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A new taxon of a primitive moth (Insecta: Lepidoptera: Eolepidopterigidae) from the latest Middle Jurassic of northeastern China

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Abstract.—A new genus and species, *Aclemus patulus* n. gen. n. sp., is described based on a new specimen collected from the latest Middle Jurassic Jiulongshan Formation in Inner Mongolia, China. Based on a combination of characters from this fossil, including a homonomous fore- and hindwing, a 3-branched media vein, wings lacking long cilia on their margins; and a cross-vein absent between subcosta and radius, we establish a new genus assigned to the Eolepidopterigidae. In addition, the diagnosis of *Longcapitalis excelsus* Zhang, Shih, Labandeira and Ren 2013, is emended based on new fossil material.

Introduction

The mid-Mesozoic Eolepidopterigina is an extinct suborder of moths within the Lepidoptera. A single family, the Eolepidopterigidae, constitutes this suborder. The Eolepidopterigidae is inferred to have fed on pollen and to have laid eggs as elongate lesions in plant substrates (Rasnitsyn, 1983). Within the Eolepidopterigina, another closely related lineage, the Undopterigidae, was erected to accommodate the genus *Undopterix* Skalski, 1979. However, subsequent examination of these specimens showed that the long apophyses in the female genitalia and the wing venation of *Undopterix* are similar to those present in the Eolepidopterigidae. Consequently, the Undopterigidae is considered a junior synonym of the Eolepidopterigidae (Rasnitsyn, 1983; Skalski, 1990; Sohn et al., 2012; Zhang et al., 2013).

To date, 15 fossil species of Eolepidopterigidae have been reported worldwide. The type genus *Eolepidopterix* is represented by *Eolepidopterix jurassica* Rasnitsyn, 1983, restricted to the Upper Jurassic of Transbaikalia, Russia. Seven species described from the latest Middle Jurassic of China currently are the oldest known eolepidopterigid records (Zhang et al., 2013). In addition to *Eolepidopterix*, the following eolepidopterigids have been reported: *Palaeolepidopterix aurea* Kozlov 1989, from the Late Jurassic deposits of Kazakhstan; *Daiopterix rasnitsyni* Skalski 1984 and *D. olgae* Kozlov 1989, from the Upper Jurassic deposits of Russia (Skalski, 1984; Kozlov, 1989); and *Netoxena nana* (Martins-Neto, 1999), *Undopterix caririensis* Martins-Neto and Vulcano 1989 and *Gracileopterix pulchra* Martins-Neto and Vulcano 1989, from the late Early Cretaceous of Brazil (Martins-Neto and Vulcano, 1989). Additionally, *Undopterix sukatshevae* Skalski 1979, placed

originally in Micropterigidae, was formally transferred to Eolepidopterigidae (Skalski, 1979, 1990; Kozlov, 1988).

Recently, we collected well-preserved fossil moths from the Jiulongshan Formation near Daohugou Village, Ningcheng County of Inner Mongolia, in northeastern China. The geological age of the Daohugou fossil-bearing beds formerly was considered as mid Middle Jurassic, based on a radioisotopic date of 165 Ma (Ren et al., 2002; Gao and Ren, 2006). Because of new calibrations established for the Jurassic System (Walker et al., 2013), this site now should be considered as latest Middle Jurassic, corresponding to a late Callovian Age. The Jiulongshan Formation is considered part of the Yanliao Biota, yielding a *Lagerstätte* of excellently preserved plants, insects, dinosaurs, pterosaurs, birds, and mammals (Ji et al., 2006; Ren et al., 2010; Gao et al., 2012; Gu et al., 2012; Yang et al., 2012). From this deposit, a new genus and species, *Aclemus patulus* n. gen. n. sp., assigned to the Eolepidopterigidae, is described herein. In addition, the diagnosis of *Longcapitalis excelsus* Zhang, Shih, Labandeira and Ren 2013, is emended based on additional new material.

Material and methods

This study is based on two specimens housed at the fossil insect collection of the Key Lab of Insect Evolution and Environmental Changes at the College of Life Sciences, Capital Normal University (CNU), in Beijing, China. Camera Lucida drawings were prepared with the aid of drawing tube attached to a Leica MZ12.5 stereomicroscope. The drawings were imported into a computer by an Epson 5100 scanner, and color- and contrast-balanced with Adobe Photoshop CS2 graphics software. Photographs were acquired by a Nikon DXM1200C Digital Camera.

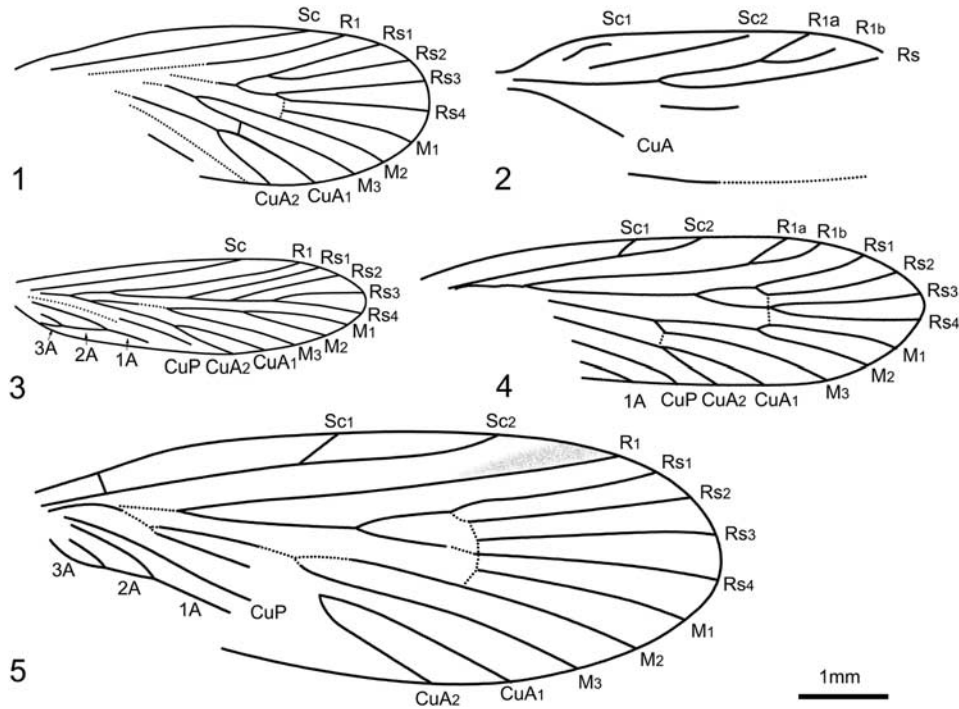


Figure 1. Camera lucida drawing of the forewings. (1) *Aclemus patulus* n. gen. n. sp. (2) *Eolepidopterix jurassica* Rasnitsyn, 1983 (modified from Rasnitsyn, 1983). (3) *Grammikolepidopteron extensus* Zhang, Shih, Labandeira and Ren, 2013 (modified from Zhang et al., 2013). (4) *Daiopterix rasnitsyni* Skalski, 1984 (modified from Skalski, 1984). (5) *Longcapitalis excelsus* Zhang, Shih, Labandeira and Ren, 2013 (modified from Zhang et al., 2013).

We follow the wing venation nomenclature of Wootton (1979). The relevant abbreviations are: C, costa; Sc, subcosta; R, radius; R_{1a} and R_{1b} , anterior and posterior branches of the anterior radius, respectively; Rs, posterior branch of R (composed of the Rs_1 , Rs_2 , Rs_3 , and Rs_4); M, media; M_{1+2} , anterior branch of the M, with M_1 and M_2 fused; M_{3+4} , posterior branch of the M, with the M_3 and M_4 fused; Cu, cubitus; CuA , anterior branch of the cubitus (composed of the CuA_1 and CuA_2); CuP , posterior branch of the cubitus; and 1A, 2A, and 3A, the first, second, and third branches of the anal vein.

The body length was measured along the midline from the anterior margin of the frons to the apex of the abdomen, minus appendicular structures. The width was measured across the broadest part of the body along the sagittal axis, at the thorax. The wing length was measured from the basal zone of articulatory sclerites to the apex of the wing. The wing index is defined as the ratio of wing width/wing length. All measurements are given in millimeters.

Systematic paleontology

Order Lepidoptera Linné, 1758
 Suborder Eolepidopterigina Rasnitsyn, 1983
 Family Eolepidopterigidae Rasnitsyn, 1983
 Genus *Aclemus* new genus

Type species.—*Aclemus patulus* n. sp., by monotypy.

Diagnosis.—As for the type species by monotypy (see below).

Etymology.—The generic name, *Aclemus*, is a combination of the Greek A-, meaning “lack of” or “absence”, and the

Latin-clemus, meaning “twig” or “branch,” which refers to both the Sc and R_1 veins lacking a bifurcation. The sex is masculine.

Occurrence.—Daohugou locality, Inner Mongolia Autonomous Region, in northeastern China.

Aclemus patulus new species
 Figures 1, 2

Type.—Holotype; male; specimen CNU-LEP-NN-2013-001; hindleg, abdomen, and wings clearly visible, but basal and anal area of fore- and hindwings poorly preserved.

Diagnosis.—The new fossil species can be identified by the following combination of characters: all legs with setae; metatibia with one pair of medial spurs and one pair of apical spurs; forewings and hindwings lacking cilia on their anterior margins; forewing veins Sc and R_1 unfurled, cross-veins r-m and m_3 - cua_1 present; hindwing veins, Sc and R_1 unfurled, cross-vein m_3 - cua_1 present.

Aclemus n. gen. (Fig. 1.1) is differentiated from the type genus of Eolepidopterigidae, *Eolepidopterix* Rasnitsyn, 1983 (Fig. 1.2), in having the forewing with Sc and R_1 unfurled (vs. forewing with Sc and R_1 bifurcated). The Sc unfurled condition is a derived character. *Aclemus* shares this character with *Palaeolepidopterix*, *Netoxena*, *Gracileopterix*, and *Grammikolepidopteron*. R_1 unfurled also is considered a derived character. *Aclemus* shares this character with *Netoxena*, *Grammikolepidopteron*, and *Longcapitalis*.

The venation of *Aclemus* resembles that of *Grammikolepidopteron* Zhang et al., 2013 (Fig. 1.3), but *Aclemus* differs from the latter by the R vein bifurcated into R_1 and Rs veins, which

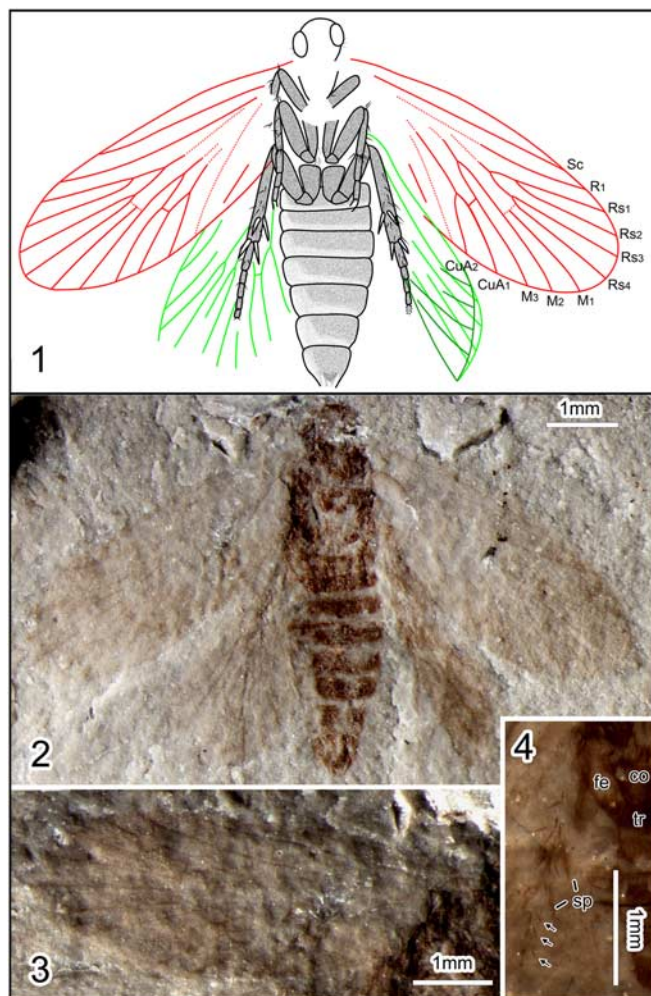


Figure 2. (1) Camera lucida drawing of *Aclemus patulus* n. gen. n. sp., holotype, ♂, CNU-LEP-NN-2013-001. (2–4) Photographs of *Aclemus patulus* n. gen. n. sp., holotype, ♂, CNU-LEP-NN-2013-001. (2) General habitus. (3) Forewing. (4) Hindleg. co, coxa; fe, femur; sp, spur; tr, trochanter. Arrowhead indicates terminal spinules for each tarsomere.

further subdivide into the veins Rs_{1+2} and Rs_{3+4} and then into the 4 branches of Rs_1 , Rs_2 , Rs_3 and Rs_4 , deployed in successively stepped branching points (vs. branching points of R_1 and Rs_1 to Rs_3 that are linearly aligned). In the primitive moths, Rs veins usually present as in *Aclemus*. Thus the former arrangement of Rs veins is inferred to be the primitive state. In Eolepidopterigidae, only *Netoxena nana* and *Grammikolepidopteron extensus* possess the derived state.

Aclemus resembles *Longcapitalis* Zhang et al., 2013 (Fig. 1.5), but it differs from the latter by the following: (1) the forewing with the Sc is unforked (vs. forewing with the Sc bifurcated); (2) the presence of an m_3-cua_1 cross-vein in both the forewing and hindwing (vs. m_3-cua_1 crossvein absent)—the presence of a cross-vein between M and CuA is probably the homoplasious condition, which *Aclemus* shares with *Daiopterix rasnitsyni*; and (3) all legs bear setae (vs. legs lacking setae). The presence or absence of leg setae is highly variable within the family and the genus. Consequently, this character is viewed as a homoplasy. Setae occur in a number of Eolepidopterigidae, such as *Aclemus patulus*, *Eolepidopterix*

jurassica, *Daiopterix olgae*, *Akainalepidopteron elachipteron*, and *Dynamilepidopteron aspinosus*, but are lost in the other species.

Aclemus shows similarity to the genus *Daiopterix* Skalski, 1984 (Fig. 1.4), but it differs from the latter in the following characters: (1) the forewing has the Sc and R_1 unforked (vs. forewing with Sc and R_1 veins bifurcating), (2) the hindwing with the R_1 is unforked (vs. the R_1 forked), and (3) the hindleg possesses setae (vs. a hindleg without setae).

Occurrence.—This specimen was collected near Daohugou Village, Shantou Township, Ningcheng County, of the Inner Mongolia Autonomous Region, in northeastern China. The fossil bed is the latest Middle Jurassic and late Callovian in age.

Description.—Eyes oval, with sparse pubescence along the outer ocular margin. Mesofemora longer than mesotibiae; mesotibiae with irregularly arranged setae; mesotibial spurs difficult to identify. Hindlegs well preserved; metafemora 0.6 times as long as metatibiae; metatibiae with irregularly arranged setae, and with one pair of medial spurs and one pair of apical spurs; both pairs of spurs approximately 1–1.5 times as long as the diameter of the tibiae (Fig. 2.4); metatibiae 1.2 times as long as metatarsi. Tarsi 5-segmented, with terminal spinules at each tarsomere (Fig. 2.4, black arrows); tarsomere I longest, about 2.0 times as long as tarsomere II; tarsomeres II, III, IV subequal to each other, with tarsomere IV slightly longer than tarsomere V.

Forewing moderately broad, and with a rounded margin distally (Figs. 1.1, 2.3). Wing index of forewing ca. 0.25. Sc unforked, extending to the costal margin at two-thirds length of the wing from its base. R_1 unforked; Rs 4-branched; Rs_4 extending to apex of forewing; Rs_{1+2} and Rs_{3+4} furcations arising at about the same level. M 3-branched. CuA bifurcated; CuA furcation beyond M furcation. Cross-vein m_3-cua_1 present, originating at 1/3 length of M_3 from M_{2+3} furcation and terminating at one-third length of CuA_1 from CuA furcation. CuP and anal veins not preserved. Hindwing venation resembling forewing. Sc and R_1 unforked; Rs 4-branched, Rs_{1+2} and Rs_{3+4} furcations arising at the same level; M 3-branched; CuA bifurcated; cross-vein m_3-cua_1 present. Measurements: body length ca. 5.2, width 1.3; forewing length 4.8, width 1.8.

Etymology.—The specific name is derived from the Latin, *patulus* (unfolding), referring to the unfolded posture of the insect body.

Remarks.—An affiliation to the Lepidoptera is supported by the absence of the M_4 vein on the forewing, and an M_1 vein with a markedly angulate position at the junction with cross-vein $r-m$, which is a previously unrecognized autapomorphy of the Lepidoptera (Huang et al., 2010).

This genus is assigned to the family Eolepidopterigidae by a combination of the following four features: (1) the fore- and hindwings are homonomous, (2) the M vein is three-branched, (3) the wings lack long cilia on their margin, and (4) a cross-vein is absent between the Sc and R veins.

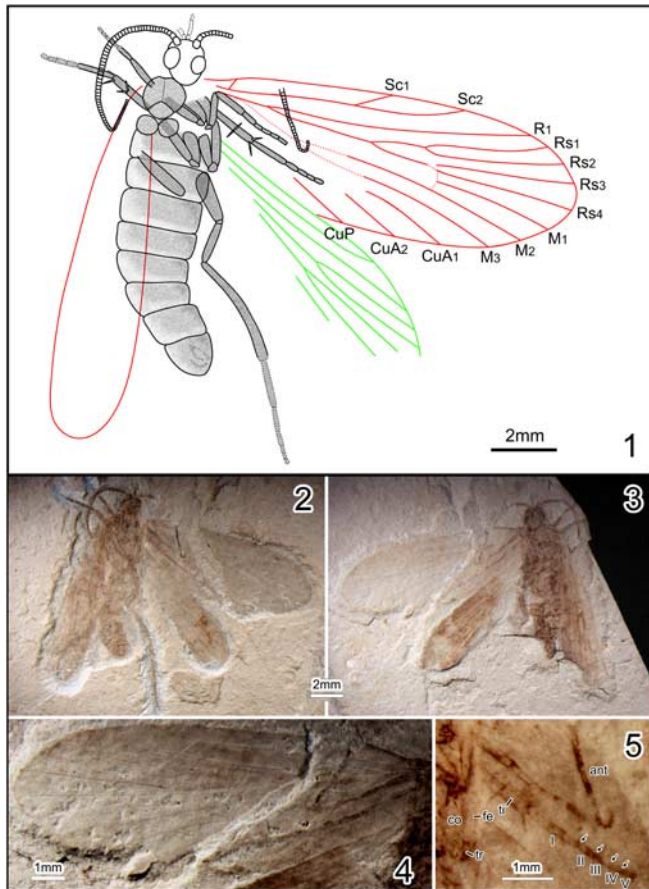


Figure 3. (1) Camera lucida drawing of *Longcapitalis excelsus* Zhang, Shih, Labandeira and Ren 2013, ♂, CNU-LEP-NN-2013-004P/C, new material. (2–5) Photographic images of *Longcapitalis excelsus* Zhang, Shih, Labandeira and Ren 2013, ♂, CNU-LEP-NN-2013-004P/C. (2) General habitus, counterpart. (3) General habitus, part. (4) Forewing. (5) Foreleg, mid leg and antennal articles. ant, antenna; co, coxa; fe, femur; ti, tibia; tr, trochanter; I–V, tarsomeres I–V. Arrowhead indicates boundaries between tarsomeres.

Longcapitalis Zhang, Shih, Labandeira and Ren, 2013

Type species.—*Longcapitalis excelsus* Zhang, Shih, Labandeira and Ren, 2013; by monotypy.

Diagnosis.—As for the type species, by monotypy (see below).

Occurrence.—Daohugou locality, Inner Mongolia Autonomous Region, northeastern China.

Longcapitalis excelsus Zhang, Shih, Labandeira and Ren, 2013
Figure 3

2013 *Longcapitalis excelsus* Zhang, Shih, Labandeira, and Ren,
p. 16, fig. 11

Holotype.—CNU-LEP-NN-2012-025P/C (part and counterpart).

Diagnosis.—The diagnostic characters of the legs are added. (1) Mesotibiae have two pairs of spurs. (This feature excludes this taxon from *Eolepidopterix*, *Seresilepidopteron* and *Quadruplecivena*.) (2) The absence of setae on all tibiae.

Table 1. Tibial spur formula of non-Glossatan families and the suborder Glossata

Non-Glossatan and Glossata	Tibial Spur Formula
Micropterigidae	0-0-4
Agathiphagidae	1-4-4
Heterobathmiidae	0-0-4
Mesokristenseniidae	1-1-4
Glossata	commonly 0-2-4

(This feature excludes this taxon from *Eolepidopterix jurassica* and *Daoipterix olgae*.)

Occurrence.—This specimen was collected from the same locality where the holotype was collected.

Description.—Characters of the antennae and legs are added, based on the new specimen, as follows. Antenna with scape swollen, scape and pedicel broader than flagellomeres, flagellum filiform, length of segments less than their diameters, total length of antenna subequal to half the length of the forewing. Last segments of labial palpi visible, protruding from head underside. Forefemora subequal to foretibiae; foretibiae 0.6 times as long as foretarsi; foretarsi 5-segmented, tarsomere I longest. Mesofemora longer than forefemora, slightly shorter than mesotibiae; mesotibiae with one pair of medial spurs and one pair of apical spurs; mesotibiae 0.6 times as long as mesotarsi. Mesotarsi 5-segmented (Fig. 3.5); tarsomere I as long as the total length of the rest segments; tarsomere II subequal to tarsomere III; slightly longer than tarsomere IV; tarsomere IV subequal to tarsomere V. Hindleg very long, about 1.5 times as long as mid leg. All legs lacking setae. Characters on thorax and wings are the same as the holotype specimen. Measurements (new material): body length 10.5 and width 2.5, forewing length 11.8 and width 4.2.

Material.—Male, specimen CNU-LEP-NN-2013-004P/C (part and counterpart); well-preserved left forewing and legs, parts of head and left hindwing.

Remarks.—The diagnosis of the genus is emended, based on the new fossil specimen that has good preservation of the fore-, mid- and hindlegs. Our comparison of this new specimen to the holotype revealed that Zhang et al. (2013) confused the midlegs with the hindlegs.

Discussion

The Eolepidopterigidae, proposed by Rasnitsyn in 1983, was based on only one specimen of *Eolepidopterix jurassica* with limited diagnosable characters. Subsequently, 14 genera with 16 species in this family, including the new taxon reported here, have been documented from Russia, Kazakhstan, China, and Brazil. These species collectively improve the morphological definition of the Eolepidopterigidae. The tibial spur formula is considered one of the important diagnosable elements for distinguishing basal lepidopteran families, because it is typically consistent within a family (Table 1). However, there are exceptions, such as Psychidae with tibial spurs 0-2-4, 0-1-1 or absent (Nielsen and Common, 1991), and Hesperiidae with

tibial spurs 0-2-4 and rarely 0-2-2. Rasnitsyn (1983) proposed that the mesotibiae of Eolepidopterigidae possessed two apical spurs, although the presence of preapical spurs was not excluded. Among the specimens previously reported, only *Eolepidopterix jurassica*, *Seresilepidopteron dualis*, *Quadruplicivena celsa*, and *Longcapitalis excelsus* have well-preserved mesotibiae. Two apical mesotibial spurs are visible on the first three species. The new material of *Longcapitalis excelsus*, bearing two medial and two apical spurs on their mesotibiae, provides a new character for the Eolepidopterigidae. Our update of the tibial spur formula of Eolepidopterigidae provides for a common presence of 0-2-4 and the rare occurrence of 0-4-4.

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