



Earliest true moth lacewing from the Middle Jurassic of Inner Mongolia, China

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A new moth lacewing *Guithone bethouxi* gen. et sp. nov., is described from the Middle Jurassic Jiulongshan Formation (Inner Mongolia, China). This taxon is characterized by robust body, head retracted under pronotum, and remarkable costal space (expanded basad, narrowed distad). Herein, we propose a detailed definition of the lineages of Ithonidae sensu lato (moth lacewings, giant lacewings, and montane lacewings) based on extant groups in order to clarify the systematics of fossil species within the taxon. The comparison shows that *Guithone bethouxi* gen. et sp. nov. unquestionably represents the earliest true moth lacewing, implying that lineage differentiations within Ithonidae sensu lato must have taken place before the Middle Jurassic. Furthermore the new genus possessing some particular venation characters, such as irrecurrent humeral veinlet and simplified crossveination in radial sector, represents an important intermediate group in the evolution of Ithonidae sensu lato.

Introduction

Three distinct family-level lineages have been assigned to the ithonid-like lacewings, namely “Ithonidae” sensu stricto (moth lacewings), “Polystoechotidae” (giant lacewings), and “Rapismatidae” (montane lacewings). Based on their phylogenetic analysis incorporating both molecular and morphological data, Winterton and Makarkin (2010) formally synonymized Polystoechotidae and Rapismatidae with Ithonidae. The new status of Ithonidae sensu lato has now been accepted (Yang et al. 2012; Wang et al. 2013; Makarkin et al. 2014). However, there is a possible source of confusion due to the use of taxonomic reference using an “-id” ending (such as “ithonid”), indicative of family-level rank, and because of the various senses given to “Ithonidae”. In the following we propose to refer to the ithonid, polystoechotid and rapismatid genus-groups.

Although a few extinct genera were included (*Allorapisma* Makarkin and Archibald, 2009; *Principiala* Makarkin and Menon, 2007) in Winterton and Makarkin’s (2010) phylogenetic reconstruction, the systematic position of most fossil taxa remains to be clarified as they previously were collectively attributed to Ithonidae sensu lato without the further assignment (Makarkin et al. 2014). Therefore, essentially based on Winterton and Makarkin’s (2010) results, herein we propose a workable definition for the three lineages of Ithonidae based

on wing venation, and this attempt aims to better integrate data obtained from both fossil and extant forms.

Up to date, about 10 genera and 26 species ranging from the Early Jurassic to early Eocene were identified as Ithonidae sensu lato (Makarkin et al. 2014). Noteworthy, only the polystoechotid genus-group has been found in the earliest strata (Early to Late Jurassic) (Martynov 1925, 1937; Panfilov 1980; Ren et al. 2002), while major diversification of the rapismatid genus-group seems to have started in the Early Cretaceous (Makarkin and Menon 2007; Makarkin and Archibald 2009). To date, no genuine fossil of the ithonid genus-group has been described. Herein, a new, convincing moth lacewings fossil is described from the Middle Jurassic of northeastern China. The new insect shares the typical features of extant representatives of the ithonid genus-group, representing the earliest occurrence of this lineage.

Institutional abbreviations.—CNU, Capital Normal University, Beijing, China.

Other abbreviations.—A1–A3, anal veins; CuA, anterior cubitus; CuP, posterior cubitus; f, frenulum; hv, humeral veinlet; MA, anterior branches of media; MP, posterior branches of media; R1, first branch of radius; Rs, radial sector; Sc, subcosta; tr, trichosors (wing venation terminology after Barnard 1981).

Material and methods

The specimen which is the focus of this study (CNU-NEU-NN 2015003P/C) is deposited in the Key Lab of Insect Evolution & Environment Change, Capital Normal University, Beijing, China. Draft drawing was produced using a LEICA MZ75 dissecting microscope equipped with a drawing tube. Photographs used to produce the combined photographs on Fig. 1A₁, B (see details below) were taken with a Canon EOS 5D Mark III digital camera, and photographs of Figs. 1A₂ and 3A, B were taken with Canon EOS 70D digital camera, both of which coupled to a Canon MP-E 65 mm macro lens (all lenses equipped with polarizing filters), under dry condition.

Photographs in Fig. 1 were produced as follows. Original photographs used the “matrix white balance” technique (Cui et al. 2015). Both sides of the specimen were photographed under both dry and ethanol conditions. The “P-side” of the specimen was fragmented during collection, and those fragments were glued loosely. Rather than undertaking a hazardous physical res-

toration of the specimen, we opted for a digital reconstruction. Each “fragment” photograph was isolated (simultaneously on both dry and ethanol photographs). Fragments were then tightly adjusted using their outline, and landmarks from the other side of the specimen (CNU-NEU-NN2015003C). Two photographic combinations were then produced. The one reproduced on Fig. 1A is a combination of ethanol photographs of both sides of the specimen, and of the side CNU-NEU-NN2015003C under dry condition; the photograph reproduced on Fig. 1B is a combination of ethanol photographs of both sides of the specimen (combination techniques exemplified in Béthoux 2015).

Systematic palaeontology

Order Neuroptera Linnaeus, 1758

Family Ithonidae Newman, 1853 sensu Winterton and Makarkin (2010)

Genera included: Ithonid genus-group: *Ithone* Newman, 1838, *Megalithone* Riek, 1974, and *Varnia* Walker, 1860, *Guithone* gen. nov.; polystoechotid genus-group: *Fontecilla* Navás, 1931, *Platystoechotes* Carpenter, 1940, *Polystoechotes* Burmeister, 1839, *Elektrithone* Makarkin, Wedmann, and Weiterschan, 2014, *Jurapolystoechotes* Ren, Engel, and Lü, 2002, *Kirgisella* Martynov, 1925, *Lasiosmylus* Ren and Guo, 1996, *Mesopolystoechus* Martynov, 1937, *Osmyloides* Panfilov, 1980, *Palaeopsychops* Andersen, 2001, *Paleopterocalla* (Panfilov, 1980), *Panfilovdvia* (Panfilov, 1980), *Polystoechotites* Cockerell, 1908; rapismatid genus-group: *Adamsiana* Penny, 1996, *Narodona* Navás, 1929, *Oliarces* Banks, 1908, *Rapisma* McLachlan, 1866, *Allorapisma* Makarkin and Archibald, 2009, *Principiala* Makarkin and Menon, 2007.

Remarks.—Winterton and Makarkin (2010) proposed a broad definition of Ithonidae (sensu lato), inclusive of three traditional families. However, interrelationships within the family were not fully resolved due to the uncertain placement of some genera (e.g., *Oliarces* Banks, 1908; *Platystoechotes* Carpenter, 1940) and the absence of most fossil taxa in the analysis.

Because the systematics of fossil insects is essentially based on wing venation, herein we reviewed the subdivision of the family in the framework of Winterton and Makarkin's (2010) phylogenetic work and propose some putative diagnostic features of wing venation.

The first lineage to consider is the ithonid genus-group (moth lacewings) consisting of the three extant genera that are restricted to Australia. These genera share the following character states combination: distal parts of Sc and R1 separated; Sc and R1 reaching the anterior margin straightly before the apex of wing; MP fork distant to the wing base, beyond the MA divergence (from Rs); and MP2 dichotomously branched. Noteworthy, few fossil insects could undoubtedly be assigned to this lineage to date.

The polystoechotid genus-group (giant lacewings) includes three living genera, but this assemblage is not well grouped due to the lack of the definitive synapomorphic character (Winterton and Makarkin 2010). Considering the diverse fossil taxa related to this group (about ten extinct taxa are assigned to this group temporarily), we outlined some remarkable venational features, including: distal parts of Sc and R1 closely approximated in extant genera or evidently fused in the fossil taxa; Sc and R1 distinctly bent posteriad and terminating close to the wing apex; crossveins regularly arranged and presence of the least well-defined outer gradate series in radial sector; MP forked distant from wing base, beyond MA divergence.

The heterogeneous rapismatid genus-group is represented by four extant genera *Adamsiana* Penny, 1996, *Narodona* Navás, 1929, *Oliarces*, and *Rapisma* McLachlan, 1866 and two extinct genera *Allorapisma* and *Principiala*. Although this clade has not received a firm support in the phylogenetic analysis of Winterton and Makarkin (2010), they share some distinctive features, including: distal parts of Sc and R1 separated; Sc and R1 distinctly bent posteriad, and the ending close to the wing apex;

Table 1. Comparisons of *Guithone* gen. nov. with three lineages of Ithonidae. Putatively apomorphic states in bold. ¹ Separated Sc and R1 occurs in all extant ithonid genus-group and most rapismatid genus-group (unknown in *Principiala*). In polystoechotid genus-group, the extant genera also have the separated Sc and R1, but Sc and R1 are distinctly approximated distad in fossil polystoechotid genus-group (e.g., *Palaeopsychops* Andersen, 2001) that is different to the other groups. ² Sc and R1 in ithonid genus-group commonly straightly (or slightly bent) reach the anterior margin, however, Sc and R1 in the other groups distinctly incline posteriad and ending close to wing apex. ³ Regular arrangement of crossveins in radial sector occurs in extant giant genus-group. Although some Eocene giant genus-group also show the complicated crossvenation, these species generally possess one row of outer gradate series at least. Contrarily, crossveins in radial sector in the other groups are always numerous and irregularly arranged. Few and irregular crossveins as a particular state are only found in some fossil taxa, e.g., *Guithone* gen. nov., *Lasiosmylus* Ren and Guo, 1996, *Paleopterocalla* (Panfilov, 1980), *Panfilovdvia* (Panfilov, 1980).

Characters	<i>Guithone</i> gen. nov.	Ithonid genus-group	Polystoechotid genus-group	Rapismatid genus-group
Humeral veinlet	simple (irrecurrent)	recurrent	recurrent	recurrent
Distal parts of Sc and R1 ¹	distinctly separated	distinctly separated	closely approximated (or fused in fossil taxa)	distinctly separated
Termination position of Sc and R1 ²	reaching the anterior margin straightly before wing apex	reaching the anterior margin straightly before wing apex	distinctly bent posteriad, ending close to the wing apex	distinctly bent posteriad, ending close to the wing apex
Crossveins in radial sector ³	few and irregular arrangement	numerous and irregular arrangement	regular arrangement and forming one row of outer gradate series at least	numerous and irregular arrangement
Position of MP first fork	distant from wing base, beyond MA divergence	distant from wing base, beyond MA divergence	distant from wing base, beyond MA divergence	proximal MA divergence
Branching pattern of MP2	dichotomously branched	dichotomously branched	pectinately branched	dichotomously branched

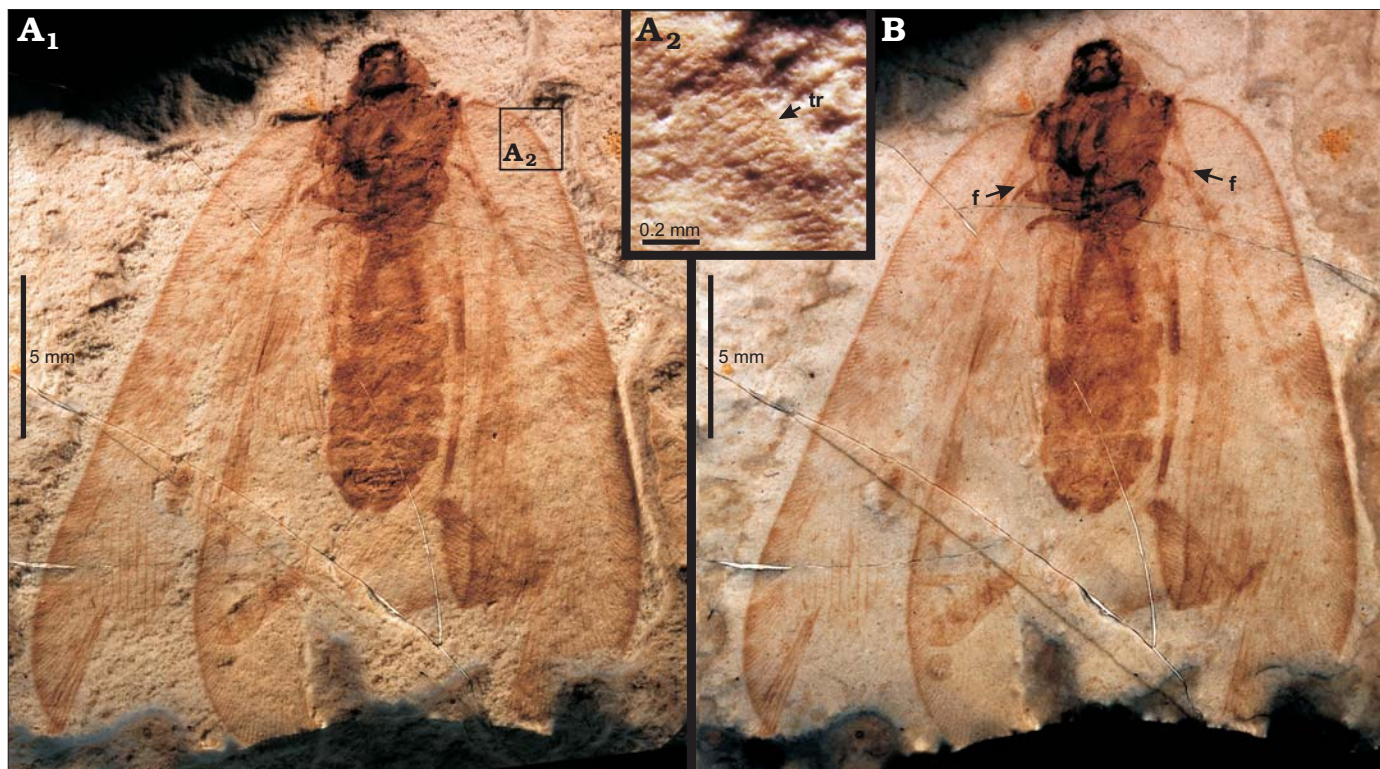


Fig. 1. Moth lacewing *Guithone bethouxi* gen. et sp. nov. holotype (CNU-NEU-NN2015003P/C) from Bathonian–Callovian boundary (Middle Jurassic) of Jiulongshan Formation of Daohugou, China. Photographs: dry-ethanol (A) and ethanol-ethanol (B) composites; detail (A₂). tr, trichosors; f, frenulum.

numerous and irregular crossveins arranged in radial sector; MP forked proximad of MA divergence.

The abovementioned combinations of character states can be used to differentiate the three main lineages of the family. This work must be considered as a preliminary arrangement at the genus level, based on the available data. It could be greatly helpful to reconsider the classification of Ithonidae including both fossil and extant species in the future.

Stratigraphic and geographic range.—Jiulongshan Formation, Middle Jurassic; Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China.

Genus *Guithone* nov.

Etymology: From Chinese *gu*, ancient; and the extant genus name *Ithone*.

Type species: *Guithone bethouxi* gen. et sp. nov., monotypic, see below.

Diagnosis.—The same as for the monotypic type species.

Remarks.—Although the specimen of the type species of this genus is only sub-complete, useful characters could be investigated. The new genus is assigned to the Ithonidae according to the following characters: stout body, head hypognathous and concealed under pronotum, and extremely broad costal space at the base (Fig. 1A₁, B). To determine the systematic position of *Guithone* gen. nov. within Ithonidae, a comparison was conducted between the new genus and the three main lineages (Table 1). It is noticeable that a simple humeral veinlet (irrecurrent) occurs in the new genus, in contrast to the other genera of Ithonidae that commonly possess the recurrent humeral vein-

let. Makarkin et al. (2013) pointed that the recurrent humeral veinlet as an apomorphy of Neuroptera independently evolves in different families within this order. As for Ithonidae, the recurrent humeral veinlet should be a possible synapomorphy of this family considering the general occurrence at most known genera. Essentially, the humeral veinlet of *Guithone* gen. nov. also exhibits a “recurrent trend” in comparison with other genera (Figs. 2A, B, 3A). Consequently we consider that the form of humeral veinlet in *Guithone* gen. nov. represents an intermediate state in the evolution of the character within the Ithonidae.

The Table 1 summarized the distribution of wing venation character states among three genus-groups of Ithonidae, as compared to the states exhibited by *Guithone* gen. nov. It shows that the new genus shares most character states with the ithonid genus-group. Therefore, we propose that *Guithone* gen. nov. should be assigned to this group, hence representing its eldest record of this lineage, as well as the first record in the Northern Hemisphere.

Stratigraphic and geographic range.—As for the type species by monotypy.

Guithone bethouxi sp. nov.

Figs. 1–3.

Etymology: In honour of Olivier Béthoux to acknowledge his sincere help to Bingyu Zheng.

Holotype: CNU-NEU-NN2015003P/C, a nearly completely preserved male specimen with clearly visible structures, and four overlapping, sub-complete wings, partially folded.

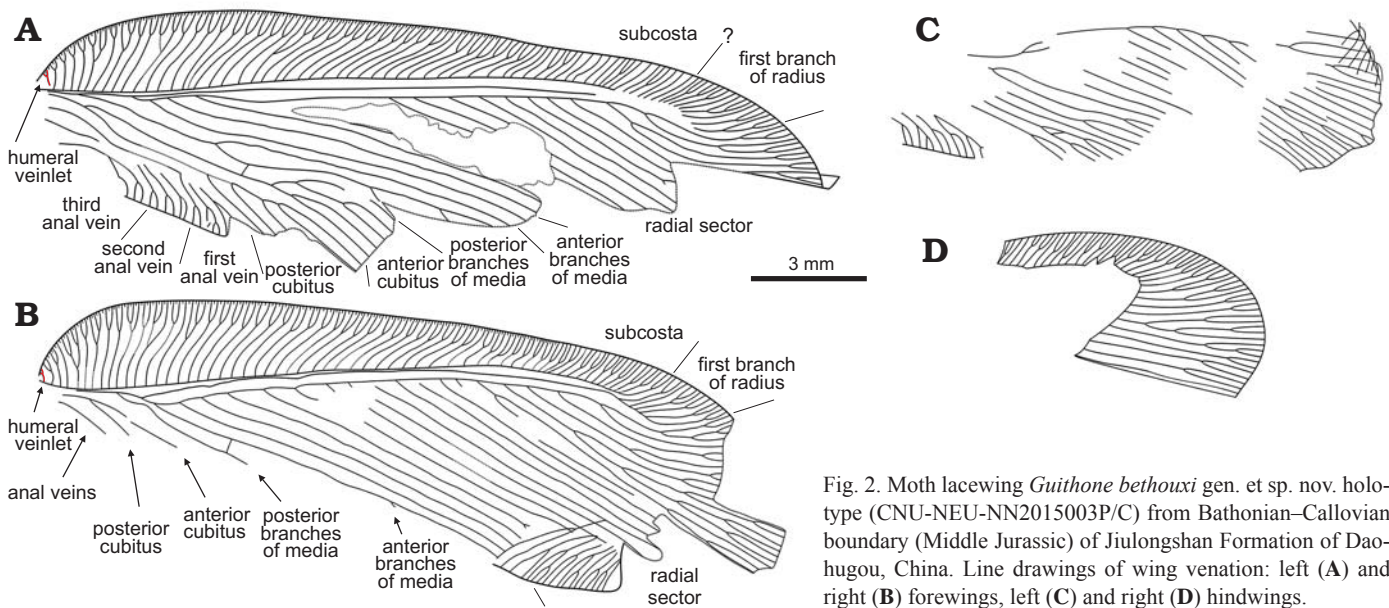


Fig. 2. Moth lacewing *Guithone bethouxi* gen. et sp. nov. holotype (CNU-NEU-NN2015003P/C) from Bathonian–Callovian boundary (Middle Jurassic) of Jiulongshan Formation of Daohugou, China. Line drawings of wing venation: left (A) and right (B) forewings, left (C) and right (D) hindwings.

Type locality: Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China.

Type horizon: Jiulongshan Formation, Bathonian–Callovian boundary beds (165 Ma), Middle Jurassic.

Diagnosis.—Trichosors present along the anterior margin; humeral veinlet simple, not recurrent; costal crossveins sinuous at their base, with distal dichotomous forks (rarely trichotomous); Sc and R1 reaching the anterior margin separately; few crossveins in the radial sector; MP fork beyond the separation of MA from Rs.

Description.—*Body*: well preserved, ca. 14.5 mm long, robust, with few hairs on the surface; head hypognathous, concealed under pronotum, ca. 1.2 mm long; antennae not preserved; compound eyes large, as wide as the half of frons; ocelli absent; mandible stout, apical portion sharp; thorax stout, less hairy; scutums in mesoscutum nearly round on both sides; mesoscutum of similar size as metascutum; legs medium-sized (ca. 1.5 mm), covered by abundant setae; tarsal claws short, sharp, with arolium at base of each; abdomen stout. Gender masculine.

Forewing: slender, ca. 19.3 mm long and 5.2 mm wide as preserved; dense hairs along margin and veins. Trichosors distributed (Fig. 1A₂) along the proximal half of anterior margin; nygmata not detected; costal area shrinking gradually from the base to apex (2.2 mm maximum width, 0.9 mm minimum width); humeral veinlet not recurrent (Figs. 2A, B, 3A); costal crossveins slightly sinuous at the base, and dichotomously forked distally (rarely trichotomous); Sc and R1 separated distally, reaching the anterior margin before wing apex (Fig. 3B); subcostal space narrowed basad and broadened distad (possibly as a consequence of compression); Rs slightly zigzagged in distal portion, with 17 regularly pectinate branches; MA simple, and the divergence of MA close to the origin of Rs; MP forked beyond the divergence point of MA from Rs; MP2 only partly preserved, first fork near mid-length of wing; CuA simple; CuP pectinately branched; anal region well developed, A1–A3 each with 2–4 distal branches.

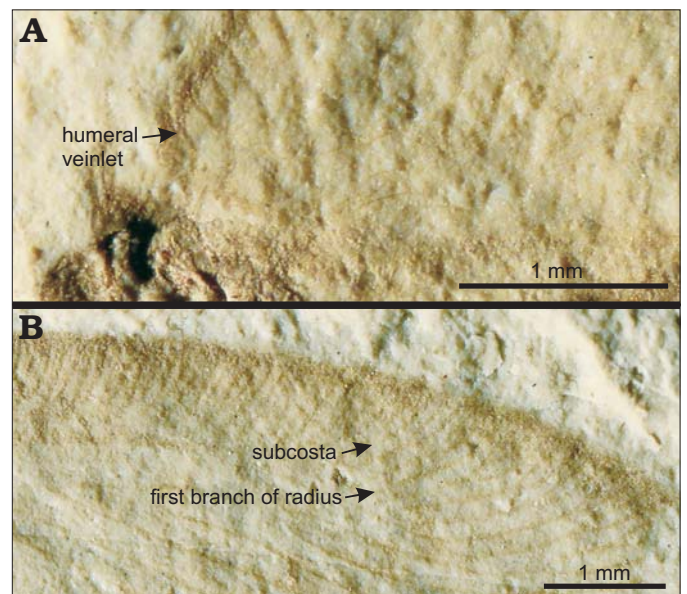


Fig. 3. Moth lacewing *Guithone bethouxi* gen. et sp. nov. holotype (CNU-NEU-NN2015003P/C) from Bathonian–Callovian boundary (Middle Jurassic) of Jiulongshan Formation of Daohugou, China. Dry photographs of details of the left forewing venation: proximal part of costal area (A), distal of subcosta and first branch of radius (B).

Hindwing: incompletely preserved, main veins hardly identifiable; trichosores not detected; frenulum well preserved, visible on both hindwings (Fig. 1B). Wing membrane tinged with irregular pale brown shades.

Concluding remarks

Ithonidae had its golden time in the Mesozoic, however, most fossil taxa of this family have no further subdivisions due to the lack of identified characters of the subclades. Based on available data, we aimed to provide some diagnostic wing venation features of the three principle lineages, which allowed

us to preliminarily allocate fossil taxa to one of the three genus-groups. Additionally, a new, convincing moth lacewing is described from the Middle Jurassic of China, representing the first record of this lineage in the Northern Hemisphere. Before the finding of *Guithone* gen. nov., the Gondwanan origin of moth lacewings was inferred from the constricted distribution of the extant genera. Nevertheless, the new genus provides the new insights on the evolution of moth lacewings. It indicates that differentiation between the giant lacewings and moth lacewings must have occurred before the Middle Jurassic. Additionally, a remarkable disjunct distribution across the fossil and extant genera within the moth lacewings implies that the pattern of moth lacewings evolution was probably more complicated than previously thought.

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