# Jurassic mimicry between a hangingfly and a ginkgo from China

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A near-perfect mimetic association between a mecopteran insect species and a ginkgoalean plant species from the late Middle Jurassic of northeastern China recently has been discovered. The association stems from a case of mixed identity between a particular plant and an insect in the laboratory and the field. This confusion is explained as a case of leaf mimesis, wherein the appearance of the multilobed leaf of *Yimaia capituliformis* (the ginkgoalean model) was accurately replicated by the wings and abdomen of the cimbrophlebiid *Juracimbrophlebia ginkgofolia* (the hangingfly mimic). Our results suggest that hangingflies developed leaf mimesis either as an antipredator avoidance device or possibly as a predatory strategy to provide an antiherbivore function for its plant hosts, thus gaining mutual benefit for both the hangingfly and the ginkgo species. This documentation of mimesis is a rare occasion whereby exquisitely preserved, co-occurring fossils occupy a narrow spatiotemporal window that reveal likely reciprocal mechanisms which plants and insects provide mutual defensive support during their preangiospermous evolutionary histories.

Cimbrophlebiidae | insect–plant association | Mecoptera | Mesozoic | Yimaiaceae

**M**ore than 100 years ago, S. H. Scudder noticed in Late Carboniferous strata an impressive resemblance between the pinnules of a well-known seed fern and a particular cockroach species (1), a similarity that recently earned these ancient species the designation of "pinnule insects" (2). This convergence in plant and insect identity has provided confusion that continues to befuddle fossil collectors to the present day. Recently, other fossil reports of leaf-mimicking insects have crept to the fore, including grasshoppers (3), katydids (4), and of course, leaf insects (5). Earlier, Chopard had documented a dazzling wealth of leaf mimicry by modern grasshoppers, katydids, and other orthopterans from the modern tropics—resemblances that not only extended to the basic appearance of a leaf, but also imitations that included lifelike details of insect feeding damage and fungal necroses (6). Based on these observations of fossil and modern Orthoptera and Phasmatodea, it would appear that if the phenomenon of leaf mimesis were sufficiently common in these groups, it should be detectable in other, spatiotemporally removed fossil plant and insect taxa. What does the fossil record say about the antiquity of leaf mimesis? In particular, what may have been the response of natural selection during the mid-Mesozoic, where a record of broadleaved gymnosperms with a profusion of varied leaf shapes may have interacted with co-occurring insect groups bearing a similar diversity of wing forms?

One mid-Mesozoic group of sites where fossil conditions are ideal for examining the possible presence of leaf mimesis is Daohugou, in northeastern China's Inner Mongolia. The encompassing Jiulongshan Formation is dated as late Middle Jurassic (7) and represented several subenvironments within and surrounding a large lake basin (8). The site previously has provided two examples of leaf mimesis, in particular two species of *Bellinympha*, extinct saucrosmyline lacewings that exhibited strong resemblances to small, pinnate cycadophyte leaves (9, 10),

a type of relationship absent in modern neuropterans (9). Here, we propose a likely leaf mimesis that occurred between a very different pair of interactors—a species from the insect order Mecoptera (scorpionflies) and a species from the diverse seed plant order Ginkgoales (ginkgos), representing a linked, finely honed association. Both groups were more diverse and had a greater breadth of life habits during the Mesozoic than their present diversities would indicate (11–13). Our reconstruction of leaf mimesis was based on morphological and other biological evidence (14), and we used several principles to guide our process of establishing this initially putative association (15, 16).

Extant Mecoptera is a nondiverse group in the modern insect fauna, including ~32 genera in nine families. By contrast, fossil mecopterans are three times more diverse at the genus level, representing 98 genera accommodated in 34 extinct families (17, 18). This pattern suggests that recent Mecoptera are relictual, a status also supported by a long and diverse evolutionary history extending to the Permian (11). Mecopterans obtain their scorpionfly namesake from male members of the Panorpidae, a mecopteran clade characterized by distinctive, scorpion-like terminalia. Extant hangingflies (Bittacidae) are a subset of scorpionflies that bear long legs and have a habitus paralleling that of crane flies (Diptera), exhibiting gross morphological convergence. The extant Eomeropidae are considered to possess many plesiomorphic features, and consist of one extant species in the Chilean rainforest with a very cockroach-like body (18). Despite these resemblances to other arthropods, there has been no evidence indicating that any fossil or modern mecopterans inordinately resemble the foliage of co-occurring plants.

We report on a previously undescribed mecopteran, *Juracimbrophlebia ginkgofolia* Wang, Labandeira, Shih and Ren gen. et sp. nov., a member of the extinct family Cimbrophlebiidae from the Jiulongshan Formation in northeastern China. Our data indicate that *J. ginkgofolia*, when stretching its wings, would very closely resemble a particular, multilobed, co-occurring leaf of the ginkgoalean *Yimaia capituliformis* Zhou, Zheng & Zhang (Figs. 1–3), a member of the Yimiaceae. Three other morphotype names for *Gingko*-like leaves from the same deposit have been proposed (as *Ginkgoites* sp.) that are affiliated with the reproductive organ of *Y. capituliformis* (19). However, *Y. capituliformis* is generally accepted as the valid name for these three, *Gingko*-like foliar morphotypes. We infer, based on evidence presented below, that *J. ginkgofolia* might have lived on *Y. capituliformis* and developed a protective, mimetic relationship with individual leaves of this woody, tree-statured plant. It is possible that other cimbrophlebiids with similar appearances to
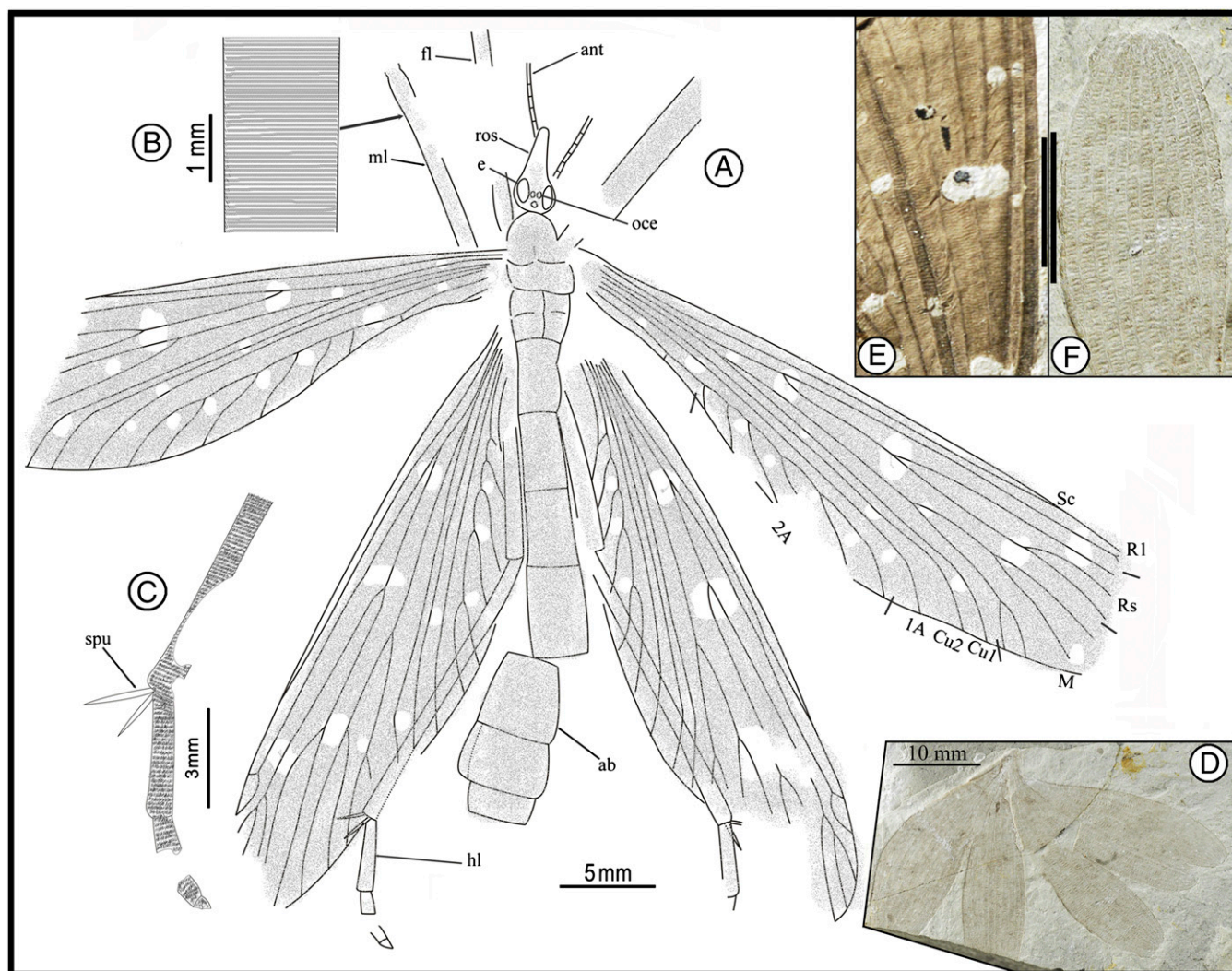
**Fig. 1.** (*A*–*C*) Camera lucida drawings of *J. ginkgofolia* gen. et sp. nov., holotype CNU-MEC-NN-2010–050P. (*A*) Habitus of holotype. (*B*) Highly enlarged portion of the midleg, showing annulately distributed pubescence. (*C*) Portion of hindleg, displaying two spurs at the femur–tibia joint. (*D*) *Y. capituliformis* leaf specimen of *Ginkgoites* (CNU-PLA-NN-2010-396), with rugose surface for comparison. (*E*) A portion of the wing from the paratype of *J. ginkgofolia* (CNU-MEC-NN-2010-012P). (*F*) Lobe of a *Ginkgoites* leaf from *Y. capituliformis* (CNU-PLA-NN-2010-396) for comparison. ab, abdomen; ant, antennae; e, compound eyes; fl, foreleg; hl, hindleg; ml, midleg; oce, ocelli; ros, rostrum; spu, tibial spurs. (Scale bars: 5 mm, *E* and *F*.)

*J. ginkgofolia* occupied the same habitat and assumed similar relationships, although compelling evidence is lacking. The resemblance of *J. ginkgofolia* with *Y. capituliformis* suggests an extraordinary association during the late Middle Jurassic in northeastern China. This finding reveals an interesting and unique behavioral mode for hangingflies and a mimetic association between an insect and a plant, which minimally lasted the duration of Jiulongshan deposition, perhaps >1 million years (8).

## Systematic Paleontology

The systematic paleontology is as follows: Insecta Linnaeus, 1758; Mecoptera Packard, 1886; Raptipeda Willmann, 1977; Cimbrophlebiidae Willmann, 1977; *Juracimbrophlebia ginkgofolia* Wang, Labandeira, Shih et Ren gen. et sp. nov.

**Holotype.** Holotype CNU-MEC-NN-2010-050P/C (Figs. 1 *A*–*C* and 3*C*) had a well-preserved, nearly complete body with most of four wings present, but wing apexes, genital region, and parts of antennae and legs were not preserved. Paratypes were as follows: CNU-MEC-NN-2010-022 (Fig. 3*H*); CNU-MEC-NN-2010-037P/ C, single forewing preserved; CNU-MEC-NN-2010-023, overlapped wings, with parts of body and antennae; and CNU-MEC-

NN-2010-012P/C (Fig. 1*E*), single forewing missing basal area. Specimens are deposited in the Key Laboratory of Insect Evolution and Environmental Changes, Capital Normal University.

**Etymology.** The generic name *Juracimbrophlebia* is the combination of *Jura-* and *cimbrophlebia* (the type genus of the family Cimbrophlebiidae), referring to the Jurassic age and scorpionfly nature of the species. The specific name *ginkgofolia* is the combination of Latin words *ginkgo* and *-folia*, referring to the distinctively ginkgoalean, leaf-like wings.

**Locality and Age.** All specimens were collected from the Jiulongshan Formation, of late Middle Jurassic age (Bathonian–Callovian boundary interval) from Daohugou Village, Shantou Township, Ningcheng County, of Inner Mongolia Autonomous Region in China. Ar-Ar and SHRIMP U-Pb dating results indicate an absolute age of 164–165 Ma (7).

**Diagnosis.** The previously undescribed genus and species are distinguished from other cimbrophlebiid species by the following wing characters. The 2A vein with six or more pectinate primary branches separates the previously undescribed genus from

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*Perfecticimbrophlebia*, which has one branch of 2A with a distal bifurcation, and from two species of *Cimbrophlebia* (*Cimbrophlebia flabelliformis* and *Cimbrophlebia brooksi*), of which the 2A has no more than four branches. The 2A, with only primary branches, separates the genus from *Malmocimbrophlebia*, *Telobittacus*, and three other species of *Cimbrophlebia* (*Cimbrophlebia leahyi*, *Cimbrophlebia westae*, and *Cimbrophlebia bittaciformis*), which collectively possess distally bifurcating 2A branches.

**Description.** Body is ∼38.5 mm long as preserved. Head is compressed dorsally; antennae are filiform, covered by numerous setae; compound eyes are conspicuously occupying most of the lateral head exposure; three ocelli are arranged triangularly; rostrum is prolonged and gradually narrowed distally (Fig. 1*A*).

Thorax is poorly preserved and slightly deformed, with dimensions of 6.8 mm long by 3.7 mm wide. Prothorax is vaulted anteriorly; metathorax is well differentiated, with prescutum and scutellum easily discernable. Legs are extremely long and gracile, like most hangingflies, and are covered by abundant annulate pubescence (Fig. 1*B*). Foreleg and midlegs are partly preserved and extended anteriad. Hindlegs are modified for grasping and become slender, with femora ∼11.6 mm long, tibia 16.4 mm long, and basitarsi 3.9 mm long (Fig. 1*C*); tibial spurs are elongate. Abdomen is 26.5 mm long as preserved, with eight visible segments, but the terminal abdominal segments are not preserved; sex is unknown.

Forewing is slightly broader than hindwing, at 32.4 mm long as preserved, with the proximal part minimally 2.1 mm wide and the rounded apex maximally 8.9 mm wide. Forewing exhibits light coloration and a field of transparent spots. Membrane is distinctly rugose, and a similar condition is present among co-occurring *Yimaia* leaves (Fig. 1 *D–F*) and other cimbrophlebiids (20).

Venation is typically cimbrophlebiid-like: subcosta vein (Sc) ends at costa vein (C), ∼2/3 of wing length; first branch of radial vein (R$_1$) branches near pterostigma; radial sector (Rs) has five dichotomous branches; media (M) has four branches, fused with cubitus vein (Cu) toward the base; the divergence of the anterior branch of cubitus vein (Cu$_1$) and Cu$_2$ is closed to the wing base; Cu$_2$ bent sharply toward posterior wing margin close to the termination; the first anal vein (1A) has a single branch, curved and entering the posterior margin; the second anal vein (2A) has six or more pectinate primary branches, and a short crossvein occurs close to the wing base. Hindwing is similar to the forewing in size and venation, at 33.8 mm long and 8.6 mm wide (maximum).

## Discussion

The Cimbrophlebiidae is an extinct family of Mecoptera erected in 1977 that was based on an Eocene specimen from Denmark (21). Like their sister group, the Bittacidae, the Cimbrophlebiidae are commonly known as hangingflies (20, 21). The oldest fossil record of Cimbrophlebiidae was from the lower Toarcian of Central Europe and England. Unfortunately, this important specimen was never described, limiting its usefulness for systematic studies (22). There is limited understanding of the morphology of the family, largely attributable to incomplete descriptions, although early Eocene species of *Cimbrophlebia* were described in detail (20, 21). Until 2009, only two valid genera were formally described: *Cimbrophlebia* Willmann, 1977, and *Malmocimbrophlebia* Bechly and Schweigert, 2000 (21, 23). A third genus, *Telobittacus* Zhang, 1993, was assigned to Bittacidae; subsequently, authors considered the possibility that it might indeed belong to the Cimbrophlebiidae (20, 24, 25). We provisionally accept this assignment, which our cladistic analysis supports (see *SI Text* and Fig. S1), and is included in our analyses here. A considerable amount of cimbrophlebiid material has
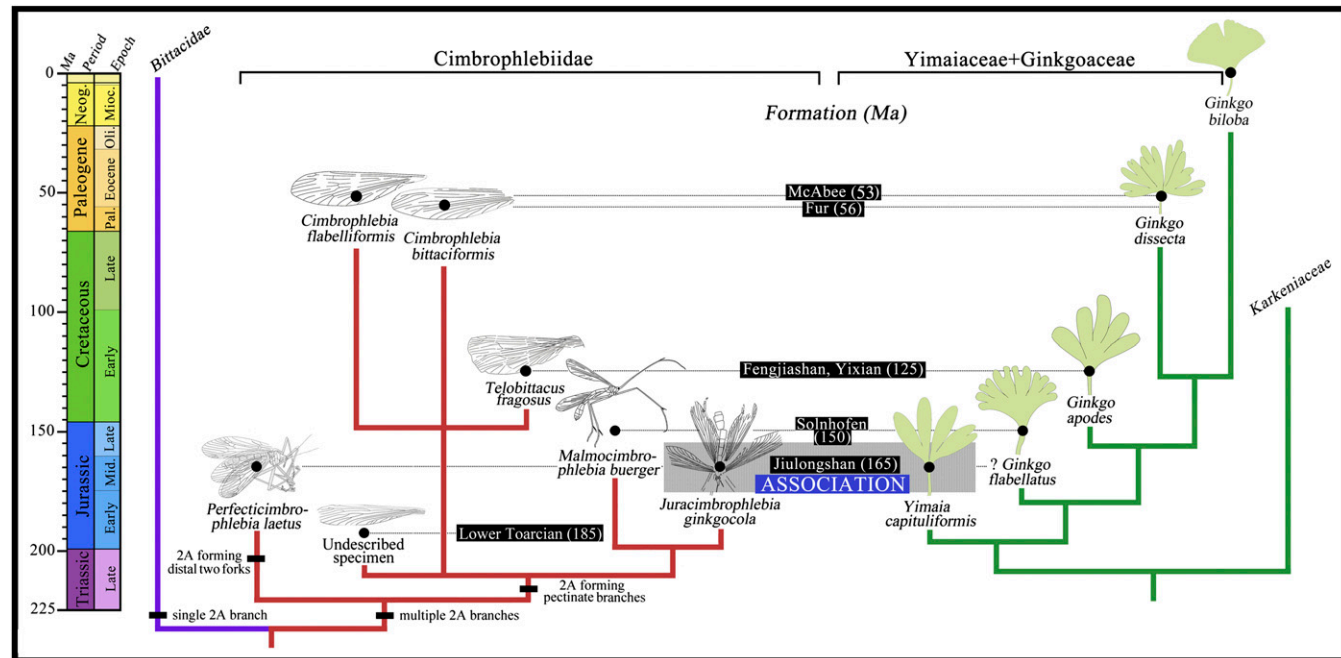


**Fig. 2.** Possible associations between Middle Jurassic-Eocene members of the hangingfly lineage Cimbrophlebiidae and co-occurring taxa of the ginkgoalean clade Yimiaceae–Ginkgoaceae. Note that only Jiulongshan taxa exhibit compelling evidence for an association. The phylogeny of Cimbrophlebiidae is based on one of the most parsimonious trees of PAUP v4.0b10, using an exhaustive search (tree length, 11; consistency index, 0.9091; retention index, 0.8889; for details, see *SI Text* and Fig. S1). Ginkgoalean phylogenetic relationships are based on refs. 39 and 40; selected multilobed *Ginkgoites* or *Ginkgo* leaves of Yimiaceae or Ginkgoaceae taxa from each locality were the closest possible matches of relevant, available species present at the same locality or in a spatiotemporally proximal locality. The data sources are the Solnhofen Formation: *Malmocimbrophlebia buergeri*, *Ginkgo flabellus* (23, 41); the Fengjiashan and Yixian Formations: *Telobittacus fragosus*, *Ginkgo apodes* (24, 42); and the McAbee and Fur Formations: *Cimbrophlebia flabelliformis*, *Ginkgo dissecta* (20, 43). The single positive match (*Discussion*) is *Ginkgoites* sp. from *Y. capituliformis*, coexisting with *J. ginkgofolia* in the same deposit (19), from the Middle Jurassic Jiulongshan Formation of northeastern China, indicated by the gray horizontal bar.

been found from the Middle Jurassic of northeastern China, including *Perfecticimbrophlebia* Yang, Shih et Ren, 2012 from the same locality as *J. ginkgofolia* (26). It allowed us to conduct a preliminary cladistic analysis to infer the phylogeny of Cimbrophlebiidae for which we have sufficient morphological data. The best supported tree and key character transformations are shown in Fig. 2 (details are provided in *SI Text*, Fig. S1, and Tables S1 and S2).

Although the systematic position of *J. ginkgofolia* within Cimbrophlebiidae is not fully resolved, its discovery provides additional insight into the poorly understood evolutionary history of the Cimbrophlebiidae. The wings and abdomen of *J. ginkgofolia* have a palmate appearance, with the vertex of this radiate arrangement centered at the head region. The abdomen assumed a central position, with the diverging left forewing and hindwing couplet configured to the left and similarly the right forewing and hindwing pair to the right (Fig. 3 *C* and *D*). This five-lobed, palmate presentation would have closely resembled the multilobed leaf forms of *Y. capituliformis* (Fig. 3 *A*, *B*, *E*, and *F*; ref. 19). We considered a configuration whereby the splayed-



**Fig. 3.** (*A–F*) Mimesis of *Ginkgoites* leaves from *Y. capituliformis* with the hangingfly *J. ginkgofolia*, from the Middle Jurassic Jiulongshan Formation of northeastern China. (*A*) *Ginkgoites* leaf of *Y. capituliformis* (CNU-PLA-NN-2009-733P). (*B*) A *Ginkgoites* leaf of *Y. capituliformis* (CNU-PLA-NN-2010-044). (*C*) Holotype of *J. ginkgofolia* (CNU-MEC-NN-2010-050P), with an appearance similar to *Y. capituliformis*. (*D*) A cimbrophlebiid specimen (CNU-MEC-NN-2010-017P). (*E*) A *Ginkgoites* leaf of *Y. capituliformis* (CNU-PLA-NN-2010-371P). (*F*) A *Ginkgoites* leaf of *Y. capituliformis* (CNU-PLA-NN-2010-501). (*G*) Artist's reconstruction of *J. ginkgofolia* mimetic on *Ginkgoites* leaves of *Y. capituliformis*. (*H–K*) Comparisons of single *J. ginkgofolia* wings to single *Y. capituliformis* leaf lobes. (*H*) Right forewing of paratype of *J. ginkgofolia* (CNU-MEC-NN-2010-022). (*I*) Right forewing of a cimbrophlebiid specimen (CNU-MEC-NN-2010-017P). (*J*) Lobe of a *Ginkgoites* leaf from *Y. capituliformis* (CNU-PLA-NN-2009-733P). (*K*) Lobe a *Ginkgoites* leaf from *Y. capituliformis* (CNU-PLA-NN-2010-371P). (Scale bars: 10 mm.)

out posture of these fossil insects would be similar to *Bellinympha*, representing a specialized behavioral adaptation (9). However, some *Juracimbrophlebia* specimens were found with a posture of overlapping wings, and we compared only a single forewing and hindwing with a single lobe of the Mesozoic ginkgoalean leaf (Fig. 3 *H–K*). It is clear that a single wing of *Juracimbrophlebia* exhibits a high degree of shape and size similarity to a single lobe of some ginkgoalean leaves. Additionally, the rugose texture of *J. ginkgofolia's* wing membrane is similar to other Mesozoic ginkgoalean leaves other than those of *Y. capituliformis* (Fig. 1 *E* and *F*), further enhancing a predilection for leaf imitation. Another interesting finding is the particular stripes and spotted patterns on the cimbrophlebiid wings. These features likely represent forms of disruptive camouflage that imitate the dappled patterns produced by sunlight passing through leaves, further strengthening the match between the insects and their background. Therefore, even assuming a rest position without wing extension, a potential benefit would accrue from incomplete leaf mimesis. Furthermore, another contemporaneous cimbrophlebiid specimen (Fig. 3 *D* and *I*) displays a potential resemblance to *Ginkgoites* leaves, indicating that this phenomenon may have involved other cimbrophlebiids and ginkgoaleans during the late Middle Jurassic.

Did Mesozoic bittacids sharing a similar morphology with cimbrophlebiids also evolve a mimetic biological association? We performed a quantitative analysis to evaluate similarity among cimbrephlebiids, bittacids, and ginkgoaleans (*SI Text*, Figs. S2–S5, and Table S3). In the geometric morphometric analysis, cimbrophlebiids show less shape variation compared with ginkgoalean leaves than do bittacids (Fig. S4 *A* and *B* and S5 *A* and *B*). These data provide direct evidence to indicate that cimbrophlebiids possess a more significant morphological foundation for mimicking ginkgoalean leaves than bittacid insects. It also suggests that bittacids overwhelmingly had an open, nonmimetic lifestyle, instead of evolving a specialized dependence on ginkgoaleans, a potential feature accounting for their survival to the present day.

Why did *J. ginkgofolia* form this particular morphological trait? This insect had a comparatively large body size of >30 mm in length compared with other contemporaneous mecopteran taxa, resulting in easy detection by the diverse predator fauna at Daohugou, including larger predaceous insects, mammals, pterosaurs, and small arboreal dinosaurs (27–30). Possessing unusually long and slender legs, cimbrophlebiids were not built for cursoriality, and with weakly constructed wings they were poor fliers as well, as in extant bittacids and craneflies. One avenue for predator avoidance would be use of ginkgoalean foliage as shelter or, perhaps more efficiently, employing leaf mimesis as additional or alternative protection. We identified five species of multilobed, broadleaved ginkgoaleans at Daohugou, representing ~12.4% of the total number of plant specimens documented (Table S4). This foliage provided a rich, cryptic habitat of foliage for retreat into leafy interstices or for engaging in leaf mimesis to avoid predators (Fig. 3*G*).

There is another possible explanation for this specialized morphology. As a leaf-mimicking predator, *J. ginkgofolia* could have induced potential prey to approach within striking distance (31, 32). Although extant *Ginkgo biloba* is considered to be minimally herbivorized (33–35), related Daohugou taxa such as *Y. capituliformis*, a highly lobate variant of the standard *Y. capituliformis* leaf form (19), exhibited relatively high levels of insect consumption, comparable to other mid-Mesozoic plant groups (Fig. 4) (36, 37), and providing potential food to a diverse herbivore fauna. It is possible that the association between *J. ginkgofolia* and *Ginkgoites*-type leaves of *Y. capituliformis* was a mutualism, by which the plant host provided leaves for crypsis while the associated leaf mimetic predator provided an antiherbivore function for its plant host (38). This association implies that the taxonomically rich ginkgoalean flora with various multilobed leaves at Daohugou provided raw material for an
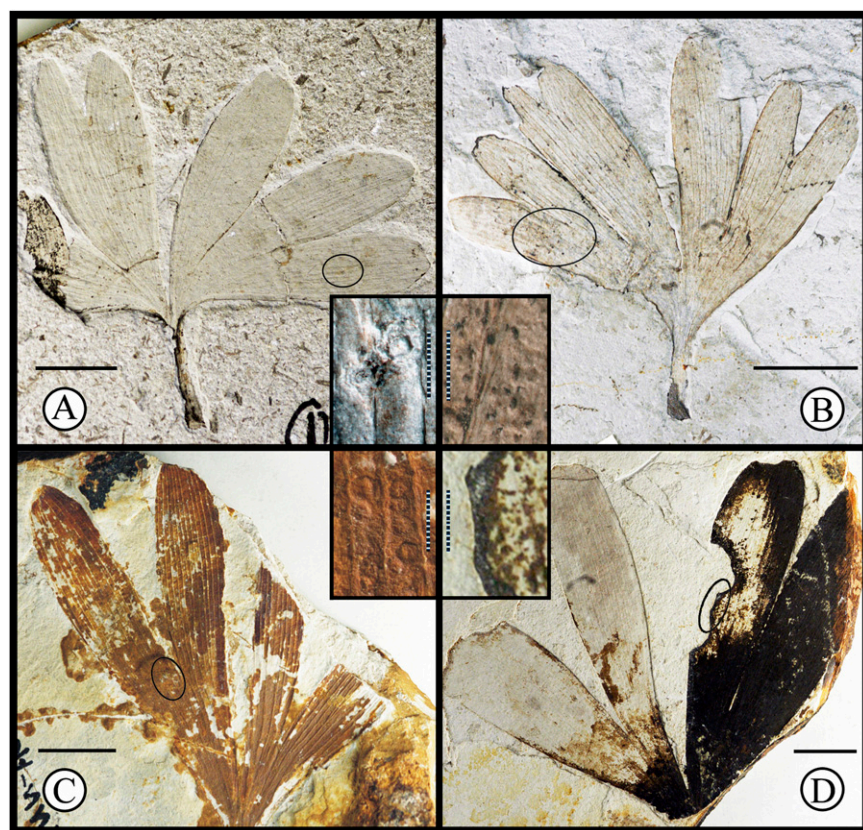


**Fig. 4.** Insect herbivore damage on *Ginkgoites* leaves of *Y. capituliformis* from the Middle Jurassic Jiulongshan Formation of northeastern China. *Insets* are enlargements of damaged areas circled from respective leaves and using the damage type (DT) system of reference (44). (*A*) Gall damage (DT80; CNU-PLA-NN-2010-605P). (*B*) Piercing-and-sucking damage (DT48; CNU-PLA-NN-2010-044). (*C*) Rows of small circular galls (DT80; CNU-PLA-NN-2010-548). (*D*) Margin feeding (DT12; CNU-PLA-NN-2010-521). (Scale bars: solid, 10 mm; dashed, 1 mm in *A–C*, 2 mm in *D*.)

exceptional time of innovation, such as leaf mimesis (9, 38). The type of indirect evidence that supports the *J. ginkgofolia–Y. capituliformis* association could be applied to other coexisting insect and plant taxa. Such reconstructions of organismic behavior and assessments of the functions of structures are accomplished through exploration of ecological and evolutionary puzzles that are informed by unique discoveries (15).

We explored other biotas with well-documented cimbrophlebiid and ginkgoalean taxa, selecting those candidates with the most similar combination of insect body and wing shape and size that matched similar co-occurring ginkgoalean leaf forms (Fig. 2). Interestingly, the occurrences of cimbrophlebiids were occasionally coincident with multilobed ginkgoalean species. Although no convincing matches equivalent to that of *J. ginkgofolia* and the *Ginkgoites* leaves of *Y. capituliformis* were found, some cimbrophlebiids possessed appearances similar to *J. ginkgofolia*, perhaps representing a continuation of their interactions with ginkgoaleans. It is possible that various associations between cimbrophlebiids and ginkgoaleans may have lasted >100 million years, from the Middle Jurassic to the Early Eocene.

Nevertheless, at least during the time represented by deposition of the Jiulongshan Formation, an opportunity was present wherein, through leaf mimesis, an increase in fitness either accrued only to the insect (commensalism) or, alternatively, to the plant and insect partners (mutualism). This association joins a previously published instance of leaf mimesis from the same deposit by another group of insects, the Neuroptera, whereby two species of saucrosmyline lacewings were mimetic, although only their forewings resembled particular cycadophyte leaves (9). The association of *J. ginkgofolia* and the *Ginkgoites*

leaves of *Y. capituliformis* considerably extend this phenomenon. More importantly, it adds a more finely tuned example of leaf mimesis wherein the entire insect body participates in the deception. This mimicry would necessitate a quantum increase in the coordination and integration of somatic development to achieve replication of a leaf model in size, shape, surface texture, and probably behavioral control of motion, sufficient to either deceive a potential predator or prey item. This similarity only could occur during an interval wherein the multilobed ginkgoalean leaf (the model) was present in sufficient numbers to continue the deception. In any event, *Y. capituliformis* became extinct during the Jurassic–Cretaceous boundary (19), as possibly did its mimic, *J. ginkgofolia*, significantly before the initial appearance of angiosperms during the mid Early Cretaceous. The interpretations of these two different examples of leaf mimesis can provide unusual insight (2, 16) into a preangiospermous world of elevated counterdefensive plant–insect associations such as leaf mimesis.

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ECOLOGY

# Supporting Information

## Wang et al. 10.1073/pnas.1205517109

### SI Text

**Cladistic Analysis.** *Methods.* We conducted a preliminary cladistic analysis to infer the systematic position of the mecopteran, *Juracimbrophlebia ginkgofolia* Wang, Labandeira, Shih et Ren gen. et sp. nov., within the Cimbrophlebiidae. Because of the limitations of the fossil material, only wing characters were used in this study. Six representative cimbrophlebiid species and one undescribed specimen from all reported genera with sufficiently preserved characters were selected for the analysis (Table S1). Two fossil species of the Bittacidae, *Preanabittacus validus* Yang, Shih et Ren 2012 (1) and *Megabittacus colosseus* Ren 1997 (2), were selected as outgroups for the analyses. The Bittacidae is accepted as the sister group of the Cimbrophlebiidae (3). The character matrix, consisting of eight taxa and seven morphological characters, each with multiple character-states, is provided in Table S2. The character matrix was edited using Version 5.0 of the Nexus Data Editor. All characters were treated as unordered and were weighted equally. Parsimony analysis was performed by using the exhaustive search option under PAUP (Version 4.0b10; ref. 4). Bootstrap values for clades were calculated in PAUP (Version 4.0b10), using a general heuristic search (1,000 replicates), and the branches with bootstrap values < 50% were collapsed.

*Descriptions of characters.*

*i*) *Wing membrane.* States: 0), smooth or slightly rugose at the anterior margin; 1), rugose. A satiny membrane occurs in most Mecoptera, and is treated as a plesiomorphy.

*ii*) *Number of M branches.* States: 0), four branches; 1), more than four branches. State (0) occurs in the outgroups and in two genera of Cimbrophlebiidae, which is considered a plesiomorphy.

*iii*) *Configuration of vein 2A.* States: 0), single branch; 1), distally dichotomously forked; 2), with pectinate branches. The multiple branches of vein 2A is considered a synapomorphy of the Cimbrophlebiidae.

*iv*) *Number of vein 2A branches.* States: 0), one branch; 1), two branches; 2), less than four basal branches; 3), more than four basal branches. State (0) occurs among the outgroups, which is assigned to a plesiomorphy. State 1 only occurs in *Perfecticimbrophlebia*.

*v*) *Configuration of vein 2A branches.* States: 0), only forming primary branches; 1), possessing secondary branches. Bittacids possess a single vein 2A; therefore, this character is not applicable to Bittacidae. Within the Cimbrophlebiidae, the formation of primary branches (without secondary branches) is considered a plesiomorphy.

*vi*) *Length of vein 2A.* States: 0), distinctly shorter than vein 1A; 1), long, approximately equal to vein 1A. The extended 2A vein is considered as a synapomorphy of the Cimbrophlebiidae.

*vii*) *Configuration of vein 1A.* States: 0), oblique, and entering the posterior margin at about 30 degrees; 1), bent sharply distally, entering the margin at more than 40 degrees. State (0) occurs in the outgroups and in *Perfecticimbrophlebia*. State (1) only occurs in the Cimbrophlebiidae.

*Phylogenetic results and discussion.* The cladistic analysis resulted in 21 parsimonious trees (tree length = 11, consistency index = 0.9091, retention index = 0.8889), and the best-supported tree is shown in Fig. S1. In the results, the monophyly of Cimbrophlebiidae is supported by the following synapomorphic characters: rugose membrane and multibranched 2A and 1A veins

that are bent sharply distally and enter the margin by >40 degrees. The genus *Perfecticimbrophlebia* is represented as the earliest diverging clade, and is basalmost within the Cimbrophlebiidae. The bittacid-like appearance of *Perfecticimbrophlebia* also exhibits a close relationship with the Bittacidae, including relatively narrow wings, a short main branch of the 2A vein, and an oblique branch of the 1A vein. Consequently, *Perfecticimbrophlebia* is an intermediate condition between the Bittacidae and the Cimbrophlebiidae, indicating an earlier evolutionary differentiation of both families than previously thought.

The other "typical" cimbrophlebiid genera are grouped based on the sharing of four synapomorphic characters. The characters are more than two pectinate and multiple branches of the 2A vein, a long main branch of the 2A vein, and a sharply bent 1A vein. Although the interrelationships within the large clade were not determined, there are three paraphyletic lineages. The first is the oldest lineage of the Cimbrophlebiidae, an undescribed specimen from the lower Toarcian (5); the second is the *Juracimbrophlebia* + *Malmocimbrophlebia* clade; and the third is the *Cimbrophlebia* + *Telobittacus* clade. Further resolution of the position of *Juracimbrophlebia* and *Malmocimbrophlebia* is not determinable from the results. This lack of resolution likely is caused by poor preservation of some characters in *Malmocimbrophlebia*. The Cretaceous genus *Telobittacus* and the Eocene *Cimbrophlebia* form a clade that diverged after *Juracimbrophlebia* and *Malmocimbrophlebia*. This clade is supported by one synapomorphic character: the presence of secondary branches in vein 2A. However, the internal relationships of this clade are not well resolved, because *Cimbrophlebia* and *Telobittacus* are rendered paraphyletic. This result partly supports Novokshonov's views that *Telobittacus fragosus* is likely a congener of *Cimbrophlebia bittaciformis* (6, 7). Because we did not examine the type of *Telobittacus fragosus*, we provisionally accept the validity of *Telobittacus*.

Although the phylogeny of the Cimbrophlebiidae is not completely resolved, our results provide a unique perspective on the evolution of Cimbrophlebiidae and allow an assessment of the temporal sequence of key character transformations within a phylogenetic framework (Fig. 2 and Fig. S1). *Perfecticimbrophlebia*, with a distally bifurcating 2A vein, represents the basalmost Cimbrophlebiidae and an intermediate transition between the Bittacidae and the Cimbrophlebiidae. Typical Cimbrophlebiidae have characteristics involving complex 2A branches. The multiple, pectinate, primary 2A branches without distal bifurcations is found in a Lower Jurassic undescribed specimen and in the Middle Jurassic *Juracimbrophlebia*, indicating that the typical configuration of the 2A vein apparently undergo an evolutionary change from simple to complex branches.

**Geometric Morphometric Analysis.** *Methods.* Geometric morphometric analysis is considered a useful way to determine shape differences, and the resulting phenograms from Procrustes distances indicate phenetic relationships among samples, summarizing overall patterns of similarity (8–10). Although there is no biological homology between insect wings and plant leaves, we performed a morphometric analysis to compare the forewing outlines of cimbrophlebiids and bittacids with single lobes from a large pool of ginkgoalean leaves to evaluate their shape similarity. To conduct a quantitative analysis, we needed to select fossil specimens with complete preservation of shape outlines. We selected 10 representatives each of cimbrophlebiids, bittacids, and *Yimaia* leaf lobes from the same locality, as shown in

Table S3. Before the analysis, we drew the shapes of forewings and leaf lobes under CorelDraw 12 graphic software to obtain exact outlines (Fig. S2). The line drawings were inputted to tps-UTILS 1.38 to obtain TPS files (11). Cartesian coordinates of the semilandmarks were digitized with tps-DIG 2.16 (12), and 100 semilandmarks were resampled by length for curvature. The coordinates were analyzed using tps-RELW 1.49 (13). Semi-landmark configurations were scaled, translated, and rotated against the consensus configuration using the GLS Procrustes superimposition method (14). Procrustes distances, considered as the best method for measuring shape differences (8, 15–19), were produced by the tps-SPLIN 1.20 (20). The Procrustes distance matrix was subjected to unweighted pair group method using arithmetic averages (UPGMA) generated by NTSYSpc to determine the phenetic relationships among the samples (21). We also performed an analysis to estimate the similarities among the average outline shape of cimbrophlebiids, bittacids, and ginkgoaleans. The average landmark configurations for cimbrophlebiids, bittacids, and ginkgoaleans were respectively computed using tps-SUPER (22) and then served as input to tps-UTILS 1.38 to obtain the combined TPS file. The new TPS file was analyzed by using tps-RELW 1.49, tps-SPLIN 1.20, and NTSYSpc by the same, previously mentioned methods.

*Results and discussion.* The consensus configuration of the samples using the GLS Procrustes superimposition method and distributions of 100 semilandmarks is shown in Fig. S3. The first two relative warps of the semilandmarks (accounting for 56.97% of the variation among the specimens) are plotted to indicate variation along the two axes (Fig. S4*A*). The shape changes of different specimens are shown as deformation of the GLS reference using thin-plate splines (Fig. S4*A*). A UPGMA phenogram of the studied shape outlines based on Procrustes distance matrix is presented in Fig. S4*B*.

Geometric morphometric analysis provided a straightforward way to interpret the relationships among Cimbrophlebiidae, Bittacidae, and ginkgoalean leaf lobes. The bittacids are well grouped and are separate from cimbrophlebiids and ginkgoaleans in the UPGMA phenogram (Fig. S4*B*). The splines of bittacids show relatively high deformation to the consensus reference (Fig. S3), in comparison with cimbrophlebiids and ginkgoalean leaf lobes (Fig. S4*A*). Interestingly, the bittacid-like species *Perfecticimbrophlebia laetus* Yang, Shih et Ren 2012 (C3), attributed to Cimbrophlebiidae, shows more similarities with bittacids than with cimbrophlebiids and ginkgoleans. It supports the hypothesis that *P. laetus* represents an intermediate state between bittacids and cimbrophlebiids. Other Middle Jurassic cimbrophlebiids and ginkgoaleans nest together in the phenogram, implying less shape variation among them (Fig. S4*B*). These quantitative analyses show that cimbrophlebiids are not easily distinguished from ginkgoaleans based on shapes of the forewings and leaf lobes.

A comparison of the results of average outline shapes is displayed in Fig. S5. Comparisons among the average outline shapes are given as the deformation of the GLS reference, using thin-plate splines (Fig. S5*A*). The phenetic relationships among these outline shapes are shown in Fig. S5*B*. Based on the morphometric analysis, the average outline shape of cimbrophlebiids shows more similarity to ginkgoaleans than to bittacids. In summary, the results of the geometric morphometric analysis support our hypothesis that the wings of cimbrophlebiids are more similar in shape to ginkgoaleans than are bittacids to ginkgoaleans.

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21. Rohlf FJ (2007) NTSYS-pc Numerical Taxonomy and Multivariate Analysis System (Exeter Software, New York), Version 2.20 for Windows.
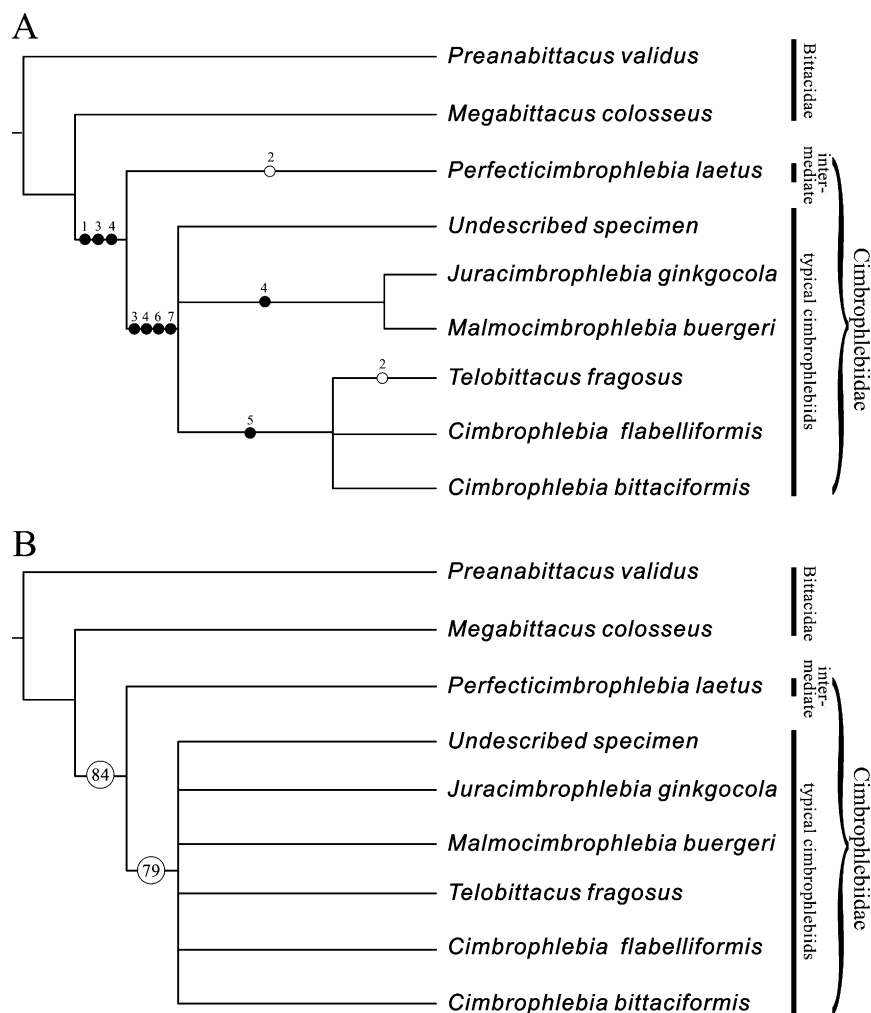22. Rohlf FJ (2004) tps-SUPER (State Univ of New York, Stony Brook, NY), Version 1.14.

**Fig. S1.** Results of the cladistic analysis. (*A*) The best-supported tree from the most parsimonious trees). (*B*) The strict consensus tree from the most parsimonious trees. The filled circles represent apomorphic characters, and open circles represent parallelisms and reversals. Bootstrap values are provided in the circles at the internodes.
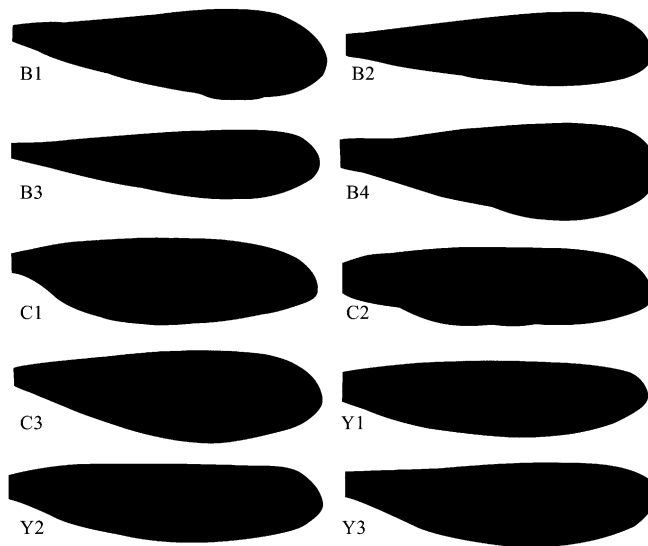
**Fig. S2.** Wing and leaf-lobe shape outlines of the samples. B1, forewing of *M. daohugouensis* (NIGPAS 133709); B2, forewing of *F. macularis* (CNU-MEC-NN-2007-001); B3, forewing of *L. longantennatus* (L91001); B4, forewing of *P. validus* (CNU-MEC-NN-2010-005); C1, forewing of *J. ginkgofolia* (CNU-MEC-NN-2010-022); C2, forewing of Cimbrophlebiidae sp. 1 (CNU-MEC-NN-2010-017P); C3, forewing of *P. laetus* (CNU-MEC-NN-2010-004P); Y1, a lobe of *Y. capituliformis* (CNU-PLA-NN-2009-733); Y2, a lobe of *Y. capituliformis* (CNU-PLA-NN-2010-371P); Y3, a lobe of *Y. capituliformis* (PB20233).



**Fig. S3.** Consensus configuration of samples with 100 semilandmark distributions.

**Fig. S4.** Among-sample differences in outline shape. (*A*) The first two relative warps computed from the data set show the relationships among the samples to the reference configuration situated at the origin. Thin-plate spline deformation grids show the shape changes along the relative warp axes. (*B*) Phenetic trees of outlined semilandmarks compiled using NTSYSpc and UPGMA statistical methods on a Procrustes distance matrix. B1, forewing of *M. daohugouensis* (NIGPAS 133709); B2, forewing of *F. macularis* (CNU-MEC-NN-2007-001); B3, forewing of *L. longantennatus* (L91001); B4, forewing of *P. validus* (CNU-MEC-NN-2010-005); C1, forewing of *J. ginkgofolia* (CNU-MEC-NN-2010-022); C2, forewing of Cimbrophlebiidae sp. 1 (CNU-MEC-NN-2010-017P); C3, forewing of *P. laetus* (CNU-MEC-NN-2010-004P); Y1, a lobe of *Y. capituliformis* (CNU-PLA-NN-2009-733); Y2, a lobe of *Y. capituliformis* (CNU-PLA-NN-2010-371P); Y3, a lobe of *Y. capituliformis* (PB20233).
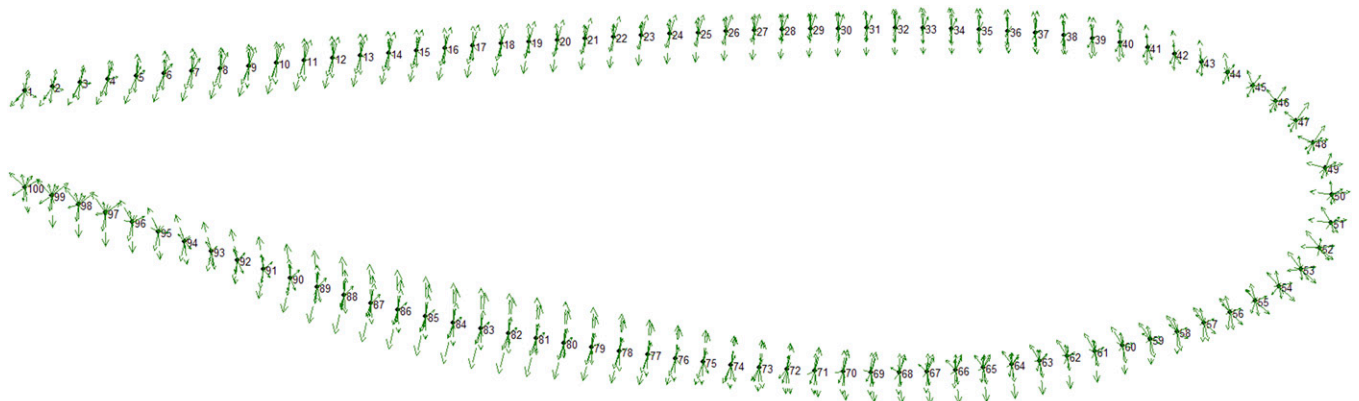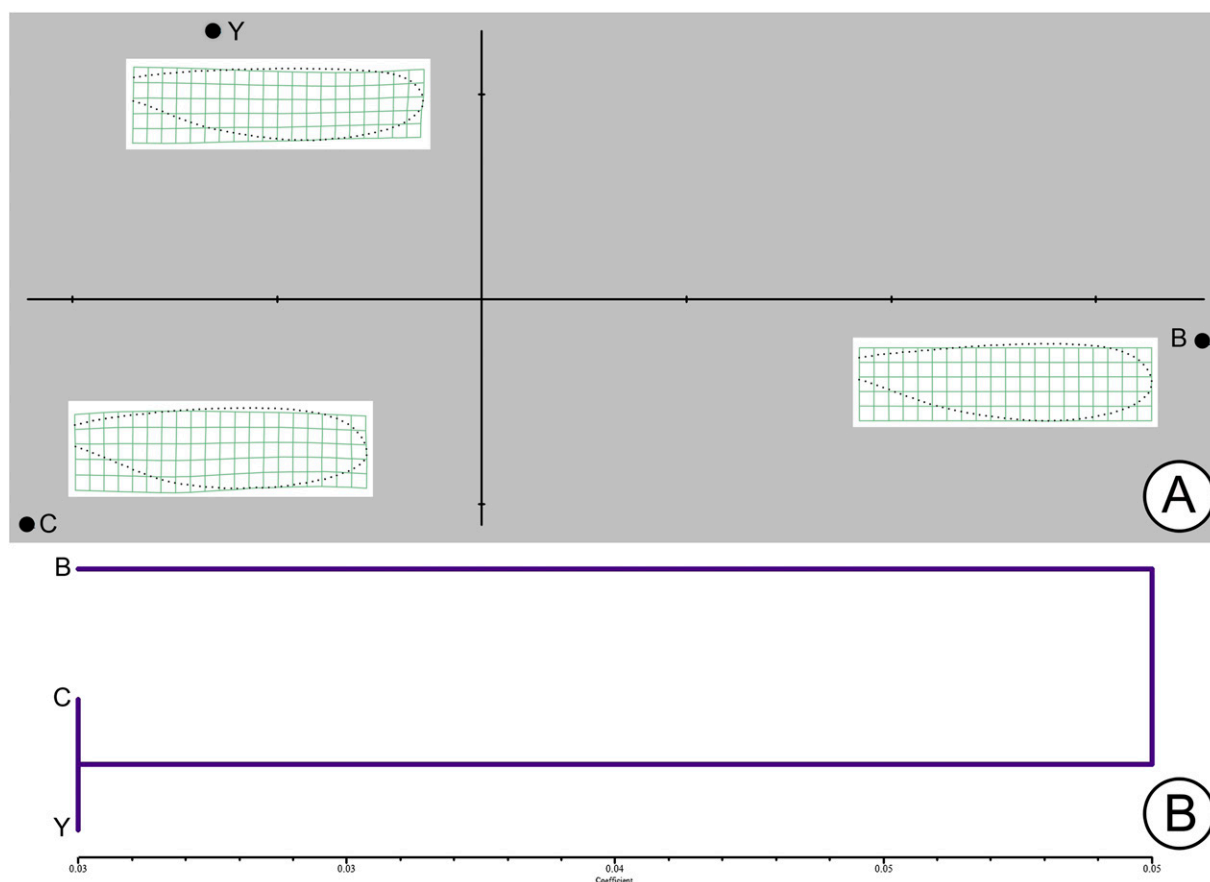
**Fig. S5.** Average differences in outline shape. (*A*) Shape changes shown as the deformation of GLS reference. (*B*) Phenetic tree compiled using NTSYSpc and UPGMA statistical methods on Procrustes distance matrix. B, average outline shape of Bittacidae; C, average outline shape of Cimbrophlebiidae; Y, average outline shape of *Y. capituliformis*.

**Table S1. Taxa studied for the cladistic analysis**

| Taxa | Geological age and formation | Source |
|------|------------------------------|--------|
| Outgroups | | |
| *Preanabittacus validus* | Middle Jurassic, Jiulongshan Fm. | 1 |
| *Megabittacus colosseus* | Early Cretaceous, Yixian Fm. | 2 |
| Ingroups | | |
| *Perfecticimbrophlebia laetus* | Middle Jurassic, Jiulongshan Fm. | 1 |
| *J. ginkgofolia* gen. et sp. nov. | Middle Jurassic, Jiulongshan Fm. | This work |
| *Malmocimbrophlebia buergeri* | Late Jurassic, Solnhofen Fm. | 3 |
| *Telobittacus fragosus* | Early Cretaceous, Fengjiashan Fm. | 4 |
| *Cimbrophlebia bittaciformis* | Early Eocene, Fur Fm. | 5 |
| *Cimbrophlebia flabelliformis* | Early Eocene, McAbee Fm. | 6 |
| Undescribed specimen | Early Jurassic, Lower Toarcian | 7 |

1. Yang XG, Shih CK, Ren D, Petrulevičius JF (2012) New Middle Jurassic Hangingflies (Insecta: Mecoptera) from Inner Mongolia, China. *Alcheringa* 36:195–201.
2. Ren D (1997) Studies on late Jurassic scorpion-flies form northeast China (Mecoptera: Bittacidae, Orthophlebiidae). *Acta Zootax Sin* 22:75–85.
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7. Ansorge J (2003) Insects from the Lower Toarcian of Middle Europe and England. *Acta Zool Cracov* S46:291–310.

**Table S2. Character matrix used in the cladistic analysis**

| Taxa | Characters | | | | | | |
|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| *Preanabittacus validus* | 0 | 0 | 0 | 0 | — | 0 | 0 |
| *Megabittacus colosseus* | 0 | 0 | 0 | 0 | — | 0 | 0 |
| *Perfecticimbrophlebia laetus* | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| *J. ginkgofolia* gen. et sp. nov. | 1 | 0 | 2 | 3 | 0 | 1 | 1 |
| *Malmocimbrophlebia buergeri* | ? | ? | 2 | ? | 0 | 1 | 1 |
| *Telobittacus fragosus* | ? | 1 | 2 | 2 | 1 | 1 | 1 |
| *Cimbrophlebia flabelliformis* | 1 | 0 | 2 | 2 | ? | 1 | 1 |
| *Cimbrophlebia bittaciformis* | ? | 0 | 2 | 2 | 1 | 1 | 1 |
| Undescribed specimen | ? | 0 | 2 | 2 | 0 | 1 | 1 |

—, not applicable; ?, unknown.

**Table S3. Selected representatives for the geometric morphometric analysis**

| Taxa | Sampled part | Source |
|---|---|---|
| Cimbrophlebiid species | | |
| *J. ginkgofolia* gen. et sp. nov. | Forewing of CNU-MEC-NN-2010-022 | This work |
| Cimbrophlebiidae sp1 | Forewing of CNU-MEC-NN-2010-017P | Fig. 3 |
| *P. laetus* Yang, Shih et Ren, 2012 | Forewing of CNU-MEC-NN-2010-004P | 1 |
| Bittacid species | | |
| *Mongolbittacus daohugouensis* Petrulevičius, Huang et Ren, 2007 | Forewing of NIGPAS 133709 | 2 |
| *Liaobittacus longantennatus* Ren, 1993 | Forewing of L91001 | 3 |
| *Formosibittacus macularis* Li, Ren et Shih, 2008 | Forewing of CNU-MEC-NN-2007-001 | 4 |
| *Preanabittacus validus* Yang, Shih et Ren, 2012 | Forewing of CNU-MEC-NN-2010-005 | 1 |
| Ginkgoalean species | | |
| *Y. capituliformis* | The lobe of CNU-PLA-NN-2010-371P | This work |
| *Y. capituliformis* | The lobe of CNU-PLA-NN-2009-733 | This work |
| *Y. capituliformis* | The lobe of PB20233 | 5 |

1. Yang XG, Shih CK, Ren D, Petrulevičius JF (2012) New Middle Jurassic hangingflies (Insecta: Mecoptera) from Inner Mongolia, China. *Alcheringa* 36:195–201.
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**Table S4. Abundance of examined plant specimens from the Daohugou biota**

| Plant group | No. of specimens | Relative percentage, % |
|---|---|---|
| Bennettitaleans | 314 | 26.04 |
| Bryophytes | 9 | 0.75 |
| Coniferaleans | 294 | 24.38 |
| Cycadaleans | 38 | 3.15 |
| Czekanowskialeans | 100 | 8.29 |
| Filicaleans | 36 | 2.99 |
| Ginkgoaleans | 149 | 12.35 |
| Gnetaleans | 1 | 0.08 |
| Lycopods | 14 | 1.16 |
| Plants Incertae Sedis | 12 | 1.00 |
| Pteridospermae | 5 | 0.41 |
| Sphenopds | 234 | 19.40 |
| Total | 1,206 | 100.00 |

The list is based on plant fossil collection at CNU. The plant fossils were examined under the Leica MZ 7.5 dissecting microscope.