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Source: Journal of Orthoptera Research, 19(1) : 41-56

Published By: Orthopterists' Society

URL: https://doi.org/10.1665/034.019.0110

Revision and new taxa of fossil Prophalangopsidae (Orthoptera: Ensifera)

Submitted December 21, 2009, accepted March 22, 2010

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Abstract

Taxonomy is investigated and revised for some prophalangopsid insects, yielded by the Middle Jurassic Jiulongshan and Upper Jurassic-Lower Cretaceous Yixian formations in China. *Flexaboilus retinervius* Li, Ren & Meng, 2007 and *Furcaboilus excelsus* Li, Ren & Meng, 2007 are considered as synonyms of *Allaboilus gigantus* Ren & Meng, 2006. *Protaboilus lini* Ren & Meng, 2006 is considered a synonym of *Aboilus stratosus* Li, Ren & Wang, 2007. *Hebeihagla* Hong, 1982b, *Habrohagla* Ren, Lu, Guo & Ji, 1995, *Grammohagla* Meng & Ren, 2006, *Trachohagla* Meng, Ren & Li, 2006 are considered as synonyms of *Parahagla* Sharov, 1968; *Athehagla* Meng & Ren, 2006 is considered a synonym of *Ashanga* Zherichin 1985. Genera *Allaboilus*, *Circulaboilus* Li, Ren & Wang, 2007 and *Ashangopsis* Lin, Huang & Nel, 2008 are revised. In addition, one new genus *Scalpellaboilus gen. nov.* and four new species: *Scalpellaboilus angustus sp. nov.*, *Circulaboilus priscus sp. nov.*, *Allaboilus robustus sp. nov.* and *A. hani sp. nov.* are described. Some wing venation variability in Prophalangopsidae is briefly discussed.

Key words

Prophalangopsidae, new taxa, synonyms, Middle Jurassic, Upper Jurassic-Lower Cretaceous, China

Introduction

Prophalangopsidae is a rather peculiar family of Ensifera that prospered from the Middle to Late Jurassic. This lineage is now represented by the relict subfamily Prophalangopsinae and probably also by Cyphoderrinae (Morris & Gwynne 1978; Gorochov 1995, 2001b, 2003; Liu *et al*. 2009). It is the only family group of ensiferans which can be traced from the Mesozoic to now. It includes five fossil subfamilies (Protaboilinae, Aboilinae, Chifengiinae, Termitidiinae and Tettohaglinae). Its earliest fossils were collected from the Lower Jurassic Upkurgan coal deposit, Kirgizia, these being assigned to Protaboilinae. Five species of Aboilinae (three of them were originally assigned to Haglidae) were found in the Lower Jurassic deposit of Xinjiang, Inner Mongolia and Shanxi, all in the Province of China.

There was an explosive evolutionary radiation of this group in the period from Middle to Late Jurassic, documented by about 20 new genera (only valid names counted) described from that period. The fossil record of this family is known from China, Central Asia, Russia, Europe and even from New Zealand. As a member of that explosive evolutionary radiation, Aboilinae were widespread in Eurasia. The oldest Chifengiinae are known from Russia, from the same time. Based on these data, Aboilinae were the most diverse and widespread of ensiferans during that time, as indicated by the number of specimens, diversity of species or their distribution. Most of the specimens and taxa were collected in Karatau Formation of Kazakhstan and Jiulongshan Formation of China.

During Early Cretaceous, Prophalangopsidae continued its radiation, all the subfamilies arising in this period, being distributed in China, Japan, Russia, Central Asia, Europe, England, and Brazil. In terms of the fossil record the Cenozoic period is very poor for Prophalangopsidae: only a few specimens of two species being found in China and Canada from the Paleocene (Lin & Huang 2006b, Kevan & Wighton 1981). The recent members of this family (including Cyphoderrinae) occur only in northwestern America, far east of Russia, southwestern China and northern India. But hitherto, no fossil records are known for either of these subfamilies. Their habitat is confined to the high mountains (Morris & Gwynne 1978; Gorochov 2001a, 2001b), and most of them are rarely encountered. They are considered as the primitive representatives of the superfamily Tettigonioidea (Gorochov 2001b, 2003).

In China, research on this group was started by Lin (1982) and Hong (1982a), who described 14 species belonging to 12 genera. Then Hong (1983-1988), Lin & Huang (2006a, 2006b), Zhang (1993), Ren *et al.* (1995), Zhang (1996), Wang & Liu (1996), Meng *et al.* (2006), Meng & Ren (2006), Li *et al.* (2007), Fang *et al.* (2007, 2009) and Lin *et al.* (2008) described more material, collected mainly from Yanliao Biota and Jehol Biota during the last two decades. Taxonomic placement of some taxa is not reliable: some new synonyms were discovered, some descriptions and illustrations are found to be inaccurate or erroneous. Thus a general review of the group is needed.

Recently, many well-preserved specimens of the compression fossils from the Middle Jurassic Jiulongshan Formation in Daohugou Village, Ningcheng County, Inner Mongolia and the Upper Jurassic-Lower Cretaceous Yixian Formation in Huangbanjigou, Chaomidian Village, Shangyuan Township, Beipiao City, Liaoning Province in Northeastern China were collected. They allow us to give a more detailed description of their morphology and to provide revisions of the prophalangopsid insects.

However a number of difficulties prevented an extensive revision of Prophalangopsidae from being carried out. First, some contributions failed to provide accurate morphological data in illustrations or descriptions, preventing identification of synonyms and correct taxonomic placement. In addition, the type specimens of the more than 16 described species from China are scattered in various collections, often without depository information.

Materials and methods

All the type specimens (part and counterpart) of the new species and new materials mentioned in this paper are housed at the Key Lab of Insect Evolution & Environmental Changes, Capital Normal University, Beijing, China. The specimens were examined with a Leica MZ12.5 dissecting microscope and illustrated with the aid of a drawing tube attached to the microscope. Line drawings were prepared with CorelDraw 12 graphic software. The photographs were taken by Epson Perfection 1650, Nikon DMX1200C and Canon G10.

The wing venation nomenclature used in this paper is based on the interpretation of Béthoux & Nel (2001, 2002): C, costa; ScA, anterior subcosta; ScP, posterior subcosta; RA, anterior radial; RP, posterior radial; MA, anterior media; MP, posterior media; CuA, anterior cubitus; CuPaα, the anterior branch of first posterior cubitus; CuPaβ, the posterior branch of first posterior cubitus; CuPb, the second posterior cubitus. The term 'handle' describes a strong cross-vein appearing as a main vein.

Systematic Palaeontology

Order Orthoptera Olivier, 1789
Suborder Ensifera Chopard, 1920
Family Prophalangopsidae Kirby, 1906
Subfamily Aboilinae Martynov, 1925
Scalpellaboilus gen. nov.

Etymology.—The generic epithet prefix is from Latin *scalpell-*, referring to the shape of the forewing, and *Aboilus*, the type genus of the subfamily. Gender: masculine.

Type species.—*Scalpellaboilus angustus sp. nov.*

Diagnosis.—Female, forewing only. Forewing extremely long and narrow, ratio of length to width more than 5; C developed, not fused with anterior margin and ScA, R undulate, M + CuA curved.

Comparison.—The genus *Scalpellaboilus gen. nov.* is similar to *Turkestania* Sharov, 1968 of Haglidae in forewing shape, but it can be assigned to subfamily Aboilinae of Prophalangopsidae based on the broad costal area, well-developed ScA and the absence of fusion between MA and RP. This genus differs from all other genera of the subfamily in its extreme wing length, high ratio of length to width and apparently developed C.

***Scalpellaboilus angustus* sp. nov.**
Fig. 1

Material.—Holotype, female forewing, part and counterpart, CNU-ORT-NN2009007P C.

Etymology.—The specific epithet derives from Latin '*angustus*', for its high ratio of length to width.

Horizon and locality.—The Jiulongshan Formation, Middle Jurassic, Daohugou Village, Ningcheng County, Inner Mongolia, China.

Diagnosis.—As for genus.

Description.—Forewing: extremely long and narrow; length about 95 mm, greatest measurable width 15.2 mm (probably 16 to 19 mm in fact), ratio of length to width more than 5; C apparently developed, preserved length 37.0 mm, straight, the end of C extends towards ScA, but is not fused with its anterior margin; area between C and ScA broad and numerous veinlets coupled with relatively simple cross-veins at its base, loose veinlets (not shown) make up distal part; ScA extremely long, probably reaching anterior margin at 2/3 basal tegminal length, slightly arched, distal part straight, not fused with C; ScP apparently long, S-shaped, reaching anterior margin at 3/4 basal tegminal length, branches of ScP numerous, oblique and regularly spaced, presence of network of irregular cross-veins between each branch (unavailable for drawing due to poor preservation); area between ScP and RA narrow at its basal part (probably caused by extrusion during fossilization); stem of R long and undulate, R

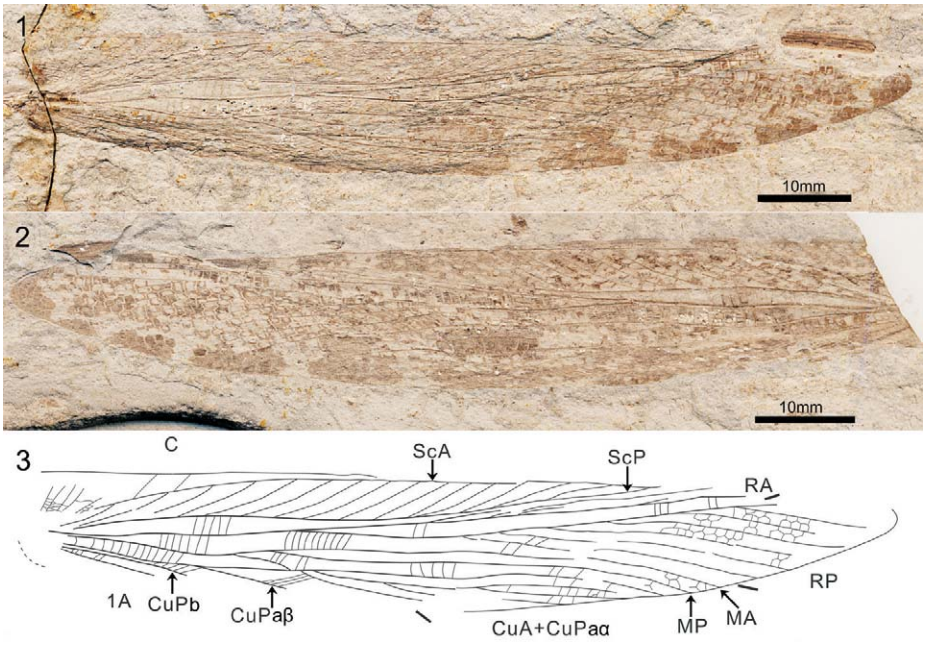


Fig. 1. *Scalpellaboilus angustus sp. nov.*: photograph and line drawing of holotype specimen CNU-ORT-NN2009007PC (part and counterpart), female.

forked before the end of C, RA branched at about 1/2 basal tegminal length, pectinate with more than 5 terminal branches and reaching apex of the wing, RP branched beyond the first branch of RA, pectinate with 7 terminal branches at least, the branches irregularly curved and regular cells between them; area between RA and RP with straight cross-veins; area between M + CuA and R extremely narrow at its base, M + CuA bowed towards posterior margin at its distal part, basal free part of M straight and forking into MA and MP before the origin of RP, MA and MP subparallel and not smooth; basal free part of CuA gently curved and longer than basal free part of M; area between R and M + CuA, M + CuA and CuPaα with slightly curved and more or less parallel cross-veins; area between M + CuA and CuPaβ broad, CuA and CuPaα remaining united as CuA + CuPaα for an apparent distance, but shorter than the cross-veins between CuA and CuPaβ, exhibiting 5 terminal branches, first anterior branch of CuA + CuPaα oriented towards MP at its midlength, arched and reaching posterior margin distal of the end of ScP; second anterior branch of CuA + CuPaα pectinate with three branches and oriented towards anterior margin at same level of first branch of CuA + CuPaα; CuPaα longer than CuA before their fusion; CuPaβ straight in preserved part; CuPb very close to CuPβ.

Discussion.—Area between ScP and RA near apex of the specimen is disrupted and slightly overlapped, basal part of posterior wing margin is invisible. This could indicate that the wing might have experienced extrusion or damage before being fossilized, but the arrangement of veins looks normal and there is no presence of an apparent pleat. Therefore, we can consider the profile of the wing as not seriously damaged and without distinct deformation. This will not essentially affect the high ratio of length to width of the wing, although the real width must be wider than its visible state. So we consider the forewing shape of this specimen as an available character.

Circulaboilus Li, Ren & Wang, 2007

Type species.—*Circulaboilus aureus* Li, Ren & Wang, 2007 [= *Circulaboilus amoenus* Li, Ren & Wang, 2007: Fig. 6, new synonym, as the first female individual of *Circulaboilus aureus*; holotype: CNU-ORT-NN-2006023.]

Revised diagnosis.—Forewing oval, apex pointed, ScA long, distinct beyond the midlength of the wing, branches of ScP spaced out, R forked distally, area between divergence of R and M markedly widening and broad, handle long and straight in male.

Included species.—*Circulaboilus aureus*, *Circulaboilus priscus sp. nov.*

Remarks.—Species *Circulaboilus aureus* was established as the type species of this genus by Li, Ren & Wang 2007, but has been erroneously illustrated previously. The type specimen is investigated again and a new description with new illustration provided.

Circulaboilus aureus Li, Ren & Wang, 2007
Fig. 2

[= *Circulaboilus amoenus* Li, Ren & Wang, 2007, *syn. nov.*]

Materials.—Holotype: CNU-ORT-NN2006022; other materials: CNU-ORT-NN2006023, CNU-ORT-NN2009025PC and CNU-ORT-NN2009027PC.

Horizon and locality.—The Jiulongshan Formation, Middle Jurassic, Daohugou Village, Ningcheng County, Inner Mongolia, China.

Description.—Male forewing, oval and large size, apex pointed, 44 to 66 mm long, estimated width 19 to 24 mm; anterior margin probably arched, area between ScA and anterior margin long; ScA curved and extremely long, cutting most branches of ScP, reaching anterior margin beyond midlength of the wing, and beyond the divergence of R; ScP long and slightly undulate, attaining anterior margin at the same distal plane where the first anterior branch of CuA + CuPaα reaches posterior margin, spaced out and parallel branches of ScP filled the area between ScP and ScA; area between ScP and R narrow, stem of R long, forking into RA and RP close to 1/2 of wing length, RA pectinate with 5 branches in total, RP branched at the same level with RA and posteriorly pectinate with 6

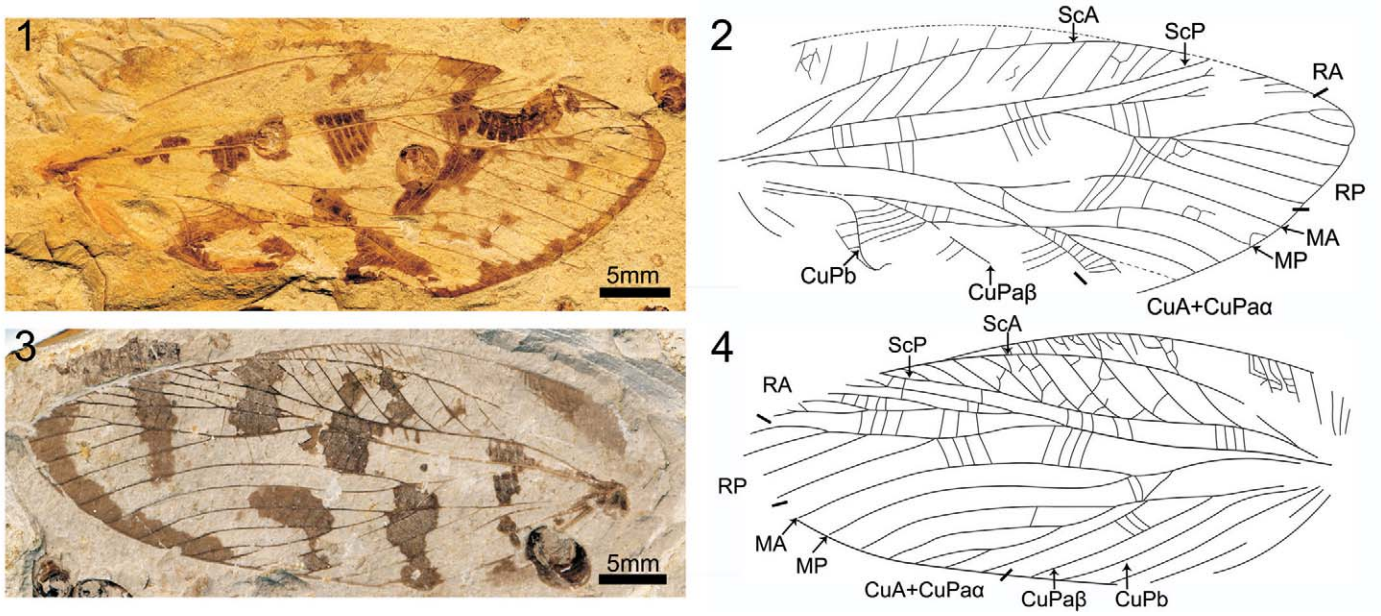


Fig. 2. *Circulaboilus aureus* 2007. 1, 2: new photograph and line drawing of holotype specimen CNU-ORT-NN-2006022, male. 3, 4: new photograph and line drawing of specimen CNU-ORT-NN-2006023 (holotype of *C. amoenus* Li Ren & Wang 2007), female.

branches, areas between the branches with regular reticulate cross-veins, area between RA and RP broad; M + CuA divided into M and CuA distant to divergence of R; free part of M short, forking into MA and MP, MP S-shaped, curved towards posterior margin at its base, then reaching wing margin and parallel with MA; area between M + CuA and R distinctly widened in middle part of wing, cross-veins in this part long and strong; CuA twice the length of M; the fusion of CuA and CuPaα lies beyond the divergence of M; CuPaα longer than CuA before their fusion; CuA fused with CuPaα and ramified immediately, probably with 5 terminal branches; CuPaβ oblique, straight in preserved part; the handle vein long and straight, a row of straight cross-veins filling up the area between handle and CuPaα; CuPb strongly curved and steep, area between CuPb and CuPaβ very broad with long and straight cross-veins; 1A a little distance to CuPb in middle part; CuPb and 1A fused together and then given off as separate branches; the colorations exhibit a pattern of patches rather than irregular bands.

Female forewing: 45 mm long, width 18 mm, various cross-veins filling the veinlets between ScA and anterior margin; RP branched opposite to the second branch of RA, RA pectinate with 7 branches, RP with at least 5 branches; MP parallel with MA, but not sigmoidal; CuA nearly the same length as free part of M; CuA+ CuPaα with 5 branches, first posterior branch emitted slightly before the fusion of CuA and CuPaα; CuPaβ oblique and straight; CuPb slightly curved in basal part.

Discussion.—Species *Circulaboilus amoenus* Li, Ren & Wang, 2007 is identified as a female individual of *Circulaboilus aureus* by this investigation; specimen CNU-ORT-NN-2006023 shows these differences from CNU-ORT-NN-2006022: area between R and M narrow, less curved MA and MP, free part of CuA short. But these kinds of differences should be treated as sexual differences and intraspecific variability rather than as specific characters.

Circulaboilus priscus sp. nov.
Fig. 3

Etymology.—The specific epithet derives from Latin '*priscus*', for its primitive character statement of R.

Materials.—Holotype: CNU-ORT-NN2009024PC.
Paratype: CNU-ORT-NN2009026PC.

Horizon and locality.—The Jiulongshan Formation, Middle Jurassic, Daohugou Village, Ningcheng County, Inner Mongolia, China.

Diagnosis.—Male, forewing only. Forewing oval, anterior margin arched, R forked very distally, M + CuA curved towards R, area between origin of RP and M distinctly broad, 1A bowed towards posterior margin and distant to CuPb.

Description.—Male forewing, oval and large size, left wing fragment of holotype 60 mm long (estimated length about 64 mm), 28 mm wide (estimated width about 29 mm), forewings of paratype 45 mm long and 24mm wide in preserved part; anterior margin arched, area between ScA and anterior margin long, filled with several veinlets

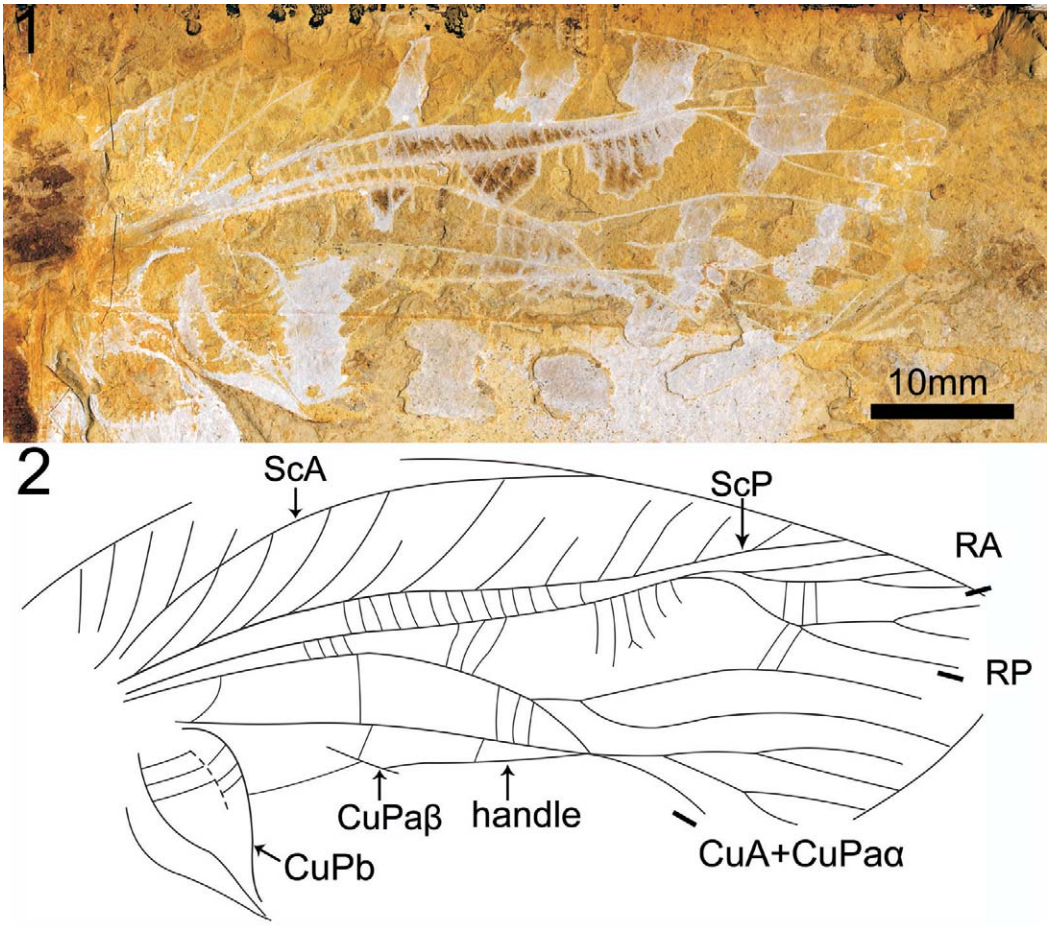


Fig. 3. *Circulaboilus priscus sp. nov.*: photograph and line drawing of holotype specimen CNU-ORT-NN-2009024PC, male.

aligned with branches of ScP; ScA curved and extremely long, reaching anterior margin beyond midlength of the wing, but before the divergence of R; ScP long and slightly undulate, attaining anterior margin basad of the first anterior branch of CuA + CuPaα attaining posterior margin, ScP with spaced out and parallel branches of which at least 7 branches basad of ScA reach the anterior margin; area between ScP and R narrow, stem of R extremely long, forking into RA and RP close to 2/3 basal wing length, RA pectinate with 3 branches, RP curved upwards basad, free part of RP slightly sigmoidal, branched beyond first branch of RA, posteriorly pectinate with 3 branches at least, areas between the branches with regular and straight cross-veins in preserved part; M + CuA curved towards R basally, divided into M and CuA before the end of ScA; free part of M short, forking into MA and MP, MP curved towards posterior margin at its base, then reaching wing margin and parallel with MA; area between M + CuA and R very narrow at its basal part, then distinctly widened, cross-veins in this part long and strong, probably curved at the area between origin of RP and MA; CuA nearly twice the length of M; the fusion of CuA and CuPaα at the level of M forking; CuPaα longer than CuA before their fusion; CuA fused with CuPaα and ramified immediately, probably exhibiting 5 terminal branches at least; the fragmentary CuPaβ indicates that CuPaβ is very oblique, the handle vein long and straight, a row of straight cross-veins filling up the area between handle and CuPaα; CuPb strongly curved and steep, area between CuPb and CuPaβ very broad with long and straight cross-veins; 1A invisible, but the cross-veins between CuPb and A veins indicate that 1A is close to CuPb and with similar shape, 2A bowed towards posterior margin and very distant to CuPb in middle part; CuPb, 1A, 2A and 3A probably fused together and then given-off as separate vein branches.

Discussion.—This new species shows a primitive character of R forked very distally and beyond 2/3 of the wing length. It's very similar to some Tuphellid insects which are only found in the Triassic and to Haglinae; however this taxon shares with Aboilinae a well-developed ScA which, cutting the branches of ScP, MA and MP, is simple and without any anastomosis with RP; a series of straight cross-veins fill up the proximal part of CuPb and CuPaβ. Furthermore, it can be assigned to *Circulaboilus* by its wing shape, mode of ScA, by the widened area between R and M + CuA and a long handle.

It is similar to *Circulaboilus aureus* Li, Ren & Wang, 2007, (Cyrtophyllitinae) but we can separate it by the following characters: M + CuA strongly curved towards R, R forked very distally at about 2/3 of the wing length, RP basally curved, 2A bowed towards posterior margin and distant to CuPb. It is also similar to *Barchaboilus mongolicus* Gorochov, 1988 and *Tettaboilus pulcher* Gorochov, 1988, but they are different in their divergence of R, long ScA, more widened area between R and M + CuA and strongly oblique CuPaβ. We can also separate it from *Allaboilus gigantus* and *Novaboilus multifurcatus* by its wing shape, R forked distally, curved M + CuA and steep CuPb.

Allaboilus Ren & Meng, 2006

[=*Flexaboilus* Li, Ren & Meng, 2007, *syn. nov.*; *Furcaboilus* Li, Ren & Wang, 2007, *syn. nov.*]

Type species.— *A. dicrus* Ren & Meng, 2006

Diagnosis.—Forewing large size, ScA long and reaching anterior margin close to midlength of forewing, ScP slightly sigmoidal, RA, RP and CuA + CuPaα with numerous branches, ovipositor long and stout.

Discussion.—The genus *Allaboilus* Ren & Meng 2006 was erected on the basis of two female and male specimens and assigned to subfamily Protaboilinae Gorochov 1995. The genus *Protaboilus* was erected by Gorochov 1988 and promoted to subfamily Protaboilinae by Gorochov 1995, this subfamily differs from all other Prophalangopsidae in the presence of arched cross-veins (transverse veinlets) between proximal parts of CuPaβ and CuPb in the male forewing (Gorochov 1995, 2003). Questionably, the type species *A. dicrus* of *Allaboilus* Ren & Meng, 2006 and *A. gigantus* didn't show any diagnostic characters that can assign them to Protaboilinae. It is appropriate to assign these taxa to Aboilinae rather than to Protaboilinae by the following characters: cross-veins between proximal part of CuPaβ and CuPb straight in male forewings, RA and RP branched relatively earlier. In addition new materials we describe here give further support to this assignment.

This genus is similar to *Tettaboilus* Gorochov and *Barchaboilus* Gorochov, but we can distinguish it by the following characters: ScA is close to midlength of forewing, CuPb is not distinctly steep, CuPaβ isn't broken (divided into two parts) by the handle in the male, first branch of CuA + CuPaα bends towards to MP; it also differs from *Apsataboilus* by its long ScA, gently curved CuPb, sigmoidal ScP and numerous branches of RA, RP and CuA + CuPaα.

Included species.—The type species *A. dicrus* Ren & Meng, 2006; *A. gigantus* Ren & Meng, 2006; *A. robustus sp. nov.*, *A. hani sp. nov.*

A. gigantus Ren & Meng, 2006
Figs 4-5

Flexaboilus retinervius Li, Ren & Meng, 2007, p. 175. fig. 1; new synonymy; holotype: CNU-ORT-NN2006107
Furcaboilus excelsus Li, Ren & Wang, 2007, p. 414. fig. 7; new synonymy; holotype: CNU-ORT-NN2006109

Materials.—Holotype: male, CNU-ORT-NN2006002.

Other materials.—Male: CNU-ORT-NN2006107/031, CNU-ORT-NN2008001-003, CNU-ORT-NN2009046-48; Female: CNU-ORT-NN2006026/29/81/97, CNU-ORT-NN2008021-027/29/133 and CNU-ORT-NN2009029-45/54.

Horizon and locality.—The Jiulongshan Formation, Middle Jurassic, Daohugou Village, Ningcheng County, Inner Mongolia, China.

Revised diagnosis.—Forewing: ScA long and arched, reaching anterior margin at midlength or slightly beyond, ScP long and slightly undulate, with numerous branches; MP curved towards posterior margin at its base and the first anterior branch of CuA + CuPaα apparently oriented towards MP in male forewing, not very steep CuPb in male and slightly sigmoidal CuPb in female.

Description.—**Male, forewing:** large size, estimated length 74 to 88 mm, width 27 to 32 mm (opposite the divergence of R); area between ScA and anterior margin broad, filled with several veinlets aligned with branches of ScP; ScA long, probably reaching anterior wing margin at midlength, ScP apparently long and undulate, branches of ScP numerous and mostly with a secondary vein between them, formed into two rows of cells regularly disposed; after the end of ScA, branches of the ScP strongly directed towards the wing apex; area between ScP and R broad, stem of R long and strong, forking into RA and RP at about 1/3 basal tegminal length, RA posteriorly

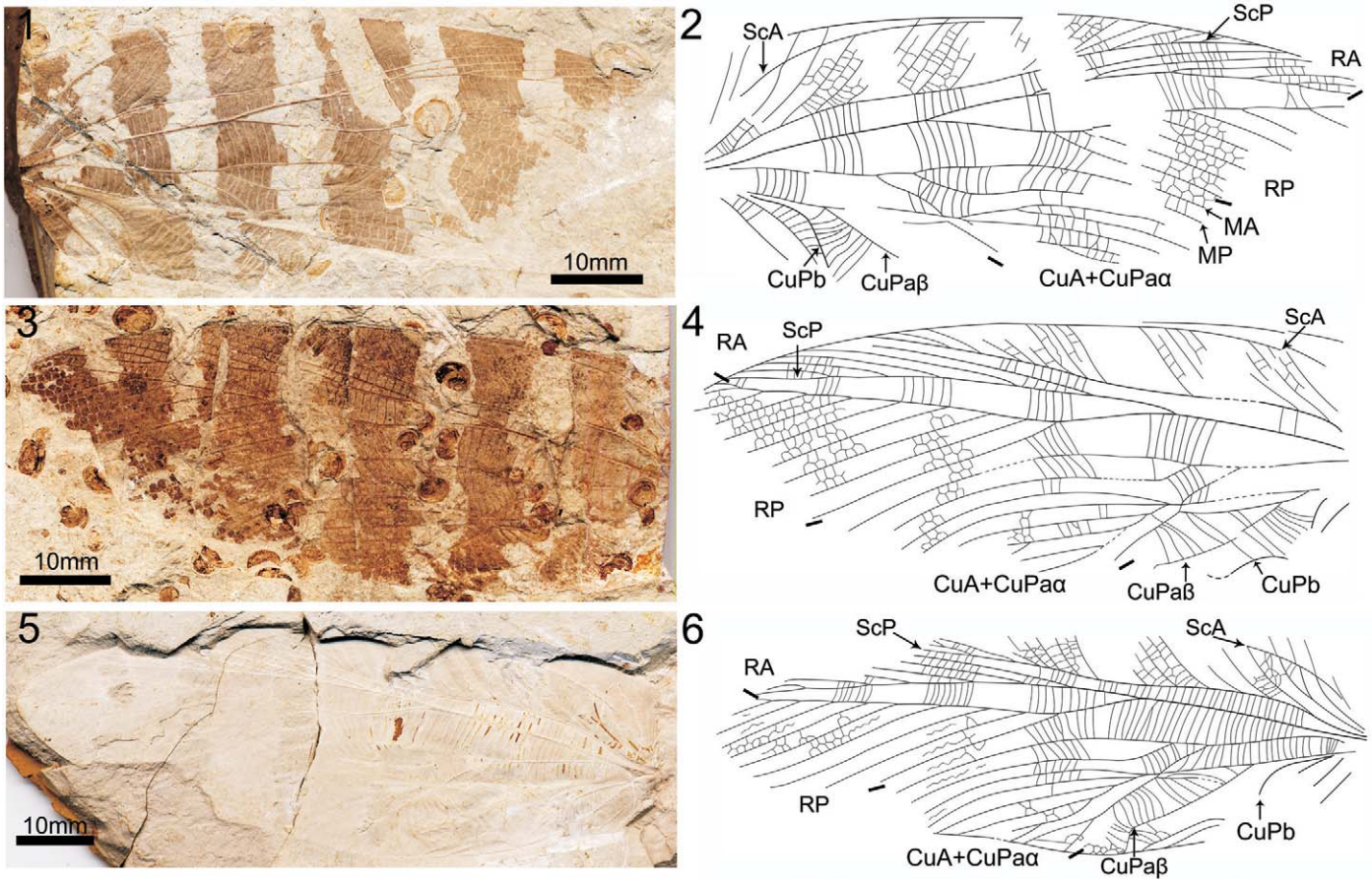


Fig. 4. *A. gigantus* Ren & Meng, 2006. 1, 2: new photograph and line drawing of holotype specimen CNU-ORT-NN2006002, male. 3, 4: new photograph and line drawing of specimen CNU-ORT-NN2006107 (holotype of *Flexaboilus retinervius* Li, Ren & Meng, 2007), male. 5, 6: photograph and line drawing of specimen CNU-ORT-NN2006031, male.

pectinate with more than 6 branches, RP branched slightly beyond or opposite the origin of first branch of RA, probably posteriorly pectinate with 10 branches, areas between the branches with regular reticulate cross-veins, a series of straight cross-veins regularly arranged between RA and RP; M + CuA curved towards R basally, divided into M and CuA before the divergence of R; M forking into MA and MP, MP curved towards posterior margin at its base, then reaching wing margin and parallel with MA; CuA gently curved and nearly twice the length of M; point of fusion of CuA and CuPaα beyond the divergence of M; CuPaα longer than CuA before their fusion; CuA fused with CuPaα and ramified immediately, forming a complex branching pattern, probably exhibiting 8 terminal branches at least, first anterior branch of CuA + CuPaα oriented towards MP, beyond gently curved, last posterior branch simple or forking, cross-veins between branches of CuA + CuPaα straight in basal part, reticulated in distal part; CuPaβ oblique, distal part sharply curved and nearly formed into a right angle, area between CuPaβ and last posterior branch of CuA + CuPaα apparently broad and filled with straight or curved cross-veins in most part, cross-veins near posterior margin formed into network; handle long and slightly curved; CuPb sharply curved and long, area between CuPb and CuPaβ narrower than area between CuPaβ and last posterior branch of CuA + CuPaα, filled in with straight or gently curved cross-veins; 1A similar to CuPb in shape and fused with CuPb at their middle length, then running to posterior margin.

Male Hindwing: RP branched before RA, RA and RP with numerous pectinate branches, distal part of RA and RP very close to each other. **Female:** compound eyes oval, 4 mm wide. **Forewing:** large size, length 78 to 91mm, width 25 to 28 mm (opposite the divergence of R), area between ScA and anterior margin broad and subtriangular shape, the basal part covered by an abundance of tiny cells; RA posteriorly pectinate with 5 to 7 branches, RP posteriorly pectinate 8 to 10 branches; free part of CuA more than two times as long as free part of M or slightly longer than it; CuA fused with CuPaα and ramified immediately or running an ultrashort interval, probably exhibiting 4 to 5 terminal branches and varied branching pattern; CuPaβ oblique, CuPb slightly sigmoidal. In specimen CNU-ORT-NN2006081, compound eyes oval, 4 mm wide, hind femur 32 mm long (in preserved part) and incrassate basally, hind tibiae with 11 spines, hind tarsus truely four segmented, first segment long and with two euplantulae; mid femur with two rows of spinules, mid and fore tibiae stout and with a row of rather strong spines, four spines preserved; fore tarsi poorly preserved; ovipositor slightly curved, long and stout, 26 mm long in preserved part (estimated length about 30 mm), 27 mm long in specimen CNU-ORT-NN2008027, 24 mm long in specimen CNU-ORT-NN2009054, it is incrassate basally.

Discussion.—The species *A. gigantus* Ren & Meng, 2006 (=*Flexaboilus retinervius* Li, Ren & Meng, 2007, *syn. nov.*, *Furcaboilus excelsus* Li, Ren & Wang, 2007, *syn. nov.*; the synonyms are established because the holotype of these two described species are almost indistinguishable) was erected just on the basis of a single male forewing. Here we found four new male and 11 female specimens which can be

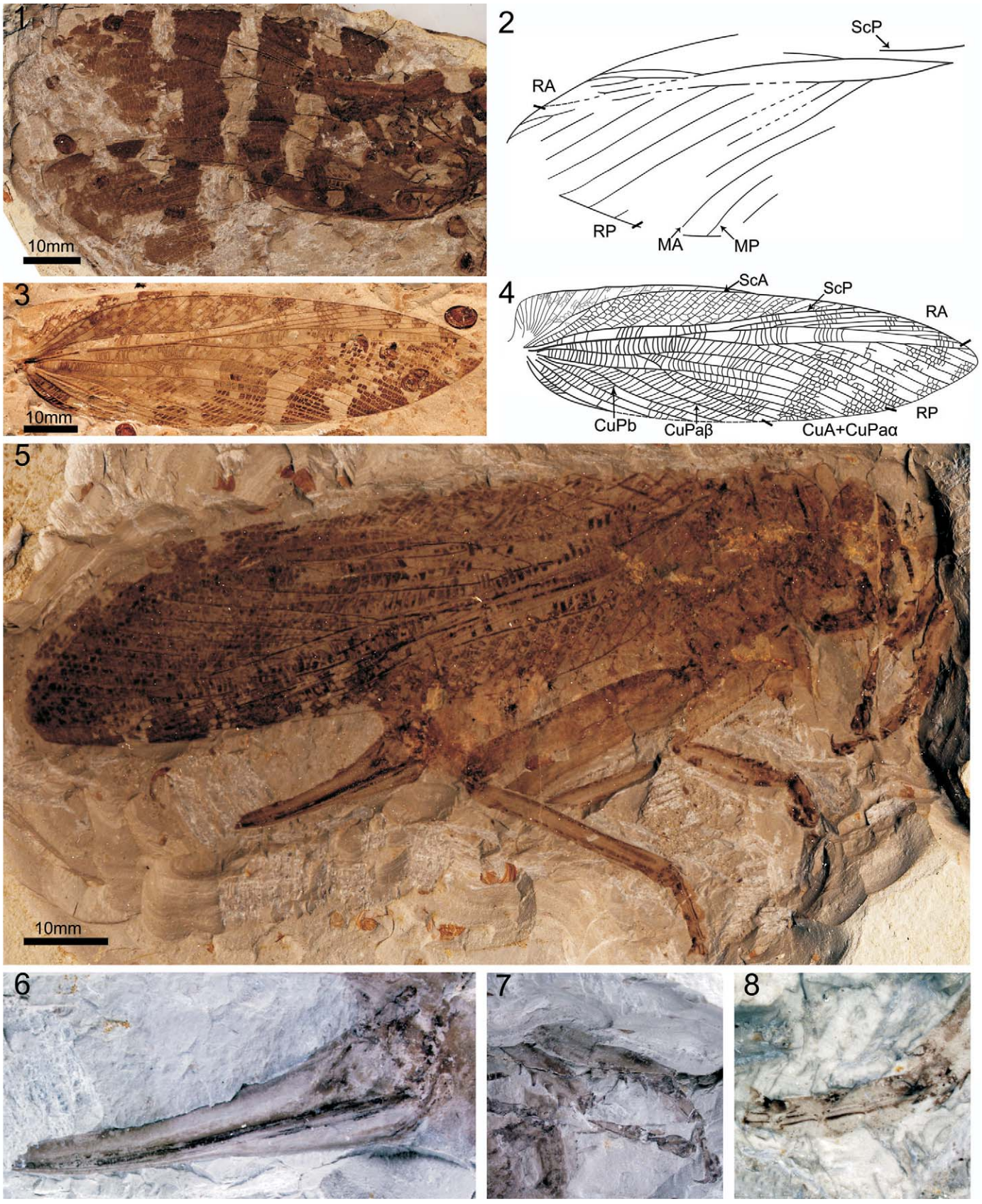


Fig. 5. New materials of *A. gigantus* Ren & Meng, 2006. 1, 2: photograph and line drawing of specimen CNU-ORT-NN2008002, male. 3, 4: photograph and line drawing of specimen CNU-ORT-NN2006021, female. 5-8: photographs of specimen CNU-ORT-NN2006081; 5. whole body, 6. ovipositor, 7. fore tibiae with alcohol, 8. hind tarsus with alcohol.

characterized to *A. gigantus* by their wing shape: long and curved ScA. The female forewings are slightly larger than male's; the venation of the female forewing is almost the same as the male forewing, except for the stridulatory apparatus, and all the specimens were collected from the same locality. So we would like to assign these female specimens to *A. gigantus*.

A. robustus sp. nov.
Fig. 6.

Material.—Holotype. Male, CNU-ORT-NN2006080.

Etymology.—The specific epithet derives from Latin '*robustus*', for its strong legs.

Horizon and locality.—The Jiulongshan Formation, Middle Jurassic, Daohugou Village, Ningcheng County, Inner Mongolia, China.

Diagnosis.—Forewing: MA reduced, not reaching posterior margin; MP basally forking into MP1 and MP2; branch of CuA + CuPaα forming a complex branching pattern, last posterior branch ramified. Hindwing: RP with pectinate and dichotomous branches.

Description.—Forewing: large size, distinctly longer than body, length 81 mm, width about 26 mm; area between ScA and anterior margin broad. ScA reaching anterior wing margin at midlength of wing, ScP apparently long and undulate, branches of ScP numerous and mostly with a secondary vein between them; after the end of ScA, branches of the ScP strongly directed towards the wing apex; area between ScP and R broader than area between R and M + CuA in basal part, R forking into RA and RP at about 1/3 basal tegminal length, RA probably posteriorly pectinate with six branches, RP branched at the level of RA, posteriorly pectinate eight branches, areas between the branches with regular reticulate cross-veins for most part, a series of straight or gently curved cross-veins regularly arranged between RA and RP; M + CuA curved towards R basally, divided into M and CuA before the divergence of R; M forking into MA and MP, MA curved towards and close to RP, probably partly reduced or possibly fused with first branch of RP at anterior half (part of area between first branch of RS and MA lost); MP forking into MP1 and MP2, curved and reaching posterior margin and parallel with each other; CuA gently curved, point of fusion of CuA and CuPaα at the level of divergence of M; CuA fused with CuPaα and ramified immediately, forming a complex branching pattern, probably exhibiting nine terminal branches, first anterior branch of CuA + CuPaα simple and apparently oriented towards MP, last posterior branch dichotomously ramified, cross-veins between branches of CuA + CuPaα straight or reticulated; CuPaβ strongly oblique, area between CuPaβ and last posterior branch of CuA + CuPaα filled with straight or curved cross-veins; part of area between CuP and posterior margin lost, CuPb sharply curved.

Hindwing: ScP slightly undulate, area between ScP and RA with straight cross-veins; RA distally branched with six pectinate branches, RP branched before RA with more pectinate and dichotomous branches than RA, reticulated cross-veins between the branches; M forking into MA and MP at the level of divergence of R; CuA fused with CuPaα, running a while and forking into three branches.

Body badly damaged, estimated abdomen length 48 mm, pronotum saddle shaped, foreleg stout, tibiae with a row of strong spines preserved.

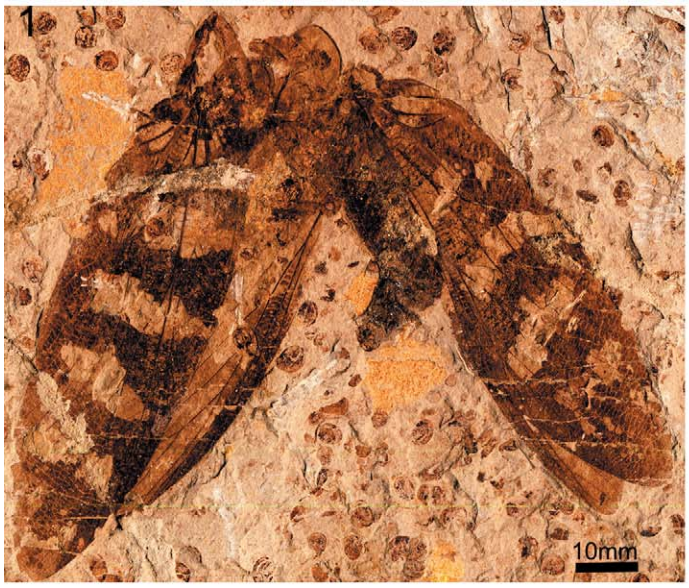
Discussion.—This new species is similar to *A. gigantus* Ren & Meng, 2006 in shape and venation, but it can be distinguished from the latter by the following characters: MA probably partly reduced; MP basally forking into MP1 and MP2; different mode of CuA + CuPaα branching; most of branches of RP ramified in hindwing.

A. hani sp. nov.
Fig. 7

Material.—Holotype: female, CNU-ORT-LB2009049.

Etymology.—In honor of Mr. Gang HAN, donor of the type specimen.

Horizon and locality.—The Yixian Formation, Upper Jurassic-Lower Cretaceous, Huangbanjigou, Chaomidian Village, Shangyuan Town-



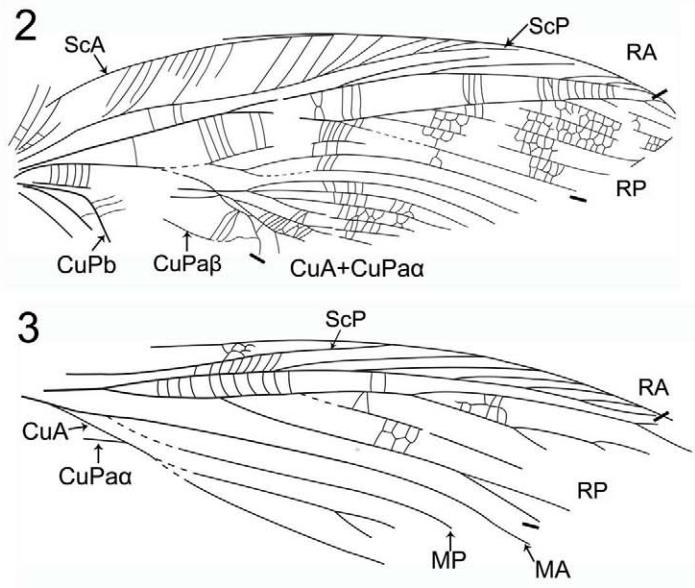


Fig. 6. *A. robustus sp. nov.*: 1: photograph of holotype specimen CNU-ORT-NN2006080, male. 2, 3: line drawings of forewing and hindwing of holotype respectively.

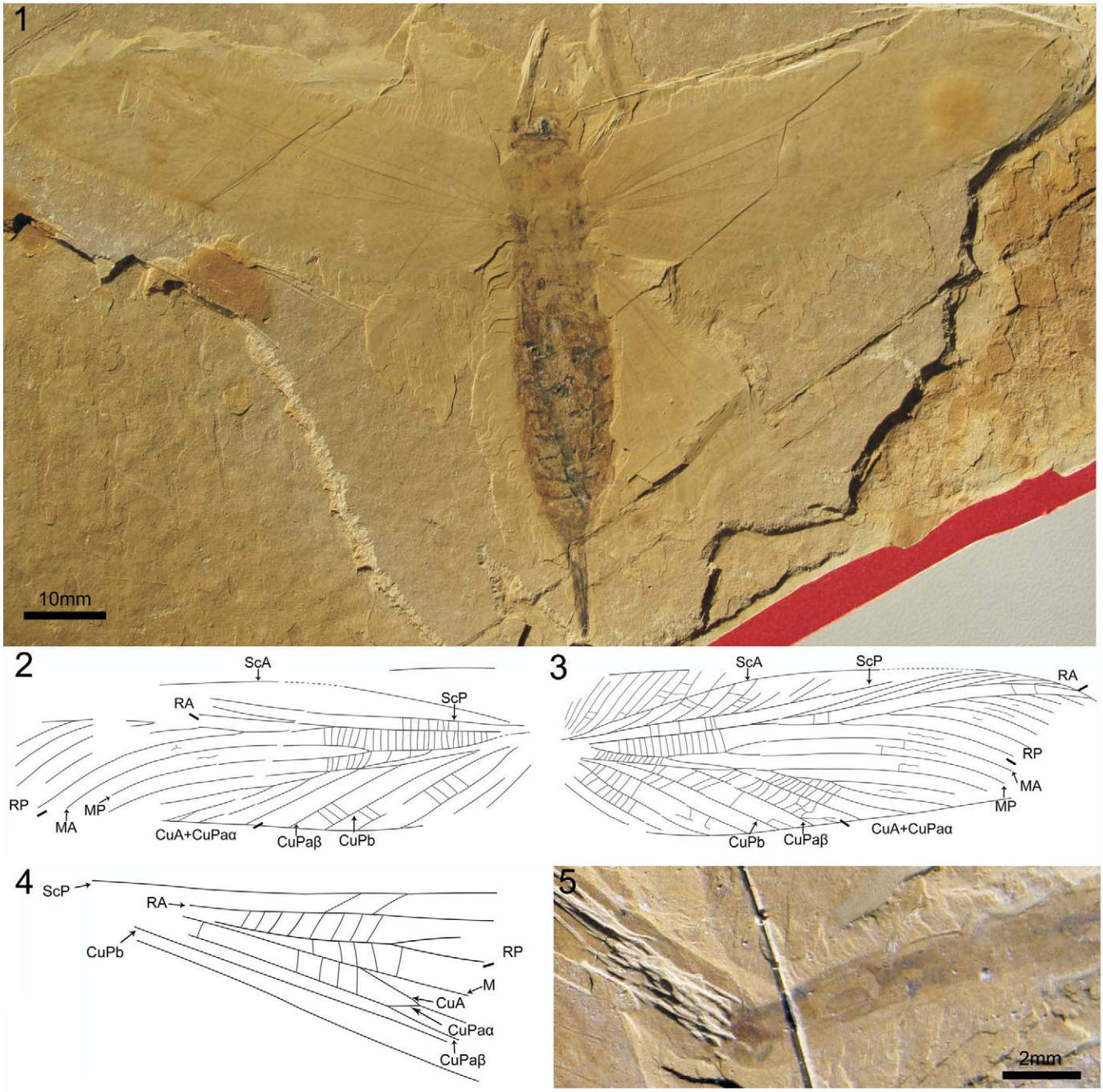


Fig. 7. *A. hangi sp. nov.* 1: photograph of holotype specimen CNU-ORT-LB2009049, female. 2-4: line drawings of forewings and hindwing of holotype respectively. 5: auditory organ of holotype.

ship, Beipiao City, Liaoning Province, China.

Diagnosis.—Only female known: forewing slim, ScA nearly straight, area between M + CuA and CuPa narrow, free part of M and CuA long, CuPb straight.

Description.—Forewing: slim and large size, longer than the insect's body, length 60 mm, greatest width about 16 mm; area between ScA and anterior margin broad and of subtriangular shape; ScA long and straight, reaching anterior wing margin at midlength and cutting the branches of ScP; ScP apparently long and nearly straight, branches of ScP numerous and connected by simple cross-veins; R forking into RA and RP at about 2/5 basal tegminal length, RA posteriorly pectinate with with 7 branches, RP branched after the first branch of RA, probably posteriorly pectinate with 8 branches, areas between the branches with regular reticulate cross-veins for the most part, a series of straight cross-veins regularly arranged between RA and RP; M + CuA straight, divided into M and CuA, M long and forking into MA and MP before the divergence of R, MA and MP parallel and reaching posterior margin, cross-veins between them formed into network in visible area; CuA slightly longer than free part of M, gently curved, point of fusion of CuA and CuPaα beyond the

divergence of M; CuA fused with CuPaα and then ramified with 5 or 6 terminal branches immediately, cross-veins between branches of CuA + CuPaα straight in basal part, reticulated in distal part; CuP differentiates into CuPa and CuPb very basal of the wing; CuPaα shorter than CuA before their fusion, CuPaβ and CuPb straight and strongly oblique; A veins straight.

Hindwing: only basal part preserved, anterior margin and ScP almost straight in preserved part; area between ScP and anterior margin with straight and strong oblique veinlets; R forked into RA and RP beyond the divergence of M + CuA; CuA fused with CuPaα, and free part of CuA distinct longer than CuPaα; CuPa and CuPb straight.

Body 45 mm long (without ovipositor), ovipositor 14 mm long as preserved; fore tibia with two inner spines and one outer spine preserved, internal auditory organ perserved, tympanum longer than broad, widely ovoid auditory openings of a swollen tympanal chamber plainly visible just below the femoro-tibial joint

Discussion.—It can be distinguished from *A. dicrus* and *A. gigantus* by its nearly straight ScA, long free part of M and CuA, straight CuPb. In addition, it was yielded from a different geological age.

It is rare to find hearing organs in fossils. Wang and Liu (1996) described a species, *Laiyangohagla beipoziensis,* (erected based on a single male specimen) with hearing organs of both sides preserved, collected from the Lower Cretaceous deposition of Shadong, China; its interior tympanum is partially covered and narrower than its outer tympanum. Our new finding of tympanal remains is more ovoid. Its shape is quite different from that of many modern tettigoniid insects, but is similar to some (modern) Pseudophyllinae. This kind of ovoid auditory opening might appear to be the plesiomorphic state of Tettigonioidea. As stridulatory devices are known to be established in Hagloidea since the Early Mesozoic, the possible function of this structure might be as a sound receptor related to detection of stridulation.

***Aboilus* Martynov, 1925**
Parahagla Lin, 1982
Linhagla Mayer, 2004
***Aboilus stratosus* Li, Ren & Wang, 2007**
Fig. 8

Protaboilus lini Ren & Meng, 2005, p. 514, fig. 3; new synonymy; holotype: CNU-ORT-NN2006003

Discussion.—This female forewing was originally described as a new species of *Protaboilus* Gorochov 1988, but in this investigation, we discern that it exhibits an early divergence of R which supports it belonging to Aboilinae. Meanwhile, it is the same as *Aboilus stratosus* in venation, only somewhat different in wing size; thus it would be better to assign it to *Aboilus stratosus*.

***Ashangopsis* Lin, Huang & Nel, 2008**
Lin, Huang & Nel, 2008, p. 206-208, fig. 1-4

Type species.—*Ashangopsis daohugouensis* Lin, Huang & Nel, 2008.

Revised diagnosis.—Forewing broad and short, ScA straight and nearly parallel with ScP, main longitudinal vein stout and strong, body characters as per the original diagnosis.

Remarks.—This genus was originally assigned to Chifengiinae by Lin *et al.* (2008), but would be better assigned to Aboilinae. Details to be presented later in Discussion.

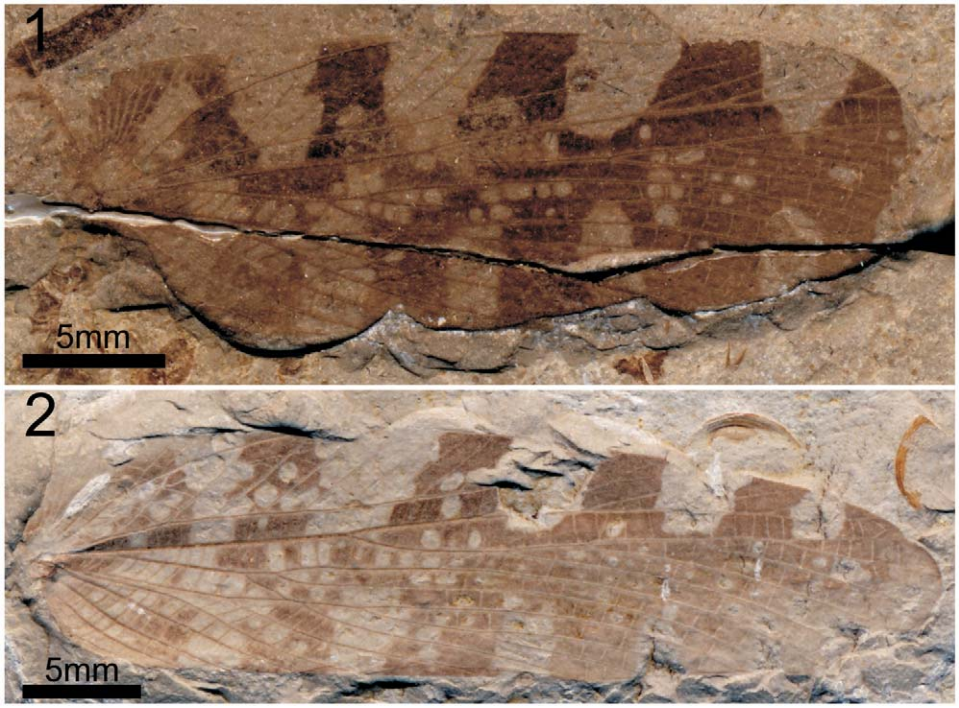


Fig. 8. *Aboilus stratosus* 2007. 1: photograph of holotype specimen CNU-ORT-NN2006010, female. 2: photograph of specimen CNU-ORT-NN2006003, female.

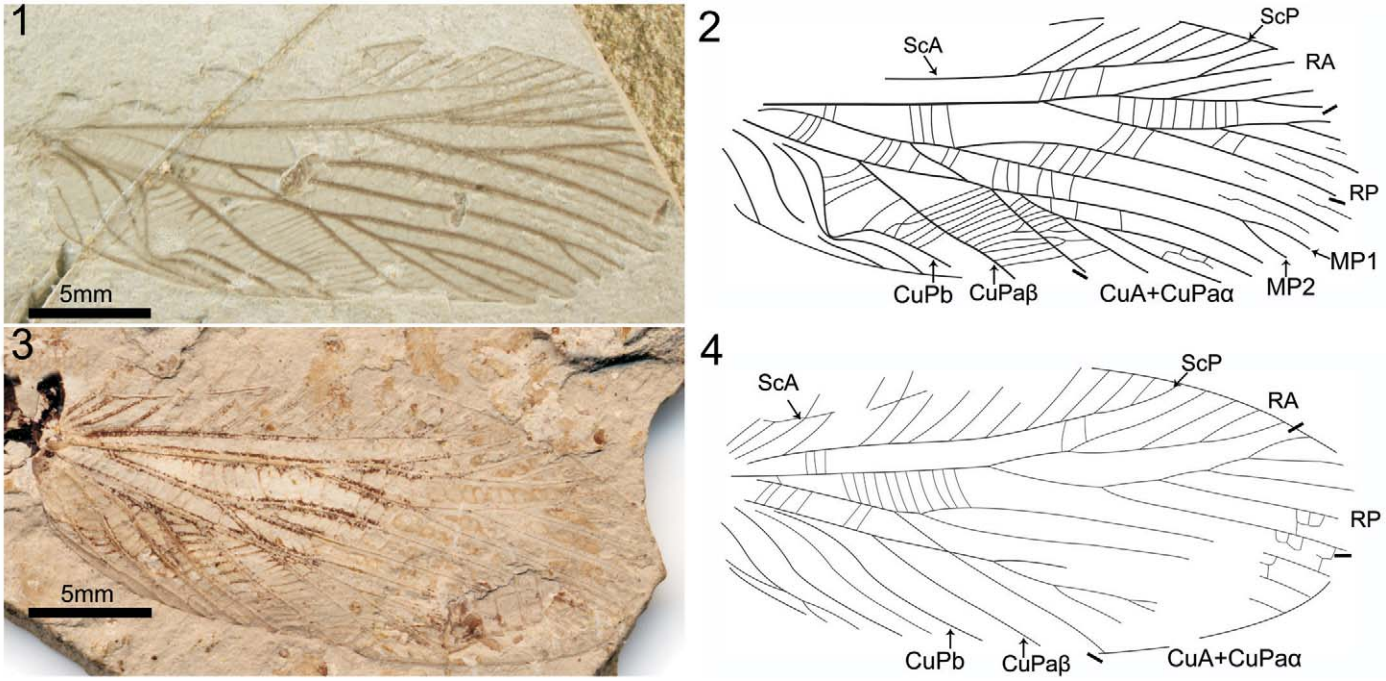


Fig. 9. *Ashangopsis* Lin, Huang & Nel, 2008. 1, 2: photograph and line drawing of specimen CNU-ORT-NN-2009010, male. 3, 4: photograph and line drawing of specimen CNU-ORT-NN-2009020, female.

***Ashangopsis daohugouensis* Lin, Huang & Nel, 2008**
Fig. 9.

Diagnosis.—As for genus.

New materials.—Male: CNU-ORT-NN2009010.
Female: CNU-ORT-NN2009019-22/23PC.

Horizon and locality.—The Jiulongshan Formation, Middle Jurassic, Daohugou Village, Ningcheng County, Inner Mongolia, China.

Description.—Male: forewing broad and short, lacks for the most part the area between anterior margin and ScA; length 26 mm, greatest width 10 mm (both measures preserved part); ScP straight, with oblique and regularly spaced branches, filled with simple cross-veins; R long and straight, forking into RA and RP close to midlength of forewing, RA with 5 and RP with 4, pectinate branches (preserved part), RP branched beyond first branch of RA; M + CuA probable origin from basal stem of R, and divided into M and CuA very basal to base of forewing; M forking into MA and MP before the divergence of R; MA simple, curved towards RP, MP distally forking into MP1 and MP2, stem of MP straight; CuA longer than M, fused with CuPaα slightly beyond divergence of M, then running a while and ramified with 5 terminal branches; CuPaβ oblique, area between CuPaβ and CuA + CuPaα broad, with straight and regularly arranged cross-veins; CuPb sharply curved and undulate, 1A fused with CuPb at their mid-length, then reaching posterior margin, probably 2A S-shaped and very close to the fusion of 1A and CuPb .
Female. Forewing broad and short, most part of area between anterior margin and ScA preserved; estimated length 29 mm and greatest width 12 mm of specimen CNU-ORT-NN2009023PC; ScA visible and straight, cutting the branches of ScP; ScP straight, with oblique and regularly spaced branches, filled with simple cross-veins, the branches aligned with the veinlets between ScA and anterior margin, R long and straight, forking into RA and RP close to mid-length of forewing, RA with 4 and RP with 5, pectinate branches, RP branched beyond first branch of RA; M + CuA probably originating from basal stem of R, and divided into M and CuA close to base of forewing; M forking into MA and MP before the divergence of R; MA and MP simple, parallel with each other; CuA longer than M, fused with CuPaα slightly beyond the origin of MP, then ramified with at least 5 terminal branches; CuPaβ oblique and straight; CuPb slightly sigmoidal; 1A, 2A, 3A similar to CuPb in shape, 4A fused with 3A for a while, then running to posterior wing margin.

Discussion.—Lin, Huang & Nel described the species *Ashangopsis daohugouensis* on the basis of three well-preserved specimens. Lin *et al.* (2008) considered the specimens (holotype and paratype) to be male and characterized this genus by the following characters: CuPb not strongly curved, absence of anastomosis between branches of anal veins, a very strong cross-vein connecting bases of CuA and CuPaα and forming a triangular cell filled with three cross-veins, forewing broader and shortened. Upon further detailed examination, we found that all three of their specimens are female per the absence of any stridulatory apparatus. In detail, CuPb is slightly sigmoidal; no anastomosis between CuPb and anal veins; area between CuPb and CuA + CuPaα narrow. These characters mentioned above clearly support that all specimens of *A. daohugouensis* describe by Lin *et al.* (2008) are female. Furthermore, the new material we described here shows apparently male characters: CuPb is sharply curved and fused with 1A at a point; area between CuPb and CuA + CuPaα broad. This further supports the conclusion proposed above.

The new material CNU-ORT-NN2009010 shows MP distally forking into MP1 and MP2, which is better considered as an intraspecific variability of wing venation. Also, on the basis of the new material, for which the area between ScA and the anterior margin is partly visible: ScA is long and straight, meanwhile cutting the branches of ScP. This character is shared with all taxa of Aboilinae,

but differs from Chifengiinae as also does MA and MP, being without any constriction. Thus it would be better to assign this taxon to Aboilinae rather than to Chifengiinae.

Subfamily: Chifengiinae Hong, 1982

Type genus.—*Chifengia* Hong, 1982.

Included genera.—*Chifengia* Hong, 1982a, *Alloma* Hong, 1982a, *Parahagla* Sharov, 1968, *Ashanga* Zherichin, 1985, *Aenigmoilus* Gorochov, Jarzembowski & Coram, 2006.

Revised diagnosis of Chifengiinae—Forewing large size, ScA reduced, reaching or paralleling with branch of ScP, cross-veins between branches of ScP usually straight, area between MA and MP usually distinctly narrower in basal part and broader in middle part; hindwing: ScP sigmoidal, posterior branch of CuA + CuPaα not reaching CuPaβ; ovipositor well developed and longer than pronotum.

Discussion.—This subfamily was established by Hong in 1982; it includes *Chifengia* Hong, 1982a, *Parahagla* Sharov, 1968, *Ashanga* Zherichin, 1985, *Aenigmoilus,* Gorochov, Jarzembowski & Coram, 2006 — and some other described genera which should be synonyms of the former. *Hebeihagla* Hong, 1982b and *Alloma* Hong, 1982a were originally assigned to Haglinae, but on the basis of the illustrations of the type specimens, the wing venation supports assigning these two genera to Chifengiinae Hong, 1982, by the following characters (which are distinctly different from Haglinae): branch of ScP simple, MA and MP constricted in basal part.

Among *Hebeihagla*, *Alloma*, *Sinohagla*, *Yenshania*, *Habrohagla* and *Trachohagla* — *Hebeihagla* could be identified as a synonym of *Parahagla* while the status of *Alloma* needs to be investigated by checking the type specimen. Meanwhile, *Sinohagla* Lin, 1965 and *Yenshania* Hong, 1982a are very similar to Chifengiinae, but this still needs an investigation of the type specimens to make sure of their position. Other described genera, *Habrohagla* Ren, Lu, Guo & Ji, 1995, *Trachohagla* Meng, Ren & Li, 2006, *Grammohagla* Meng & Ren, 2006, are also synonyms of *Parahagla* Sharov, 1968.

Based on the abundance of specimens which can be assigned to *Parahagla sibirica*, the character, area between MA and MP distinct narrower in basal part and about two times broader in middle part, is stable. This character has been overlooked by previous authors especially those not providing accurate descriptions. However, it also happened in *Chifengia*, *Alloma* and *Ashanga hongi comb. nov.* (*Athehagla hongi* Meng & Ren, 2006); it is not investigated in *Ashanga clara* and *Aenigmoilus minutus*.

Parahagla Sharov, 1968

[=*Hebeihagla* Hong 1982; *Habrohagla* Ren, Lu, Guo & Ji, 1995; *Grammohagla* Meng & Ren, 2006 syn. nov.; *Trachohagla* Meng, Ren & Li, 2006 *syn. nov.*]

Type species.—*Parahagla sibirica* Sharov, 1968.

Included species.—Only type species *Parahagla sibirica* Sharov, 1968.

Revised Diagnosis.—ScA reduced and parallel with branches of ScP, area between MA and MP distinctly narrower in basal part and about two times broader in middle part, M + CuA emitted from stem of R, CuPaβ broken by a straight handle in male forewing; hindwing: anterior margin and ScP sigmoidal, posterior branch of CuA + CuPaα not reaching CuPaβ; hind tibia with four spurs. Ovipositor well developed and apparently longer than pronotum.

Parahagla sibirica Sharov, 1968
Fig. 10.

Chifengia lata Meng, Ren & Li, 2006, p. 753, fig. 2; new synonymy; holotype: CNU-ORT-LB2006009
Chifengia angustata Meng, Ren & Li, 2006, p. 754, fig. 3; new synonymy; holotype: CNU-ORT-LB2006006
Chifengia amans Meng & Ren, 2006, p. 286, fig. 7-8; new synonymy; holotype: CNU-ORT-LB2005003
Grammohagla latibasis Meng, Ren & Li, 2006, p. 756, fig. 8; new synonymy; holotype: CNU-ORT-LB2006007
Grammohagla striata Meng & Ren, 2006, p. 283, fig. 1-4; new synonymy; holotype: CNU-ORT-LB2005001
Trachohagla jeholia Meng, Ren & Li, 2006, p. 753, fig. 1; new synonymy; holotype: CNU-ORT-LB2006008
Hebeihagla songyingziensis Hong, 1982b, p. 447, fig. 1; new synonymy; holotype: 75LII-2b
Habrohagla curtivenata Ren, Lu, Guo & Ji, 1995, p. 64, fig. 3-20; new synonymy; holotype: CH93301

New materials.—CNU-ORT-LB2006020/054/059/103/105/106, CNU-ORT-LB2008079/081, CNU-ORT-LB2009079, CNU-ORT-LB2009050-52

Description of Specimen CNU-ORT-LB2006020.—Hindwing broader, but probably slightly shorter than forewings, anterior margin and ScP sigmoidal, RA branched distally, RP pectinate with at least 8 branches, area between RA and ScP very narrow; M + CuA separate before the divergence of R; MA and MP reaching posterior margin, area between MA and MP narrow in the distal part; free part of M and CuA short; CuA fused with CuPaα, running for a moderate while and then forked with two branches, the branches not reaching CuPaβ in the preserved part, the posterior one very close to CuPaβ; CuPb straight; anal area enlarged, A veins straight.

Hind tibia long, with a row of spines and four spurs preserved; ovipositor long, about 23 mm length preserved.

Discussion.—*Parahagla* was erected by Sharov in 1968; the specimen was collected from Russia. In the last three decades, seven described genera which can be assigned to Chifengiinae were published in China; all of them were established by single specimen. Among them, four described genera are almost indistinguishable from *Parahagla* by their illustrations.

With plenty of well-preserved specimens recently collected from the Yixian Formation, a new investigation based on wing venation has been conducted.

First, all the new materials mentioned here and the specimens of *Parahagla sibirica*, *Chifengia lata*, *C. angustata*, *C. amans*, *Grammohagla latibasis*, *G. striata*, *Trachohagla jeholia*, *Hebeihagla songyingziensis* and *Habrohagla curtivenata*, share the following characters: a straight ScA parallel with branches of ScP, ScP straight with regularly arranged branches, branches of ScP connected by straight cross-veins, area between MA and MP distinctly narrower in basal part and about two times broader in middle part, M + CuA emitted from stem of R, area between CuPa and M + CuA narrow, CuPaβ broken by a straight handle in male forewing, CuA + CuPaα ramified and second

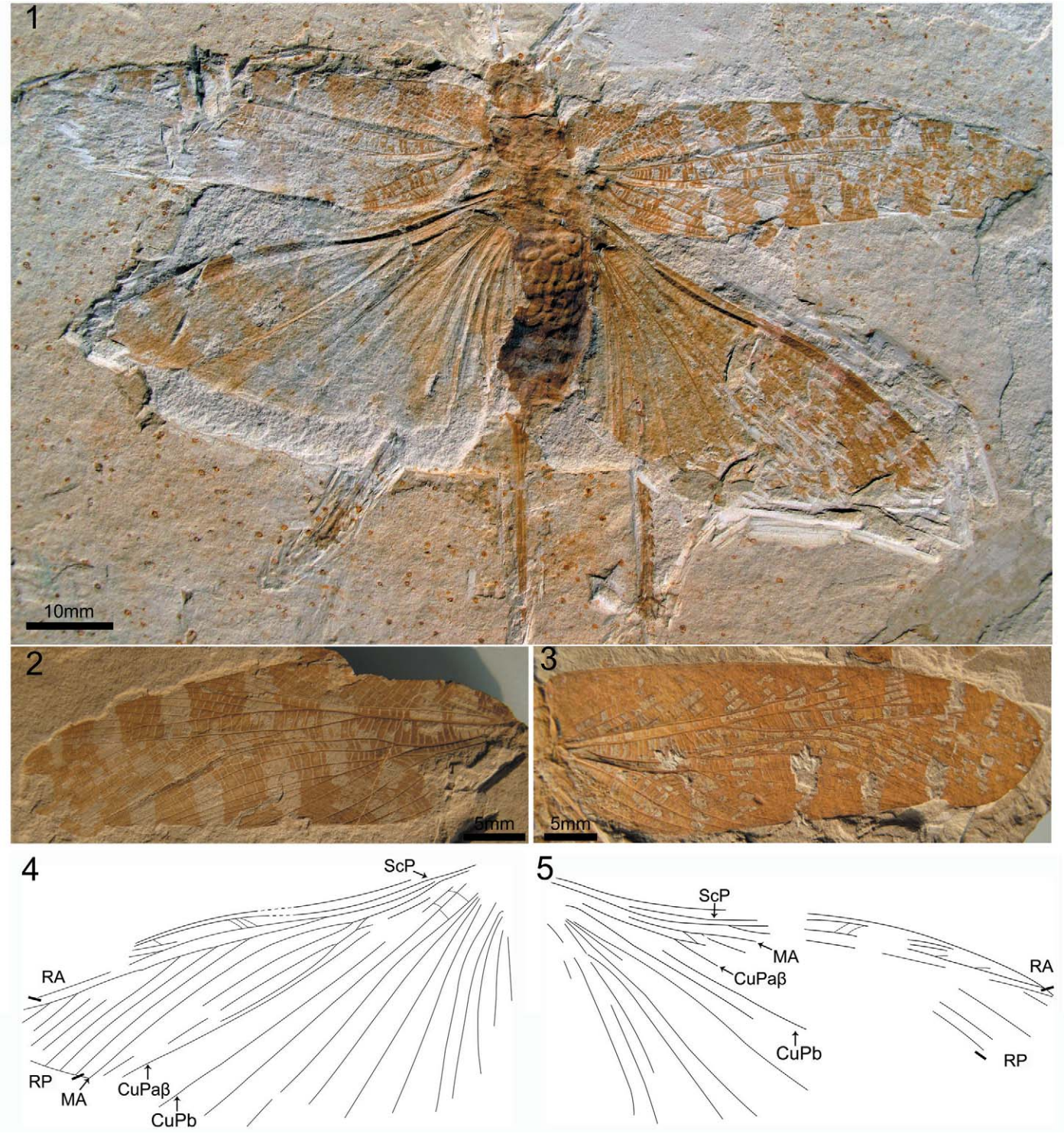


Fig. 10. New materials of *P. sibirica* Sharov, 1968. 1: photograph of specimen CNU-ORT-NN200.

anterior branch pectinate with several branches, CuPaβ curved and broken by a straight handle. Meanwhile, they only differ in number of branches of RA and RP, the relative position of RP branching, the length of the free part of CuA, and the branch numbers of CuA + CuPaα, which were used to characterize different genera by the original descriptions. These kinds of characters are always unstable in different individuals of the same species, with variation even existing between the left wing and right wing of one individual.

Second, up to now, only two specimens with a hind wing were found. The well-preserved collections reveal more about the morphology of Chifengiinae hind wings. These show a distinct difference from Aboilinae hind wings in that the posterior branch of CuA + CuPaα is close to, but not reaching, CuPaβ, and also in that the branches of CuA + CuPaα probably fuse together and become lost in the network cross-veins.

Fig. 11. *Ashanga hongi* comb. nov., holotype specimen CNU-ORT-LB2005002.

***Ashanga* Zherichin 1985**

[=*Athehagla* Meng & Ren *syn. nov.*]

Type species.—*Ashanga clara.*

Included species.—*Ashanga clara* Zherichin, 1985, *Ashanga hongi comb. nov.*

Ashanga hongi comb. nov.
Fig. 11.

Athehagla hongi Meng & Ren, 2006 p. 286, figs 5-6.

Holotype.—CNU-ORT-LB2005002

New material.—CNU-ORT-LB2006042

Revised diagnosis.—ScA oblique and straight, fused with two branches of ScP before reaching anterior margin, CuA + CuPaα running for a moderate while before ramification.

Discussion.—This specimen was briefly described as a new genus of Chifengiinae by Meng & Ren (2006). After a new examination of the type specimen, we consider this female forewing as a member of *Ashanga* Zherichin, 1985, for the following reasons: 1) ScA straight but not parallel with branches of ScP, instead fusing with two branches of it. It is very similar to *Ashanga clara* (fusing with one branch of ScP before reaching the anterior margin); 2) CuA + CuPaα running for a discernable distance rather than ramifying immediately as in *Ashanga clara*. However, it shares the major characters of *Ashanga clara*: *e.g.*, forewing shape, ScP oblique, straight and with straight and regularly arranged branches, cross-veins between the branches of ScP simple, divergence of R close to wing base. Because of the characters mentioned above, *Athehagla* is transferred to *Ashanga* as *Ashanga hongi comb. nov.*

Discussion

Comparison and systematic position.—Gorochov (2003) considered Protaboilinae as a primitive group of Prophalangopsidae, possibly ancestral for all other subfamilies. The first Protaboilinae was described by Gorochov (1988); it was collected from the Lower Jurassic deposit, Kirgizia. In 2006, five new specimens collected from the Upper Jurassic-Lower Cretaceous Yixian Formation, Fengning County, Hebei, and the Middle Jurassic Jiulongshan Formation, Daohugou, Inner Mongolia, China, were described as five new species of two genera and assigned to Protaboilinae by Ren & Meng (2006). But in our investigation, all of these new taxa have been transferred to Aboilinae; of them four specimens are females, which share almost all characters in wing venation with Aboilinae. The cross-veins between the proximal part of CuPb and CuPaβ of the described species *Allaboilus gigantus*, are also similar to Aboilinae, but distinctly different from those of Protaboilinae. Thus, up to now, Protaboilinae consists of only one genus and species. In addition, *Protaboilus praedictus*, the type species of Protaboilinae, was considered as a sister species of *Aboilus columnatus* in a cladistic analysis of Palaeozoic and Mesozoic Ensifera (Béthoux & Nel 2002). This species differs from Aboilinae only in stridulatory apparatus and a slightly later origin of branches of RA and RP. In general, the position of Protaboilinae is still uncertain.

Aboilus Martynov 1925 is the type genus of Aboilinae and 19 described species are hitherto assigned to this genus. But some species within *Aboilus* are still questionable: *e.g.*, *Aboilus zebra* Gorochov 1988 probably belongs to another genus, and there are probably synonyms. Therefore, new investigations of the type specimens (which are scattered in various institutions, often without specified depository) is needed. Some species described from China in the last two decades were originally attributed to Haglidae, with subfamily assignment incorrect or lacking, but undoubtedly they can be assigned to Aboilinae or Chifengiinae of Prophalangopsidae. They include *Alloma* Hong, 1982a, *Habrohagla* Ren, Lu, Guo & Ji, 1995, *Hebeihagla* Hong, 1982b, which can be assigned to Chifengiinae based on their reduced ScA and basally narrower part of the area between MA and MP; also *Huabeius* Hong, 1982b, *Mesohagla* Zhang, 1996, *Shangxiania* Zhang, 1993, *Shanxius* Hong, 1984, *Sinoprophalangopsis* Hong, 1984 and *Zhemengia*, Hong 1982b, which can be assigned to Aboilinae based on their long ScA cutting branches of ScP. Some genera, *e.g.*, *Sunoprophalangopsis* Hong, 1982b and *Brunneus* Hong, 1983, have been assigned to Aboilinae by Gorochov (2003).

Intraspecific variability.—Variability in forewing size and wing-venation pattern is poorly known for prophalangopsid insects, because most of the species are described upon only a few specimens, some of them being poorly preserved. Only by Gu *et al.* (2009) was some variation of *Sigmaboilus* discussed and displayed: there were some differences between left and right forewings of the same individual.

On the basis of the recent collections (some completely preserved forewing pairs), a further investigation was carried out. One of the structures which varies the most is the branching number of ScP, RA and RP. This takes place in such species as *Circulaboilus aureus* (Fig. 2), *Allaboilus gigantus* (Figs 4, 5), *Ashangopsis daohugouensis* (Fig. 9), *Parahagla sibirica* (Fig. 10), *Sigmaboilus peregrinus* and *S. fuscus* (Gu *et al.* 2009). The location of the first fork of RP is also a highly

variable structure in the forewings of *Parahagla sibirica* and *Circulaboilus aureus*. In *A. daohugouensis*, MP is simple in the holotype NIGP 143692a-b (Lin *et al.* 2008) and CNU-ORT-NN2009019/023, but forking distally in CNU-ORT-NN2009010. The branching pattern and number of CuA + CuPaα exhibit a wide range variation in such species as *A. gigantus*, *A. hani* (Fig. 7), *P. sibirica*, *A. daohugouensis*, *C. aureus*; the pattern is relatively stable in *P. sibirica*. The free part of CuA is slightly longer, or more than two times longer, than the free part of M of *A. gigantus* (Figs 4, 5). Documentation of such variation might prevent the erection of invalid taxa in the future.

Conclusion

Eleven Prophalangopsid species described from Yanliao Biota (Jiulongshan Formation) and Jehol Biota (Yixian Formation and Jiufuotang Formation) are determined to be synonyms. As a result, Aboilinae, as the most diverse group of Prophalangopsidae, includes 11 genera found in China; Protaboilinae Gorochov 1995 consists only of one genus *Protaboilus*; Chifengiinae includes genera *Chifengia*, *Ashanga*, *Parahagla*, *Aenigmoilus* and *Alloma*.

This revision suggests that substantial additional investigations on prophalangopsid insect taxa will be necessary. However a number of difficulties make extensive revisions of Prophalangopsidae a challenge. First, some published contributions fail to provide accurate morphological data in their illustrations or descriptions. They do not allow identification of synonyms and correct taxonomic placement for many taxa. In addition, the type specimens of the more than 16 described species from China are scattered in various collections, without specific published indication of their depository. Unavailability of such type materials makes their comparison and related taxonomic decisions very difficult.

Acknowledgments

We are grateful to Professor Glenn K. Morris (University of Toronto, Mississauga, Canada) and an anonymous reviewer for their valuable comments. We thank Dr. Alexey Yu. Solodovnikov (Zoological Museum, Natural History Museum of Denmark, University of Copenhagen, Danmark), for his improvement of our manuscript. We thank Dr. A.V. Gorochov and Dr. Shi Fu-Ming for providing their authored documents. We thank Dr. O. Béthoux for his suggestions and help. We thank Dr. Shih Chung-kun for donating collection CNU-ORT-NN2009045 and for his improvement of this manuscript. This research is supported by the National Natural Science Foundation of China (No. 40872022), the Nature Science Foundation of Beijing (No.5082002), the Key and PHR Program of Beijing Municipal Commission of Education, the Chinese Municipal Education Commission Discipline Construction and Graduate Education Construction Project, a grant (No.O529YX5105) from the Key Laboratory of the Zoological Systematics and Evolution of the Chinese Academy of Sciences and a Research Fund of the Orthopterists' Society.

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Table. 1. A list of the fossils mentioned in this contribution. J_1 - Early Jurassic; J_2 - Middle Jurassic; J_3 - Late Jurassic; K_1 - Early Cretaceous; F. - Formation; G. - Group.

Subfamily	Species	Locality	Geol. age
Aboilinae	*Allaboilus. dicrus* Ren & Meng 2006	Jiulongshan F., Inner Mongolia, China	J_2
	A. gigantus Ren & Meng 2006	Jiulongshan F., Inner Mongolia, China	J_2
	=*Flexaboilus* Li, Ren & Meng 2007	Jiulongshan F., Inner Mongolia, China	J_2
	=*Furcaboilus* Li, Ren & Wang 2007	Jiulongshan F., Inner Mongolia, China	J_2
	A. robustus sp. nov	Jiulongshan F., Inner Mongolia, China	J_2
	A. hani sp. nov.	Yixian F., Liaoning, China	J_3-K_1
	Aboilus stratosus Li, Ren & Wang 2007	Jiulongshan F., Inner Mongolia, China	J_2
	=*Protaboilus lini* Ren & Meng 2006	Jiulongshan F., Inner Mongolia, China	J_2
	Ashangopsis daohugouensis Lin, Huang & Nel 2008	Jiulongshan F., Inner Mongolia, China	J_2
	Circulaboilus aureus Li, Ren & Wang 2007	Jiulongshan F., Inner Mongolia, China	J_2
	=*C. amoenus* Li, Ren & Meng 2007	Jiulongshan F., Inner Mongolia, China	J_2
	C. priscus sp. nov.	Jiulongshan F., Inner Mongolia, China	J_2
	Huabeius suni Hong 1982b	Jiufotang F., Hebei, China	K_1
	Mesohagla xinjiangensis Zhang 1996	Badaowan F., Xinjiang, China	J_1
	Scalpellaboilus angustus sp. nov.	Jiulongshan F., Inner Mongolia, China	J_2
	Shangxiania fengjiashanensis Zhang 1993	Fengjiashan F., Shaanxi, China	K_1
	*Shanxius reticulatus*Hong 1984	Shanxi, China	J_1
	*Shanxius meileyingziensis*Hong 1988	Shahai F., Liaoning, China	K_1
	*Sinoprophalangopsis reticulata*Hong 1984	Haifanggou F., Liaoning, China	J_2
Chifengiinae	*Zhemengia sinica* Hong 1982b	Inner Mongolia, China	J_1
	Aenigmoilus minutus Gorochov, Jarzembowski & Coram 2006	Wealden G., England	K_1
	*Alloma huanghuachunensis*Hong 1982a	Jiufotang F., Hebei; Liaoning, China	K_1
	A. fasicata Hong 1982a	Liaoning, China	J_3
	Ashanga clara Zherichin 1985	Russia	J_2-J_3
	A. hongi comb. nov.	Yixian F., Liaoning, China	J_2-J_3
	Parahagla sibirica Sharov 1968	Russia	K_1
	=*Chifengia lata* Meng, Ren & Li 2006	Yixian F., Liaoning, China	J_3-K_1
	=*C. angustata* Meng, Ren & Li 2006	Yixian F., Liaoning, China	J_3-K_1
	=*C. amans* Meng & Ren 2006	Yixian F., Liaoning, China	J_3-K_1
	=*Grammohagla latibasis* Meng, Ren & Li 2006	Yixian F., Liaoning, China	J_3-K_1
	=*G. striata* Meng & Ren 2006	Yixian F., Liaoning, China	J_3-K_1
	=*Habrohagla curtivenata* Ren, Lu, Guo & Ji 1995	Yixian F., Hebei, China	J_3-K_1
	=*Hebeihagla songyingziensis* Hong 1982a	Yixian F., Hebei, China	J_3-K_1
	=*Trachohagla jeholia* Meng, Ren & Li 2006	Yixian F., Liaoning, China	J_3-K_1