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. Speciality 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 holometabolon 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 Mesozioc (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...
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, Anzorge [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 M1, separated from the M2 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 $^{40}$K/$^{40}$Ar at

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**Figure 1. A stem-group amphiesmenopteran, lepidopterans, and a trichopteran.** (A), A stem-group amphiesmenopteran, Necrotaulus 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 Rs1+4 furcation beyond the M1+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
| Suborder          | Family            | Genus             | Species            | Epoch | Country         | Reference |
|-------------------|-------------------|-------------------|--------------------|-------|-----------------|-----------|
| ?                 | Archaeolepidae    | Archaeolepia      | Whalley, 1985      | A. mano Whalley, 1985 | J1 United Kingdom | [18]      |
| Eolepidopterigina | Eolepidopterigidae| Eolepidopterix     | Whalley, 1983      | E. jurassica Whalley, 1983 | J3 Kazakhstan | [4]       |
| Eolepidopterigina | Eolepidopterigidae| Palaeoepidopterix | Kozlov, 1989       | P. aurea Kozlov, 1989 | J3 Kazakhstan | [40]      |
| Eolepidopterigina | Eolepidopterigidae| Dasiopterix       | Skalski, 1984      | D. ransitynsi Skalski, 1984 | K1 Russia | [23]      |
| Eolepidopterigina | Eolepidopterigidae| Dasiopterix       | Kozlov, 1989       | D. olgae Kozlov, 1989 | K1 Russia | [40]      |
| Eolepidopterigina | Eolepidopterigidae| Netoxena Sohn, 2012| N. nana (Martins-Neto, 1999) | K1 Brazil | [24,52] |   |
| Eolepidopterigina | Eolepidopterigidae| Undopterix Skalski, 1979 | U. sukatheeva Skalski, 1979 | K1 Russia | [10] |   |
| Eolepidopterigina | Eolepidopterigidae| Undopterix Skalski, 1979 | U. caririensis Martins-Neto & Vulcano, 1989 | K1 Brazil | [39] |   |
| Eolepidopterigina | Eolepidopterigidae| Gracileopterix Neto & Vulcano, 1989 | G. pulchra Martins-Neto & Vulcano, 1989 | K1 Brazil | [39] |   |
| Zeugloptera       | Micropterigidae   | Sabatinca Walker, 1863 | S. perveta (Cockerell, 1919) | K1 Burma | [12,42] |   |
| Zeugloptera       | Micropterigidae   | Parasabatinca Whalley, 1978 | P. aftimacrai Whalley, 1978 | K1 Lebanon | [45] |   |
| Zeugloptera       | Micropterigidae   | Parasabatinca Whalley, 1978 | P. calcadae Martins-Neto & Vulcano, 1989 | K1 Brazil | [39] |   |
| Zeugloptera       | Micropterigidae   | Palaeosabatinca Kozlov, 1988 | P. zherichini 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] |   |
| Zeugloptera       | ?                  | ?                   | ? Burns | [52,56] |   |
| Zeugloptera       | ?                  | ?                  | A. mirabilis Kozlov, 1989 | J3 Kazakhstan | [40] |   |
| Zeugloptera       | ?                  | ?                  | A. minima Kozlov, 1989 | J3/K1 Mongolia | [40] |   |
| Zeugloptera       | ?                  | ?                  | ? J3/K1 France | [9,16] |   |
| ?                 | Mesokristenseniidae| Mesokristensenia Huang et al., 2010 | M. latipenna Huang et al., 2010 | J2 China | [25] |   |
| ?                 | Mesokristenseniidae| Mesokristensenia Huang et al., 2010 | M. sinica Huang et al., 2010 | J2 China | [25] |   |
| ?                 | Mesokristenseniidae| Mesokristensenia Huang et al., 2010 | M. angustipenna Huang et al., 2010 | J2 China | [25] |   |
| Glossata          | Bucculaticidae    | Bucculatrix Zeller, 1839 | B. platani Kozlov, 1988 | K2 Kazakhstan | [16] |   |
| Glossata          | Incurvariidae     | ?                  | K2 Russia | [10] |   |
| Glossata          | Incurvariidae     | ?                  | K1 Brazil | [5] |   |
| Glossata          | ?                  | ?                  | K1 Lebanon | [45] |   |
| Glossata          | ?                  | ?                  | K2 Russia | [5,58] |   |
| Glossata          | ?                  | ?                  | K2 Russia | [10] |   |
| Glossata          | ?                  | ?                  | P. cuprealata Kozlov, 1989 | J3 Kazakhstan | [40] |   |
| Glossata          | ?                  | ?                  | K. lapidaria Kozlov, 1989 | J3 Kazakhstan | [40] |   |
| ?                 | ?                  | ?                  | Archiptilia Handlirs, 1939 | A. ovata Handlirs, 1939 | J1 Germany | [21,59] |   |
| ?                 | ?                  | ?                  | Epidendontus Handlirs, 1939 | E. genizans Handlirs, 1939 | J1 Germany | [21,59] |   |
| ?                 | ?                  | ?                  | Metarchitaulius Handlirs, 1939 | M. longus Handlirs, 1939 | J1 Germany | [21,59] |   |
| ?                 | ?                  | ?                  | Nannotrichopteron Handlirs, 1906 | N. gracile Handlirs, 1906 | J1 Germany | [20,21] |   |
| ?                 | ?                  | ?                  | Palaeothitaulius Handlirs, 1939 | P. vicinus Handlirs, 1939 | J1 Germany | [21,59] |   |
| ?                 | ?                  | ?                  | Pararchitaulius Handlirs, 1939 | P. ovalis Handlirs, 1939 | J1 Germany | [21,59] |   |
| ?                 | ?                  | ?                  | Parataulius Handlirs, 1939 | P. jursicus Handlirs, 1939 | J1 Germany | [21,59] |   |
| ?                 | ?                  | ?                  | Pseudorthophlebia Handlirs, 1906 | P. platyptera Handlirs, 1906 | J1 Germany | [20,21] |   |
| ?                 | ?                  | ?                  | Paratrichopteridium Handlirs, 1906 | P. efassum Handlirs, 1939 | J1 Germany | [21,59] |   |
| ?                 | ?                  | ?                  | Paratrichopteridium Handlirs, 1906 | P. costale Handlirs, 1939 | J1 Germany | [21,59] |   |
| ?                 | ?                  | ?                  | Necrotaulius Handlirs, 1906 | N. tener Sukatsheva, 1990 | K1 Russia | [50,60] |   |
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 Mesokristenseni-
da. 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 stereomi-
croscope 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 microtographic
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
microtographic aspect, spot size or accelerating voltage; we
strived 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
polyallin film, used in industrial kitchens to shrink-wrap food. In
contrast to polyester shrink-wrap, polyallin film does not melt or
release gas in the vacuum chamber. The shrink-wrapping of stub-
mounted specimens in polyallin 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). Amphimesme-
nopteran and lepidopteran apomorphies are taken from Kristen-
sen and Skalski [15] and Huang et al. [25]. Family-level
classification follows Nieukerken et al. [1]. Wing venation nomen-
clature 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.

Table 1. Cont.

| Suborder     | Family       | Genus | Species | Epoch | Country | Reference |
|--------------|--------------|-------|---------|-------|---------|-----------|
| Glossata     | ?            | ?     | ?       | K1    | Burma   | [54]      |
| Glossata     | ?            | ?     | ?       | K2    | USA     | [61]      |
| Glossata     | Nepticulidae | ?     | ?       | K1    | USA     | [13]      |
| Glossata     | Gracillariidae | ?     | ?       | K1    | USA     | [13]      |
| Glossata (larva) | ? | ?     | ?       | K1    | Lebanon | [62]      |
| Glossata (larva) | ? | ?     | ?       | 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.
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 proboscis ……………………Glossata
   –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…………………………………….Heterobathmiidae
   –Sc unforked; crossvein absent between Sc and R; pterostigma present…………………………………….Micropterigidae

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 M1, after separation from M2, 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 M1+2 and M4 consisting of smooth and sublinear veins. Abbreviation: ny, nygmata.
doi:10.1371/journal.pone.0079500.g002
5. Metatibia without medial spur; R₁ forked.

6. Mesotibia with medial spur; crossvein m-cua and crossvein cua-cup present. Agathiphagidae

Mesotibia without medial spur; crossvein m-cua and crossvein cua-cup absent. Mesokristensenidae

Suborder Eolepidopterina Rasnitsyn, 1983.

Family Eolepidopteridae Rasnitsyn, 1983.

Type genus. Eolepidoptera Rasnitsyn, 1983 [4].

Emended diagnosis. Head with mandibulate mouthparts. Antennae filiform, less than half the length of forewing. Foretibia with an epiphysis. Metatibia 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—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—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—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—pairs of spurs. 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Both pairs of wings homoneurus (the venation of the forewings and hind wings alike). Wings covered with scales. Forewing with jugum and number of vein branches as follows: Sc—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—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—pairs of spurs. Both pairs of wings homoneurus (the venation of the forewings and hind wings alike). Wings covered with scales. Forewing with jugum and number of vein branches as follows: Sc—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—pairs of spurs. Both pairs of wings homoneurus (the venation of the forewings and hind wings alike). Wings covered with scales. Forewing with jugum and...
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).
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 tarwal 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; Rs₂ 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. Mesocutum, mesoscutellum, metascutum and metacetum all 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 R₂ 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.

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

urn:lsid:zoobank.org:act:017DB748-9F58-407E-87AF-75063A531CCA.

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

Etymology. The specific name is derived from the Greek, elachipteron (small), referring to the wing of this species that is shorter than its body length.

Type materials. Holotype: CNU-LEP-NN-2012-024; Q; well preserved fore and hind wings; anal area covered by body and portions of the legs. Paratypes: CNU-LEP-NN-2012-023; Q; 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. 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), crosstvein absent between Sc and R.

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

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

Compared with Undopterix, Nachialedipopteron 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 Nachialedipopteron (vs. lacking cilia); and 3), the metatibiae has spines in Nachialedipopteron (vs. lacking spines).

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

urn:lsid:zoobank.org:act:61EBD55-F1FA-4F7F-BA7E-B95CD0C0F65.

Etymology. The specific name is derived from the Greek, elachy (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; Q; well preserved fore and hind wings; anal area covered by body and portions of the legs. Paratypes: CNU-LEP-NN-2012-023; Q; 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. Mesocoxa more slender than mesocoxae; mesocoxae longer than metacoxa; two long spines present at the end of mesofemora; metatibia 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), Piliform 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
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. Cu₄ bifurcated; CuP simple; anal area not well preserved. Cu₂ divergent from M. R forks immediately after M–Cu₂ 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. Cu₄ bifurcated; CuP simple. Crossvein cua–cup slanted obliquely. Ptiliform scales ranging from 0.12 to 0.21 mm in length, present on veins Sc, R₁+₂, R₃, R₂, R₃, 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.

Ptiliform scales, with lengths between 0.07 and 0.08 mm, are present on some lepidopterans, e.g. *Heterobathmia pseudoerocaria* 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 ptiliform scales along the veins of *H. pseudoerocaria*.

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

urn:lsid:zoobank.org:act:31AD01ED-D78A-45D0-8E80-AB92CC9497F7

**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 *pterion*, 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 *Akazanilepidopteron* 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-F755D5B1EEDE8

**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; ₁; 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...
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; mesoscutellar flabellate, relatively large, nearly equal to mesoscutum in length; metascutum dumbbell shaped; metascutellum smaller than mesoscutellum. Metaabdomen 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 length 6.7; width ca. 2.4. Hind wing length ca. 5.5. Measurements (in mm). Body length 7.0; width 1.9. Forewing length 6.7; width ca. 2.4. Hind wing length ca. 5.5.

Quadruplecivena Zhang, Shih, Labandeira & Ren gen. nov. urn:lsid:zoobank.org:act:878C3B3C-643E-4C46-B56A-ABDA90AEB775.

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

Comparison. Quadruplecevisa differs from Seresilepidopteron in the following characters: in the forewing, 1), the M 1+2 distinctly extends beyond the Rs 3+4 furcation (vs. the M 1+2 and Rs 3+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–r crossvein near the R 1 furcation (vs. the sc–r crossvein considerably removed from the R 1 furcation). Quadruplecivena differs from Akainalepidopteron in the following characters: 1), the M 1+2 furcation distinctly extends beyond the Rs 3+4 furcation (vs. the M 1+2 and Rs 3+4 furcations occurring at the same level); 2), the M 1 is not sharply angulate at the junction with the r–m crossvein (vs. M 1 sharply angulate at the junction with r–m crossvein); 3), the hind wing lacks spines (vs. hind wing with spines); 4), the sc–r 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).

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

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.
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; Rs1+2 stalked ca. 0.2 of their total length; Rs1+2 forked at the same level as Rs3+4 furcation; Rs4 and M1 respectively above and below wing apex. M 3-branched; M1 and M2 stalked; M1+2 forked beyond Rs3+4 furcation. CuA bifurcated. Anal veins not preserved. In hind wing, Sc not forked. R1 forked; crossvein sc–r1 present and slightly curved and oblique, originating near end of Sc and terminating near R1 furcation; Rs 4-branched; stem Rs1+2 slightly longer than Rs3+4. M 3-branched; M1+2 forked beyond Rs3+4 furcation; M3 curved at 2/3 the length of vein M3 from its base. CuA bifurcated.

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
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 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 anteroes; and 4) crossvein absent between Sc and R.

Comparison. **Petilicorpus** gen. nov. is assigned to the Eolepidoptera for having a long apophyses in the abdomen and the M vein 3-branched in the forewing. **Petilicorpus** resembles Eolepidoptera in having the presence of a slender body and similar forewing length and antennal length. However, **Petilicorpus** differs from *Eolepidoptera* 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 *Paleoepidoptera* is not well preserved. Based on the present specimen, **Petilicorpus** can be differentiated from *Paleoepidoptera* by its longer head and shorter pronotum. The venation of **Petilicorpus** resembles *Daiopterix* 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 *Daiopterix* 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; Q; 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 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.
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; Rs3+2 stem slightly shorter than Rs5+4 stem. M 3-branched. Hyaline zones surround r–m crossvein and at Rs5+4 and M1+2 furcations. Crossvein m present, originating near M1+2 furcation and terminating at the midpoint of M2. Hind wing ca. 2.3 times as long as wide. Veneration 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.
Diagnosis. Head longer than wide. Metatibiae lacking spines. Anterior margin of wings lacking cilia. Humeral vein in forewing present. Sc forked. R1 not forked. All furcations of Rs1+2, Rs3+4, and M1+2 almost at the same level with each other. Anal veins looping into a double-Y configuration. Hind wing with Sc and R1 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 R1 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 R1 is not forked in both fore- and hind wings (vs. R1 forked in the fore- and hind wings); 2), the Rs1+2 stem is as long as the Rs3+4 stem (vs. the Rs1+2 stem shorter than the Rs3+4 stem); and 3), the anal veins form a double-Y loop (vs. the anal veins forming a single-Y loop). *Longcapitalis* differs from *Alkainalepidopteron* by the following characters: 1), the R1 is not forked in both fore- and hind wings (vs. R1 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).

**Diagnosis.** Head longer than wide. Metatibiae lacking spines. Anterior margin of wings lacking cilia. Humeral vein in forewing present. Sc forked. R1 not forked. All furcations of Rs1+2, Rs3+4, and M1+2 almost at the same level with each other. Anal veins looping into a double-Y configuration. Hind wing with Sc and R1 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 R1 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 R1 is not forked in both fore- and hind wings (vs. R1 forked in the fore- and hind wings); 2), the Rs1+2 stem is as long as the Rs3+4 stem (vs. the Rs1+2 stem shorter than the Rs3+4 stem); and 3), the anal veins form a double-Y loop (vs. the anal veins forming a single-Y loop). *Longcapitalis* differs from *Alkainalepidopteron* by the following characters: 1), the R1 is not forked in both fore- and hind wings (vs. R1 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-B866E1DD0055.

**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; R; 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. Metanota with a spine at the end of femora. Metabasitibiae with one pair medial spurs and one pair apical spurs. Metatarsi 5-segmented, all tarsal segments with terminal spines. Forewing 2.7 times as long as wide, bearing a humeral vein; pterostigma present. Sc forked, at distal 3/5 of the stem, Sc1, almost extending to the midpoint of wing costal margin, Sc2
extending to costal margin of wing, beyond 2/3 length of wing from base. R1 not forked; Rs 4-branched; Rs3 extending to apex of forewing; Rs1+2 stalked ca. to 0.4 of the total vein length; Rs3 and R4 free; and Rs 1+2 stem subequal to Rs 1+4 stem. M 3-branched. Hyaline zones surround r–m crossvein at Rs1+4 furcation, and at the Rs1, M1+2, M1+4, and M1+2–M3 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. R1 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-B794-4239-9FEE-BE4B8F8A3D9D

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

**Etymology.** The generic name is from the Greek, combining grammus (line, linear), in reference to the linearly aligned branching points of veins R1 and Rs to Rs4; and lepidopteron, meaning “scale” or “falte,” 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 R1 not forked. Rs3 terminating only slightly before wing apex. Branching points of R1 and Rs1 to Rs3 linearly aligned. M divided into M3 and M1+2–M1+4 subdivide iteratively into veins M1 and M2 at an angle of ca. 15 degrees; M1 linear and smooth. CuA bifurcated; CuP simple. Three anal veins looping into a double-Y configuration. Apophyses short.

An Eolepidopteridae 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 M4 vein extending beyond the CuA furcation (vs. the CuA furcation extending beyond the M4 vein); 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 Micropterix, Micropterix percuta Cockerell, 1919 [42]. However, Grammikolepidopteron differs from *M. percuta* in: 1), the forewing having Sc and R1 veins that are not forked (vs. Sc and R1 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:4D3BC4A4-5935-48A3-823F-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); C right forewings well preserved; body hind wing not well preserved. Forewings asymmetrical; left hind wing 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; mesocutellum 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. R1 not forked, extending to costal margin of wing at a point 4/5 length of wing from base; Rs 4-branched; Rs3 terminating slightly before wing apex; branching points of R1 and Rs3 to Rs5 linearly aligned. M arising from CuA, 3-branched; M1 and M2 stalked, ca. 0.4 of their total length. CuA furcation distal of M furcation and before the M1+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 R1 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 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 palp long. Mesothidia lacking medial spurs; spurs of formula of legs: 1–1–4. Number of forewing veins branches: Sc–2, R1–1, Rs–4, M–4, CuA–2, CuP–1, A–3; Rs3 and R5 separate. Ovipositor nonpiercing, with anterior apophyses.

The synapomorphies for the Mesokristenseniidae are mesothidia with only an apical spur, wings homoneurous, R1 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 M1 sharply angulate at the junction with r–m crossvein.

**Genera included.** Kludolepidopteron gen. nov. and Mesokristensisia 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; 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; mesocutellum 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.

Mesothidia with only an apical spur, wings homoneurous, R1 unforked, M vein 4-branched, and ovipositor with anterior apophyses.

The synapomorphies for the Mesokristenseniidae are mesothidia with only an apical spur, wings homoneurous, R1 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 M1 sharply angulate at the junction with r–m crossvein.
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; C; 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 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
of the stem; Sc₂ extending to costal margin of wing at 2/3 length from wing base; sc–r crossvein absent. R₁ not forked; Rs 4-branched; Rs₃ slightly below the apex of forewing; Rs₁+₂ stalked ca. 0.3 of their total length. M 4-branched, stem M₁+₂ longer than stem M₃+₄. Hyaline zones surrounding r–m crossvein at Rs₃+₄ and M₁+₂ furcations. Cuₐ forked before M₃+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 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
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; Sc extending to costal margin of wing at 2/3 distance from wing base; sc–r crossvein absent. R1 not forked; Rs 4-branched; R5 extending to the apex of forewing; Rs5+2 stalked ca. 1/3 of their total length; Rs5 and Rs4 free. M 4-branched; M1+2 stem longer than M3+4 stem. Hyaline zones surround r–m crossvein at Rs3+2, Rs3+4 and M1+2 furations. CuA forked before M3+4 furation; 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.
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), R₁ 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).

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

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 Sc₂); 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); Q; 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, Rs1+2 stem shorter than Rs3+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. Mesoscutum fan-shaped; metascutum dumbbell shaped; metasculum 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; Sc2 extending to costal margin of wing at 3/5 length of wing from base. Crossovein sc–r present. R1 not forked; Rs4-branched; Rs4 extending to the apex of forewing; Rs1 and Rs2 stalked; Rs1+2 stalked ca. 0.38 of their total length; Rs3 and Rs4 free. M 4-branched; stem M1+2 longer than stem M3+4. M1 after separation from M3 subtending an angle of 60 degrees, sharply angulate at junction with crossovein r–m. Crossovein m–ca. originating near M1+2 furcation and terminating near the midpoint of M3. Hyaline zones surrounding r–m crossovein at Rs3+4 and M1+2 furcations. CuA1+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. R1 not forked; Rs 4-branched; Rs3+4 stem ca. 2 times as long as stem Rs1+2. Abdomen lacking specialized integumental modifications. Ovipositor long; apophyses not evident.

**Measurements (in mm).** Body length ca. 6.3; width 1.1. Forewing length 4.3; width 1.6. Hind wing length ca. 5.6; width 1.3.

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

- **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 Rs1+2 and Rs3+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 Rs3+4 subequal in length. 

**Comparison.** Kladolepidopteron. *subaequalis* resembles *K. oviformis* in: 1), the forewing index (0.32 vs. 0.31); and 2), the wing apex forkings almost at the same level as Rs3+4. *Kladolepidopteron parva* 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 Rs3+4 stem than the Rs3+4 stem only half length of Rs3+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; Sc2 extending to costal margin of wing at 3/5 length of wing from base. Crossvein sc–r present. R1 not forked; Rs 4-branched; Rs4 extending to the apex of forewing; Rs1 and Rs2 stalked, Rs3+2 stalked ca. 0.35 of their total length; Rs3 and Rs4 free; Rs3+4 furcation almost at same level as Rs3+4. Crossvein s-present (Figs. 16C, D). M 4-branched; M1, after separation from M2 subtending an angle of 75–80 degrees, sharply angulate at junction with r–m crossvein (Figs. 16C, D); stem M1+2 longer than stem M3+4. CuA bifurcated; CuP simple. Three main 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. R1 not forked; Rs 4-branched; Rs branching into veins Rs1+2 and Rs3+4, and then further subdividing into four branches of Rs1, Rs2, Rs3, and Rs4; furcations of Rs1+2 and Rs3+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)

- **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); sex unknown; 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 Rs1+2 forking almost at the same level as Rs3+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. 5.3 mm long); 2), short forewing length of 4.1 mm (vs. long forewing length of 4.8 mm); and 3), the Rs3+4 stem slightly shorter than the Rs3+4 stem (vs. the Rs3+4 stem only half length of the Rs3+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                           |
| Subcostal vein (Sc)            | forked                          | not forked or forked            |
| Radial vein (R1)               | not forked                      | not forked or forked            |
| Furcations of Rs1+2 and Rs3+4  | Furanct of Rs1+4 distally, distinctly beyond furcation of Rs1+2 | approximately at the same level to each other |
| Crossvein m-cua                | Present                         | absent                          |
| Crossvein m-cup                | Present                         | Present                         |

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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. CuA1 bifurcated; CuP simple. Hind wing Sc not forked.

Forewing length ca. 4.1; width ca. 1.3. Hind wing length ca. 3.4.

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

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

**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.

**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
**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 *Ascololepidopterix* gen. nov.

Key to known genera of Ascololepidopterigidae fam. nov.

1. Forewing with Sc not forked.................................................................*Ascololepidopterix* gen. nov.
   - Forewing with Sc forked........................................................................2
2. Forewing length more than 7.0 mm; forewing lacking crossvein Rs1-Rs2; crossvein r present ..................
   - Forewing length less than 5.0 mm; forewing with crossvein Rs1-Rs2; crossvein r absent..........................

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

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

**Type species.** *Ascololepidopterix 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+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.](image-url) 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 multinevus** Zhang, Shih, Labandeira & Ren sp. nov. (Fig. 18)

urn:lsid:zoobank.org:act:7B3EA090-9A7A-4AE9-AD90-7075315CCB91.

**Etymology.** The specific name is derived from the Latin, *multi* (many, much), and *neris* (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. 2.3 times as long as wide; lacking humeral vein; prominent pterostigma present. Sc not forked. R₁ forked distally; R₁b curved; Rs 4-branched; Rs₄ to the apex of forewing; Rs₅+₂ stalked ca. 0.45 of vein total length; stem Rs₅+₂ as long as stem Rs₅+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 M₁₄ shorter than stem M₃+₄; m crossvein originating near M₁₂ furcation, ending at M₃+₄; CuA bifurcated; CuP simple. Crossvein m₃+₄–cu₁ originating at ca. 1/3 length of M₃+₄ from its base and terminating near CuA furcation; cu–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 Rs₁₂ longer than stem Rs₃+₄. M 4-branched; M₁ and M₂ stalked; furcation of M₁₂ at same level with furcation of Rs₁₂; CuA bifurcated; CuP simple. Crossvein m₃–cu₁₁₁ 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. Cuvium R₁ absent, r–m crossvein weak. Stem M₁₂ longer than stem M₃+₄; m₃+₄–cu₄ crossvein originating near M furcation and terminating at midpoint of CuA. Cuvium cu–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), R₇ forked; 4), M 4-branched; and 5), crossveins m–cu₄ and cu₄–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 s–r crossvein is absent (vs. the s–r crossvein present); 3), the r crossvein is present (vs. the r crossvein absent); 4), the location of the m₄+₃–cu₄ 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-BA00-1589FECF707C.

**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; Q; 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. Cuvium s–r absent. R₁ forked from distal 1/4 of stem, slightly beyond the Rs₁₂ furcation; Rs 4-branched; Rs₁₂ stalked ca. 0.45 of their vein length; stem R₄+₂ as long as stem R₅+₂; 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 M₃+₄; m crossvein originating near M₁₂ furcation and terminating near the midpoint of CuA. Hyaline zones surrounding r–m crossveins at Rs₁₂, Rs₅+₂, and M₃+₂ furlcations. CuA bifurcated; CuP simple; cu–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. Cuvium m₃–cu₁₁₁ present between M₁ and CuA; cu₄–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:B2E52225-7FFD-4E66-B153-D6D638B6056E.

**Type species.** *Trionolepidopteron admarginis* Zhang, Shih, Labandeira & Ren sp. nov.
**Etymology.** The generic name is derived from the Greek τριόν (three) for the threefold branched Rs vein in the hind wing; and λεπίδος (scale, flake), referring to the Lepidoptera, the order to which this taxon is assigned; and πτερόν (a bird’s wing, fin). The gender is masculine.

**Distribution.** Inner Mongolia Autonomous Region, China.

**Diagnosis.** Body small; forewing with Sc forked. R₁ forked. Crossvein Rs₁–Rs₂ present. Stem M₁+₂ longer than stem M₃+₄. Crossvein m₃+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), R₁ 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 R₁ forked veins; 2), the M vein is 4-branched; 3), a free M₁ vein; and 4), presence of the m₃+₄–cua crossvein. *Trionolepidopteron* is differs from *Pegolepidopteron* by the following characters: 1), Rs₁–Rs₂ crossveins are present on the forewing (vs. absent); 2), r crossvein is absent on forewing (vs. present); 3), m₃+₄–cua crossvein is present.

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![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](image-url)
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 rs1–rs2 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; S2 extending to costal margin of wing, beyond 2/3 length of wing from base. R3 forked; sc–r crossvein absent; Rs 4-branched; Rs4 terminating at forewing apex; Rs4+5 stalked ca. 0.37 of their total length; stem Rs4+5 subequal to stem Rs5+4. Crossvein r5–r6 present and located near the costal margin of forewing. M 4-branched; stem M1+2 longer than stem M3+4; after separation from M2 at an angle of ca. 70 degrees, sharply angulated at junction with r-m crossvein. Hyaline zones surround r-m crossveins at R5+6, R5+6, M1+2, and M1+2-M5 furcations. CuA bifurcated. Crossvein m3+4–cua present, originating on M3+4 and terminating near the CuA furcation. Hind wing ca. 2.5 times as long as wide. Sc and R3 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
mesothorax and metathorax 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 autopomorphy 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 autopomorphies. 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 autopomorphies.

Although Kristensen listed 23 autopomorphies for adult Lepidoptera [44], few of these can be observed on compression fossils. Grimaldi [8] specified three critical, external autopomorphies that should be present in adults of early lepidopteran fossils: 1) absence of a forewing M4 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 piliform 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 autopomorphies [15,25] are sufficient for identifying specimens in this report as Amphiesmenoptera (Table 3):  

1. **The forewing anal veins form a “double-Y” loop.**
2. **The hind wing M vein bears at most three branches.** This condition also indicates that veins M₃ and M₄ are entirely merged.
3. **The pronotum has paired setose prominences.**
4. **The anterior margin of female segments VIII and IX are accompanied by long, rod-like apodemes.**
5. In addition, we cite the following, additional nine lepidopteran apomorphies [15,25] as providing evidence for an affiliation to the Lepidoptera (Table 3):

6. **The median ocellus is absent.** The loss of median ocellus represents an autopomorphy 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, Petricorpus 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.

7. **The foretibia possesses an epiphysis.** Except for the fossil genus Mesokristensensia, 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 autopomorphous 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 Sericolepidopteron 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.

8. **The foretibia bears at most a single apical spur.** Except for the Agathiphagidae and Mesokristensenidae that possess a single apical spur on their foretibiae, most other Lepidoptera lack foretibial spurs. A spur is absent on the foretibia of Quadriplectena 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.

9. **The mesothorax 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.

10. **Absence of nygmata on the wings.** Nygmata are distinctive pustulate structures located at the base of the Rs₄–Rs₅ 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.

11. **Forewing M vein is 3-branched.** A 3-branched medial vein, M, has long been considered a lepidopteran autopomorphy [6], but exceptions occur in both Lepidoptera and Trichoptera. For example, the M₃ is present in the Aglossata, Mesokristensenidae and Ascololepidopterigidae fam. nov. (Lepidoptera); and the M₄ is absent in the extinct family Dysoneuridae (Trichoptera). In spite of these
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 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 monotrysian 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.

Table 3. Amphiesmenopteran and Lepidopteran apomorphies for our specimens.

| Genus and Species | Specimen | Amphiesmenopteran apomorphies | Lepidopteran apomorphies |
|------------------|----------|-------------------------------|--------------------------|
| Sereslepidopteron S. dualis | CNU-LEP-NN-2006-001 | O O ? ? | O O O O ? |
| Akainalepidopteron A. elachipteron | CNU-LEP-NN-2012-023 | ? ? ? ? | ? ? ? O O ? |
| Dynamilepidopteron D. aspinosus | CNU-LEP-NN-2012-014 | ? ? ? ? | O O O ? |
| Quadruplicivena Q. celsa | CNU-LEP-NN-2012-027 | ? O ? ? | O X ? |
| Petiolaris P. cristatus | CNU-LEP-NN-2012-007 | ? O ? O | O ? O O ? |
| Longicapillus L. excelsius | CNU-LEP-NN-2012-025 | O O ? ? | ? ? ? O O ? |
| Grammikolepidopteron G. extensus | CNU-LEP-NN-2012-006 | O ? ? O | ? ? ? ? O X ? |
| Mesokristensenia M. sinica | CNU-LEP-NN-2009-003 | ? ? ? ? | ? ? ? O X O ? |
| M. trichophora | CNU-LEP-NN-2012-032 | O ? ? ? | O ? X O ? |
| Kladelepopteron K. oviformis | CNU-LEP-NN-2009-007 | O ? ? ? | O ? X O ? |
| K. subaequalis | CNU-LEP-NN-2012-020 | O O ? ? | ? ? ? ? X O ? |
| K. parva | CNU-LEP-NN-2012-011 | ? O ? O | ? ? ? ? X O ? |
| Ascololepidopterix A. multinerve | CNU-LEP-NN-2012-028 | O O ? ? | ? ? ? ? X O ? |
| Pegolepidopteron P. latiala | CNU-LEP-NN-2012-001 | O O ? O | ? ? ? ? X O ? |
| Trionolepidopteron T. admarginis | CNU-LEP-NN-2012-012 | ? O ? ? | ? ? ? ? X O ? |
| Incertae sedis | CNU-LEP-NN-2012-013 | ? ? ? ? | O O O ? |

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