New species and material of Hagloidea (Insecta, Ensifera) from the Yanliao biota of China

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Abstract
A new species of Cyrtophyllitinae, Archaboilus polyneurus sp. nov. Gu, Yue & Ren, is described from the Middle Jurassic Jiulongshan Formation, Daohugou Village, Inner Mongolia, China. The species is characterized by its ScA reaching the anterior wing margin at the level of the divergence of M+ CuA, distally branched RP, lengths of free CuA and free M equal, and numerous branches of CuA + CuPa. A new fossil of Liassophyllum caii Gu & Ren, 2012 is described which increases knowledge of its wing venation and indicates that Liassophyllum should be assigned to the Tuphellidae.

Keywords
Archaboilus, Daohugou, Cyrtophyllitinae, Liassophyllum, Middle Jurassic, Orthoptera, systematic palaeontology, Tuphellidae

Introduction
The superfamily Hagloidea (Orthoptera) sensu Gorochov 1995 was widespread from the Late Triassic to the Early Cretaceous and consists of the families Haglidae, Tuphellidae, Prophalangopsidae, Hagloedischiidae (Gorochov 1995). A cladistic analysis based on wing venation suggests that it is paraphyletic (Béthoux and Nel 2002).
The Prezottophlebiidae was erected by Martins-Neto (2007) and assigned to the Hagloidea on the basis of a new species from the Early Cretaceous Santana Formation of Brazil. Although Haglidae are extinct and Prophalangopsidae are now considered to be relicts, they are the most diverse Hagloidea in the fossil record (Gorochov 1995; Wappler 2001; Gu et al. 2010).

The non-marine Jurassic and Cretaceous deposits of northern China are rich and diverse in fossil insects (Wang et al. 2012; Cai and Huang 2014; Fang et al. 2020; Gao et al. 2021; Yang et al. 2021). In the Yanliao and Jehol biota, Prophalangopsidae are the most diverse and abundant Orthoptera with over thirty valid species, while the Haglidae have lower diversity and abundance. Lin (1965) described two haglid species from the Lower Jurassic of Inner Mongolia, but they were erected based on female wings, which are difficult to compare with known haglid species, which are based on males. *Alloma* Hong, 1982 (Hong 1982a) and *Hebeihagla* Hong, 1982 (Hong 1982b), are considered as synonyms of *Parahagla* Sharov, 1968 of Chifengiinae, which were originally assigned to Haglineae of Haglidae (Hong 1982a, b). The family assignment of *Yenshania hebeiensis* Hong, 1982 (Hong 1982a) is questionable, as the type specimen is very fragmentary. Although *Isfaroptera yujiagouensis* Hong, 1983 was also erected based on a very fragmentary specimen, its preserved characters are sufficient to support its assignment to Haglidae. Gu et al. (2012a, b) described two Jurassic hagloid species, *Archaboilus musicus* Gu, Engel & Ren, 2012, and *Liasophyllum caii* Gu & Ren, 2012. The broad winged species *Vitimoilus ovatus* Gu, Tian, Yin, Shi & Ren, 2017, was described from the Early Cretaceous Dabeigou Formation, the most recently described haglid species from China (Gu et al. 2017).

Here, we report a new species of the haglid subfamily Cyrtophyllitinae and describe a new fossil of *Liasophyllum caii* Gu & Ren, 2012, increasing the diversity of Haglidae and knowledge of their wing venation.

**Method and materials**

The specimens were examined with a Nikon SMZ 25 microscope and photographed with a Nikon DS-Ri 2 digital camera system. Line drawings were prepared using Adobe Illustrator CC 2017 and Adobe Photoshop CC 2017 software. Measurements were taken using Adobe Illustrator. The specimens are housed at the Key Lab of Insect Evolution and Environmental Changes, Capital Normal University (CNU), Beijing, China.

Wing venation terminology follows the interpretation proposed by Béthoux and Nel (2002). Another commonly used Orthoptera venational terminology is that of Sharov (1968; and see e.g., Gorochov 1995). These mainly differ by their interpretations of the media and cubitus areas. For ease of comparison, we also provide the Sharov venation system in parentheses. Corresponding abbreviations used are: ScA (C), anterior subcosta; ScP (Sc), posterior subcosta; RA (RA), RP (Rs), anterior and posterior radius, respectively; MA (MA1), MP (MA2), anterior, posterior media, respectively; CuA (MP), CuP, anterior, posterior cubitus, respectively; CuPaα (CuA1),...
the anterior branch of first posterior cubitus; CuPaβ (CuA2), the posterior branch of first posterior cubitus; CuPb (CuP), the second posterior cubitus; AA1 (1A), first branch of anterior anal vein.

**Systematic palaeontology**

Class Insecta Linnaeus, 1758  
Order Orthoptera Olivier, 1789  
Suborder Ensifera Chopard, 1920  
Superfamily Hagloidea Handlirsch, 1906  
Family Haglidae Handlirsch, 1906  
Subfamily Cyrtophyllitinae Zeuner, 1937

**Archaboilus** Martynov, 1937

**Composition.** A. kisylkiensis Martynov, 1937, A.martynovi Gorochov, 1988, A. musicus Gu, Engel & Ren, 2012, A. shurabicus Martynov, 1937, A.similis Zherikhin, 1985, Archaboilus polyneurus sp. nov.

**Archaboilus polyneurus** sp. nov. Gu, Yue & Ren

http://zoobank.org/59886EC8-2ABE-4064-868D-8A0867FE5F34  
Fig. 1

**Diagnosis.** ScA reaches anterior wing margin at level of divergence of M+ CuA, RP branched distally, lengths of free CuA and free M equal, CuA + CuPα with numerous branches.

**Material examined.** Holotype, CNU-ORT-NN2009018PC. Paratype, CNUORT-NN2009011.

**Locality and age.** Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China; Jiulongshan Formation, Bathonian–Callovian boundary interval (Ren et al. 2019), Middle Jurassic.

**Description.** Forewing oval, estimated length ca 33 mm. ScA crossing area between ScP and anterior wing margin, reaching margin at level of divergence of M+ CuA; basal part of ScP slightly anteriorly curved, ScP reaching anterior margin at 3/4 to wing base with numerous oblique branches uniformly distributed; branches of ScP with secondary vein between them, formed by two rows of cells; most cross-veins between ScP and R straight; stem R slightly undulate; RA basally branched, pectinate with 4–7 terminal branches; base of RP curved towards to posterior margin, RP very distally branched with less branches than RA; area between RA and RP with series of regular arranged cross-veins; area between R and M expanding when R dichotomous, with series of long cross-veins, cross-veins of expanded area curved; presence
of a transverse veinlet connecting MA and base of RP (asterisk on Fig. 1B, D, F); M separated from M + CuA distant to origin of RP; MA probably undulate; MP strongly curved basally (not preserved in holotype); lengths of free CuA and free M equal; CuA + CuPaα with numerous branches; CuPaβ oblique; “handle” straight; CuPb strongly oblique, basal part and middle part (where bearing teeth) forms obtuse angle.

**Etymology.** From the Latin “polyneurus”, referring to its numerous branches of CuA + CuPaα.

**Discussion.** Although the preservation and deformation of the specimens makes it difficult to identify the complete structure of ScA, this new species can be assigned to Archaboilus Martynov, 1937 by a combination of its ScA crossing the area between ScP and the anterior wing margin, the base of MP strongly curved, and the presence of a transverse veinlet connecting MA and the base of RP. Besides these diagnostic characters of the genus, *A. polyneurus* sp. nov. shares with *A. musicus* from the same locality a slightly sigmoidal ScP, but it differs from it by its much more distally branched RP and distinctly smaller forewing. Although the holotype and single known specimen of *A. kisylkiensis* Martynov, 1937 is only the basal half of a forewing, its free CuA is much longer than its free M, not as in the new species. *A. polyneurus* sp. nov. differs from all other Archaboilus species by its shorter ScA, very distally branches of RP, and
numerous branches of CuA + CuPaα. Although the terminals numbers of RA and CuA + CuPaα are different between the holotype and paratype, this kind of difference has been shown to be intra-specific variation in orthopterans and their relatives (Béthoux 2008; Gu et al. 2010, 2011).

**Family Tuphelidae Gorochov, 1988**

**Genus Liassophyllum Zeuner, 1935**

*Liassophyllum caii* Gu & Ren, 2012

Fig. 2

**Material examined.** CNU-ORT-NN2020001.

**Locality and age.** Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China; Jiulongshan Formation, Bathonian–Callovian boundary interval (Ren et al. 2019), Middle Jurassic.

**Description of new material.** Isolated left forewing with negative and positive imprint; preserved length 41 mm, estimated complete length ca 49 mm, distal part of subcostal area, R, M, part of posterior margin all missing. Preserved forewing venation

![Figure 2](image_url)

*Figure 2.* Photo (A) and drawing (B) of *Liassophyllum caii* Gu & Ren, 2012, CNU-ORT-NN2020001. Scale bar: 5 mm.
almost the same as previously described fossils of the species. Forewing elongated, not typically oval; the anterior wing margin is slightly flattened in its basal part, then arched upwards; there is no curved ScA crossing area between ScP and anterior wing margin; area between ScP and anterior margin basally narrowed, gradually widened to the middle; area between CuPb and CuPa β broad, very basal cross-veins strongly curved and connected, formed into several irregular cells.

**Discussion.** Although the distal part of the forewing is absent, we assign the new fossil to *L. caii* Gu & Ren, 2012 by the following: R is simple for a long distance and is strongly arched toward the anterior margin distal to the redirection of ScP; MA is undulate; and the area between R and MA is distinctly broad. *Liassophyllum caii* Gu & Ren, 2012 was erected based on 11 specimens. The holotype is an isolate forewing with the basal area between ScP and the anterior margin missing, the paratypes are well preserved but with wings strongly overlapped and their subcostal area is not clear. The basal part of the subcostal area of the type species *L. abbreviatum* Zeuner, 1935 is also unknown. The new material described here has a clear subcostal area, improving the knowledge of this important area. It lacks an arched ScA crossing the subcostal area positioned very close to the anterior wing margin. The basal-most area between ScP and anterior wing margin has fan-like veinlets. Zeuner (1939) and Gu et al. (2012a) attributed *Liassophyllum* to Cyrtophyllitinae, but Gorochov (1995) and Gorochov et al. (2006) excluded the genus from the subfamily, not mentioning its higher-rank assignment. The new material reported here supports exclusion of *Liassophyllum* from the Cyrtophyllitinae by its absence of an arched ScA crossing the area between ScP and the anterior margin. Further, the undulate MA, the long and more or less undulate stem of R, the very distal dichotomous R, and the broad and long area between CuPb and CuPa β of *Liassophyllum* species strongly indicate that this genus belongs to the Tuphellidae.

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