

New Fossil Lepidoptera (Insecta: Amphiesmenoptera) from the Middle Jurassic Jiulongshan Formation of Northeastern China

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Abstract

Background: The early history of the Lepidoptera is poorly known, a feature attributable to an inadequate preservational potential and an exceptionally low occurrence of moth fossils in relevant mid-Mesozoic deposits. In this study, we examine a particularly rich assemblage of morphologically basal moths that contribute significantly toward the understanding of early lepidopteran biodiversity.

Methodology/Principal Findings: Our documentation of early fossil moths involved light- and scanning electron microscopic examination of specimens, supported by various illumination and specimen contrast techniques. A total of 20 moths were collected from the late Middle Jurassic Jiulongshan Formation in Northeastern China. Our principal results were the recognition and description of seven new genera and seven new species assigned to the Eolepidopterigidae; one new genus with four new species assigned to the Mesokristenseniidae; three new genera with three new species assigned to the Ascololepidopterigidae fam. nov.; and one specimen unassigned to family. Lepidopteran assignment of these taxa is supported by apomorphies of extant lineages, including the M₁ vein, after separation from the M₂ vein, subtending an angle greater than 60 degrees that is sharply angulate at the junction with the r–m crossvein (variable in Trichoptera); presence of a foretibial epiphysis; the forewing M vein often bearing three branches; and the presence of piliform scales along wing veins.

Conclusions/Significance: The diversity of these late Middle Jurassic lepidopterans supports a conclusion that the Lepidoptera–Trichoptera divergence occurred by the Early Jurassic.

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Introduction

The Lepidoptera, or butterflies and moths, are one of the most speciose lineages of herbivores, currently including about 157,500 described species encompassing the four suborders of Zeugloptera, Aglossata, Heterobathmiina, and Glossata [1]. In contrast to the documented paleodiversity of other diverse insect lineages [2], the Lepidopteran fossil record is depauperate [3]. Only two extant suborders, Zeugloptera and Glossata, and an extinct suborder, Eolepidopterigina proposed by Rasnitsyn [4], are represented in the fossil record. Speciosity of the basal lepidopteran lineages is minimal in the fossil record, as in the extant fauna. This may be a consequence of the Lepidoptera once constituting a minor group

of the world's fauna, following their evolution from the stem-group, the Amphiesmenoptera (Fig. 1A) [5], a major holometabolan lineage comprising two distinctive insect orders, the Lepidoptera and the Trichoptera. The taxonomic boundary between Lepidoptera and Trichoptera is often obscured in their early fossil record [3], attributable to an overall morphological similarity and presence of few apomorphic characters visible in fossil specimens [5].

Because of the rarity of Mesozoic Lepidoptera, only 24 genera, of which two are extant, have been described from the Mesozoic (Table 1) [3,6–8]. In addition, undescribed Mesozoic fossils have been reported, including unequivocal Lepidoptera larvae [5,9], and other evidence such as unequivocal or possible Lepidoptera

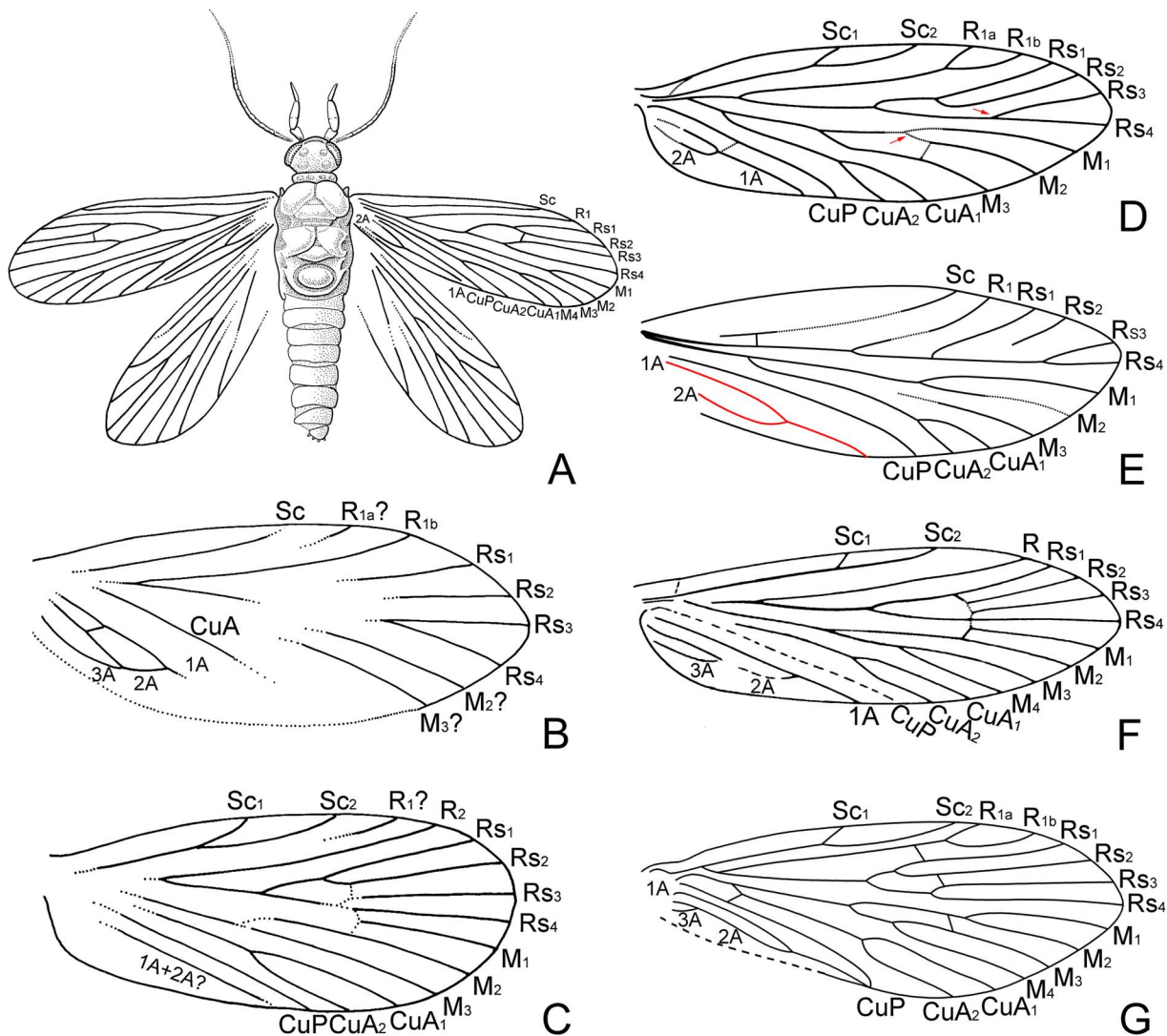


Figure 1. A stem-group amphiesmenopteran, lepidopterans, and a trichopteran. (A), A stem-group amphiesmenopteran, *Necrotaulius tener*, modified after Grimaldi and Engel [5]. (B-F), Lepidopteran forewings. (B), *Archaeolepis mane*, from Grimaldi and Engel [5]. (C), Forewing of an Early Jurassic Germany lepidopteran, from Grimaldi and Engel [5]. (D), *Undopterix sukatshevae*, modified after Skalski [10]; the red arrowhead showing Rs_{3+4} furcation beyond the M_{1+2} furcation. (E), *Netoxena nana*, modified after Martins-Neto [24]; red line indicates a single-Y configuration. (F), *Mesokristensenia sinica*, modified after Huang *et al.* [25]. (G), A trichopteran, *Juraphilopotamus lubricus*, modified after Gao *et al.* [43]. doi:10.1371/journal.pone.0079500.g001

wing scales [10–12] and unequivocal Lepidoptera leaf mines [13,14]. Mesozoic fossil Lepidoptera are principally assigned to two extinct families, the Eolepidopterigidae and the Mesokristenseniidae, and an extant family, the Micropterigidae, the latter considered the most basal extant lineage of Lepidoptera [15,16]. In addition, Kozlov erected an extinct family, the Undopterigidae to accommodate *Undopterix* Skalski, 1979 [10], but its phylogenetic placement is uncertain.

The earliest unequivocal lepidopteran fossil hitherto established is *Archaeolepis mane* Whalley, 1985 (Fig. 1B) from the Early Jurassic, about 190 million years ago (Ma), of Dorset, England [5,18,19]. The next, more recent, early fossils are eight non-monophyletic genera, dated to approximately 180 Ma, from the uppermost Lias of Dobbertin, Germany [5], which were described by Handlirsch as *Necrotauliidae*. However, Ansorge [21,22] disputed the necrotaulid affiliations of the Handlirsch's specimens and other well-preserved wings from the Grimmen locality of Germany, and

assigned most of these to the Lepidoptera on the basis of the 3-branched M vein and the presence of scales on the forewings. These fossils overwhelmingly are represented by wings. A representative forewing is shown in Fig. 1C, indicating a M with 3 branches and the M_1 , separated from the M_2 at an angle of about 70 degrees, and sharply angulate at the junction with crossvein r-m. Additionally, a forewing of *Undopterix sukatshevae*, within the Undopterigidae [23], is shown in Fig. 1D, as is a forewing of *Netoxena nana* in the Eolepidopterigidae [3,24], in Fig. 1E. Huang *et al.* [25] described *Mesokristensenia sinica* in the Mesokristenseniidae, the forewing of which is shown in Fig. 1F. For comparison, the forewing of a trichopteran, *Juraphilopotamus lubricus* Wang, Zhao & Ren, 2009 [17], is shown in Fig. 1G.

Recently, we collected 20 well-preserved, nearly complete fossil lepidopterans from the Jiulongshan Formation at Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, in China. This deposit was radiometrically dated by $^{40}\text{K}/^{40}\text{Ar}$ at

Table 1. Known fossil records of Mesozoic Lepidoptera.

Suborder	Family	Genus	Species	Epoch	Country	Reference
?	Archaeolepididae	<i>Archaeolepis</i> Whalley, 1985	<i>A. mane</i> Whalley, 1985	J1	United Kingdom	[18]
Eolepidopterigina	Eolepidopterigidae	<i>Eolepidopterix</i> Rasnitsyn, 1983	<i>E. jurassica</i> Rasnitsyn, 1983	J3	Kazakhstan	[4]
Eolepidopterigina	Eolepidopterigidae	<i>Palaeolepidopterix</i> Kozlov, 1989	<i>P. aurea</i> Kozlov, 1989	J3	Kazakhstan	[40]
Eolepidopterigina	Eolepidopterigidae	<i>Daiopterix</i> Skalski, 1984	<i>D. rasnitsyni</i> Skalski, 1984	K1	Russia	[23]
Eolepidopterigina	Eolepidopterigidae	<i>Daiopterix</i> Skalski, 1984	<i>D. olgae</i> Kozlov, 1989	K1	Russia	[40]
Eolepidopterigina	Eolepidopterigidae	<i>Netoxena</i> Sohn, 2012	<i>N. nana</i> (Martins-Neto, 1999)	K1	Brazil	[24,52]
Eolepidopterigina	Eolepidopterigidae	<i>Undopterix</i> Skalski, 1979	<i>U. sukatshevae</i> Skalski, 1979	K1	Russia	[10]
Eolepidopterigina	Eolepidopterigidae	<i>Undopterix</i> Skalski, 1979	<i>U. cariensis</i> Martins-Neto & Vulcano, 1989	K1	Brazil	[39]
Eolepidopterigina	Eolepidopterigidae	<i>Gracileopterix</i> Neto & Vulcano, 1989	<i>G. pulchra</i> Martins-Neto & Vulcano, 1989	K1	Brazil	[39]
Zeugloptera	Micropterigidae	<i>Sabatinca</i> Walker, 1863	<i>S. perveta</i> (Cockerell, 1919)	K1	Burma	[12,42]
Zeugloptera	Micropterigidae	<i>Parasabatinca</i> Whalley, 1978	<i>P. aftimacrai</i> Whalley, 1978	K1	Lebanon	[45]
Zeugloptera	Micropterigidae	<i>Parasabatinca</i> Whalley, 1978	<i>P. caldasae</i> Martins-Neto & Vulcano, 1989	K1	Brazil	[39]
Zeugloptera	Micropterigidae	<i>Palaeosabatinca</i> Kozlov, 1988	<i>P. zherichini</i> Kozlov, 1988	K1	Russia	[16]
Zeugloptera	Micropterigidae	?	?	J1	Germany	[21,22]
Zeugloptera	Micropterigidae	?	?	K1	Lebanon	[53]
Zeugloptera	Micropterigidae	?	?	K1	Burma	[5,52,54]
Zeugloptera	Micropterigidae	?	?	K1	Spain	[52,55]
?	?	?	?	?	Burma	[52,56]
Zeugloptera	?Micropterigidae	<i>Auliepterix</i> Kozlov, 1989	<i>A. mirabilis</i> Kozlov, 1989	J3	Kazakhstan	[40]
Zeugloptera	?Micropterigidae	<i>Auliepterix</i> Kozlov, 1989	<i>A. minima</i> Kozlov, 1989	J3/K1	Mongolia	[40]
Zeugloptera	?Micropterigidae	?	?	J3/K1	France	[9,16]
Zeugloptera	?Micropterigidae	?	?	J3/K1	France	[57]
?	Mesokristenseniidae	<i>Mesokristensenia</i> Huang et al., 2010	<i>M. latipenna</i> Huang et al., 2010	J2	China	[25]
?	Mesokristenseniidae	<i>Mesokristensenia</i> Huang et al., 2010	<i>M. sinica</i> Huang et al., 2010	J2	China	[25]
?	Mesokristenseniidae	<i>Mesokristensenia</i> Huang et al., 2010	<i>M. angustipenna</i> Huang et al., 2010	J2	China	[25]
Glossata	Bucculatricidae	<i>Bucculatrix</i> Zeller, 1839	<i>B. platani</i> Kozlov, 1988	K2	Kazakhstan	[16]
Glossata	Incurvariidae	?	?	K2	Russia	[10]
Glossata	Incurvariidae	?	?	K1	Brazil	[5]
Glossata	Incurvariidae	?	?	K1	Lebanon	[45]
Glossata	?Mnesarchaeidae	?	?	K2	Russia	[5,58]
Glossata	?Lophocoronidae	?	?	K2	Russia	[10]
Glossata	?	<i>Protolepis</i> Kozlov, 1989	<i>P. cuprealata</i> Kozlov, 1989	J3	Kazakhstan	[40]
Glossata	?	<i>Karataunia</i> Kozlov, 1989	<i>K. lapidaria</i> Kozlov, 1989	J3	Kazakhstan	[40]
?	?	<i>Archiptilia</i> Handlirsch, 1939	<i>A. ovata</i> Handlirsch, 1939	J1	Germany	[21,59]
?	?	<i>Epididontus</i> Handlirsch, 1939	<i>E. geinitzianus</i> Handlirsch, 1939	J1	Germany	[21,59]
?	?	<i>Metarchitaulius</i> Handlirsch, 1939	<i>M. longus</i> Handlirsch, 1939	J1	Germany	[21,59]
?	?	<i>Nannotrichopteron</i> Handlirsch, 1906	<i>N. gracile</i> Handlirsch, 1906	J1	Germany	[20,21]
?	?	<i>Palaeotaulius</i> Handlirsch, 1939	<i>P. vicinus</i> Handlirsch, 1939	J1	Germany	[21,59]
?	?	<i>Pararchitaulius</i> Handlirsch, 1939	<i>P. ovalis</i> Handlirsch, 1939	J1	Germany	[21,59]
?	?	<i>Parataulius</i> Handlirsch, 1939	<i>P. jurassicus</i> Handlirsch, 1939	J1	Germany	[21,59]
?	?	<i>Pseudorthophlebia</i> Handlirsch, 1906	<i>P. platyptera</i> Handlirsch, 1906	J1	Germany	[20,21]
?	?	? <i>Paratrachopterygidium</i> Handlirsch, 1906	<i>P. efoffum</i> Handlirsch, 1939	J1	Germany	[21,59]
?	?	? <i>Paratrachopterygidium</i> Handlirsch, 1906	<i>P. costale</i> Handlirsch, 1939	J1	Germany	[21,59]
?	?	<i>Necrotaulius</i> Handlirsch, 1906	<i>N. tener</i> Sukatsheva, 1990	K1	Russia	[50,60]

Table 1. Cont.

Suborder	Family	Genus	Species	Epoch	Country	Reference
Glossata	?	?	?	K1	Burma	[54]
Glossata	?	?	?	K2	USA	[61]
Glossata ¹	Nepticulidae	?	?	K1	USA	[13]
Glossata ¹	Gracillariidae	?	?	K1	USA	[13]
Glossata (larva)	?	?	?	K1	Lebanon	[62]
Glossata (larva ²)	?	?	?	K2	Canada	[9]
Glossata (larva)	?	?	?	K1	Lebanon	[5]
?	?	?	?	K1	Spain	[63]

Notes: ¹Leaf mine;

²Head capsule. J1, Early Jurassic; J2, Middle Jurassic; J3, Late Jurassic; K1, Early Cretaceous; K2, Late Cretaceous.

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164–165 Ma [26], a date supported by slightly younger isotopic dates from overlying volcanic deposits [26,27]. This date corresponds to the Callovian–Oxfordian boundary interval of the latest Middle Jurassic, using the most recent, standard international time scale [28]. The deposit contain beautifully preserved fossils of insects and other animals [29–33]. After comparison of these fossils to other Mesozoic lepidopteran specimens, we recognized below eleven new genera and fourteen new species, assigned to the three families, the Eolepidopterigidae, the Mesokristenseniidae, and the Ascololepidopterigidae fam. nov. We used additional taxa to emend diagnoses of the two previously named families, the Eolepidopterigidae and the Mesokristenseniidae. With the fossils reported by Huang *et al.* [25], these new findings, now document the third oldest-known lineage of lepidopterans.

Materials and Methods

Light Microscopy, Image Processing and Line Drawings

All specimens were microphotographed and illustrated using a Leica MZ12.5 dissecting microscope accompanied with a drawing tube attachment in Beijing, and an Olympus SZX12 stereomicroscope in Washington, DC. Images were captured using dissecting microscopes equipped with digital cameras and image processing software. The image processing software for the Beijing computer–microscope–camera system was a Nikon DXM 1200C, with NIS-elements D 2.30; and in Washington, DC, an Image-Pro 6.1 (Media Cybernetics) platform. Alcohol was used to increase the contrast of specimen structures for some images. Line drawings in Beijing were made in conjunction with Photoshop CS2 graphic software.

Electron Microscopy

We used a Philips XL30 environmental scanning electron microscope to examine shrink-wrapped specimens. Compression fossils, such as the material studied herein, generally present minimal topographic relief. This absence of microtopographic differentiation and the uncoated state of the specimens, posed a demand on specimen imaging. By varying the microscopy conditions for each specimen, including sources of illumination, such as back-scattered electrons, gas emission secondary electrons and particle detector adjustment; or alternatively, varying microtopographic aspect, spot size or accelerating voltage; we strove to find the best combination of imaging conditions within a challenging SEM environment.

The fossil specimens studied under vacuum conditions of the electron microscope necessitated a modification of specimen preparation. The presence of a poorly consolidated sedimentary matrix surrounding the fossils resulted in the spalling of particles that interfered with normal operation of the vacuum tube. A protocol was devised that solved this problem. Any matrix material that sloughed from the specimen was isolated by heat-resistant polyalfin film, used in industrial kitchens to shrink-wrap food. In contrast to polyester shrink-wrap, polyalfin film does not melt or release gas in the vacuum chamber. The shrink-wrapping of stub-mounted specimens in polyalfin film reduced the likelihood of costly specimen chamber contamination. Thereafter, the wrapping was carefully heat-sealed to reduce specimen bulk and promote ease of further examination. When the specimen was ready for microscopy, a window was opened over the area of interest by careful cutting of the wrapping, leaving a hole for specimen access. A thorough dusting of particles attached to the wrapping is necessary immediately preceding insertion of the specimen into the specimen chamber, particularly if the fossil has remained in storage for some time.

Measurement and Anatomical Conventions

Measurements, including body length and width, wing length and width, and wing index, follow Kristensen and Nielsen [34]. The wing index is defined as the ratio of wing width/wing length. All measurements are given in millimeters (mm). Amphimesopteran and lepidopteran apomorphies are taken from Kristensen and Skalski [15] and Huang *et al.* [25]. Family-level classification follows Nieukerken *et al.* [1]. Wing venation nomenclature is based on Wootton [35]. A proposed hypothetical forewing for Lepidoptera, modified from Kristensen and Skalski [15], is illustrated in Fig. 2A. In contrast, a hypothetical forewing for Trichoptera, modified from Holzenthal *et al.* [36], is presented in Fig. 2B. Wing veins are given as combinations of vein abbreviation and the number of vein branches. For example, Rs–4 means that the Rs has four branches; Sc–1/2 indicates that the Sc has one or two branches. Wing vein forking of branches are described as occurring at the same level (equidistant) or at a different level (variable distance) from the base of the wing. The Lepidoptera ovipositor is defined as a composite of abdominal segments VIII, IX+X and associated intersegmental membranes. Additional abbreviations of morphology are provided in the figure captions.

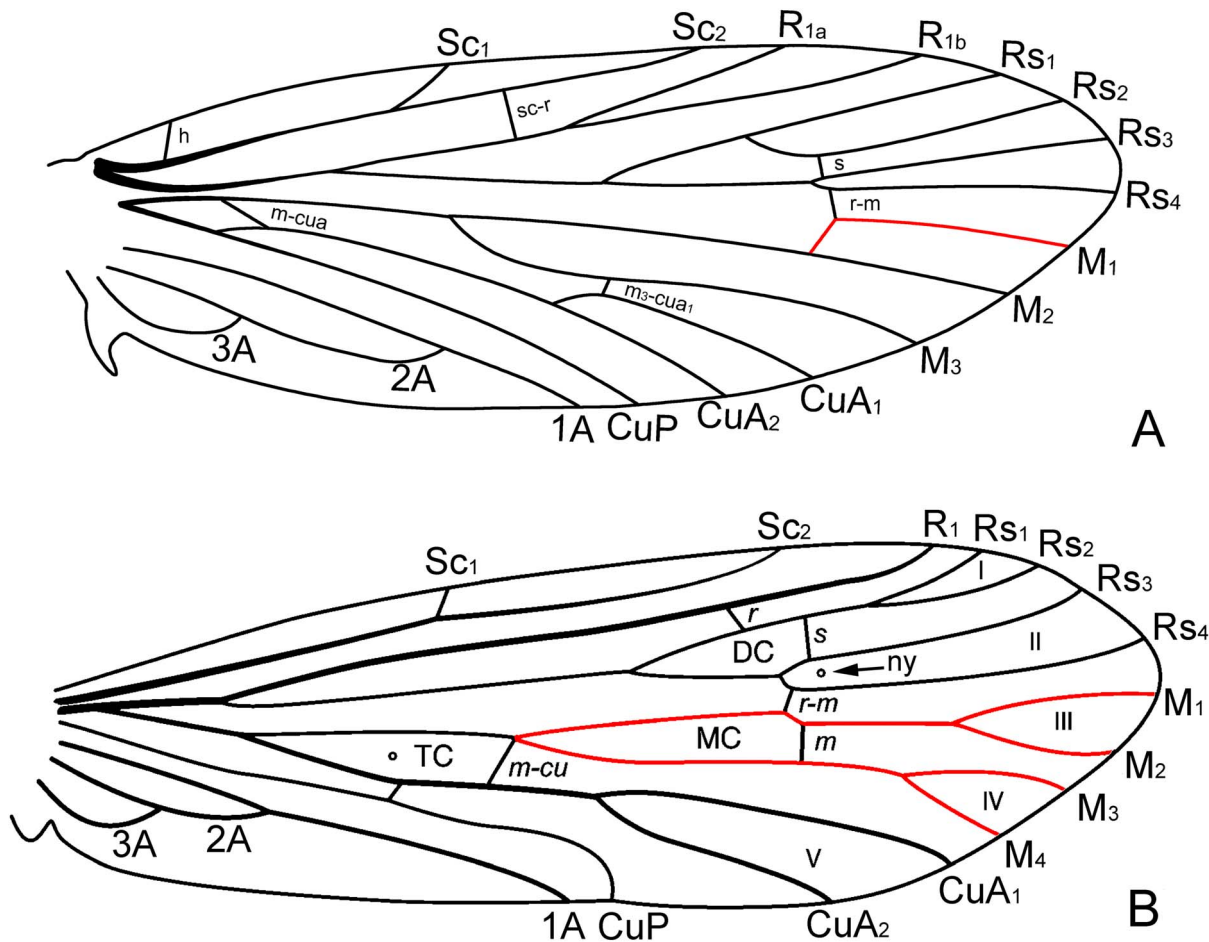


Figure 2. A hypothetical forewing of the Lepidoptera and Trichoptera. (A), A hypothetical forewing of the Lepidoptera modified after Kristensen & Skalski [15]; red line indicates that M_1 , after separation from M_2 , subtends an angle greater than 60 degrees and is sharply angulate at the junction with the r-m crossvein. (B), A hypothetical forewing of the Trichoptera modified after Holzenthal *et al.* [36]; red line indicates the separation of M_{1+2} and M_1 consisting of smooth and sublinear veins. Abbreviation: ny, nygmata.
doi:10.1371/journal.pone.0079500.g002

Etymological Sources

The primary source for Latin and Greek etymology is Simpson [37], buttressed by Brown’s compendium [38]. Linnaean designations of genus and species names were configured to be consistently either Latin or Greek, avoiding combinatorial forms with both languages in the same word.

Repository

All type specimens described in this report are deposited in the Key Laboratory of Insect Evolution and Environmental Change, College of Life Sciences, Capital Normal University, Beijing, China.

Nomenclatural Acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix

“http://zoobank.org/”. The LSID for this publication is: urn:lsid:zoobank.org:pub: AC86AB61-87FC-4353-96BB-AA03231E3BA5. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: PubMed Central, LOCKSS (www.lockss.org).

Results

Taxonomy

- Class Insecta Linnaeus, 1758.
- Order Lepidoptera Linnaeus, 1758.
- Key to the extant and fossil families of lepidoptera
- 1. Maxillary galeae forming a proboscisGlossata
- Maxillary galeae not forming a proboscis.....2
- 2. M 3-branched.....3
- M 4-branched.....5
- 3. Anterior apophyses present.....Eolepidopterigidae
- Anterior apophyses absent.....4
- 4. Sc forked; crossvein present between Sc and R; pterostigma absent.....Micropterigidae
- Sc unforked; crossvein absent between Sc and R; pterostigma present.....Heterobathmiidae

5. Metatibia without medial spur; R_1 forked.....
Ascololepidopterigidae fam. nov.
 –Metatibia with medial spurs; R_1 unforked,6
 6. Mesotibia with medial spurs; crossvein m-cua
 and crossvein cua–cup present.....Agathiphagidae
 – Mesotibia without medial spur; crossvein m-cua
 and crossvein cua–cup absent.....Mesokristenseniidae
 Suborder Eolepidopterigina Rasnitsyn, 1983.
 Family Eolepidopterigidae Rasnitsyn, 1983.

Type genus. *Eolepidopterix* Rasnitsyn, 1983 [4].

Emended diagnosis. Head with mandibulate mouthparts. Antennae filiform, less than half the length of forewing. Pronotum longer than one third the mesonotum length. Foretibia with an epiphysis. Mesotibia with one pair of spurs; metatibia with two pairs of spurs. Both pairs of wings homoneurous (the venation of the forewings and hind wings alike). Wings covered with scales. Forewing with jugum and number of vein branches as follows: Sc-1/2, R_1 -1/2, R_s -4, M-3, CuA-2, CuP-1, and A-2/3. Ovipositor with long apophyses anteriores; papillae anales long, non-piercing.

The synapomorphies for the Eolepidopterigidae are the mesotibia with a pair apical spurs, metatibia with a pair medial spurs and a pair apical spurs, wings homoneurous, forewing M vein 3-branched, and ovipositor with long apophyses anteriores.

This family is defined as a clade in Amphiesmenoptera, which have three branches of the M vein in the hind wing and the anterior margin of female abdominal segments VIII and IX with long, rod-like apodemes. This family can be assigned to Lepidoptera by the following characters: foretibia with an epiphysis, mesotibia lacking medial spurs, wings covered with scales, and forewing M vein 3-branched.

Distribution. China, Russia, Kazakhstan, Brazil.

Genera included. *Akainalepidopteron* gen. nov.; *Daiopterix* Skalski, 1984 [23]; *Dynamilepidopteron* gen. nov.; *Eolepidopterix* Rasnitsyn, 1983 [4]; *Gracileopterix* Martins-Neto & Vulcano, 1989 [39]; *Grammikolepidopteron* gen. nov.; *Longcapitalis* gen. nov.; *Netoxena* Sohn, 2012 [3] (= *Xena* Martins-Neto, 1999 [24]); *Palaeolepidopterix* Kozlov, 1989 [40]; *Petilicorpus* gen. nov.; *Quadruplecivena* gen. nov.; *Seresilepidopteron* gen. nov.; *Undopterix* Skalski, 1979 [10].

Key to the known genera of eolepidopterigidae.

1. Body longer than 9 mm; length of forewing nearly 10 mm;
hind wing with crossvein sc- r_1 near the R_1 furcation
.....*Quadruplecivena* gen. nov.
- Body less than 8 mm; length of forewing less than 9 mm;
hind wing lacking crossvein sc- r_12
2. Forewing with Sc not forked.....3
– Forewing with Sc forked.....6
3. Forewing with R_1 not forked.....4
– Forewing with R_1 forked.....5
4. Anal veins of a single-Y configuration (Fig. 1E).....*Netoxena*
– Anal veins of a double-Y configuration.....
.....*Grammikolepidopteron* gen. nov.
5. Forewing less than 3 mm; $R_{s_{1+2}}$ stalked,
ca. 1/3 of its total length.....*Gracileopterix*
– Forewing longer than 5 mm, $R_{s_{1+2}}$ stalked,
more than half of its total length.....*Palaeolepidopterix*
6. Forewing with R_1 not forked.....*Longcapitalis* gen. nov.
– Forewing with R_1 forked.....7
7. Sc branching near the base of forewing.....*Eolepidopterix*
– Sc branching distally.....8
8. $R_{s_{3+4}}$ forking beyond the $R_{s_{1+2}}$ furcation.....9
– $R_{s_{3+4}}$ and $R_{s_{1+2}}$ forking at the same level.....11
9. Forewing with $R_{s_{3+4}}$ forking level with M_{1+2} furcation
.....*Petilicorpus* gen. nov.

- Forewing with $R_{s_{3+4}}$ forking beyond M_{1+2} fork (Fig. 1D)
.....10
10. Humeral vein present on forewing.....*Undopterix*
– Humeral vein absent on forewing.....*Daiopterix*
11. Hind wing with spines on several veins.....
.....*Akainalepidopteron* gen. nov.
– Hind wing lacking spines.....12
12. Anterior margins of fore and hind wings lacking cilia;
metatibia with irregularly arranged spines.....
.....*Dynamilepidopteron* gen. nov.
– Anterior margins of fore and hind wings with cilia;
metatibia lacking spines.....*Seresilepidopteron* gen. nov.

Remarks. Kristensen [41] considered Skalski's family assignment of all species, except *Eolepidopterix jurassica*, to the Eolepidopterigidae [7] unconvincing due to lack of definitive apomorphies. Subsequently, Nieukerken *et al.* [1] placed only *E. jurassica* in the Eolepidopterigidae. We assign all the above-mentioned genera to this family for the following reasons. Skalski erected the genus *Undopterix* in Micropterigidae [10], with the type species as *U. sukatsheva* Skalski 1979. Another supposed congener was added, *U. caririensis* Martins-Neto & Vulcano, 1989 from the Crato Formation, Brazil [10,39]. The taxonomic position of this genus is controversial: some authors have placed it in Micropterigidae [10]; some assign it to the Undopterigidae [16]; whereas others considered it as Eolepidopterigidae [4,7]. Yet, *Undopterix sukatsheva* Skalski, 1979, exhibits no autapomorphies of the Micropterigidae [34]. The long apophyses of the last several abdominal segments are comparable to those present in the Eolepidopterigidae [4]. For wing venation, *Undopterix* shows similarity to Eolepidopterigidae, especially in the hind wing. *Undopterix* has R_1 forked, which is rare in Micropterigidae, but present in some members of Eolepidopterigidae, such as *Daiopterix* Skalski [23], *Seresilepidopteron* gen. nov., *Akainalepidopteron* gen. nov., *Quadruplecivena* gen. nov., and *Petilicorpus* gen. nov. Consequently, we believe it is more appropriate to place *Undopterix* in the Eolepidopterigidae. We agree with Skalski [7], followed by Sohn *et al.* [3], in considering the Undopterigidae a synonym of the Eolepidopterigidae. In addition, the Eolepidopterigidae are believed to have affinities with the Agathiphagidae [7], based on an ovipositor bearing long apophyses that is not present in Micropterigidae and Heterobathmiidae [34]. When *Gracileopterix* was erected, it was not assigned to a family [39], and because of its great similarity to *Undopterix*, we tentatively place this genus in Eolepidopterigidae.

Seresilepidopteron Zhang, Shih, Labandeira & Ren gen.

nov.

urn:lsid:zoobank.org:act:5AB2FE11-A3A1-4593-B01B-29E7C8E25C49.

Type species. *Seresilepidopteron dualis* Zhang, Shih, Labandeira & Ren sp. nov.

Etymology. The generic name, *Seresilepidopteron*, is derived from the Greek, *Seres* (Σηρες), the ancient Greek (and later similar Latin) name for northwestern China and its inhabitants, also referring to the land where silk originates; and *lepidos*, the Greek word for “scale” or “flake”; and *pteron*, Greek, for “wing” or “fin.” The root, *lepidos*, also refers to the Lepidoptera, the ordinal affiliation of this genus. The gender is masculine.

Diagnosis. Mesothorax slightly longer and wider than metathorax. All legs lacking spines. Forewing Sc and R_1 forked, all furcations of $R_{s_{1+2}}$, $R_{s_{3+4}}$ and M_{1+2} at the same level with each other. Humeral vein, sc-r crossvein and crossvein between R_1 and R_s present; three anal veins looping into a double-Y configuration; jugum present but short, lacking long setae. Hind wing Sc not forked; R_1 forked; sc-r crossvein present.

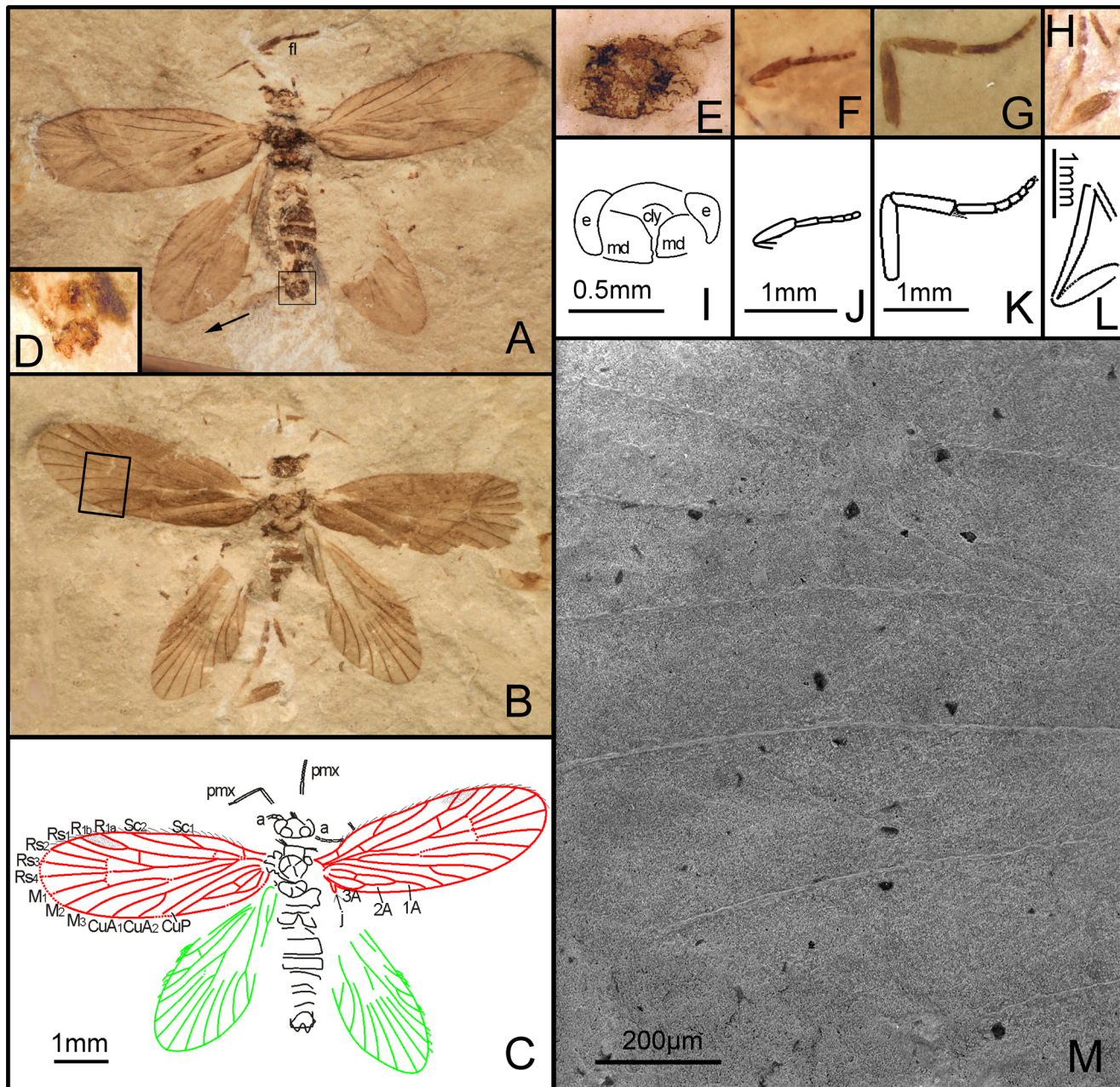


Figure 3. *Seresilepidopteron dualis* gen. et sp. nov. Male, holotype, CNU-LEP-NN-2006-001P/C. (A), Fossil specimen (counterpart). (B), Fossil specimen (part). (C), Camera lucida drawing of (A), showing overall habitus. (D), Genitalia (counterpart), outlined at (A). (E), Head and associated features (part). (F), Foreleg (counterpart). (G), Middle leg (counterpart). (H), Hind leg (part). (I) to (L), Camera lucida drawings of head (I), foreleg (J), middle leg (K), and hind leg (L). (M), SEM micrograph of left forewing venation, enlarged from the rectangular template in (B). Abbreviations: a, antennae; cly, clypeus; e, eye; fl, foreleg; j, jugum; md, mandible; pmx, maxillary palpus.
doi:10.1371/journal.pone.0079500.g003

An Eolepidopterigidae affiliation is supported by: 1), forewing with jugum; 2), M 3-branched; and 3), ovipositor segments with long apophyses anteriores.

Distribution. Inner Mongolia Autonomous Region, China.

Comparison. The venation of *Seresilepidopteron* resembles that of *Daiopterix*, but *Seresilepidopteron* differs from the latter by three anal veins looping into a double-Y configuration (vs. only two anal veins looping into a single-Y configuration). *Seresilepidopteron* resembles *Undopterix*, but it differs from the latter by: 1), having sc-r and r crossveins (vs. lacking sc-r and r crossveins); 2), the

presence of three anal veins; and 3), a double-Y configuration in the forewing (vs. two anal veins).

Seresilepidopteron dualis Zhang, Shih, Labandeira & Ren sp. nov. (Figs. 3, 4)

urn:lsid:zoobank.org:act:C4F29D5D-B13E-4BF3-84A4-A11E41319C4F.

Etymology. The specific name is derived from the Latin, *dualis* (dual, twice).

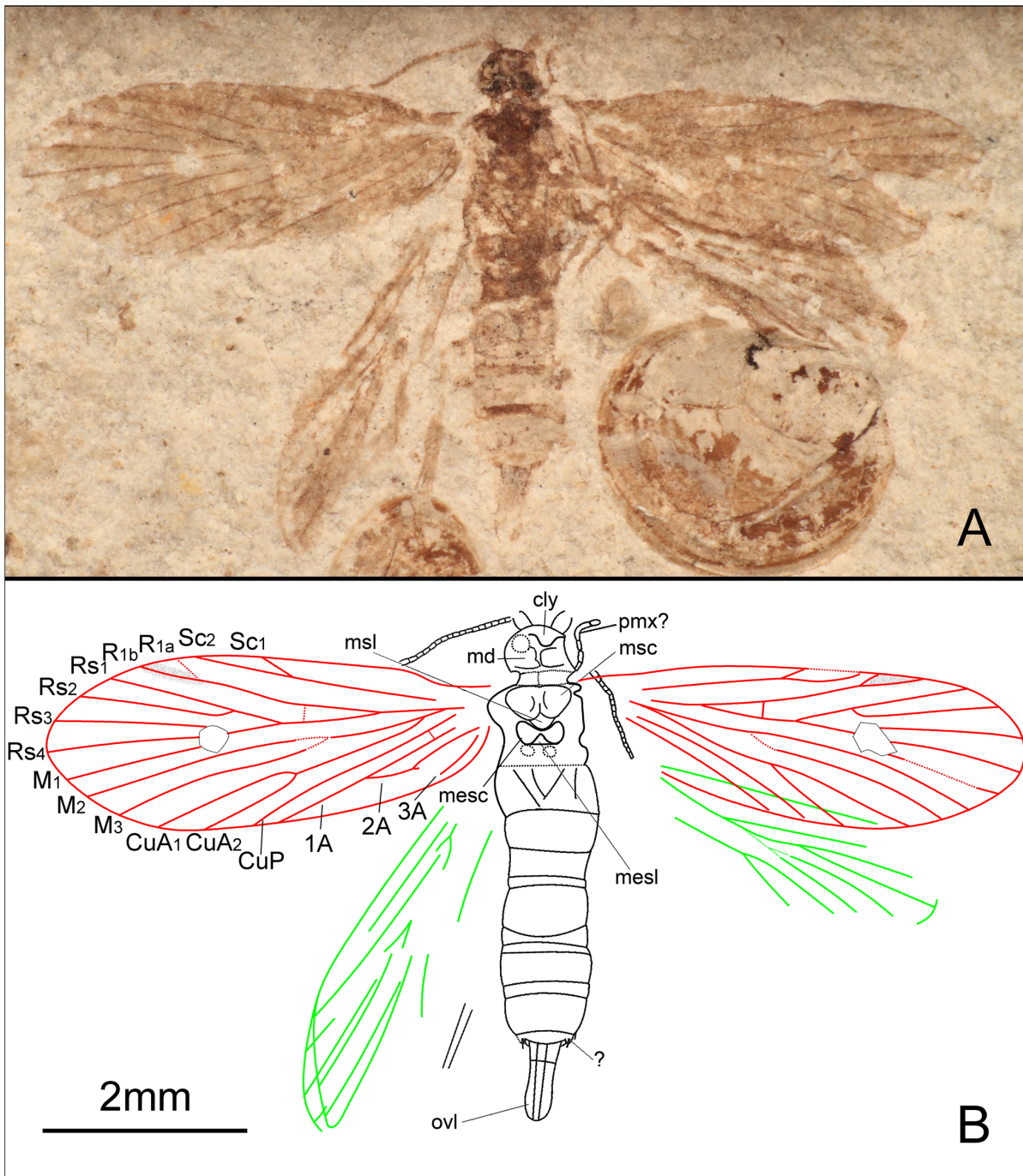


Figure 4. *Seresilepidopteron dualis* gen. et sp. nov. Female, paratype, CNU-LEP-NN-2006-002. (A), Fossil specimen, with a conchostracan at lower-right. (B), Camera lucida drawing of (A), showing overall habitus. Abbreviations: cly, clypeus; md, mandible; msc, mesoscutum; msl, mesoscutellum; mesc, metascutum; mesl, metascutellum; ovl, ovipositor lobes; pmx, maxillary palpus. doi:10.1371/journal.pone.0079500.g004

Type materials. Holotype: CNU-LEP-NN-2006-001P/C (part and counterpart); ♂; well preserved head, thorax, abdomen, fore and hind wings, parts of legs. Paratype: ♀; CNU-LEP-NN-2006-002; excellently preserved body and forewings.

Locality and horizon. These specimens were collected from Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia Autonomous Region, China. The age is latest Middle Jurassic, near the Callovian–Oxfordian boundary.

Diagnosis. Same as generic diagnosis.

Description. Male (Fig. 3). Head partially preserved; antennae filiform; compound eyes widely separated. Portions of two mandibles and clypeus visible on ventral view of head (Figs. 3E, I). Last segment of a maxillary palpus visible, with sparse setae. Mesothorax slightly longer and wider than metathorax. No traces of setal warts on thorax. Almost all segments of abdomen preserved; genitalia visible (Fig. 3D).

Foreleg (Figs. 3F, J) detached and separated ca. 0.8 mm from the head of the insect, with faint trace of epiphysis; tarsi 5-

segmented. Midleg (Figs. 3G, K) well preserved, covered with dense hairs, but detached ca. 5.0 mm from the insect. Tarsi 5-segmented, with spines; apical segment with a pair of tarsal claws. A pair of apical spurs apparent on the mesotibia (Fig. 3K). Femur of hindleg robust, detached (Figs. 3H, L); ca. 3.1 mm apart from the posterior margin of metathorax.

Forewing (Fig. 3C) with a humeral vein; costal margin bearing sparse cilia. Sc forked, stalked, gently curved; Sc₂ reaching proximal margin of pterostigma. R₁ forked, both branches of R₁ extend to pterostigma. Rs 4-branched; Rs₄ to the apex of forewing; Rs₁₊₂, Rs₃₊₄, and M₁₊₂ furcations arise at same level in the wing. Crossvein sc-r oblique, proximal to the R₁-Rs furcation. Crossvein r located midway between R₁ furcation and Rs furcation. M 3-branched, the hyaline zones surround the r-m crossvein at Rs₁₊₂, Rs₃₊₄ and M₁₊₂ furcations. CuA bifurcated; CuP simple, slightly curved terminally. Stem of M divergent from stem of R basally, just beyond humeral vein. CuA divergent from M slightly beyond R-M furcation; R forks just after M-CuA furcation. Three anal veins looping into a double-Y configuration. Crossvein between 1A and 2A present. A short, digitate jugum present in the basal posterior margin of forewing, lacking long setae. Hind wing venation (Fig. 3C) resembles forewing except Sc not forked; sc-r crossvein present proximally to R₁ furcation. Costal margin bears long bristles. Anal area poorly preserved.

Paratype: Female (Fig. 4). Head with large mandibles; antennae filiform, shorter than forewing; robust scape. Maxillary palpus 5-segmented; fourth segment longest. Mesothorax longer and wider than metathorax. Mesoscutum, mesoscutellum, metascutum and metascutellum well preserved. All abdominal segments visible; ovipositor long, well developed, with a pair of inner apophyses.

Wing venation (Fig. 4B) of female similar to male, except for the following differences: 1), Sc₂ extends to anterior wing margin at midlength in male, after midlength in female; 2), R₁ furcation in female closer to the apex than that in male; 3), in female, crossvein between R₁ and Rs located before Rs furcation on right wing, but in male after Rs furcation; 4), in female, cup-a crossvein present but no crossvein in anal area; and 5), in male, cup-a crossvein absent, but crossvein in anal area present in the female.

Measurements (in mm). CNU-LEP-NN-2006-001P/C: body length 4.3; width 0.9. Forewing length 4.7; width 1.7. Hind wing length 3.8; width 1.7. For CNU-LEP-NN-2006-002: body length 5.0 and width 1.1; forewing length 4.5 and width 1.8; and hind wing length 3.9.

Remarks. Because there are many similarities in provenance and morphology between these two specimens from the same locality, we consider these two specimens to be conspecific male and female. The minor differences in the wing venation between male and female could be attributable to either individual variation or sexual dimorphism.

Akainalepidopteron Zhang, Shih, Labandeira & Ren gen. nov.

urn:lsid:zoobank.org:act:F017D748-9F58-407E-87AF-75063A531CCA.

Type species. *Akainalepidopteron elachipteron* Zhang, Shih, Labandeira & Ren sp. nov.

Etymology. The generic name *Akainalepidopteron* is derived from the Greek *akaina*, (spine, thorn), referring to the piliform scales on the hind wing veins of this species; and “*lepidos*,” the Greek name for “scale” or “flake”; and “*pteron*,” Greek for “wing” or “fin.” The root, *lepidos*, also refers to the Lepidoptera, the ordinal affiliation of this genus. The gender is masculine.

Distribution. Inner Mongolia Autonomous Region, China.

Diagnosis. Mesotibia with few short spines; metatibia with robust spines. Forewing and hind wing bear cilia on the anterior margin. Humeral vein present in forewing. Sc and R₁ forked; all furcations of Rs₁₊₂, Rs₃₊₄, and M₁₊₂ ca. at same level with each other. Hind wing Sc not forked. R₁ forked; furcations of Rs₁₊₂, Rs₃₊₄, and M₁₊₂ almost at the same level. Long, piliform scales present on several veins of hind wing. Crossvein cua-cup present.

An Eolepidopterigidae affiliation is supported by: 1), antennae less than half the length of forewing; 2), wings homoneurous; 3), M 3-branched; and 4), crossvein absent between Sc and R.

Comparison. The diagnostic autapomorphy of *Akainalepidopteron* consists of piliform scales present on the veins of the hind wing, a character not known to exist for any other lepidopteran fossil species. *Akainalepidopteron* exhibits a great similarity to *Seresilepidopteron* in venation, but differs in the position of some crossveins. The differences are: 1), in the forewing, *Akainalepidopteron* lacks sc-r and r crossveins (vs. retention of these crossveins); 2), in the hind wing, the cua-cup crossvein is present in *Akainalepidopteron* (vs. absence); and 3), the sc-r crossvein is absent in *Akainalepidopteron* (vs. presence).

Akainalepidopteron also is similar to *Daiopterix*, especially to *D. olgae* that has wing cilia and metatibial spines. *Akainalepidopteron* is distinguished from *Daiopterix* by the following characters: 1), the cup-a crossvein is absent in *Akainalepidopteron* (vs. present); and 2), the humeral vein is present in *Akainalepidopteron* (vs. absent).

Compared with *Undopterix*, *Akainalepidopteron* is different in that: 1), it has forking of Rs₁₊₂ at the same level as forking of Rs₃₊₄ (vs. a stem Rs₁₊₂ only half length of the stem Rs₃₊₄); 2), the anterior margin of forewing and hind wing bears cilia in *Akainalepidopteron* (vs. lacking cilia); and 3), the metatibiae has spines in *Akainalepidopteron* (vs. lacking spines).

Akainalepidopteron elachipteron Zhang, Shih, Labandeira & Ren sp. nov. (Figs. 5, 6)

urn:lsid:zoobank.org:act:6D4EBD55-F1FA-4F7F-BA7E-B95C0D0C0F65.

Etymology. The specific name is derived from the Greek, *elachys* (short, small), and *pteron* (wing, fin), referring to the wing of this species that is shorter than its body length.

Type materials. Holotype: CNU-LEP-NN-2012-024; ♀; well preserved fore and hind wings; anal area covered by body and portions of the legs. Paratypes: CNU-LEP-NN-2012-023; ♀; well preserved legs; anal area covered by body and part of hind wing; and CNU-LEP-NN-2012-026; sex unknown; a well preserved forewing; anal area poorly preserved.

Locality and horizon. These specimens were collected from Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia Autonomous Region, China. The age is latest Middle Jurassic, near the Callovian-Oxfordian boundary.

Diagnosis. Same as generic diagnosis.

Description. Head length subequal to width, invested with dense setae on the anterior margin. Antennae filiform, tapered to apex; length of segments equal to their diameter. Eyes oval, with sparse setae on the outer margin.

Forecoxae more robust than forefemora; femora ca. 1.6 times as long as foretibiae, slightly longer than foretarsi. Epiphyses indiscernible. Mesocoxae more slender than forecoxae; mesofemora longer than mesotibia; two long spines present at the end of mesofemora; mesotibia with spines. Metafemora robust and short, less than half the length of metatibia; metatibia with irregularly arranged spines at the distal part, and with one pair medial spurs and one pair apical spurs. All tarsal segments with terminal spinules.

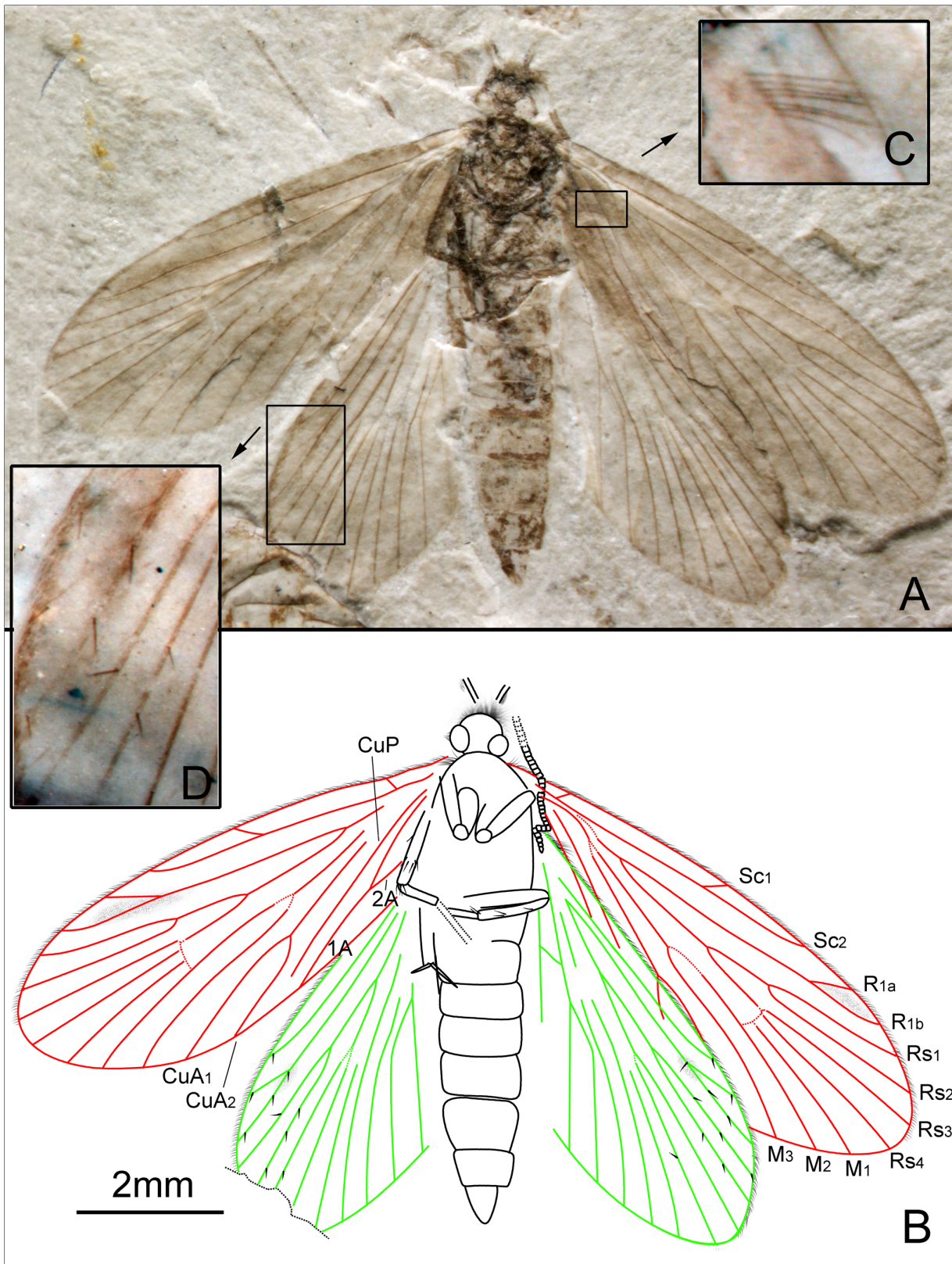


Figure 5. *Akainalepidopteron elachipteron* gen. et sp. nov. Female, holotype, CNU-LEP-NN-2012-024. (A), Fossil specimen. (B), Camera lucida drawing of (A), showing overall habitus. (C), A cluster of frenular bristles (wing coupling apparatus) on hind wing, outlined at the upper-right rectangular template in (A). (D), Piliiform scales on hind wing, outlined at the lower-left rectangular template in (A).
 doi:10.1371/journal.pone.0079500.g005

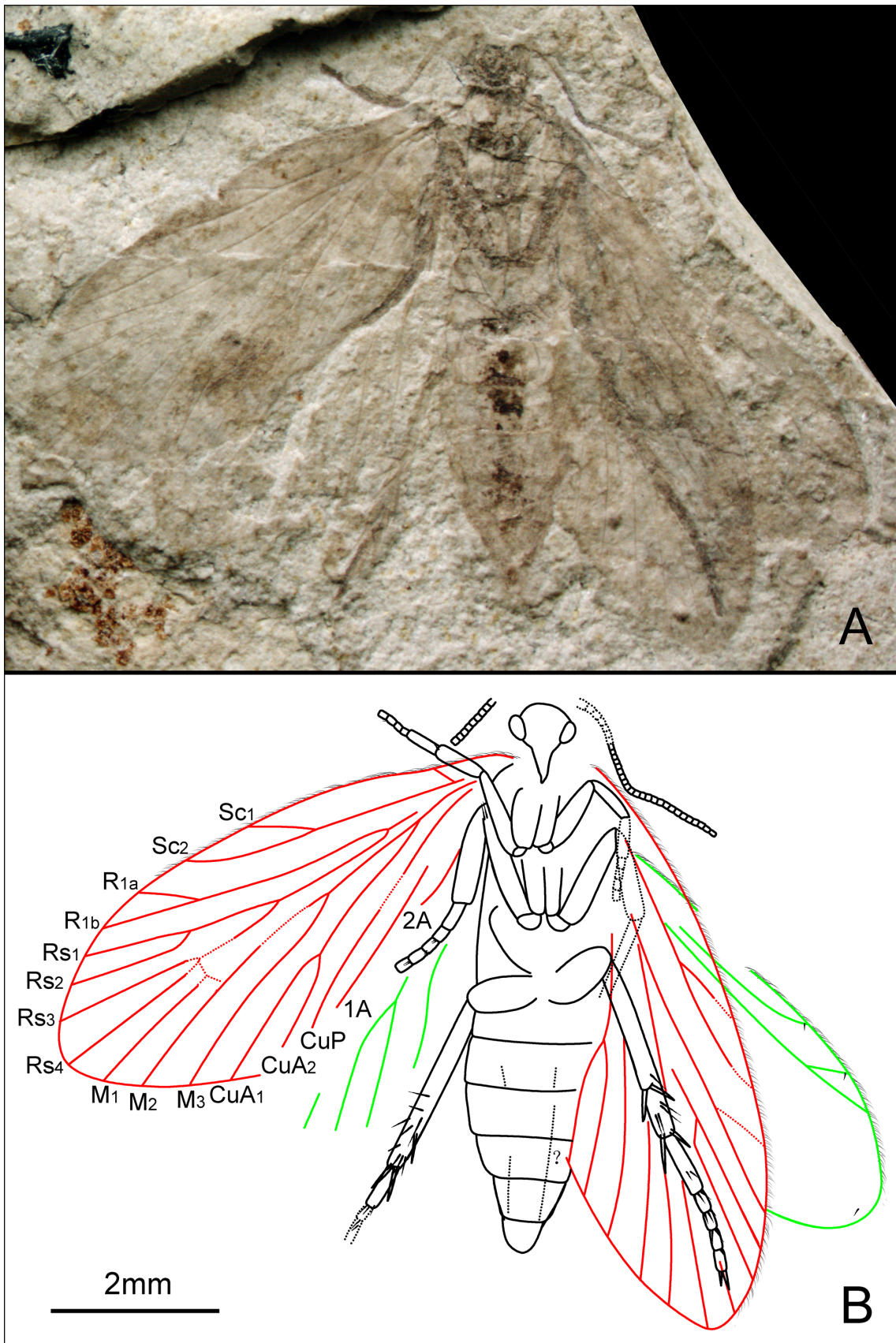


Figure 6. *Akainalepidopteron elachipteron* gen. et sp. nov. Female, paratype, CNU-LEP-NN-2012-023. (A), Fossil specimen. (B), Camera lucida drawing of (A), showing overall habitus. doi:10.1371/journal.pone.0079500.g006

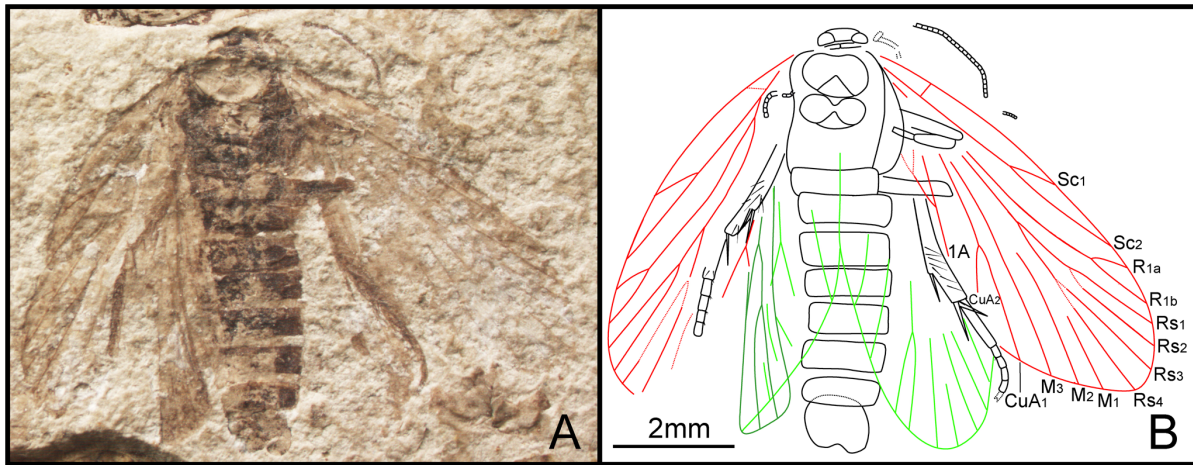


Figure 7. *Dynamilepidopteron aspinosus* gen. et sp. nov. Male, holotype, CNU-LEP-NN-2012-014. (A), Fossil specimen. (B), Camera lucida drawing of (A), showing overall habitus.
doi:10.1371/journal.pone.0079500.g007

Forewing ca. 2.9 times as long as wide; anterior margin bearing cilia; pterostigma present. Humeral vein present. Sc forked from distal 1/3 of stem; Sc₂ extending to the costal margin at 2/3 length of the wing from its base. R₁ forked distally; Rs 4-branched; Rs₄ ending slightly below the apex of forewing; Rs₁₊₂ stalked ca. 0.3–0.5 of their total length; stem Rs₁₊₂ subequal to stem Rs₃₊₄. M 3-branched. Hyaline zones surrounding r–m crossvein, at Rs₃₊₄ and M₁₊₂ furcations. CuA bifurcated; CuP simple; anal area not well preserved. CuA divergent from M. R forks immediately after M–CuA furcation. Hind wing ca. 2.4 times as long as wide; anterior margin bearing cilia, and a cluster of ca. 7 frenular bristles arising near the base of C on hind wing (Fig. 5C). Sc not forked, extending 2/3 length of the wing from its base. R₁ forked; Rs 4-branched; Rs₁₊₂ forked at the same level with Rs₃₊₄. M 3-branched. CuA bifurcated; CuP simple. Crossvein cua–cup slanted obliquely. Piliform scales ranging from 0.12 to 0.21 mm in length, present on veins Sc, R_{1a}, R_{1b}, RS₁, RS₂, RS₃ and RS₄ (Figs. 5 B,D).

Female genitalia with short ovipositor; apophyses probably present.

Measurements (in mm). CNU-LEP-NN-2012-024: body length 7.2 and width 1.5; forewing length 7.3 and width ca. 2.5; hind wing length 6.2 and width ca. 2.6. CNU-LEP-NN-2012-023: body length 6.3 and width 1.3; forewing length ca. 6.0 and width ca. 2.4; Hind wing length ca. 5.3. CNU-LEP-NN-2012-026: forewing length ca. 11.1, width 5.1.

Remarks. There are three forms of wing-coupling in Lepidoptera: the jugate, frenate and amplexi conditions. The frenular bristles on the anterior margin of the hind wing of CNU-LEP-NN-2012-024 (Fig. 5C) probably played an important role in wing-coupling. Because the jugum is not discernible in these specimens and the female possesses multiple frenular bristles, we believe that this species probably possessed a modified jugate–frenate form of wing-coupling.

Piliform scales, with lengths between 0.07 and 0.08 mm, are present on some lepidopterans, e.g. *Heterobathmia pseudierocrania* Kristensen & Nielsen, 1979, with body lengths from 3.2 to 3.6 mm and forewing lengths from 4.5 to 5.0 mm [34]. The scales present on the hind wing veins of CNU-LEP-NN-2012-024 are of similar shape and length (adjusted for lengths of body and wings) to those piliform scales along the veins of *H. pseudierocrania*.

Dynamilepidopteron Zhang, Shih, Labandeira & Ren gen. nov.

urn:lsid:zoobank.org:act:31AD01ED-D78A-45D0-8E80-AB92CC94977F.

Type species. *Dynamilepidopteron aspinosus* Zhang, Shih, Labandeira & Ren sp. nov.

Etymology. The generic name is derived from the Greek, *dynamis* (power, strength), referring to the robust hind leg of this genus; and *lepidos*, Greek for “scale” or “flake,” also referring to the ordinal name, Lepidoptera, to which this genus belongs; and *pteron*, meaning “wing” or “fin” in Greek. The gender is masculine.

Distribution. Inner Mongolia Autonomous Region, China.

Diagnosis. Body relatively large, ca. 7 mm long. Metatibia robust, with strong spines. Forewing and hind wing lack cilia on the anterior margin. Humeral vein present in forewing. Sc and R₁ forked; all furcations of Rs₁₊₂ and Rs₃₊₄ veins at same level. Hind wing lacking spines.

An Eolepidopterigidae affiliation is supported by: 1), antennae less than half the length of forewing; 2), wings homoneurous; 3), M 3-branched; and 4), crossvein absent between Sc and R.

Comparison. *Dynamilepidopteron* is similar to *Akainalepidopteron* in venation, but: 1), the former lacks cilia on the anterior wing margins (vs. both forewing and hind wing with cilia); and 2), the hind wing lacks spines on the veins (vs. spines present on the veins).

Dynamilepidopteron aspinosus Zhang, Shih, Labandeira & Ren sp. nov. (Fig. 7)

urn:lsid:zoobank.org:act:EB75EC3D-5811-43EE-9232-F755D5B1EED8.

Etymology. The specific name is derived from the Latin, *aspinosus* (the absence of spines), in reference to the hind wing lacking spines.

Type material. Holotype: CNU-LEP-NN-2012-014; ♂; well preserved forewings, thorax and hind legs.

Locality and horizon. This specimen was collected from Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia Autonomous Region, China. The age is latest Middle Jurassic, near the Callovian–Oxfordian boundary.

Diagnosis. Same as generic diagnosis.

Description. Head short and broad, possibly due to preservation. Antennae filiform; length of segments equal to their

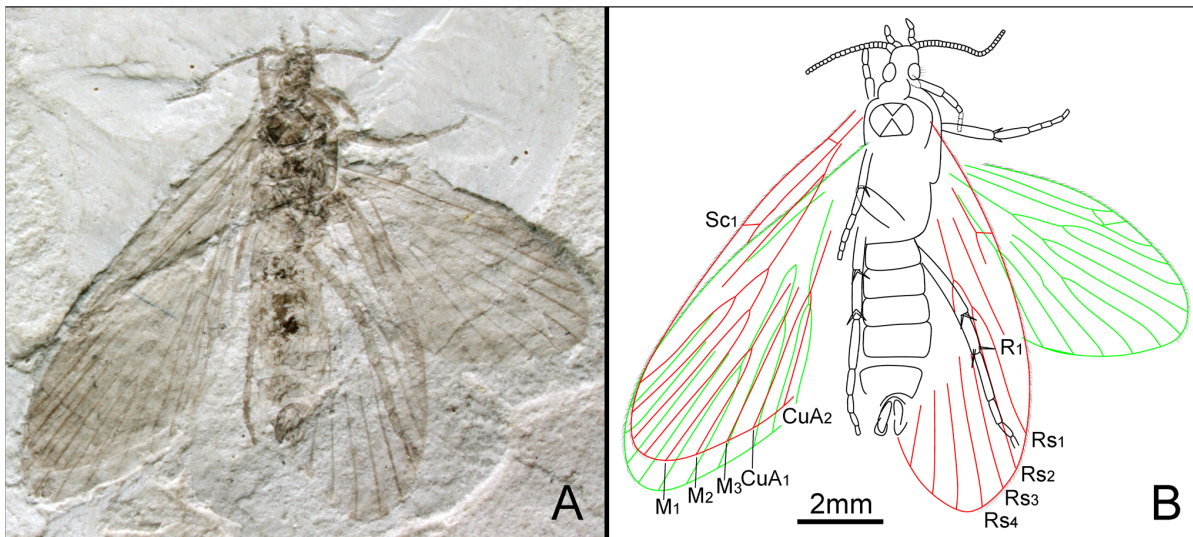


Figure 8. *Quadruplicivena celsa* gen. et sp. nov. Male, holotype, CNU-LEP-NN-2012-027. (A), Fossil specimen. (B), Camera lucida drawing of (A), showing overall habitus.

doi:10.1371/journal.pone.0079500.g008

diameter basally, the length ca. 1.5 times as long as their diameter distally. Maxillary palpus visible, obtuse aspect apically. Mesoscutum broader than long, posterior edges of mesoscutum concave along midline; mesoscutellum flabellate, relatively large, nearly equal to mesoscutum in length; metascutum dumbbell shaped; metascutellum smaller than mesoscutellum. Metatibia relatively robust; with irregularly arranged spines, bearing two pairs of spurs, one pair apically and the other pair arising slightly beyond middle of tibia; all spurs ca. 1.5–2 times as long as diameter of tibia. Metatarsi 5-segmented; tarsomere I longest, nearly equal to the total length of tarsomeres II, III, IV and V combined; two spinules at the apex of each tarsomere.

Forewing 2.8 times as long as wide. Humeral vein present. Sc forked from 2/5 of the stem length; Sc₁, extending midway along costal margin; Sc₂ beyond 2/3 the length of the wing from its base. R₁ forked distally, slightly beyond Rs₁₊₂ furcation; Rs 4-branched; Rs₄ terminating slightly below the apex of forewing; Rs₁₊₂ stalked ca. 0.3–0.4 of their total length; Rs₃ and Rs₄ free; stem Rs₁₊₂ subequal in length to stem Rs₃₊₄. M 3-branched. CuA bifurcated; CuP not preserved. Three anal veins looping into a double-Y configuration.

Measurements (in mm). Body length 7.0; width 1.9. Forewing length 6.7; width ca. 2.4. Hind wing length ca. 5.5.

***Quadruplicivena* Zhang, Shih, Labandeira & Ren gen. nov.**
urn:lsid:zoobank.org:act:878C8B3C-643E-4C46-B56A-AB-DA90AEB775.

Type species. *Quadruplicivena celsa* Zhang, Shih, Labandeira & Ren sp. nov.

Etymology. The generic name, *Quadruplicivena*, is derived from the Latin, *quadruplex* (quadruple, fourfold); and *vena* (vein, blood vessel); which jointly refers to the costal margin of hind wing that consists of a Sc, sc-r₁ crossvein and a R_{1a}, forming a quadrate configuration. The gender is feminine.

Distribution. Inner Mongolia Autonomous Region, China.

Diagnosis. Labial palpus 3-segmented. All legs lacking spines. Anterior margins of fore and hind wings with cilia. Forewing with humeral vein; Sc forked; R₁ not forked; Rs₁₊₂ forking at same level with Rs₃₊₄, and before M₁₊₂ forking. Hind wing Sc not forked; R₁ forked; sc-r₁ crossvein present.

An Eolepidopterigidae affiliation is supported by: 1), antennae less than half the length of forewing; 2), mesotibia with a pair of spurs; 3), wings homoneurous; and 4), M 3-branched.

Comparison. *Quadruplicivena* differs from *Seresilepidopteron* in the following characters: in the forewing, 1), the M₁₊₂ distinctly extends beyond the Rs₃₊₄ furcation (vs. the M₁₊₂ and Rs₃₊₄ furcations occurring at the same level); 2), the sc-r crossvein is absent (vs. presence of the sc-r crossvein); and 3), hind wing sc-r₁ crossvein is near the R₁ furcation (vs. the sc-r crossvein considerably removed from the R₁ furcation). *Quadruplicivena* differs from *Akainalepidopteron* in the following characters: 1), the M₁₊₂ furcation distinctly extends beyond the Rs₃₊₄ furcation (vs. the M₁₊₂ and Rs₃₊₄ furcations occurring at the same level); 2), the M₁ is not sharply angulate at the junction with the r-m crossvein (vs. M₁ sharply angulate at the junction with r-m crossvein); 3), the hind wing lacks spines (vs. hind wing with spines); 4), the sc-r₁ crossvein is present and the cua-cup crossvein absent (vs. the sc-r₁ crossvein absent, and the cua-cup crossvein present); and 5), the legs lack spines (vs. legs with irregularly arranged spines).

***Quadruplicivena celsa* Zhang, Shih, Labandeira & Ren sp. nov. (Figs. 8, 9)**

urn:lsid:zoobank.org:act:1EBA2307-D14A-4B56-93B2-2069AA3BA10D.

Etymology. The specific name is derived from the Latin *celsa* (eminent, noble) in reference to the labial palpi, which are prominent and resemble a crown, providing a noble or regal appearance.

Type material. Holotype: CNU-LEP-NN-2012-027; ♂; consisting of a well-preserved head, with antennae and labial palpi; well-preserved legs. Left fore- and hind wings overlapping. The right fore- and hind wings are partially preserved; the anal area is poorly preserved. The left hind wing is unusually longer than the right hind wing, probably due to deformation of the matrix or actual wing asymmetry of this particular individual.

Locality and horizon. This specimen was collected from Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia Autonomous Region, China. The age is latest Middle Jurassic, near the Callovian–Oxfordian boundary.

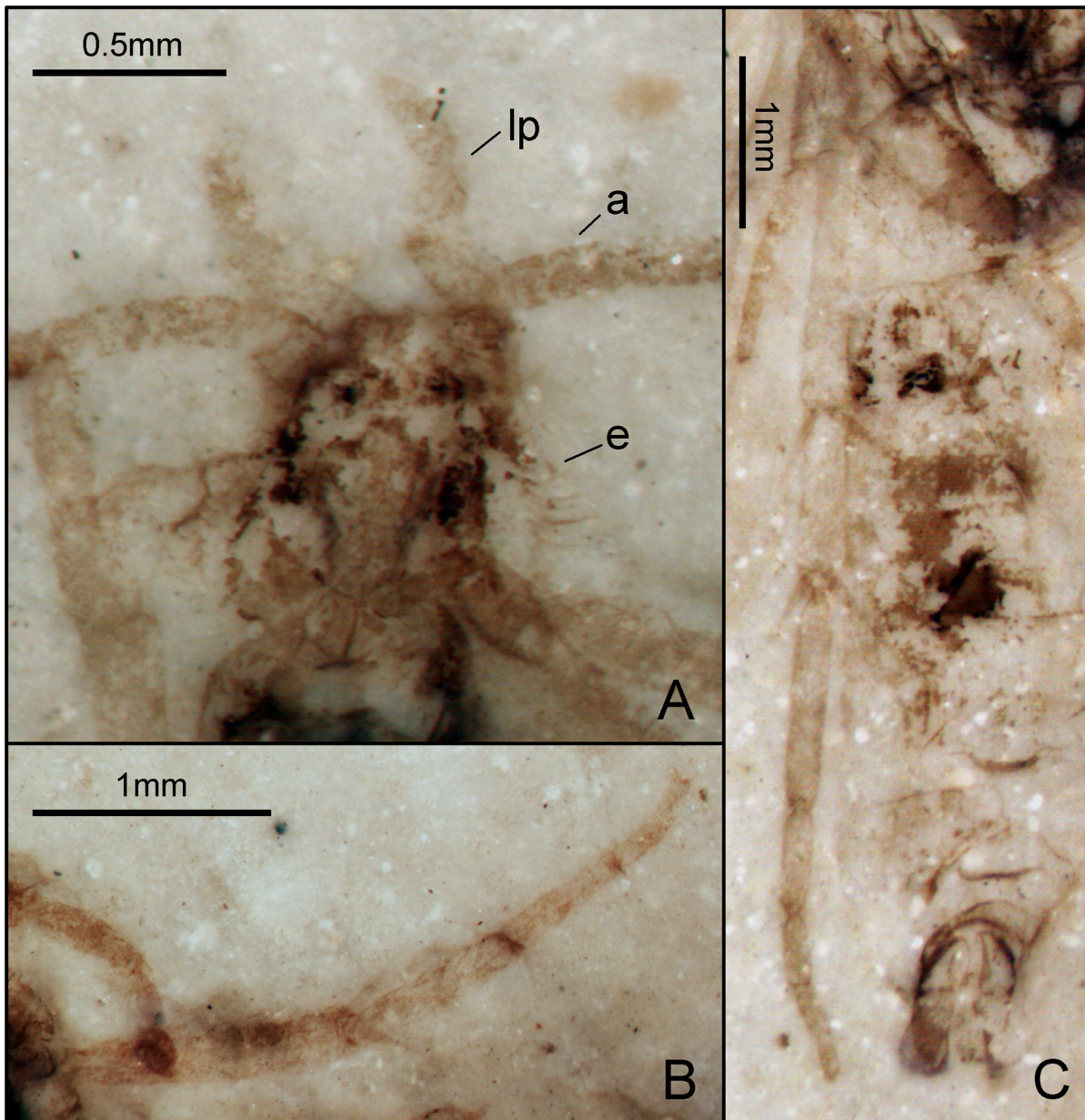


Figure 9. *Quadruplecivena celsa* gen. et sp. nov. CNU-LEP-NN-2012-027. (A), Head of fossil specimen. (B), Right mid leg. (C), Hind leg and abdomen. Abbreviations: a, antennae; e, eye; lp, labial palpus.
doi:10.1371/journal.pone.0079500.g009

Diagnosis. Same as generic diagnosis.

Description. Male. Antennae filiform, tapered to apex, ca. 1/3 as long as forewing; length of segments shorter than their diameter basally, subequal to their diameter distally. Compound eyes bearing long sparse setae. Labial palpi 3-segmented (Fig. 9A), the last two segments nearly equal in length; apical palpal segments tapered toward apex. Mesothorax with large prescutum; anterior and posterior edge of mesonotum distinctly concave along midline; mesoscutellum triangular. Foretibial epiphysis indistinct. Mesotibia with one pair of apical spurs (Fig. 9B). Metatibia with one pair of medial spurs and one pair of apical spurs (Fig. 9C). Metatarsi 5-segmented, tarsomere I ca. 1.9 times as long as tarsomere II; tarsomere II ca. 1.6 times as long as tarsomere III;

tarsomere III subequal to tarsomere IV, and slightly longer than tarsomere V. All tarsal segments lacking terminal spinules.

Forewing 3 times as long as wide; anterior margin bearing cilia. Humeral vein present. Sc forked. Rs 4-branched; Rs_{1+2} stalked ca. 0.2 of their total length; Rs_{1+2} forked at the same level as Rs_{3+4} furcation; Rs_4 and M_1 respectively above and below wing apex. M 3-branched; M_1 and M_2 stalked; M_{1+2} forked beyond Rs_{3+4} furcation. CuA bifurcated. Anal veins not preserved. In hind wing, Sc not forked. R_1 forked; crossvein $sc-r_1$ present and slightly curved and oblique, originating near end of Sc and terminating near R_1 furcation; Rs 4-branched; stem Rs_{1+2} slightly longer than Rs_{3+4} . M 3-branched; M_{1+2} forked beyond Rs_{3+4} furcation; M_3 curved at 2/3 the length of vein M_3 from its base. CuA bifurcated.

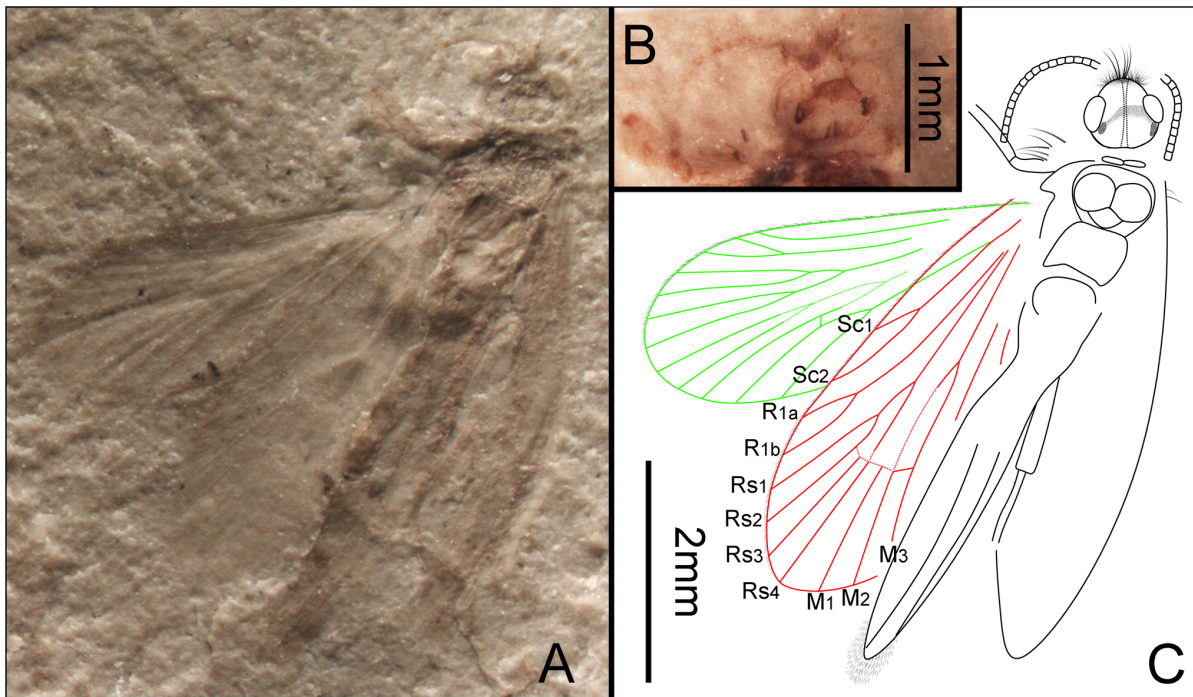


Figure 10. *Petilicorpus cristatus* gen. et sp. nov. Female, holotype, CNU-LEP-NN-2012-007. (A), Fossil specimen. (B), Head and associated structures. (C), Camera lucida drawing of (A), showing overall habitus. doi:10.1371/journal.pone.0079500.g010

Measurements (in mm). Body length ca. 9.5; width 1.9. Forewing length 9.8; width ca. 3.3. Hind wing length ca. 7.8 (right wing) and 9.8 (left wing); width 3.8 (right wing) and 3.4 (left wing).

***Petilicorpus* Zhang, Shih, Labandeira & Ren gen. nov.**

urn:lsid:zoobank.org:act:070D5F91-A174-4BE8-A0B1-503475BF1817.

Type species. *Petilicorpus cristatus* Zhang, Shih, Labandeira & Ren sp. nov.

Etymology. The generic name is derived from the Latin *petilis* (thin, slender), and *corpus* (body, substance), which collectively refers to the gracile body shape of this species. The gender is masculine.

Distribution. Inner Mongolia Autonomous Region, China.

Diagnosis. Body slender. Anterior margins of fore and hind wing with cilia. In forewing, Sc and R_1 forked; Rs branched into Rs_{1+2} , and Rs_{3+4} ; Rs_{3+4} forked beyond that of Rs_{1+2} ; Rs_{3+4} furcation nearly at same level as M_{1+2} furcation; crossvein m present. Hind wing with Sc not forked; R_1 forked. In female, apophyses well developed.

An Eolepidopterigidae affiliation is supported by: 1), wings homoneurous; 2), M 3-branched; 3), ovipositor segments with long apophyses anteriores; and 4) crossvein absent between Sc and R.

Comparison. *Petilicorpus* gen. nov. is assigned to the Eolepidopterigina for having a long apophyses in the abdomen and the M vein 3-branched in the forewing. *Petilicorpus* resembles *Eolepidopterix* in having the presence of a slender body and similar forewing length and antennal length. However, *Petilicorpus* differs from *Eolepidopterix* in the following characters: 1), the pronotum is short with a length of 0.05 mm and a width/length ratio of 8.0 (vs. pronotum relatively long with length of 0.19 mm and width/length ratio of 2.9); 2), the Sc vein is forked distally (vs. the Sc vein branching near the base of the forewing); and 3), the anterior margins of both the fore- and hind wings bear cilia (vs. lacking

cilia). The wing of *Paleolepidopterix* is not well preserved. Based on the present specimen, *Petilicorpus* can be differentiated from *Paleolepidopterix* by its longer head and shorter pronotum. The venation of *Petilicorpus* resembles *Daiiopterix* in the following characters: 1), the Sc and R_1 are forked; and 2), the Rs_{1+2} stem is shorter than the Rs_{3+4} stem. In addition, *Petilicorpus* can be separated from *Daiiopterix* by: 1), possession of a long Sc vein (vs. a short Sc vein); 2), the Sc_2 vein extending beyond the Rs_{1+2} furcation (vs. the Sc_2 not reaching the Rs_{1+2} furcation); and 3), the m crossvein is present (vs. m crossvein absent).

***Petilicorpus cristatus* Zhang, Shih, Labandeira & Ren sp. nov. (Fig. 10)**

urn:lsid:zoobank.org:act:7D597FB8-6196-4664-9BB6-087BCABF95B2.

Etymology. The specific name is derived from the Latin, *cristatus* (bearing a crest, cluster of plumes), in reference to setae on the head.

Type material. Holotype: CNU-LEP-NN-2012-007; ♀; left fore and hind wings well preserved; anal areas are obscured.

Locality and horizon. This specimen was collected from Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia Autonomous Region, China. The age is latest Middle Jurassic, near the Callovian–Oxfordian boundary.

Diagnosis. Same as generic diagnosis.

Description. Female. Body slender and entirely covered by setae. Head slightly longer than wide, anterior edge with clusters of setae pointing forward. Antennae filiform, less than half length of forewing; length of segments equal to their diameter. Eyes oval. A pair of chaetosemata present near eyes (Fig. 10B). Median ocellus absent. Prothorax much broader than length, with a pair of transverse structures that are adjacent mesially. Mesoscutum broader than long, posterior edge concave along midline; mesoscutellum flabellate, slightly shorter than mesoscutum.

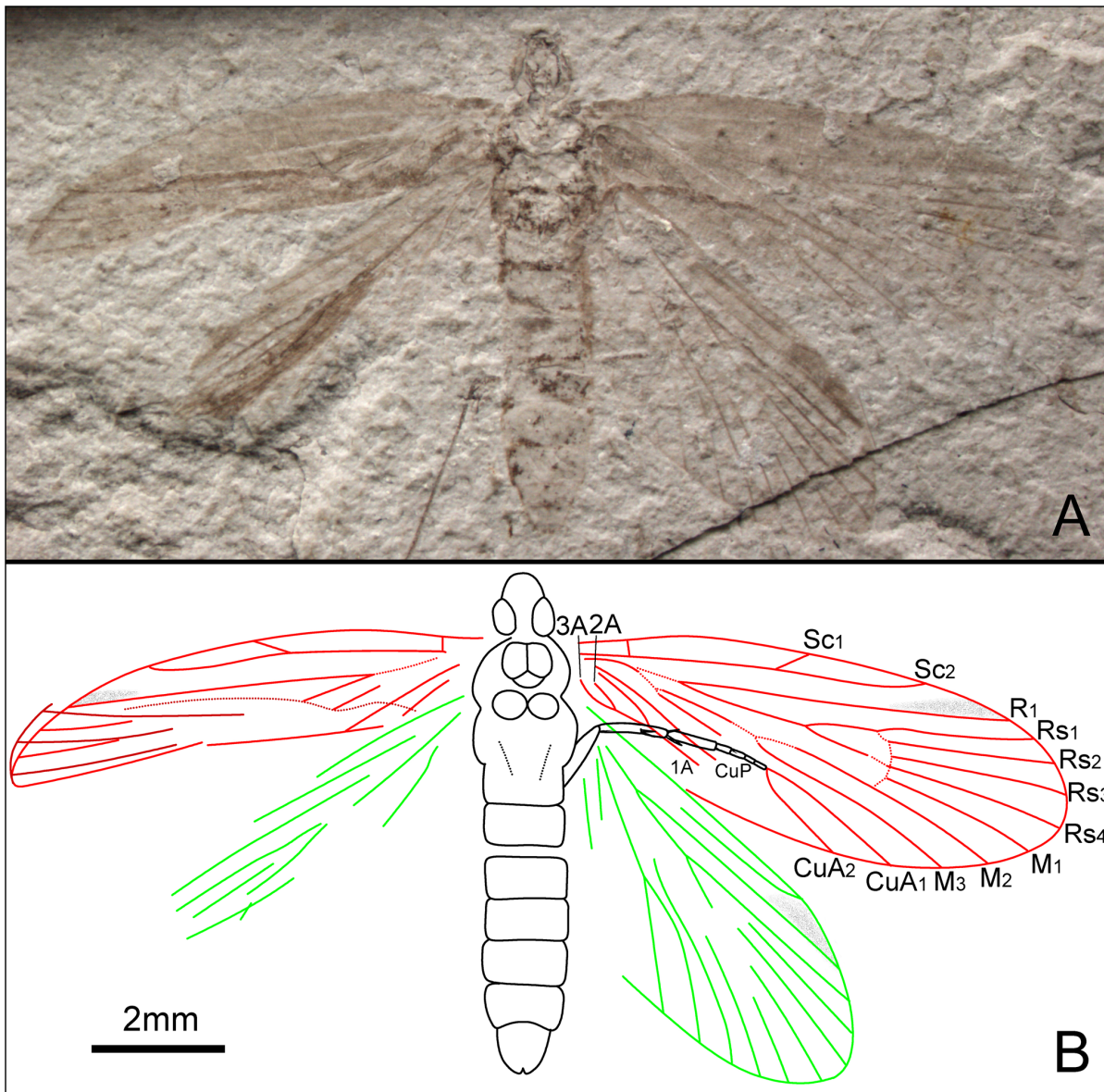


Figure 11. *Longcapitalis excelsus* gen. et sp. nov. Female, holotype, CNU-LEP-NN-2012-025P. (A), Fossil specimen. (B), Camera lucida drawing of (A), showing overall habitus.
doi:10.1371/journal.pone.0079500.g011

Mesothorax large. Long setae present on the sides of prothorax and mesothorax.

Anterior margins of both fore- and hind wings bear cilia. Forewing humeral vein indiscernible. Sc forked from distal 1/3 of the stem; Sc₁ extended to the costal margin beyond the 1/3 the length of the wing from its base; Sc₂ extended beyond the 1/2 length of the wing from its base. R₁ forked, almost at same level as the Rs₁₊₂ furcation; Rs 4-branched; Rs₄ terminating at apex of forewing; Rs₁₊₂ stalked ca. 0.4 of total vein length; Rs₃ and Rs₄ free; Rs₁₊₂ stem slightly shorter than Rs₃₊₄ stem. M 3-branched. Hyaline zones surround r-m crossvein and at Rs₃₊₄ and M₁₊₂ furcations. Crossvein m present, originating near M₁₊₂ furcation and terminating at the midpoint of M₃. Hind wing ca. 2.3 times as long as wide. Venation similar to forewing; Sc not forked, m crossvein absent and m₃-cua₁ crossvein present. CuA bifurcated. In female, apophyses slender, almost 2/3 as long as abdomen.

Abdominal terminus (possibly the papillae anales) covered by dense long setae.

Measurements (in mm). Body length 6.6; width 0.9. Forewing length 5.2; hind wing length 5.0, width ca. 2.1.

***Longcapitalis* Zhang, Shih, Labandeira & Ren gen. nov**

urn:lsid:zoobank.org:act:5DEA5662-B07C-4DF6-9784-008E56B7A61F.

Type species. *Longcapitalis excelsus* Zhang, Shih, Labandeira & Ren sp. nov.

Etymology. The generic name is derived from the Latin, *longus* (long, extended), and *capitalis* (head of a living creature), in reference to the elongate head of this species. The gender is masculine.

Distribution. Inner Mongolia Autonomous Region, China.

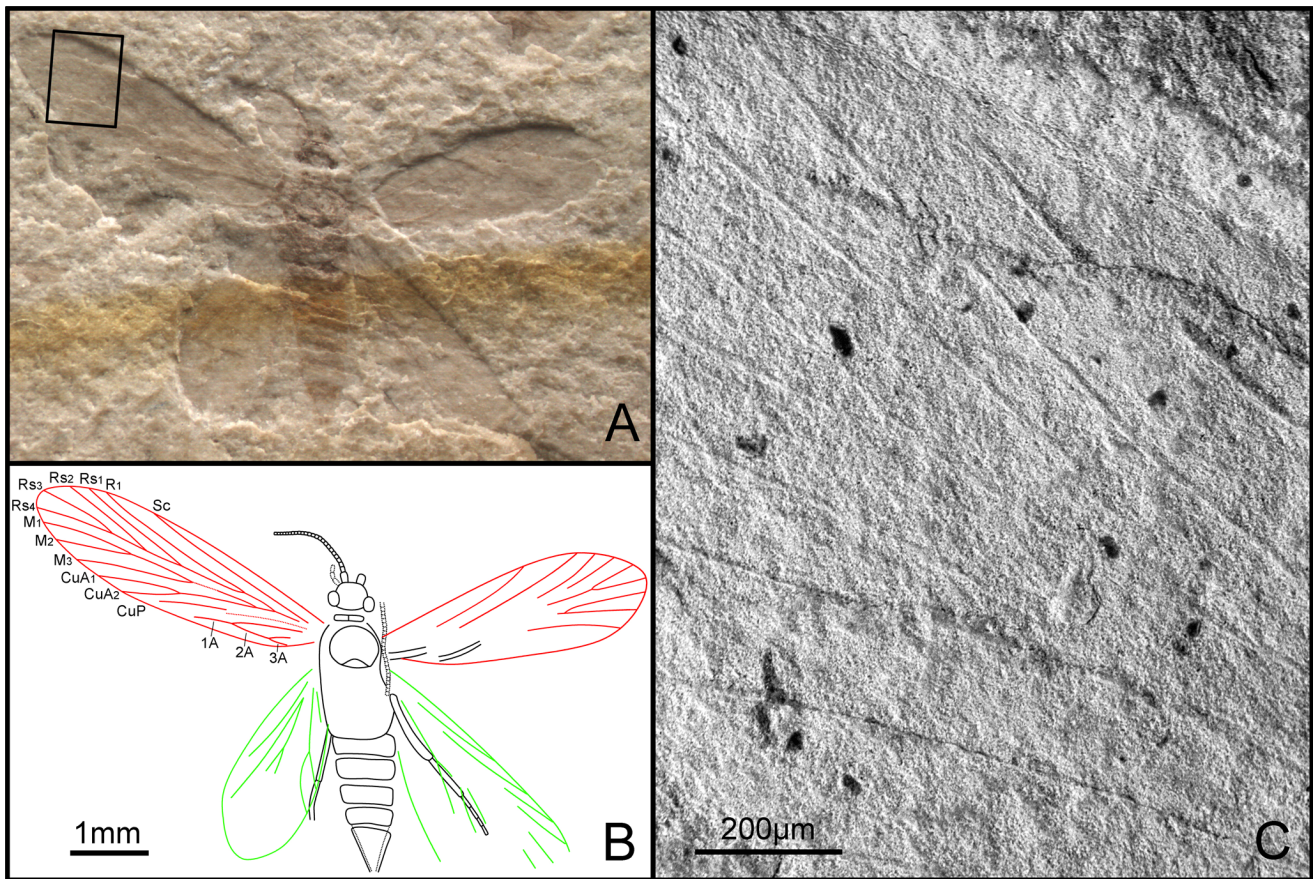


Figure 12. *Grammikolepidopteron extensus* gen. et sp. nov. Female, holotype, CNU-LEP-NN-2012-006P. (A), Fossil specimen. (B), Camera lucida drawing of (A), showing overall habitus. (C), SEM micrograph showing the left forewing venation, enlarged from the rectangular template in (A). doi:10.1371/journal.pone.0079500.g012

Diagnosis. Head longer than wide. Metatibiae lacking spines. Anterior margin of wings lacking cilia. Humeral vein in forewing present. Sc forked. R_1 not forked. All furcations of Rs_{1+2} , Rs_{3+4} , and M_{1+2} almost at the same level with each other. Anal veins looping into a double-Y configuration. Hind wing with Sc and R_1 not forked. Veins on hind wing lacking spines.

An Eolepidopterigidae affiliation is supported by: 1), wings homoneurous; 2), M 3-branched; and 3), crossvein absent between Sc and R.

Comparison. The venation of *Longcapitalis* resembles that of other Eolepidopterigidae, but this new genus lacks a R_1 furcation in the forewing, making it different from all other species of Eolepidopterigidae. *Longcapitalis* shows great similarity to the genus *Undopterix*, but it differs from the latter in the following characters: 1), the R_1 is not forked in both fore- and hind wings (vs. R_1 forked in the fore- and hind wings); 2), the Rs_{1+2} stem is as long as the Rs_{3+4} stem (vs. the Rs_{1+2} stem shorter than the Rs_{3+4} stem); and 3), the anal veins form a double-Y loop (vs. the anal veins forming a single-Y loop). *Longcapitalis* differs from *Akainalepidopteron* by the following characters: 1), the R_1 is not forked in both fore- and hind wings (vs. R_1 forked); 2), the hind wing lacks spines (vs. spines present on several veins on hind wing); 3), the wings lack cilia (vs. cilia present on anterior margins of the fore- and hind wings); and 4), the metatibiae lack spines (vs. the metatibiae bearing irregularly arranged spines).

Longcapitalis excelsus Zhang, Shih, Labandeira & Ren sp. nov. (Fig. 11)

urn:lsid:zoobank.org:act:4C76B3E1-673A-4D9C-958F-B866E4DD0055.

Etymology. The specific name is derived from the Latin, *excelsus* (tall, large), in reference to the comparatively large body size of this species.

Type material. Holotype: CNU-LEP-NN-2012-025P/C (part and counterpart); ♀; well preserved forewings, hindleg, and portion of hind wings.

Locality and horizon. This specimen was collected from Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia Autonomous Region, China. The age is latest Middle Jurassic, near the Callovian–Oxfordian boundary.

Diagnosis. Same as generic diagnosis.

Description. Head relatively long (ca. 0.9 mm), longer than wide; compound eyes elongate oval. Mesonotum slightly broader than long, with median suture; posterior edge concave along midline; mesoscutellum small, ca. half length of mesoscutum. Metafemora with a spine at the end of femora. Metatibiae with one pair medial spurs and one pair apical spurs. Metatarsi 5-segmented, all tarsal segments with terminal spinules.

Forewing 2.7 times as long as wide, bearing a humeral vein; pterostigma present. Sc forked, at distal 2/5 of the stem, Sc_1 , almost extending to the midpoint of wing costal margin; Sc_2

extending to costal margin of wing, beyond 2/3 length of wing from base. R_1 not forked; Rs 4-branched; Rs_4 extending to apex of forewing; Rs_{1+2} stalked ca. to 0.4 of the total vein length; Rs_3 and Rs_4 free; and Rs_{1+2} stem subequal to Rs_{3+4} stem. M 3-branched. Hyaline zones surround r-m crossvein at Rs_{1+2} furcation, and at the Rs_{3+4} , M_{1+2} and M_{1+2} - M_3 furcations. CuA bifurcated; CuP simple. Anal veins looping into a double-Y configuration. Hind wing 2.6 times as long as wide. Sc not forked. R_1 not forked. Rs 4-branched. M 3-branched. CuA bifurcated; CuP simple. Anal area not well preserved.

Measurements (in mm). Body length ca. 7.9; width 1.7. Forewing length 8.2; width 3.0. Hind wing length ca. 7.3; width 2.8.

Grammikolepidopteron Zhang, Shih, Labandeira & Ren gen. nov.

urn:lsid:zoobank.org:act:6EB3F8BB-B784-4239-8FEE-BEA4B8FA5D9D.

Type species. *Grammikolepidopteron extensus* Zhang, Shih, Labandeira & Ren sp. nov.

Etymology. The generic name is from the Greek, combining *grammikos* (line, linear), in reference to the linearly aligned branching points of veins R_1 and Rs_1 to Rs_3 ; and *lepidos*, meaning “scale” or “flake,” representing the Lepidoptera, the ordinal assignment of this species; and *pteron*, meaning “wing” or “fin.”. The gender is masculine.

Distribution. Inner Mongolia Autonomous Region, China.

Diagnosis. Body small, less than 4.0 mm. Forewing elongate. Humeral vein and sc-r crossvein absent. Sc and R_1 not forked. Rs_3 terminating only slightly before wing apex. Branching points of R_1 and Rs_1 to Rs_3 linearly aligned. M divided into M_3 and M_{1+2} . M_{1+2} subdivided iteratively into veins M_1 and M_2 at an angle of ca. 15 degrees; M_1 linear and smooth. CuA bifurcated; CuP simple. Three anal veins looping into a double-Y configuration. Apophyses short.

An Eolepidopterigidae affiliation is supported by: 1), antennae less than half the length of forewing; 2), M 3-branched; and 3), crossvein absent between Sc and R.

Comparison. *Grammikolepidopteron* resembles *Netoxena* Sohn, 2012, but *Grammikolepidopteron* is separated from *Netoxena* by: 1), absence of a sc-r crossvein (vs. sc-r crossvein present); 2), the M_{1+2} furcation extending beyond the CuA furcation (vs. the CuA furcation extending beyond the M_{1+2} furcation); and 3), three anal veins looping into a double-Y configuration (vs. two anal veins looping into a single-Y configuration).

Grammikolepidopteron resembles one fossil species within *Micropterox*, *Micropterox pervetus* Cockerell, 1919 [42]. However, *Grammikolepidopteron* differs from *M. pervetus* in: 1), the forewing having Sc and R_1 veins that are not forked (vs. Sc and R_1 that are forked); 2), anal veins that form a double-Y configuration (vs. 1A and 2A veins that are parallel); and 3), presence of a CuP vein (vs. absence of the CuP vein).

Grammikolepidopteron extensus Zhang, Shih, Labandeira & Ren sp. nov. (Fig. 12)

urn:lsid:zoobank.org:act:AD3B8CA4-5935-48A5-823F-46C48D0D2C01.

Etymology. The specific name is derived from the Latin, *extensus* (outstretched, extended), in reference to the expansive forewings.

Type material. Holotype: CNU-LEP-NN-2012-006P/C (part and counterpart); ♀; right forewings well preserved; body and hind wing not well preserved. Forewings asymmetrical; left forewing and right hind wing are much longer and slender than

the right forewing and left hind wing. This asymmetry probably is attributable to sediment deformation.

Locality and horizon. This specimen was collected from Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia Autonomous Region, China. The age is latest Middle Jurassic, near the Callovian-Oxfordian boundary.

Diagnosis. Same as generic diagnosis.

Description. Antennae with scape swollen; flagellum filiform; length of segments equal to their diameter. Eyes relatively small. Last segment of a maxillary (or labial) palpus visible. Posterior edge of mesoscutum concave; mesoscutellum small, half the length of mesoscutum. Metatarsi 5-segmented, tarsomere I longest, almost subequal to the total length of tarsomeres II, III, IV and V combined. Female genitalia with long ovipositor partially preserved.

Forewings distinctly narrow and elongate, slightly rounded apically, ca. 3.6 times as long as wide. Sc not forked, extending to costal margin of wing, at 2/3 the length of wing from base. R_1 not forked, extending to costal margin of wing at a point 4/5 length of wing from base; Rs 4-branched; Rs_3 terminating slightly before wing apex; branching points of R_1 and Rs_1 to Rs_3 linearly aligned. M arising from CuA, 3-branched; M_1 and M_2 stalked, ca. 0.4 of their total length. CuA furcation distal of M furcation and before the M_{1+2} furcation; CuP simple. Three anal veins looping into a double-Y configuration. Hind wing relatively elongate, rounded apically, 3 times as long as wide. Sc and R_1 not forked. CuA bifurcated.

Measurements (in mm). Body length over 3.8, as preserved (missing part of terminalia); width 0.9. Forewing length ca. 4.2 (left wing) and 3.5 (right wing); width ca. 1.1 (left wing) and 1.2 (right wing). Hind wing length ca. 2.9 (left wing) and 3.3 (right wing); width ca. 1.2 (left wing) and 1.3 (right wing).

Suborder *Incertae sedis*

Family Mesokristenseniidae Huang, Nel & Minet, 2010

Type genus. *Mesokristensenia* Huang, Nel & Minet, 2010 [25].

Distribution. Inner Mongolia Autonomous Region, China.

Emended diagnosis. Antenna less than half length of forewing. Labial palpi long. Mesotibia lacking medial spurs; spur formula of legs: 1-1-4. Number of forewing vein branches: Sc-2, R_1 -1, Rs -4, M -4, CuA-2, CuP-1, A-3; Rs_3 and Rs_4 separate. Ovipositor nonpiercing, with anterior apophyses.

The synapomorphies for the Mesokristenseniidae are mesotibia with only an apical spur, wings homoneurous, R_1 unforked, M vein 4-branched, and ovipositor with anterior apophyses.

The lepidopteran affiliation of this family has been established by Huang *et al.* [25] based on the following characters: 1), apex of the foretibia with at most one spur; 2), wings covered with overlapping scales; 3), wings lacking nygmata; and 4), the M_1 sharply angulate at the junction with r-m crossvein.

Genera included. *Kladolepidopteron* gen. nov. and *Mesokristensenia* Huang, Nel & Minet, 2010.

Mesokristensenia Huang, Nel & Minet, 2010

Type species. *Mesokristensenia latipenna* Huang, Nel & Minet, 2010.

Distribution. Inner Mongolia Autonomous Region, China.

Emended diagnosis. Antenna short, ca. 1/3 the length of forewing; scape prominently swollen; pedicel relatively robust. Metatibia with spines and two pairs of spurs. M_1 , after separation from M_2 , subtended by an angle of greater than 60 degrees, sharply angulate at junction with r-m crossvein. Crossvein sc-r absent.

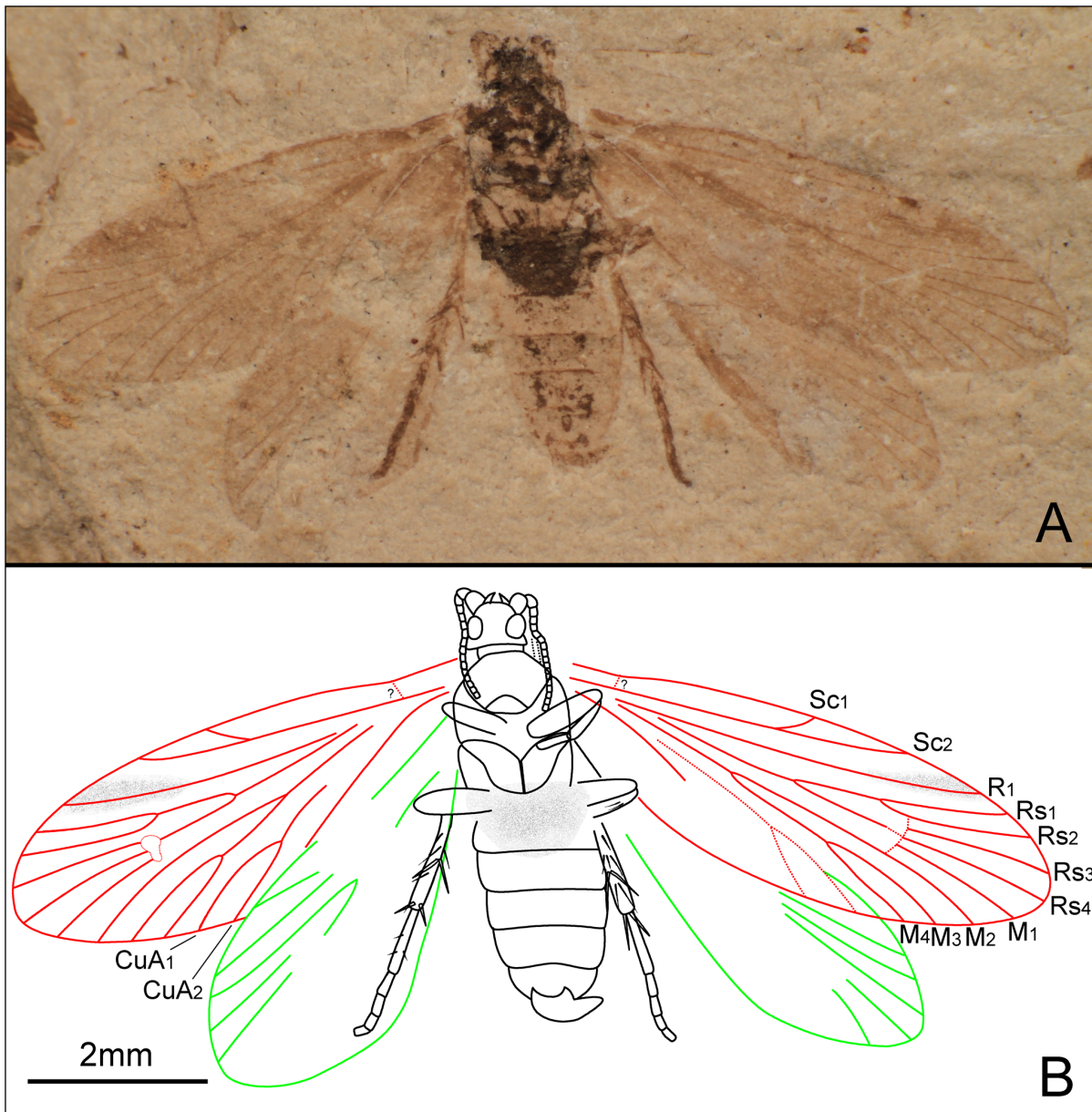


Figure 13. *Mesokristensenia sinica* Huang, Nel & Minet. Male, CNU-LEP-NN-2009-003. (A), Fossil specimen. (B), Camera lucida drawing of (A), showing overall habitus.

doi:10.1371/journal.pone.0079500.g013

Species included. *M. angustipenna* Huang, Nel & Minet, 2010 [25]; *M. latipenna* Huang, Nel & Minet, 2010 [25]; *M. sinica* Huang, Nel & Minet, 2010 [25] and *M. trichophora* sp. nov.

Mesokristensenia sinica Huang, Nel & Minet, 2010 (Figs. 1F and 13)

Type materials. Holotype NIGP-150462 deposited in Nanjing Institute of Geology and Palaeontology [25]. Additional specimen CNU-LEP-NN-2009-003; ♂; forewings well preserved anal areas are covered by hind wings.

Locality and horizon. This specimen was collected from Daohugou Village, Shantou Township, Ningcheng County, Inner

Mongolia Autonomous Region, China. The age is latest Middle Jurassic, near the Callovian–Oxfordian boundary.

Description of additional specimen. Antenna with the scape prominently swollen and pedicel relatively large; flagellum filiform; length of segments equal to their diameter. Compound eyes moderately developed. Apex of labial palpi acute. Mesothorax large; mesonotum slightly broader than long, posterior edge concave; mesoscutellum small, half the length of mesoscutum. Mesofemora and metafemora robust. Metatibia with irregularly arranged spines; a pair of apical spurs and additional spurs arising from distal third or fourth of tibia; all spurs ca. 2 times diameter of tibia. Metatarsi 5-segmented; tarsomere I longest, with short spine.

Forewing 3.2 times as long as wide; prominent pterostigma present. Humeral vein possibly present. Sc forked, from distal 1/3

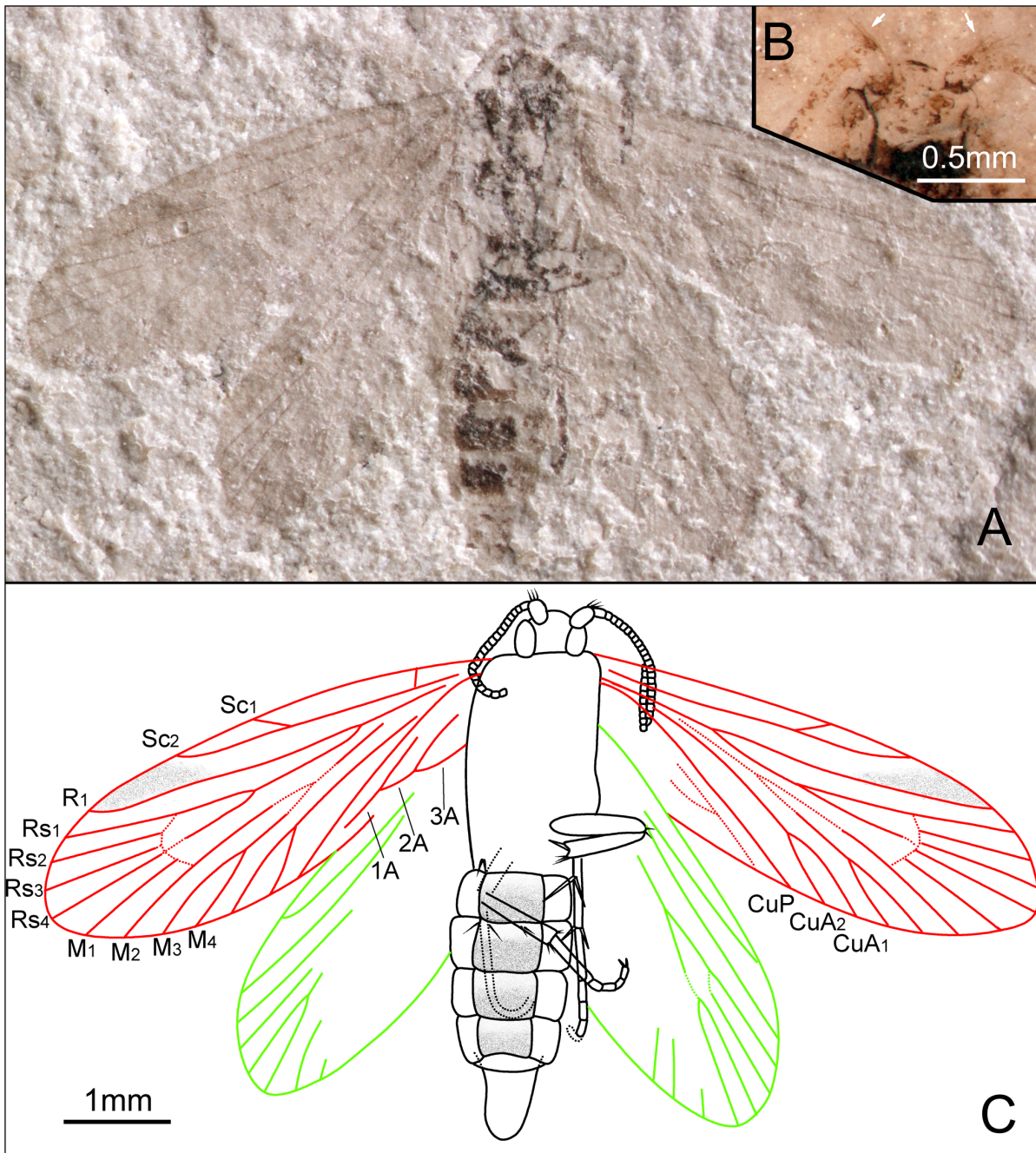


Figure 14. *Mesokristensenia trichophora* sp. nov. Female, holotype, CNU-LEP-NN-2012-032. (A), Fossil specimen. (B), Head, showing scape with setae distally. (C), Camera lucida drawing of (A), showing overall habitus. doi:10.1371/journal.pone.0079500.g014

of the stem; Sc_2 extending to costal margin of wing at $2/3$ length from wing base; $sc-r$ crossvein absent. R_1 not forked; Rs 4-branched; Rs_4 slightly below the apex of forewing; Rs_{1+2} stalked ca. 0.3 of their total length. M 4-branched, stem M_{1+2} longer than stem M_{3+4} . Hyaline zones surrounding $r-m$ crossvein at Rs_{3+4} and M_{1+2} furcations. CuA forked before M_{3+4} furcation. Hind wing 2.45 times as long as wide.

Measurements (in mm). CNU-LEP-NN-2009-003: body length ca. 5.0; width 1.5. Forewing length ca. 6.0; width 1.9. Hind wing length 4.9; width 2.0.

Remarks. This specimen, collected from the same locality as the holotype of *M. sinica*, matches the characters of *M. sinica* in the venation, wing index and body size. We deem this specimen conspecific with *M. sinica*.

Mesokristensenia trichophora Zhang, Shih, Labandeira & Ren sp. nov. (Fig. 14)

urn:lsid:zoobank.org:act:A70E3B9C-22EC-455E-8202-78153C4B8E90.

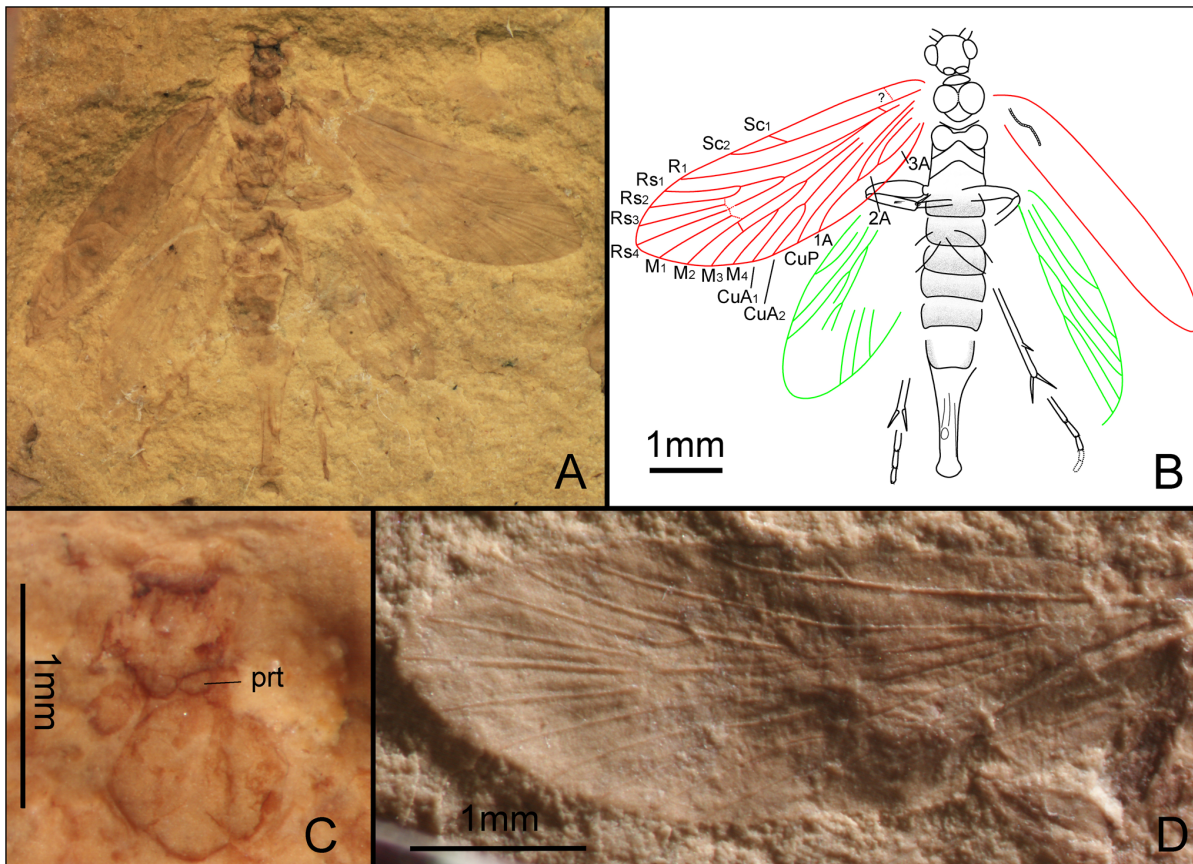


Figure 15. *Kladolepidopteron oviformis* gen. et sp. nov. Female, holotype, CNU-LEP-NN-2009-007C. (A), Fossil specimen. (B), Camera lucida drawing of (A), showing overall habitus. (C), Head and thorax. (D), Forewing. Abbreviation: prt, prothorax. doi:10.1371/journal.pone.0079500.g015

Etymology. The specific name is derived from the Greek, *trichos* (hair), and *phoro-* (bearing, carrying), in reference to hirsute antennal scape present in this species.

Type material. Holotype: CNU-LEP-NN-2012-032; ♀; wings well preserved; legs partially preserved.

Locality and horizon. This specimen was collected from Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia Autonomous Region, China. The age is latest Middle Jurassic, near the Callovian–Oxfordian boundary.

Diagnosis. Antennal scape with setae. Forewing of *M. trichophora* (with wing index of 0.34) narrower than *M. latipenna* (wing index 0.38); slightly broader than *M. sinica* (wing index 0.32/0.33), and broader than *M. angustipenna* (wing index 0.31).

Description. Compound eyes oval; antennae filiform; scape large and elongate, with setae distally placed (Fig. 14B); pedicel longer than one segment of flagellum; flagellum slender, the length of segments basally ca. 0.5 times as long as their diameter; length equal to their diameter distally. Metatibia with one pair of medial spurs, ca. 3 times as long as the diameter of the tibia; one pair of apical spurs, ca. 1.5 times as long as the diameter of the tibia; metatarsi 5-segmented, tarsomere I longest. Ovipositor relatively long and robust.

Forewing 2.9 times as long as wide; prominent pterostigma present. Forewing bearing a humeral vein. Sc forked at distal 1/3 of the stem; Sc₂ extending to costal margin of wing at 2/3 distance from wing base; sc–r crossvein absent. R₁ not forked; Rs 4-branched; Rs₄ extending to the apex of forewing; Rs₁₊₂ stalked ca. 1/3 of their total length; Rs₃ and Rs₄ free. M 4-branched; M₁₊₂

stem longer than M₃₊₄ stem. Hyaline zones surround r–m crossvein at Rs₁₊₂, Rs₃₊₄ and M₁₊₂ furcations. CuA forked before M₃₊₄ furcation; CuA₁₊₂ stalked over half of their length; CuP simple. Three anal veins looping into a double-Y configuration; 1A and 2A separate beyond basal half of vein length. Hind wing length ca. 2.6 times the width. Sc not forked; R₁ not forked; Rs 4-branched; Rs₃₊₄ stem slightly longer than stem Rs₁₊₂.

Comparison. *M. trichophora* differs from other species of *Mesokristensenia* in bearing an antennal scape with setae and in the afore-mentioned wing index.

Measurements (in mm). Body length ca. 5.1; width 1.3. Forewing length 5.0; width 1.7. Hind wing length 4.1; width 1.6.

Kladolepidopteron Zhang, Shih, Labandeira & Ren gen. nov.

urn:lsid:zoobank.org:act:3D602334-A178-4752-8EB0-03053E2982C7.

Type species. *Kladolepidopteron oviformis* Zhang, Shih, Labandeira & Ren sp. nov.

Etymology. The generic name is derived from the Greek, combining *klados* (twig, branch, stem), in reference to the presence of crossvein sc–r; and *lepidos*, meaning “scale” or “flake,” also signifying assignment to the order Lepidoptera; and *pteron*, the word for “wing” or “fin.” The gender is masculine.

Distribution. Inner Mongolia Autonomous Region, China.

Diagnosis. Vein M 4-branched in forewing. Prothorax with a pair of oval structures. Metatibia lacking spines. Crossvein sc–r present at forewing base.

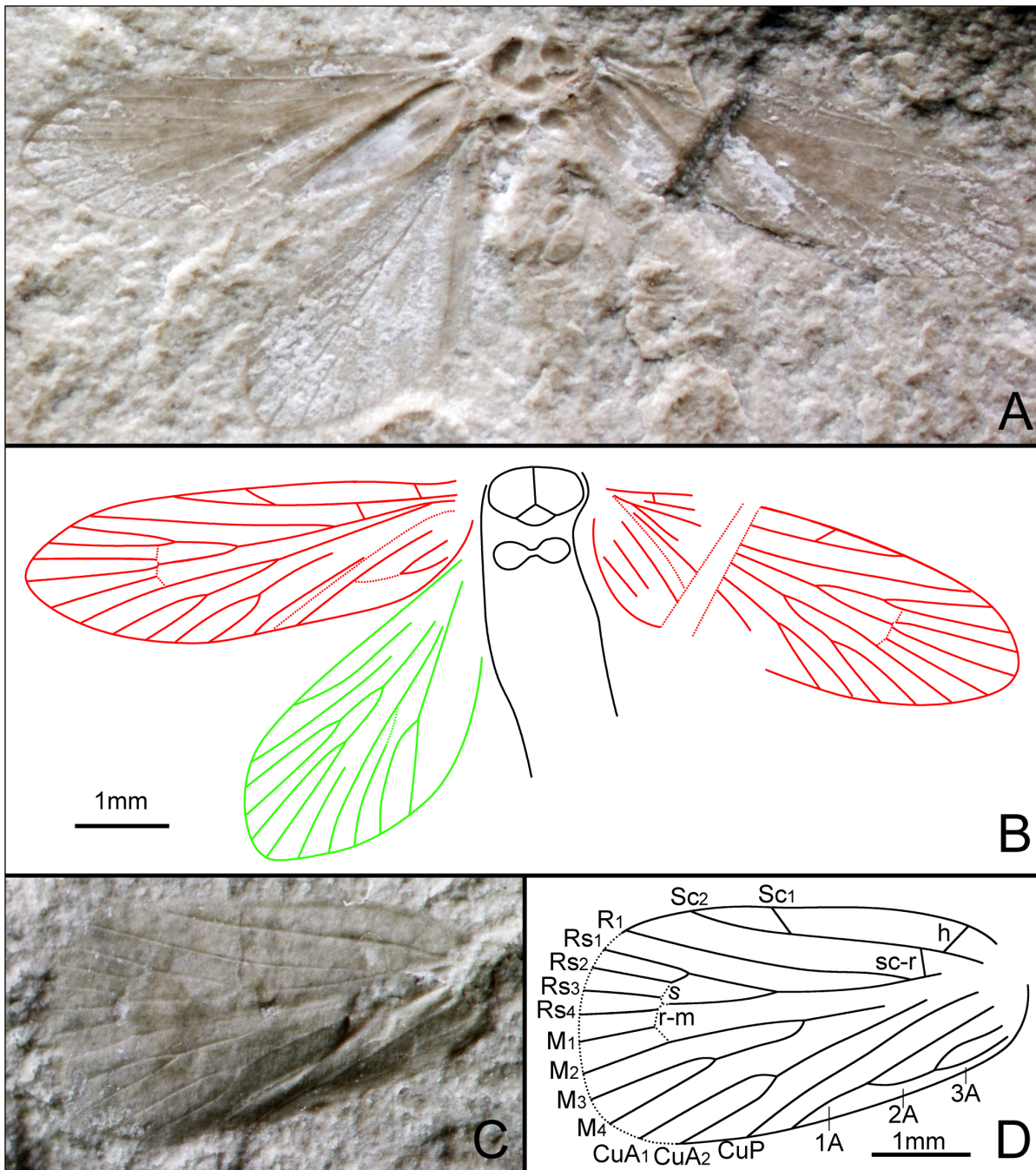


Figure 16. *Kladolepidopteron subaequalis* gen. et sp. nov. Holotype, CNU-LEP-NN-2012-020. (A), Fossil specimen. (B), Camera lucida drawing of (A), showing overall habitus. Paratype, CNU-LEP-NN-2012-022. (C), Fossil specimen. (D), Camera lucida drawing of wing at (C). doi:10.1371/journal.pone.0079500.g016

A Mesokristenseniidae affiliation is supported by: 1), antenna less than half length of forewing; 2), mesotibia with only one apical spur; 3), wings homoneurous; 4), R_1 unforked; and 5), M 4-branched.

Comparison. *Kladolepidopteron* differs from *Mesokristensenia* in: 1), having the sc-r crossvein present at the base of the forewing (vs. sc-r absence); and 2), the metatibia lacking spines (vs. hind legs bearing irregularly arranged spines).

Compared to the sole genus of the Agathiphagidae, *Agathiphaga*, *Kladolepidopteron* can be distinguished by the following characters: 1), the sc-r crossvein is present at the base of the forewing (vs. the sc-r crossvein present near the distal tip of the Sc_2); 2), absence of the m-cup and cup-a crossveins (vs. presence of the m-cup and cup-a crossveins); and 3), presence of the m crossvein (vs. absence of the m crossvein).

Species included. *Kladolepidopteron oviformis* sp. nov.; *K. parva* sp. nov.; and *K. subaequalis* sp. nov.

Kladolepidopteron oviformis Zhang, Shih, Labandeira & Ren sp. nov. (Fig. 15)

urn:lsid:zoobank.org:act:5FAB0FF0-53B9-4117-8363-FA375B4909B9.

Etymology. The specific name is derived from the Latin *ovum* (egg, egg-like); and *formis*, (shape of, likeness, form), in reference to the pair of oval structures on the prothorax.

Type material. Holotype: CNU-LEP-NN-2009-007P/C (part and counterpart); ♀; well preserved body and left forewing; mid and hind legs partially preserved.

Locality and horizon. This specimen was collected from Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia Autonomous Region, China. The age is latest Middle Jurassic, near the Callovian–Oxfordian boundary.

Diagnosis. Body relatively large. Wing index 0.33. Forewing with crossvein m present. In the hind wing, Rs_{1+2} stem shorter than Rs_{3+4} stem.

Description. Body slender. Compound eyes rounded. Antenna filiform, slender, length of segments 1.5 times their diameter.

Prothorax relatively large, with a pair of oval, slightly transverse structures that are adjacent mesially (Fig. 15C). Mesothorax with relatively large prescutum; mesoscutum broader than long;

mesoscutellum small, posterior edge concave along midline, slightly shorter than mesoscutum. Mesoscutellum fan-shaped; metascutum dumbbell shaped; metascutellum relatively large and broad. Mesofemora ca. 2 times as wide as mesotibia; mesofemora and mesotibia almost subequal in length. Mesotibia with one apical spur; two spines present at middle of mesotibia. Metatibia with one pair of medial spurs, one pair slightly longer than diameter of tibia, and other pair of apical spurs ca. 2 times as long as the diameter of the tibia. Metatarsi 5-segmented; two very short setae present on the apex of each tarsomere.

Forewings moderately slender, gradually tapering to a subacute apex (Fig. 15D). Length ca. 3.0 times the width. Forewing bearing a humeral vein. Sc forked, from distal 1/4 of the stem; Sc_2 extending to costal margin of wing at 3/5 length of wing from base. Crossvein $sc-r$ present. R_1 not forked; Rs 4-branched; Rs_4 extending to the apex of forewing; Rs_1 and Rs_2 stalked; Rs_{1+2} stalked ca. 0.38 of their total length; Rs_3 and Rs_4 free. M 4-branched; stem M_{1+2} longer than stem M_{3+4} , M_1 after separation from M_2 subtending an angle of 60 degrees, sharply angulate at junction with crossvein $r-m$. Crossvein $m-ca.$ originating near M_{1+2} furcation and terminating near the midpoint of M_3 . Hyaline zones surrounding $r-m$ crossvein at Rs_{3+4} and M_{1+2} furcations. CuA_{1+2} stalked over half of their length; CuP simple. Three anal

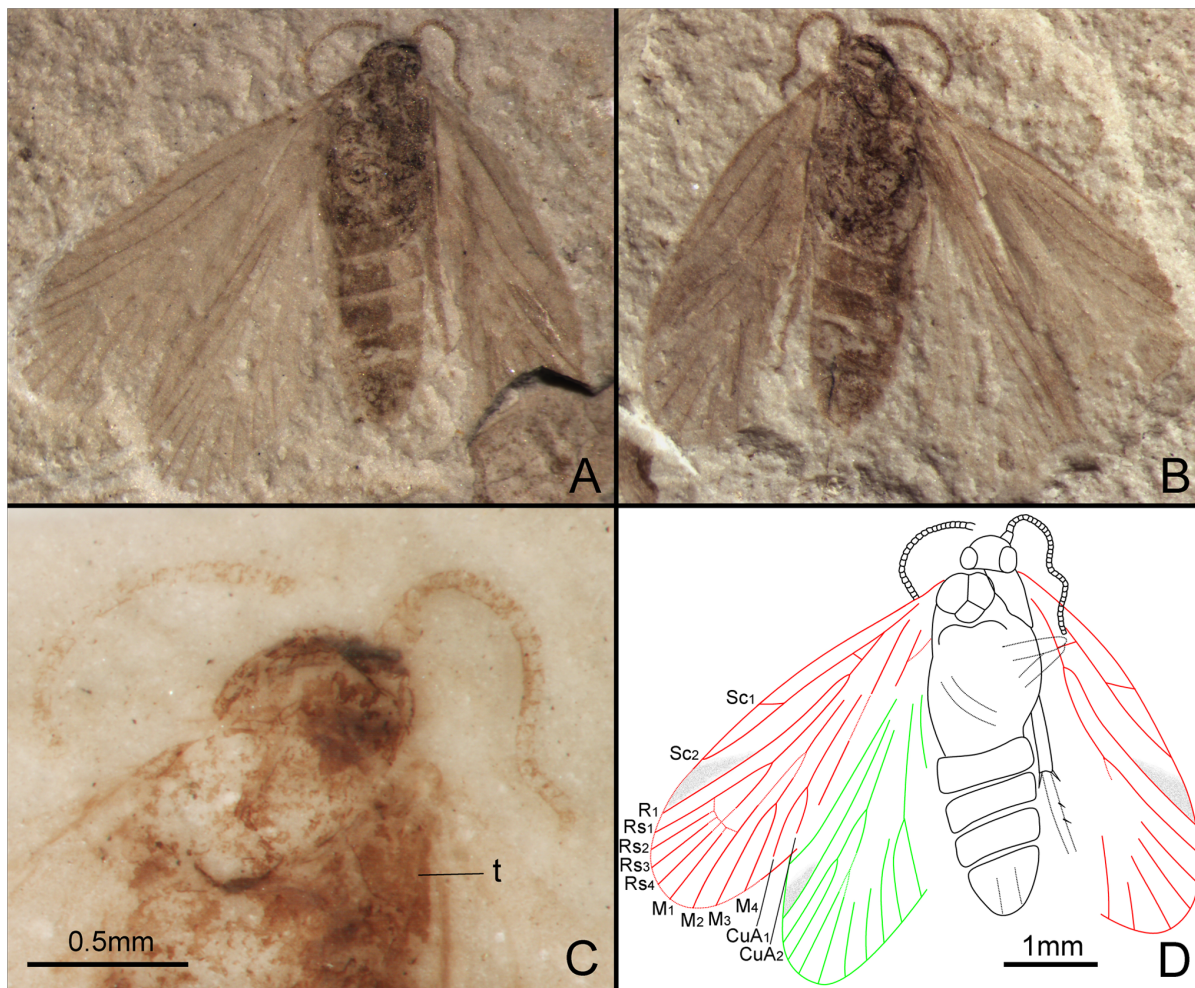


Figure 17. *Kladolepidopteron parva* gen. et sp. nov. Male, holotype, CNU-LEP-NN-2012-011P/C. (A), Fossil specimen (counterpart). (B), Fossil specimen (part). (C), Head and thorax. (D), Camera lucida drawing of (A), showing overall habitus. Abbreviation: t, tegula. doi:10.1371/journal.pone.0079500.g017

veins looping into a double-Y configuration; 1A and 2A separate at basal half. Hind wing length ca. 2.8 times the width. Sc not forked. R_1 not forked; Rs 4-branched; Rs_{3+4} stem ca. 2 times as long as stem Rs_{1+2} . Abdomen lacking specialized integumental modifications. Ovipositor long; apophyses not evident.

Measurements (in mm). Body length ca. 6.3; width 1.1. Forewing length 4.8; width 1.6. Hind wing length ca. 3.6; width 1.3.

Kladolepidopteron subaequalis Zhang, Shih, Labandeira & Ren sp. nov. (Fig. 16)

urn:lsid:zoobank.org:act:4356A7DD-DEF5-450C-B17B-389E685ABA09.

Etymology. The specific name is derived from the Latin preposition, *sub* (under, below), and *aequalis* (equal), in reference to the subequal length of the basal stems to the hind wing veins Rs_{1+2} and Rs_{3+4} .

Type materials. Holotype: CNU-LEP-NN-2012-020; sex unknown; well preserved forewings and left hind wing. Paratype: CNU-LEP-NN-2012-022; sex unknown; only forewing, with distal part not preserved.

Diagnosis. Wing index 0.32. In forewing, crossvein m absent. Hind wing relatively broad; the stem Rs_{1+2} and Rs_{3+4} subequal in length.

Comparison. *Kladolepidopteron subaequalis* resembles *K. oviformis* in: 1), the forewing index (0.32 vs. 0.33); and 2), the wing apex is moderately acute. *Kladolepidopteron subaequalis* differs from *K. oviformis* in the following characters: 1), the crossvein m absent (vs. crossvein m present); 2), the hind wing has a slightly shorter Rs_{1+2} stem than the Rs_{3+4} stem (vs. Rs_{1+2} stem only half length of Rs_{3+4} stem); and 3), the hind wing of *K. subaequalis* is broader than that of *K. oviformis*.

Description. Mesothorax large, with prominent scutum and small scutellum; prescutum not preserved. Mesoscutum with distinct median suture, broader than long, posterior edge concave along midline; mesoscutellum fan-shaped, half the length of mesoscutum; metascutum dumbbell shaped.

Forewing moderately slender, tapering gradually to apex. Length ca. 3.1 times the width. Forewing bearing a humeral vein. Sc forked from distal 1/3 of the stem; Sc_2 extending to costal margin of wing at 3/5 length of wing from base. Crossvein sc-r present. R_1 not forked; Rs 4-branched; Rs_4 extending to the apex of forewing; Rs_1 and Rs_2 stalked, Rs_{1+2} stalked ca. 0.35 of their total length; Rs_3 and Rs_4 free; Rs_{1+2} furcation almost at same level as Rs_{3+4} . Crossvein s present (Figs. 16C, D). M 4-branched; M_1 ,

after separation from M_2 subtending an angle of 75–80 degrees, sharply angulate at junction with r-m crossvein (Figs. 16C, D); stem M_{1+2} longer than stem M_{3+4} . CuA bifurcated; CuP simple. Three anal veins forming a double-Y configuration; 1A and 2A separate at basal half. Hind wing length ca. 2.3 times the width; broader than forewing. Sc not forked. R_1 not forked; Rs 4-branched; Rs branching into veins Rs_{1+2} and Rs_{3+4} , and then further subdividing into four branches of Rs_1 , Rs_2 , Rs_3 , and Rs_4 ; furcations of Rs_{1+2} , and Rs_{3+4} almost at the same level to each other. M 4-branched. CuA bifurcated; CuP difficult to discern.

Measurements (in mm). Forewing length 5.0; width 1.6. Hind wing length ca. 4.1; width 1.8.

Kladolepidopteron parva Zhang, Shih, Labandeira & Ren sp. nov. (Fig. 17)

urn:lsid:zoobank.org:act:032CD405-AC08-4D0B-A489-FB6231FE7560.

Etymology. The specific name is derived from the Latin *parva* (small, little, stunted), in reference to its small body size.

Type material. Holotype: CNU-LEP-NN-2012-011P/C (part and counterpart); ♂; well preserved forewing and hind wing; anal wing region indiscernible.

Locality and horizon. This specimen was collected from Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia Autonomous Region, China. The age is latest Middle Jurassic, near the Callovian–Oxfordian boundary.

Diagnosis. The new species has narrower wings (wing index 0.31) than *K. oviformis* (wing index 0.33) and *K. subaequalis* (wing index 0.32). Crossvein m absent in forewing. Hind wing with Rs_{1+2} forking almost at the same level as Rs_{3+4} .

Comparison. *Kladolepidopteron parva* resembles *K. oviformis* and *K. subaequalis* in venation. However, *K. parva* differs from *K. oviformis* by: 1), its short body, ca. 4.1 mm in length (vs. a relatively long body ca. 6.3 mm long); 2), short forewing length of 4.1 mm (vs. long forewing length of 4.8 mm); and 3), the Rs_{1+2} stem slightly shorter than the Rs_{3+4} stem (vs. the Rs_{1+2} stem only half the length of the Rs_{3+4} stem). *Kladolepidopteron parva* differs from *K. subaequalis* by: 1), its short forewing (vs. long forewing with a length of 5.0 mm); and 2), a forewing without a pterostigma (vs. an otherwise prominent pterostigma).

Description. Antenna filiform, ca. half the length of forewing; scape swollen; flagellum filiform; length of segments equal to their diameter. Compound eyes widely separated. Tegula large, triangular (Fig. 17C). Mesoscutum with median suture, slightly broader than long; posterior edge of mesoscutum concave

Table 2. Character comparisons of Agathiphagidae, Mesokristenseniidae and Ascololepidopterigidae.

Character	Family		
	Agathiphagidae	Mesokristenseniidae	Ascololepidopterigidae fam. nov.
Spur formula	1-4-4	1-1-4	metatibia without medial spur; foretibia and mesotibia unknown
Subcostal vein (Sc)	forked	not forked or forked	not forked or forked
Radial vein (R_1)	not forked	not forked	Forked
Furcations of Rs_{1+2} and Rs_{3+4}	Furcation of Rs_{3+4} distally, distinctly beyond furcation of Rs_{1+2}	approximately at the same level to each other	approximately at the same level to each other
Crossvein m-cua	Present	absent	Present
Crossvein cua-cup	Present	absent	Present

doi:10.1371/journal.pone.0079500.t002

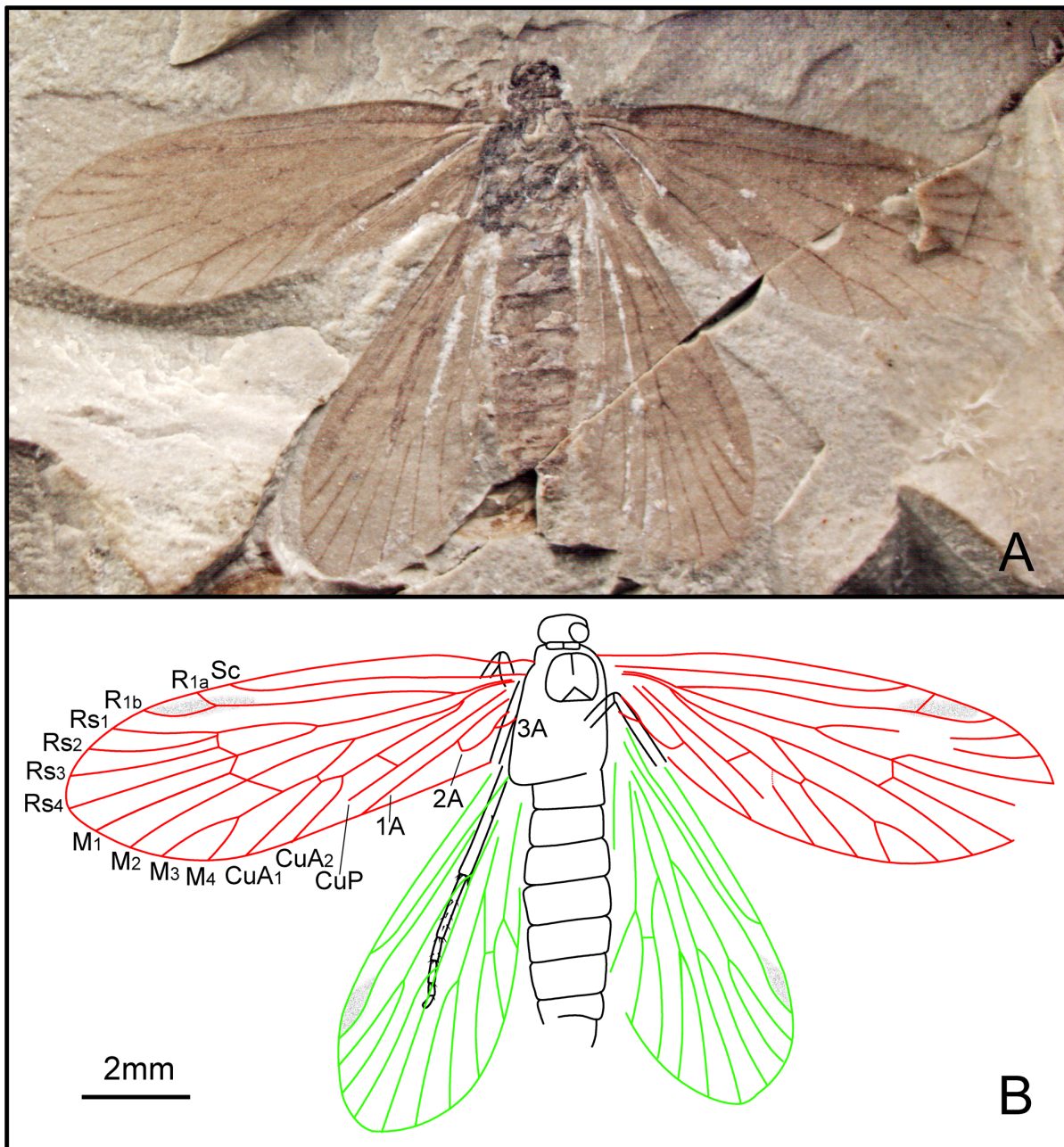


Figure 18. *Ascololepidopterix multinerve* gen. et sp. nov. Holotype, CNU-LEP-NN-2012-028. (A), Fossil specimen. (B), Camera lucida drawing of (A), showing overall habitus.
doi:10.1371/journal.pone.0079500.g018

along midline. Mesoscutellum small, fan-shaped, slightly shorter than mesoscutum. Metatibia with a pair apical spurs, ca. 1.5 times the diameter of the tibia; medial spurs difficult to discern.

Forewing ca. 3.2 times as long as wide; a prominent pterostigma present. Forewing lacking a humeral vein. Sc forked from distal 1/3 of the stem; Sc₂ extending to costal margin of wing, beyond 2/3 the length of wing from base. Crossvein sc-r present; R₁ not forked; Rs 4-branched; Rs₁₊₂ stalked ca. 1/2 of vein total length; Rs₃ and Rs₄ free. M 4-branched. Hyaline zones surrounding r-m crossvein at Rs₁₊₂, Rs₃₊₄, M₁₊₂, and M₁₊₂-M₃ furcations and along CuP. CuA bifurcated; CuP simple. Hind wing Sc not forked.

R₁ not forked; Rs 4-branched; Rs₁ and Rs₂ stalked; Rs₃ and Rs₄ stalked. M 3-branched. CuA bifurcated.

Measurements (in mm). Body length ca. 4.1; width 1.2. Forewing length ca. 4.1; width ca. 1.3. Hind wing length ca. 3.4.

Family Ascololepidopterigidae Zhang, Shih, Labandeira & Ren fam. nov.

urn:lsid:zoobank.org:act:4C3FD7D0-DD02-4575-BA4A-94600DFD80EB.

Type genus. *Ascololepidopterix* Zhang, Shih, Labandeira & Ren gen. nov.

Distribution. Inner Mongolia Autonomous Region, China.

Diagnosis. Antennae filiform, ca. half the length of forewing. Metatibiae lacking medial spurs, at most with one pair of short apical spurs. Both pairs of wings homoneurous. In forewing, number of vein branches as follows: Sc-1/2, R₁-2, Rs-4, M-4, CuA-2, CuP-1, A-3, and furcations of Rs₁₊₂, and Rs₃₊₄ almost at the same level of branching with each other. Crossveins m-cua and cua-cup present. Ovipositor with apophyses anteriores.

The synapomorphies for the *Ascololepidopterigidae* fam. nov. are: 1), metatibiae lacking medial spurs; 2), wings homoneurous; 3), forewing R₁ forked; 4), M vein 4-branched; 5), crossveins m-cua and cua-cup present; and 6), ovipositor with apophyses anteriores.

This family is defined as a clade of the Amphiesmenoptera by having a double anal furcation on the forewing and a hind wing M vein with at most three branches. This family is assigned to Lepidoptera by presence of a M₁ vein which, after separation from M₂ vein, subtends an angle greater than 60 degrees and is sharply angulate at the junction with the r-m crossvein.

Comparison. This new family with a 4-branched M is different from most other Lepidoptera, except for Agathiphagidae and Mesokristenseniidae. The differences among these three families are listed in Table 2.

Genera included. *Trionolepidopteron* gen. nov., *Pegolepidopteron* gen. nov. and *Ascololepidopterox* gen. nov.

Key to known genera of *Ascololepidopterigidae* fam. nov.

1. Forewing with Sc not forked
.....*Ascololepidopterox* gen. nov.
- Forewing with Sc forked.....2
2. Forewing length more than 7.0 mm; forewing

- lacking crossvein rs₁-rs₂; crossvein r present
.....*Pegolepidopteron* gen. nov.
- Forewing length less than 5.0 mm; forewing
with crossvein rs₁-rs₂; crossvein r absent.....
.....*Trionolepidopteron* gen. nov.

***Ascololepidopterox* Zhang, Shih, Labandeira & Ren gen. nov.**

urn:lsid:zoobank.org:act:8F418F30-2094-4D03-A8C1-455119AE64EC.

Type species. *Ascololepidopterox multinerve* Zhang, Shih, Labandeira & Ren sp. nov.

Etymology. The generic name is derived from the Greek, *a-*, meaning “not” or “without”; and *scolos*, meaning a “spur”, “thorn” or “anything pointed”, referring to the absence or reduction of metatibial spurs in this Middle Jurassic fossil; and *lepidos*, meaning “scale” or “flake,” and the ordinal name of Lepidoptera, to which the fossil belongs; and *pteron*, meaning “wing” or “fin.” The gender is feminine.

Distribution. Inner Mongolia Autonomous Region, China.

Diagnosis. Body relatively large. Forewing Sc not forked. R₁ forked. Crossveins s and r-m present. Stem M₁₊₂ shorter than stem M₃₊₄; crossvein m present, originating near M₁₊₂ furcation and terminating on M₃₊₄; crossvein m₃₊₄-cua₁, distant from the M and CuA furcations. Crossvein cua-cup originating at ca. 2/3 the length of CuA from its base and terminating beyond the midpoint of CuP. Hind wing R₁ not forked. The distal part of 2A curved upward.

An *Ascololepidopterigidae* affiliation is supported by: 1), wings homoneurous; 2), R₁ forked; 3), M 4-branched; and 4), crossveins m-cua and cua-cup present.

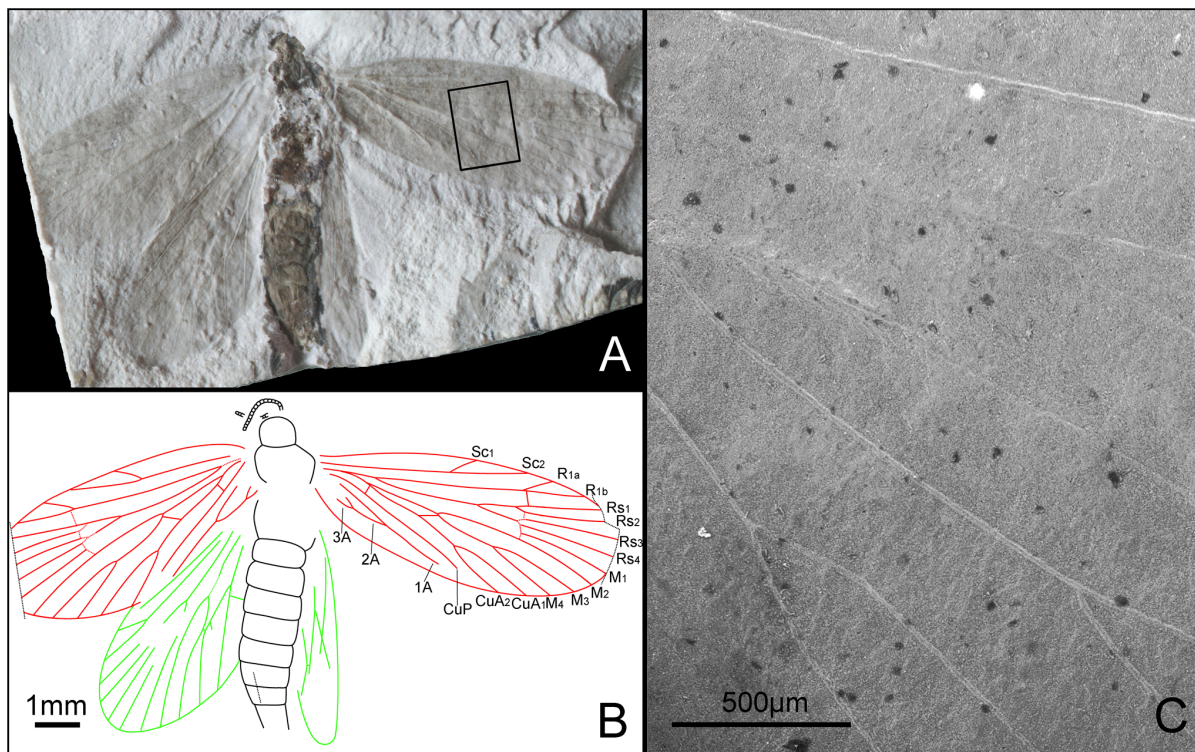


Figure 19. *Pegolepidopteron latiala* gen. et sp. nov. Female, holotype, CNU-LEP-NN-2012-001. (A), Fossil specimen. (B), Camera lucida drawing of (A), showing overall habitus. (C), SEM of right forewing venation, enlarged from the rectangular template in (A). doi:10.1371/journal.pone.0079500.g019

Ascololepidopterix multinerve Zhang, Shih, Labandeira & Ren sp. nov. (Fig. 18)

urn:lsid:zoobank.org:act:7B3EA809-9A7A-4AE9-AD90-7075315CCB91.

Etymology. The specific name is derived from the Latin, *multi* (many, much), and *nervis* (sinew, tendon, vein), in reference to the numerous crossveins in the forewings.

Type material. Holotype: CNU-LEP-NN-2012-028; sex unknown; well preserved forewings and hind wings; hind legs partially preserved.

Locality and horizon. This specimen was collected from Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia Autonomous Region, China. The age is latest Middle Jurassic, near the Callovian–Oxfordian boundary.

Diagnosis. Same as generic diagnosis.

Description. Head wider than long. Mesoscutum large, posterior edge concave along midline; mesoscutellum triangular. Metatibia with one pair apical spurs, the spurs subequal to the diameter of the tibia. Metatarsi 5-segmented; tarsomere I ca. 3 times as long as tarsomere II; metatarsi with short spines.

Forewing ca. 2.8 times as long as wide; lacking humeral vein; prominent pterostigma present. Sc not forked. R₁ forked distally; R_{1b} curved; Rs 4-branched; Rs₄ to the apex of forewing; Rs₁₊₂ stalked ca. 0.45 of vein total length; stem Rs₁₊₂ as long as stem Rs₃₊₄; s crossvein present. M 4-branched; M₁, after separation from M₂, subtends an angle of 63 (right wing) and 53 (left wing) degrees, sharply angulated at junction with r–m crossvein. Stem M₁₊₂ shorter than stem M₃₊₄; m crossvein originating near M₁₊₂ furcation, ending at M₃₊₄. CuA bifurcated; CuP simple. Crossvein m₃₊₄–cua₁ originating at ca. 1/3 length of M₃₊₄ from its base and terminating near CuA furcation; cua–cup crossvein originating at ca. 2/3 length of CuA from its base and terminating slightly beyond midpoint of CuP. Anal veins looping into a double-Y configuration; distal part of 2A curved upward. Hind wing ca. 2.6 times as long as wide. Sc not forked. R₁ not forked, the distal part curved; Rs 4-branched; stem Rs₁₊₂ longer than stem Rs₃₊₄. M 4-branched; M₁ and M₂ stalked; furcation of M₁₊₂ at same level with furcation of Rs₁₊₂. CuA bifurcated; CuP simple. Crossvein m₃–cua₁ present.

Measurements (in mm). Body length ca. 8.1; width 1.8. Forewing length 8.8; width ca. 3.1. Hind wing length ca. 7.7; width 3.0.

Pegolepidopteron Zhang, Shih, Labandeira & Ren gen. nov.

urn:lsid:zoobank.org:act:EF716898-92B6-450F-BDC6-82E71602324E.

Type species. *Pegolepidopteron latiala* Zhang, Shih, Labandeira & Ren sp. nov.

Etymology. This generic name is derived from the Greek *pegos* (strong, solid), in reference to the large body of this species, and *lepidos*, for “scale” or “flake,” also referring to this species’ assignment to the Lepidoptera; and *pteron*, for “wing” or “fin.” The gender is feminine.

Distribution. Inner Mongolia Autonomous Region, China.

Diagnosis. Body relatively large. Forewing with Sc forked, R₁ forked. Crossvein r absent, r–m crossvein weak. Stem M₁₊₂ longer than stem M₃₊₄; m₃₊₄–cua crossvein originating near M furcation and terminating at midpoint of CuA. Crossvein cua–cup located at the base of forewing. The distal part of 2A normal, not curved upward. Hind wing R₁ forked.

An Ascololepidopterigidae affiliation is supported by: 1), antennae less than half the length of forewing; 2), wings

homoneurous; 3), R₁ forked; 4), M 4-branched; and 5), crossveins m–cua and cua–cup present.

Comparison. *Pegolepidopteron* differs from *Ascololepidopterix* in the following characters: 1), the forewing Sc is forked (vs. Sc not forked); 2), the r crossvein is present (vs. the r crossvein absent); 3), the m crossveins are absent (vs. the m crossveins present); 4), 2A is rectilinear (vs. the distal part of 2A curved upward); and 5), the hind wing R₁ is forked (vs. R₁ not forked and curved). When compared to *Agathiphaga* of the monogeneric Agathiphagidae, *Pegolepidopteron* can be separated by the following characters: 1), the R₁ is forked (vs. the R₁ not forked); 2), the sc–r crossvein is absent (vs. the sc–r crossvein present); 3), the r crossvein is present (vs. the r crossvein absent); 4), the location of the m₃₊₄–cua crossvein and the cup–a crossvein; and 5), the hind wing venation of *Pegolepidopteron* is much different from that of *Agathiphaga*.

Pegolepidopteron latiala Zhang, Shih, Labandeira & Ren sp. nov. (Fig. 19)

urn:lsid:zoobank.org:act:C34FB273-675E-4A4E-BA00-1589E5F70CAD.

Etymology. The specific name is derived from the Latin of *latus* (broad, wide), and *ala*, (a bird’s wing), in reference to the broad wings of this species.

Type material. Holotype: CNU-LEP-NN-2012-001; ♀; well preserved forewings and hind wings.

Locality and horizon. This specimen was collected from Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia Autonomous Region, China. The age is latest Middle Jurassic, near the Callovian–Oxfordian boundary.

Diagnosis. Same as generic diagnosis.

Description. Antennae partially preserved, filiform, length of segments equal to their diameter.

Forewing ca. 2.5 times as long as wide; shape of wing apex unknown. Forewing lacking humeral vein. Sc forked, from distal 1/3 of vein stem; Sc₂ extending to costal margin of wing at 2/3 length of wing from its base. Crossvein sc–r absent. R₁ forked from distal 1/4 of stem, slightly beyond the Rs₁₊₂ furcation; Rs 4-branched; Rs₁₊₂ stalked ca. 0.45 of their vein length; stem Rs₁₊₂ as long as stem Rs₃₊₄; r crossvein located beyond the R₁ furcation. M 4-branched; M₁, after separation from M₂, subtending an angle of 70 (left wing) and 100 (right wing) degrees, sharply angulated at junction with r–m crossvein; stem M₁₊₂ slightly longer than stem M₃₊₄; m₃₊₄–cua crossvein slanted obliquely toward M₃₊₄, originating near M furcation and terminating near the midpoint of CuA. Hyaline zones surrounding r–m crossveins at Rs₁₊₂, Rs₃₊₄ and M₁₊₂ furcations. CuA bifurcated; CuP simple; cua–cup crossvein present, located at base of forewing. The stem of CuA diverges from stem of R basally, The stem of M diverges from stem of CuA beyond R–CuA furcation. Three anal veins loop into a double-Y configuration. Hind wing R₁ forked; Rs 4-branched. M 4-branched. Crossvein m₃–cua₁ present between M₃ and CuA; cua₂–cup crossvein present. Anal area poorly preserved.

The anterior apophyses extending forward to distal margin of segment VII.

Measurements (in mm). Body length ca. 7.7; width 1.2. Forewing length 7.2; width 2.9. Hind wing length ca. 5.8; width 2.8.

Trionolepidopteron Zhang, Shih, Labandeira & Ren gen. nov.

urn:lsid:zoobank.org:act:B2E35225-7FFD-4E66-B153-D6D638B6056E.

Type species. *Trionolepidopteron admarginis* Zhang, Shih, Labandeira & Ren sp. nov.

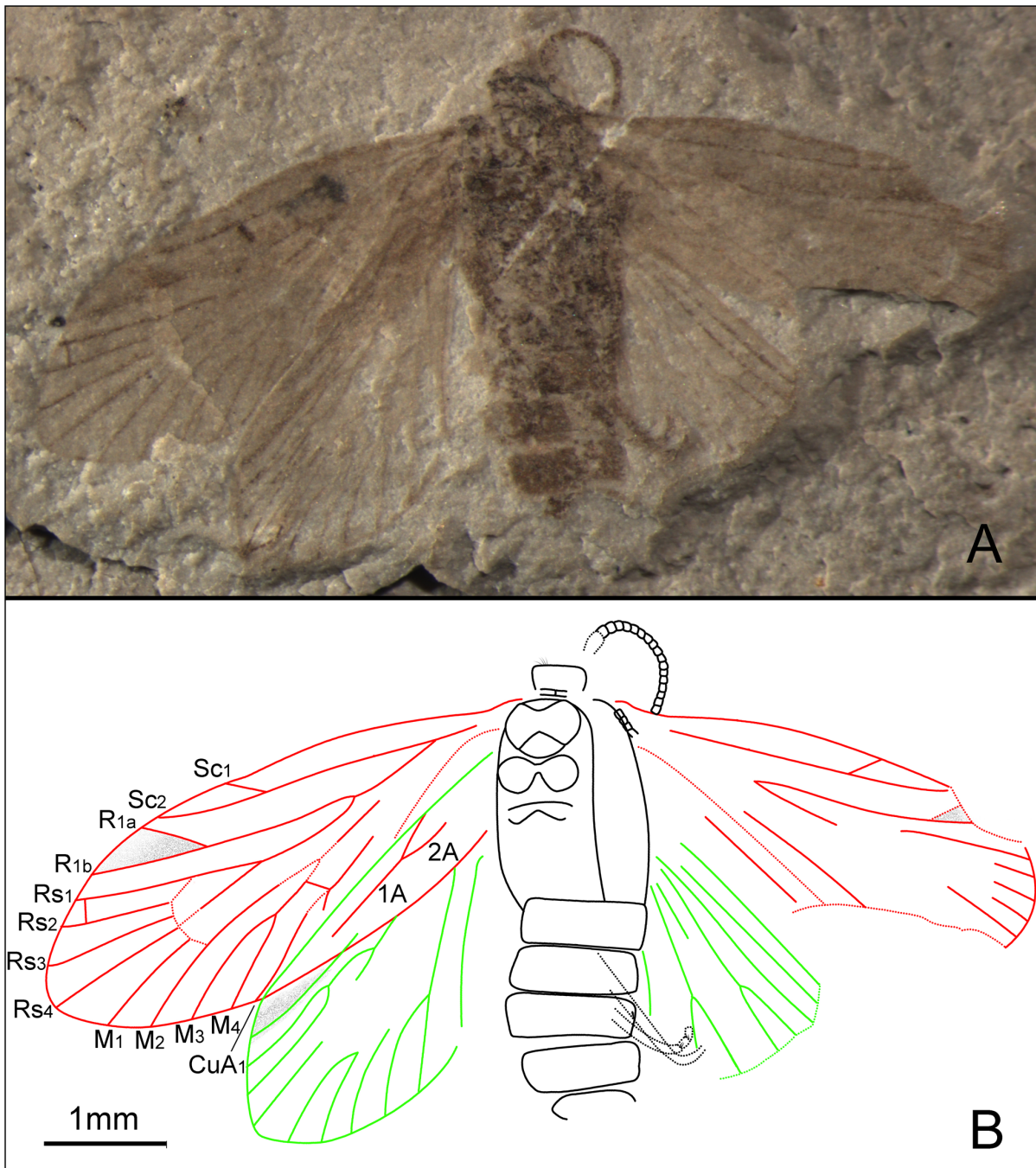


Figure 20. *Trionolepidopteron admarginis* gen. et sp. nov. Holotype, CNU-LEP-NN-2012-012. (A), Fossil specimen. (B), Camera lucida drawing of (A), showing overall habitus.
doi:10.1371/journal.pone.0079500.g020

Etymology. The generic name is derived from the Greek *trion* (three) for the threefold branched Rs vein in the hind wing; and *lepidos* (scale, flake), referring to the Lepidoptera, the order to which this taxon is assigned; and *pteron* (a bird's wing, fin). The gender is masculine.

Distribution. Inner Mongolia Autonomous Region, China.

Diagnosis. Body small; forewing with Sc forked. R_1 forked. Crossvein rs_1-rs_2 present. Stem M_{1+2} longer than stem M_{3+4} . Crossvein $m_{3+4}-cua$ located at the CuA furcation. Hind wing with both Rs and M 3-branched.

An Ascololepidopterigidae affiliation is supported by: 1), antennae less than half the length of forewing; 2), R_1 forked; 3), M 4-branched; and 4), crossvein $m-cua$ present.

Comparison. *Trionolepidopteron* resembles *Pegolepidopteron* in the venation of the forewing, including: 1), presence of the Sc and R_1 forked veins; 2), the M vein is 4-branched; (3), a free M_1 vein; and 4), presence of the $m_{3+4}-cua$ crossvein. *Trionolepidopteron* differs from *Pegolepidopteron* by the following characters: 1), rs_1-rs_2 crossveins are present on the forewing (vs. absent); 2), r crossvein is absent on forewing (vs. present); 3), $m_{3+4}-cua$ crossvein is

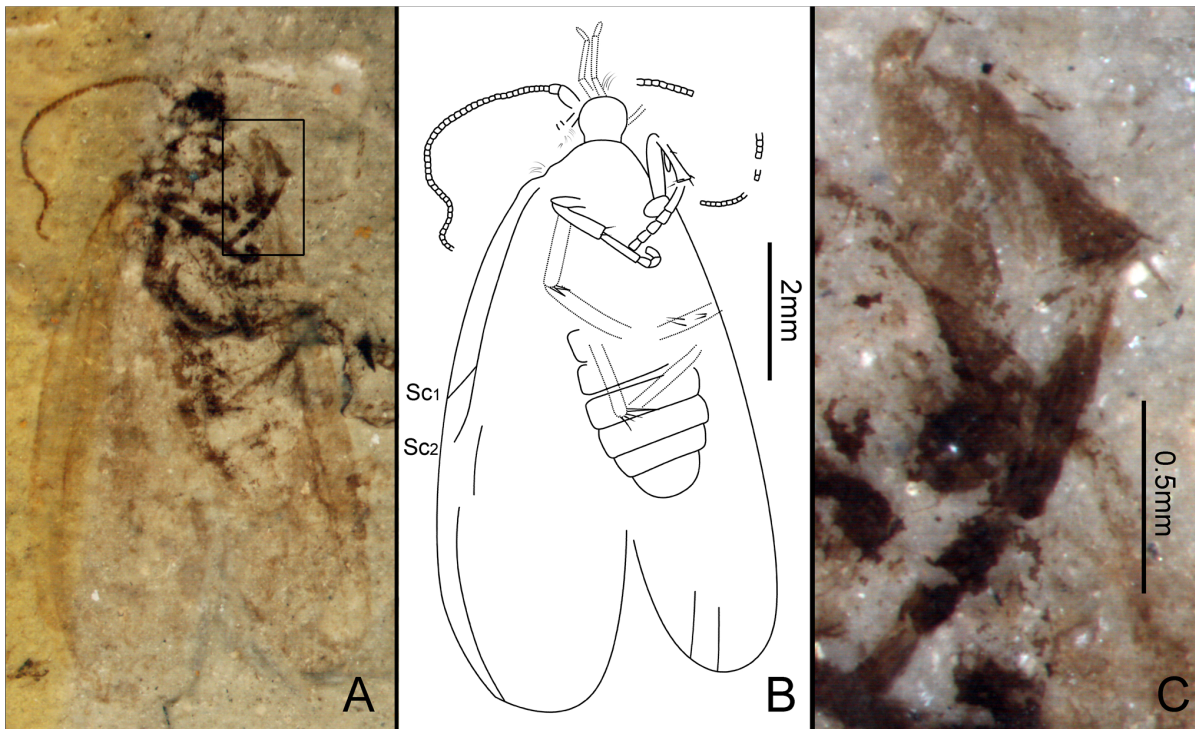


Figure 21. An unidentified moth. Male, CNU-LEP-NN-2012-013. (A), Fossil specimen. (B), Camera lucida drawing of (A), showing overall habitus. (C), Foreleg showing the tibial epiphysis, as outlined at the rectangular template in (A).
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located near the CuA furcation (vs. more remote from the CuA furcation); and 4), the hind wing has a 3-branched Rs (vs. 4-branched). Differences also occur in gross body size, with *Trionolepidopteron* having a body length of ca. 4.0 mm long (vs. body lengths of more than 7.0 mm long for *Ascololepidopterix* and *Pegolepidopteron*).

Trionolepidopteron admarginis Zhang, Shih, Labandeira & Ren sp. nov. (Fig. 20)

urn:lsid:zoobank.org:act:EC28A0BA-58AD-4630-860E-C558307500C1.

Etymology. The specific name is derived from the Latin preposition *ad* (toward, adjacent to), and *marginis* (border, edge), in reference to the rs_1 – rs_2 crossvein occurring near the costal margin of the forewing.

Type material. Holotype: CNU-LEP-NN-2012-012; sex unknown left forewing well preserved; anal area overlapping with hind wing.

Locality and horizon. This specimen was collected from Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia Autonomous Region, China. The age is latest Middle Jurassic, near the Callovian–Oxfordian boundary.

Diagnosis. Same as generic diagnosis.

Description. Antennae filiform; scape swollen; flagellum filiform; length of segments equal to their diameter. Short setae on anterior head margin. Mesothorax with small prescutum; mesoscutum broader than long; anterior and posterior edges of mesoscutum concave along midline; mesoscutellum fan-shaped, relatively large; mesoscutellum almost subequal to mesoscutum in length. Mesothorax slightly longer than metathorax; metascutum dumbbell shaped. Two short spines present on the apex of each tarsomere.

Forewing ca. 2.8 times as long as wide; pterostigma present. Humeral vein absent. Sc forked from 1/4 of vein stem distance; Sc_2 extending to costal margin of wing, beyond 2/3 length of wing from base. R_1 forked; sc–r crossvein absent; Rs 4-branched; Rs_4 terminating at forewing apex; Rs_{1+2} stalked ca. 0.37 of their total length; stem Rs_{1+2} subequal to stem Rs_{3+4} . Crossvein rs_1 – rs_2 present and located near the costal margin of forewing. M 4-branched; stem M_{1+2} longer than stem M_{3+4} ; M_1 , after separation from M_2 at an angle of ca. 70 degrees, sharply angulated at junction with r–m crossvein. Hyaline zones surround r–m crossveins at Rs_{1+2} , Rs_{3+4} , M_{1+2} , and M_{1+2} – M_3 furcations. CuA bifurcated. Crossvein m_{3+4} – cua present, originating on M_{3+4} and terminating near the CuA furcation. Hind wing ca. 2.5 times as long as wide. Sc and R_1 not forked. Rs and M 3-branched. CuA bifurcate.

Measurements (in mm). Body length over 3.8 as preserved (terminalia missing); width 1.6. Forewing length ca. 4.5; width ca. 1.6. Hind wing length ca. 3.7; width ca. 1.5.

Family *Incertae sedis*

Gen. et sp. *incertae sedis* (Fig. 21)

Material. CNU-LEP-NN-2012-013; ♂; antennae and forelegs well preserved; venation on both fore- and hind wings difficult to discern.

Locality and horizon. This specimen was collected from Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia Autonomous Region, China. The age is latest Middle Jurassic, near the Callovian–Oxfordian boundary.

Description. Antennae longer than half the length of forewing; scape swollen; pedicel relatively robust; flagellum filiform, length of flagellar segments equal to their diameter. Maxillary palpus long, the last segment short. Foretibia with epiphysis and spines (Fig. 21C); pretarsi 5-segmented. Both

mesotibia and metatibia with one pair of apical spurs; medial spurs not discernible.

Forewings extremely long, distinctly exceeding end of the abdomen. Sc forked; other wing venation not discernible.

Measurements (in mm). Body length 5.9; width 1.8. Forewing length 7.3; width ca. 2.6.

Remarks. The tibial epiphysis is well preserved on this specimen. The foretibia is characterized by well-developed epiphyses, an autapomorphy of the Lepidoptera. Based on this character, we consider this specimen is assigned to the Lepidoptera. However, due to indistinct venational characters, it cannot be placed in any lepidopteran family.

Discussion

Lepidopteran Characters from the Daohugou Specimens

Amphiesmenopteran fossils can be recognized by either the anal veins in the forewing forming a “double-Y” loop or by the hind wing M veins with at most three branches. Amphiesmenopteran specimens from the Middle Jurassic Jiulongshan Formation at Daohugou show that they had already acquired at least some lepidopteran or trichopteran apomorphies. Definitive Trichoptera and Lepidoptera from Daohugou previously have been reported by Gao *et al.* [43] and Huang *et al.* [25]. Daohugou Lepidoptera described here reveal an earlier underestimated diversity of Lepidoptera from this deposit. These specimens possess some of the most recently proposed lepidopteran autapomorphies.

Although Kristensen listed 23 autapomorphies for adult Lepidoptera [44], few of these can be observed on compression fossils. Grimaldi [8] specified three critical, external apomorphies that should be present in adults of early lepidopteran fossils: 1), absence of a forewing M_4 vein; 2), presence of an epiphysis on the foretibia of (most) species; and 3), the occurrence of wing scales on both fore- and hind wings. In addition, the presence of mandibulate mouthparts [12,40,45], a well-developed jugum and associated setae [40], and a frenulum [12,45] also are present and often used as diagnostic characters of basal moths [41].

One feature mentioned above, wing scales, have long been regarded as a diagnostic character for the Lepidoptera. Although a few trichopteran species also possess wing scales, they are always from rather derived lineages [46]. Grimaldi [8] mentioned that, differing from the Lepidoptera, the Trichoptera have wing scales that very occasionally occur on the forewings. However, some rare Trichoptera, such as *Monocentra lepidoptera* Rambur, do have wing scales on both wings [47,48]. In primitive Lepidoptera, the scales are typically “solid”, lacking a lumen; wing-surface scales are non-perforate; and the outer surface of wing scales are densely set with transverse flutes [49]. Interestingly, only one lepidopteran fossil (CNU-LEP-NN-2012-024) from Daohugou exhibits evidence of scales, as robust pilliform scales. Huang *et al.* [25] indicated the presence of wing scales from the Mesokristenseniidae, but their interpretation of the wing scales appears ambiguous. We believe that the absence of wing scales from Daohugou Lepidoptera is due to taphonomic factors. While scales are often preserved in amber [11,12], and other examples), scales are known but seldom preserved in compression fossils. Another possible explanation involves the unlikely secondary loss of wing scales from Daohugou Lepidoptera. Such an explanation, however, would require an unparsimonious assumption that these lepidopterans represent a monophyletic lineage. The morphological diversity displayed in these specimens appears to undermine such an interpretation.

Based on our survey of the literature, we consider that the following four amphiesmenopteran apomorphies [15,25] are

sufficient for identifying specimens in this report as Amphiesmenoptera (Table 3).

- The forewing anal veins form a “double-Y” loop.**
- The hind wing M vein bears at most three branches.** This condition also indicates that veins M_3 and M_4 are entirely merged.
- The pronotum has paired setose prominences.**
- The anterior margin of female segments VIII and IX are accompanied by long, rod-like apodemes.**
- In addition, we cite the following, additional nine lepidopteran apomorphies [15,25] as providing evidence for an affiliation to the Lepidoptera (Table 3).
- The median ocellus is absent.** The loss of median ocellus represents an autapomorphy of Lepidoptera, as this structure is present in Trichoptera [46]. The detailed structure of the head in most of these twenty specimens is difficult to discern. However, one of our better-preserved specimens, *Petilioxystus cristatus* gen. et sp. nov. (CNU-LEP-NN-2012-007, Fig. 10), displayed a head capsule in which a median ocellus was clearly lacking, indicating an assignment to the Lepidoptera.
- The foretibia possesses an epiphysis.** Except for the fossil genus *Mesokristensenia*, the epiphysis is a long-established and diagnostic character of modern Lepidoptera [46]. The foretibia bears a well-developed epiphysis and lacks apical spurs, often considered is an autapomorphous condition of the Lepidoptera. *Eolepidopterix jurassica*, belonging to the extinct lepidopteran family Eolepidopterigidae, possesses a foretibial epiphysis [4,6]. In addition, an epiphysis occurs on the foretibia of *Seresilepidopteron dualis* gen. et sp. nov. (CNU-LEP-NN-2006-001, Fig. 3), and on specimen CNU-LEP-NN-2012-013, the latter a species of uncertain familial status (Fig. 21), confirming assignment of these two specimens to the Lepidoptera.
- The foretibia bears at most a single apical spur.** Except for the Agathiphagidae and Mesokristenseniidae that possess a single apical spur on their foretibiae, most other Lepidoptera lack foretibial spurs. A spur is absent on the foretibia of *Quadruplecivena celsa* gen. et sp. nov. (CNU-LEP-NN-2012-027, Figs. 8, 9), and on the unaffiliated species (CNU-LEP-NN-2012-013, Fig. 21), consistent with assignment of both specimens to the Lepidoptera.
- The mesotibia lacks medial spurs.** The absence of medial spurs on the tibiae of the Aglossata is consistent with an affiliation of some Daohugou specimens to the Lepidoptera.
- Absence of nygmata on the wings.** Nygmata are distinctive pustulate structures located at the base of the Rs_3 – Rs_4 vein in almost all Trichoptera (Fig. 2B) [36]. By contrast, nygmata are absent in the Lepidoptera. All twenty specimens, except for one specimen with indeterminate wing venation, have wings that lack nygmata. The absence of nygmata on 19 specimens that exhibit good wing preservation cannot exclude the possible presence of nygmata, but strongly suggests that early Lepidoptera lacked these interesting wing structures.
- Forewing M vein is 3-branched.** A 3-branched medial vein, M, has long been considered a lepidopteran autapomorphy [6], but exceptions occur in both Lepidoptera and Trichoptera. For example, the M_4 is present in the Aglossata, Mesokristenseniidae and Ascololepidopterigidae fam. nov. (Lepidoptera); and the M_4 is absent in the extinct family Dysoneuridae (Trichoptera). In spite of these

Table 3. Amphiesmenopteran and Lepidopteran apomorphies for our specimens.

Genus	Species	Specimen	Amphiesmenopteran apomorphies ¹				Lepidopteran apomorphies ¹								
			1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Sereslepidopteron</i>	<i>S. dualis</i>	CNU-LEP-NN-2006-001	O	O	?	?	?	O	?	O	?	O	O	?	?
		CNU-LEP-NN-2006-002	?	?	?	O	?	?	?	?	?	O	?	?	?
<i>Akainalepidopteron</i>	<i>A. elachipteron</i>	CNU-LEP-NN-2012-023	?	?	?	?	?	?	?	O	?	O	O	?	?
		CNU-LEP-NN-2012-024	?	O	?	?	?	?	?	O	?	O	O	?	?
		CNU-LEP-NN-2012-026	?	?	?	?	?	?	?	?	?	O	O	?	?
<i>Dynamilepidopteron</i>	<i>D. aspinosus</i>	CNU-LEP-NN-2012-014	?	?	?	?	?	?	?	O	?	O	?	?	
<i>Quadruplecivena</i>	<i>Q. celsa</i>	CNU-LEP-NN-2012-027	?	O	?	?	?	?	O	O	?	O	X	?	?
<i>Petilicorpus</i>	<i>P. cristatus</i>	CNU-LEP-NN-2012-007	?	O	?	O	O	?	?	O	?	O	O	?	?
<i>Longcapitalis</i>	<i>L. excelsus</i>	CNU-LEP-NN-2012-025	O	O	?	?	?	?	?	?	?	O	O	?	?
<i>Grammikolepidopteron</i>	<i>G. extensus</i>	CNU-LEP-NN-2012-006	O	?	?	O	?	?	?	?	?	O	X	?	?
<i>Mesokristensenia</i>	<i>M. sinica</i>	CNU-LEP-NN-2009-003	?	?	?	?	?	?	?	O	?	X	O	?	?
	<i>M. trichophora</i>	CNU-LEP-NN-2012-032	O	?	?	?	?	?	?	O	?	X	O	?	?
<i>Kladolepidopteron</i>	<i>K. oviformis</i>	CNU-LEP-NN-2009-007	O	?	?	?	?	?	?	O	?	X	O	?	?
		CNU-LEP-NN-2012-020	O	O	?	?	?	?	?	?	?	X	O	?	?
		CNU-LEP-NN-2012-022	O	?	?	?	?	?	?	?	?	X	O	?	?
	<i>K. parva</i>	CNU-LEP-NN-2012-011	?	O	?	O	?	?	?	?	?	X	O	?	?
<i>Ascololepidopterix</i>	<i>A. multinerve</i>	CNU-LEP-NN-2012-028	O	O	?	?	?	?	?	?	?	X	O	?	?
<i>Pegolepidopteron</i>	<i>P. latiala</i>	CNU-LEP-NN-2012-001	O	O	?	O	?	?	?	?	?	X	O	?	?
<i>Trionolepidopteron</i>	<i>T. admarginis</i>	CNU-LEP-NN-2012-012	?	O	?	?	?	?	?	?	?	X	O	?	?
incertae sedis	?	CNU-LEP-NN-2012-013	?	?	?	?	?	?	O	O	O	?	?	?	?

¹Numbers refer to apomorphies listed in the text; O = character presence, X = character absence, ? = unknown state.

exceptions, most of the specimens with 3-branched M veins (Figs. 1C, D, E and 2A) are most likely Lepidoptera.

12. **Separation of the M₁ from the M₂ veins is accompanied by an angle greater than 60 degrees and a sharp, angulate intersection at the junction with the r-m crossvein** (Fig. 2A). Huang *et al.* [25] proposed that Lepidoptera can be distinguished from Trichoptera by this character of the M₁ vein. In Lepidoptera, the M₁ usually separates from M₂ at an angle greater than 60 degrees, followed by sharp angulation at junction with the r-m crossvein (Figs. 1C, F, and 2A). By contrast, nearly all Trichoptera have branches of the M₁₊₂ with the M₁ and M₂ veins at an angle of less than 45 degrees; in addition, and M₁ is linear and smooth (Figs. 1G and 2B). Not all Lepidoptera have a M₁ vein that is sharply angulated at the junction with r-m crossvein, such as *Undopterix sukatshevae* that was identified as a lepidopteran based on the presence of scales (Fig. 1D), and *Netoxena nana* based on its 3-branched M vein (Fig. 1E). If a fossil species has this feature, it is most likely a lepidopteran. Most of our twenty specimens exhibit wings with this character, except for two lacking this feature and three that have it as an ambiguous presence (as shown in Table 3).
13. **The male valva is primarily undivided.**
14. **The cerci are absent in both sexes.**

The Early Evolution of the Amphiesmenoptera

The Amphiesmenoptera likely originated from the stem panorpoid stock [15]. Although no fossils unambiguously represent the common ancestry of Lepidoptera and Trichoptera, the extinct family Necrotauliidae has been suggested as the best candidate (Fig. 1A) [5]. This family is a paraphyletic assemblage of species that existed from the Triassic to the Cretaceous [50]. The earliest fossil member of the Lepidoptera, *Archaeolepis mane* (Fig. 1B), was reported from Sinemurian Stage, of the mid Early Jurassic age, an assignment based primarily on distinctive lepidopteran scales [18]. Characters of the wing venation, legs and axial part of the body of the various new species in this report indicate the presence of autapomorphies in both the Amphiesmenoptera and the Lepidoptera. These features provide supplemental evidence to support the hypothesized divergence of the Lepidoptera and Trichoptera occurring by the Early Jurassic. This differentiation of the Lepidoptera and Trichoptera likely had transpired during the Triassic–Jurassic boundary [50], or possibly Late Triassic [6,51]. Notably, gracile, lepidopteran-like, epidermal leaf mines reminiscent of the Nepticulidae and more basal monotrystian leaf mining lineages are present in a Late Triassic (Carnian) flora from South Africa (C Labandeira, R Prevec, E Currano, J Anderson and H Anderson, unpublished data), perhaps indicating an earlier, Middle Triassic date for the origin of basalmost lepidopteran lineages.

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Conceived and designed the experiments: DR CCL CKS. Performed the experiments: WTZ CKS DRD JCS CCL JAS OF DR. Analyzed the data: WTZ CKS DRD JCS CCL JAS OF DR. Contributed reagents/materials/analysis tools: WTZ CKS DRD JCS CCL JAS OF DR. Wrote the paper: WTZ CKS CCL DRD JCS. Photographs: WTZ CKS JAS CCL. Line drawings: WTZ CKS JCS DRD.

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