part and counterpart. All wings are unfolded but poorly preserved, body and antennae are intact (Fig. 1C and Fig. S2). Deposited in the Key Laboratory of Insect Evolution and Environmental Changes, Capital Normal University, Beijing, China.

**Locality and Age.** Same as those of *B. filicifolia*.

**Diagnosis.** Forewing CuP short, not extending beyond midlength of CuA; hind wing costal cross-veins simple; wings more narrow and longer, markings more sparse, pinna-like markings weaker.

**Descriptions and Comparisons.** Body, well preserved, is 36.6 mm long. Compound eyes protrudent, antennae filiform and completely preserved. Thorax distinctly differentiated; prothorax short; sclerite in meso- and metathorax well developed. Forelegs only with tibiae and tarsi preserved, with small, fine setae; pretarsal claws distinct, simple. Abdomen with 10 segments, and caudal segment small and triangular dorsally.

Forewing elongate, 69.8 mm long, with numerous pinna-like markings. The pinna-like forewing resembles those of *B. fili-*

*cifolia*; however, the markings of *B. dancei* are sparse and less distinct compared with *B. filicifolia*. Trichosors and nygmata undetected. MA space covering a distinct, dark, rachis-like marking. Because of the incomplete preservation, the undulating margin is not well discerned in *B. dancei*. Costal cross-veins forked distally and interlinked by numerous veinlets (Fig. S4). Sc and R1 fused distally but cross-vein sc-r1 not apparent. Rs resembles *B. filicifolia*: Rs with numerous branches, and the first branch diverging from Rs stem with deep fork. MA fused with Rs; MP forked close to wing base. CuA long, with numerous complicated branches from middle to apical termination; CuP shorter than CuA, with four branches distally; cross-veins cu-cup complicated, forming two rows of cells medially. A1 long, with six pectinate branches; A2 short, nearly half the length of A1; cross-veins a1-a2 form two rows of cells.

Hind wing poorly preserved, with undulating margin; apex pointed. Membrane with three continuous markings. Venation resembles the forewing except for the simple costal cross-veins.

The venation of *B. dancei* is quite similar to that of *B. filicifolia*; however, CuP in *B. dancei* is distinctly shorter than the elongate condition observed in *B. filicifolia*. In addition, the wings of *B. dancei* are narrower, longer, and more slender, with sparser markings, than those of *B. filicifolia*. The undulating margin is not preserved and unknown for the forewing of *B. dancei*, whereas the hind wing has a distinctly undulating postero-apical margin.

## Discussion

The two species of *Bellinympha* reported here are exceptionally rare, representing only two specimens out of more than 250,000 insect fossils in the Capital Normal University (Beijing) collection. The genus is noteworthy for the large body size, elongate forewings, long filiform antennae, protrudent compound eyes, undulating margins to the forewings, disruptive pattern of coloration resembling leaf pinnae, distinctly thickened MP branches resembling a leaf rachis, complicated venation, and an appendage close to the caudal segment (Fig. 1B) that resembles the *gonapophysis lateralis* of Osmyliidae, a relatively primitive feature among Neuroptera (10). Although moderate- to small-sized lacewings are dominant among extant Neuroptera, such large species are frequently found in the Middle Jurassic, notably species of the Aetheogrammatidae, Kalligrammatidae, and Grammolingiidae (11–13). The larger body sizes render such species more vulnerable to predators because they are more conspicuous, and so it is not surprising that genera in these families often exhibit forewing wing modifications. Like *Bellinympha* and its relatives, Kalligrammatidae, Aetheogrammatidae, and Grammolingiidae have complicated venational patterns and specialized markings on the forewing, frequently resembling “eye spots” and presumably used to startle potential predators as in modern moths (14).

Unique among these Mesozoic giant lacewings, the forewing shape and patterns of *Bellinympha* are obviously irrelevant to angiosperm leaves both in construction and temporal occurrence. The numerous pinna-like markings on the wing membranes are remarkably similar to the pinnate leaves of Mesozoic Cycadales and Bennettitales: the dark posterior median (MP) region of the wing resembles the rachis of the leaf, whereas the oblique stripes resemble the pinnae (compare Fig. 1A, C, and D–G). Among the two species, *B. filicifolia* has a more obvious pattern of pinnate leaves due to a darker and better-defined coloration (Fig. 1A, B, and D), whereas *B. dancei* has a more pronounced central rachis-like region (MP region), with a similar zigzag shape near the apical area, but the oblique pinna-like stripes are less developed (Fig. 1C). Pinna-like markings on the forewings imitate contemporaneous pinnate leaves of Cycadales and Bennettitales that are frequently found in the Daohugou strata. If the distal end of the wing is aligned with the proximal end of these fossil leaves, there is a close match between insect wings and leaves (Fig. 1D–G). This marks as an important defensive strategy that evolved before the

more extensively known leaf mimesis after the rise of angiosperms. Naturally, had *Bellinympha* been perched at the apex of young leaves, which are frequently the feeding target in living cycads, it might be difficult for a predator to distinguish the insect from the surrounding foliage (Fig. S5).

When compared with coincident leaf fossils, *Bellinympha*'s imitation was not as advanced as those of living insects whereby mimesis can show an almost perfect match with various angiosperm leaves. Nonetheless, perfect representation of the mimic is not necessary to acquire an advantage because the morphology need only be close enough to elicit the appropriate response from a potential dupe. Accordingly, only a subset of visual signals may be necessary to confer sufficient crypsis as to avoid detection.

According to the material recovered to date, most wings of *Bellinympha* and its relatives are preserved in out-stretched positions rather than folded roof-like over the body as in many neuropterans. The same posture is also observed in other large and extinct lacewings contemporaneous with *Bellinympha*, such as the aforementioned families Aetheogrammatidae, Kalligrammatidae, and Grammolingiidae. It is likely that the out-stretched forewing among extremely large lacewings stems from a behavioral adaptation of “adaptive stillness” (5). *Bellinympha* with their pinnate leaf-like wings consisting of disruptive maculations likely rested and fed on the terminal pinnae of the leaves, remaining motionless or swaying gently to resemble leaves moving in the breeze, similar to modern Phasmatodea.

*Bellinympha* may not have been a swift flyer, similar to many other large neuropterans. Accordingly, there may have been several potential predators for such species among the Daohugou fauna, including, as noted, early birds, mammals, dinosaurs, pterosaurs, spiders, and other predacious insects. Although records are not numerous, early studies have documented examples of birds capturing neuropterans (15). Primitive birds, pterosaurs, and prosauropod dinosaurs discovered in the Daohugou biota possibly had also insectivorous habits, particularly arboreal dinosaurs or lizards certainly may have preyed on *Bellinympha* and its relatives (16–19). Feathered dinosaurs such as *Epidixipteryx hui* from Daohugou were likely also insectivorous (16). Most notably, this fauna contained an early gliding mammal, *Volaticotherium antiquus*, which possessed specialized dentition for feeding on insects (20). The same strata harbor other early insectivorous mammals (21, 22), demonstrating a robust fauna of potential vertebrate predators, particularly for any large, slow-flying neuropterans such as *Bellinympha*, aetheogrammatids, kalligrammatids, and the like. In addition, spiders were common predators in the Middle Jurassic, and there are numerous records from Daohugou (23). Extant neuropterans are also frequently attacked by predacious insects, such as dragonflies (Odonata), predatory flies (Diptera), and hangingflies (Mecoptera) (15). The Daohugou insect-biota was diverse, with various potential generalist insect predators, including the aforementioned dragonflies (24, 25) and hangingflies (26). Considering the multitude of contemporaneous predators, it is clear that predatory pressures were significant, and mechanisms to ease or escape predation, such as mimesis, would have been greatly favored. Certainly various behavioral and chemical mechanisms of avoiding detection must have existed, but these have left few or no fossil traces or may be determined only by specialized morphologies (e.g., nocturnality by ocellar development, integumental pigmentation). Similarly, instances of camouflage, whereby a species blends into its abiotic surroundings, may have existed in species for which coloration is not preserved. Certainly among easily discernible forms of mimicry, nothing as complex or dramatic as leaf mimesis is known before *Bellinympha*.

The eventual disappearance of *Bellinympha* and its relatives is likely the same story as has been played out by innumerable highly specialized lineages of plant-associated insects; that is, that dependent specialization that is susceptible to rapid extinction should affect the model species. In the case of *Bellinympha*, its

intimate association within a world comprising abundant gymnospermous plants with pinnate leaves left it dependent on such a flora. When the floral composition of the environment shifted in the Early Cretaceous toward a more angiosperm-dominated ecosystem and *Bellinympha*'s cycadalean and bennettitalean models waned in diversity and abundance, so too did the mimic. The disappearance of pinnate leaf mimesis coincident with declines in Cycadales and Bennettitales (27) supports the conclusion of an evolutionary tie between such plants and these *Bellinympha* neuropterans. As fewer and fewer pinnate-leaf plants were present in the flora, *Bellinympha* and its relatives would have become increasingly obvious to visual predators, leading to sharp declines in their numbers. Without rapid reversal to a more standard neuropteran wing shape and pattern or new adaptation to the increasingly abundant leaf morphologies of flowering plants, such insects were likely doomed. Such uniquely specialized morphology would have become more of a hindrance in such a changed environment and, if coupled with losses of fitness due to changing climates or its own food resources, may have led to a rapid decline. Regardless, *Bellinympha* and its relatives demonstrate that tightly associated leaf mimicry had evolved early in the Mesozoic and well before the ecological radiation of flowering plants, and that such

adaptations at one time included mimicking pinnate leaf morphologies among gymnosperms.

The discovery of *Bellinympha* is of great significance to understanding the Mesozoic evolution and diversification of insects, particularly in the context of early coevolution between plants and pollinators before angiosperms (28). These species reveal a unique pattern that seems to have disappeared in modern insects and adds to the growing body of evidence documenting that the evolution of insects was more complex before the radiation of angiosperms (29). These enigmatic scenarios of interactions between insects and gymnosperms were lost during the course of evolutionary history and show a more rich association of insects and their surrounding environment in past geological epochs than previously has been surmised.

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