New material of *Sigmaboilus* (Insecta, Orthoptera, Prophalangopsidae) from the Jurassic Daohugou Beds, Inner Mongolia, China

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ABSTRACT: Five orthopteran specimens from the uppermost Middle–lowermost Upper Jurassic of Daohugou, Inner Mongolia, China are described and attributed to the genus *Sigmaboilus* Fang, Zhang & Wang, 2007 (Prophalangopsidae); and a new species, *S. calophlebius* sp. nov., is established herein. The diagnostic characters for *Sigmaboilus* are revised and a key to species of *Sigmaboilus*, based on male forewings, is provided. Intraspecific variation in forewings of this genus is also discussed.

KEY WORDS: Intraspecific variation, key, new specimens, new species.

Prophalangopsidae belong to the superfamily Hagloidea, with a tegminal stridulatory apparatus in the male known from the Triassic onwards (Gorochov 1995, 2003). The extinct Aboilinae are the most diverse subfamily of the Prophalangopsidae, including 68 described species in 27 genera. Recently, five well preserved specimens of Aboilinae were found in the famous Daohugou beds of Inner Mongolia, China and are attributed to the genus *Sigmaboilus* Fang, Zhang, Wang & Zhang, 2007. Here we describe these specimens, assigning four to two known species and establishing a new species for the fifth. Based on these specimens, the forewing diagnostic characters for *Sigmaboilus* are revised.

1. Material and methods

All specimens described herein are preserved on the surface of grey tuffaceous siltstones and were collected from the Daohugou beds of Daohugou (41°18′N, 119°13′E) in Ningcheng County, Chifeng City, Inner Mongolia, China. The Daohugou beds are considered herein to be Callovian/Oxfordian in age (latest Middle–earliest Upper Jurassic; Zhang *et al*. 2014; Liu *et al*. 2015; Wang *et al*. 2015).

There is no consensus on the interpretation of the wing venation of Orthoptera or, consequently, its nomenclature: we here follow Béthoux & Nel (2001, 2002). The venational terms used by Zeuner (1939) and Sharov (1968, 1971), and amended by Gorochov (1986, 1995), are listed here in parentheses following the corresponding ones used by Béthoux & Nel (2001, 2002), if any notable differences are present between the terminologies. The wing-vein abbreviations used are: ScA (C) = costa; ScP (Sc) = subcosta; RA = radius anterior; RP (RS) = radial sector; M (MA) = media; MA (MA1) = media anterior; MP (MA2) = media posterior; CuA (MP) = cubitus anterior; CuPa (CuA) = first cubitus posterior; CuPaα (CuA1) = anterior branch of the first cubitus posterior; CuPaβ (CuA2) = posterior branch of the first cubitus posterior; CuPb (CuP) = second cubitus posterior; A = analis (anal); and 1A = first anal vein.

All specimens were examined dry using a Nikon SMZ1000 stereomicroscope. The photographs were taken using a Nikon D800 digital camera, and the line drawings were compiled by tracing the photographs using the image-editing software CorelDraw X5 and Adobe Photoshop CS. All specimens are deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences, Nanjing, China.

2. Systematic palaeontology

Order Orthoptera Olivier, 1789
Superfamily Hagloidea Handlirsch, 1906
Family Prophalangopsidae Kirby, 1906
Subfamily Aboilinae Martynov, 1925
Genus *Sigmaboilus* Fang, Zhang, Wang & Zhang, 2007

Type species. *Sigmaboilus gorochovi* Fang, Zhang, Wang & Zhang, 2007.

Emended diagnosis. Forewing narrow and long, ratio of length to maximal width 3.5–4.2:1; costal area subtriangular (about one third–one half total width at base) with numerous "radial veinlets" basally; ScA slightly sigmoidal, extremely long, and ending on anterior margin beyond first branch of RA; RA with 4–7 branches, RP with 6–8 branches; "handle vein" (single cross-vein traversing some of the nearest cross-veins between the base of CuA + CuPaα and CuPaβ) slightly curved, and almost parallel to nearest cross-vein between last

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branch of CuA + CuPaα and CuPaβ; CuPb slightly Z-shaped, touching 1A at point close to hind margin.

Key to species of the genus *Sigmaboilus* based on male forewing

1. Whole forewing brown..... 2
–. Colouration of forewing of irregular bands..... 3
2. Crossveins between "handle vein" and CuPaα regularly arranged and subparallel to "handle vein"..... *S. gorochovi* Fang, Zhang, Wang & Zhang, 2007
–. Crossveins between "handle vein" and CuPaα not parallel to "handle vein"..... *S. fuscus* Gu, Zhao & Ren, 2009
3. Stridulatory vein (middle part of CuPb) and posterior margin forming an acute angle..... 4
–. Stridulatory vein perpendicular to posterior margin ..... *S. calophlebius* sp. nov.
4. Crossveins between "handle vein" and CuPaα regularly arranged with last one ending in "handle vein"..... *S. sinensis* Fang, Zhang, Wang & Zhang, 2007
–. Crossveins between "handle vein" and CuPaα regularly arranged and subparallel to "handle vein" ..... *S. peregrinus* Gu, Zhao & Ren, 2009.

Sigmaboilus gorochovi Fang, Zhang, Wang & Zhang, 2007
(Fig. 1)

Holotype. NIGP148111, incomplete male forewing with anterior part slightly damaged.

New material. Specimen NIGP161451 (Fig. 1), part and counterpart, a male left forewing with costal area slightly damaged.

Horizon and locality. Uppermost Middle–lowermost Upper Jurassic; Daohugou Village, Ningcheng County, Chifeng City, Inner Mongolia, China.

Emended diagnosis. Male forewing only. ScA sigmoidal and long; RA and RP pectinate, with 5–7 anterior and seven posterior branches respectively; CuA + CuPaα with 4–5 terminal branches; "handle vein" gently curved; stridulatory vein (middle part of CuPb) and posterior margin forming an acute angle; cross-veins between "handle vein" and CuPaα regularly arranged and subparallel to "handle vein". Whole forewing brown.

Description of new specimen. Male forewing with preserved length about 36 mm, width about 9 mm, ratio of length to maximal width about 4:1. Costal area broad, with several radial veinlets preserved. ScA sigmoidal and long, probably ending in anterior margin beyond wing midlength; ScP nearly straight, ending in anterior margin at 4/5ths of wing length from base with eight branches preserved; RA and RP diverging at 11 mm distal of wing base and each with seven pectinate branches. M + CuA diverging at about 1/5 of wing length; stem CuA longer than stem M, and fused with CuPaα at about 9.5 mm distal of wing base; stem of CuA nearly straight; CuA and CuPaα fused, with five terminal branches; CuPb strongly curved and Z-shaped, 1A slightly sigmoidal, close to and touching CuPb at one point. Whole forewing brown.

Remarks. Specimen NIGP161451 shares the same pigmentation as the holotype and shows that the cross-veins between the "handle vein" and CuPaα are subparallel to the "handle vein", and therefore it should be attributed to *S. gorochovi*. But it differs from the holotype by RA and CuA + CuPaα possessing more branches and CuA connecting to CuPaα and forking earlier.

Sigmaboilus peregrinus Gu, Zhao & Ren, 2009
(Figs 2–4)

Holotype. CNU-ORT-NN2008018, male forewing with anterior part missing.

New material. Specimen NIGP164448 (Fig. 2), a pair of male forewings, with right one damaged basally and left one with costal area missing; NIGP161449 (Fig. 3), a pair of male forewings, with right one damaged anterior-medially and left one apically; NIGP161450 (Fig. 4), a male left wing with costal and anal areas partly lost.

Horizon and locality. Uppermost Middle–lowermost Upper Jurassic; Daohugou Village, Ningcheng County, Chifeng City, Inner Mongolia, China.

Emended diagnosis. Forewing only. ScA ending on anterior margin at about wing mid-length; CuA and CuPaα fused for a short distance; stridulatory vein and posterior margin forming an acute angle; cross-veins between "handle vein" and CuPaα regularly arranged and subparallel to "handle vein". Pigmentation present on most of forewing.

Descriptions of new specimens. Specimen NIGP164448. Male forewings with preserved length 35 mm (left forewing) and 30 mm (right forewing). Forewing long and narrow, base constricted. Costal area not visible; ScA slightly sigmoidal, incompletely preserved, and probably extending to wing mid-length; ScP nearly straight, ending on anterior margin at four fifths of wing length from base, with eight branches preserved; RA and RP diverging at about one third of wing length, with RA pectinately three-branched and RP seven-branched (left forewing) or six-branched (right forewing); M + CuA diverging at about one quarter of wing length; stem M short, about 2 mm long; both MA and MP very long, simple and slightly arched; stem CuA nearly straight, and as long as stem M; CuA and CuPaα fused for a short interval, with six terminal branches; CuPb strongly curved and Z-shaped; 1A slightly sigmoidal, close to and touching CuPb at one point. Pigmentation present on most of forewing.

Specimen NIGP161449. Male forewings long and narrow, with preserved length 24 mm for left forewing and 36 mm for right. Costal area broad with 11 radial veinlets preserved. ScA sigmoidal and long, probably reaching middle of anterior margin of forewing; ScP nearly straight, ending on anterior margin at four fifths of wing length from base, with numerous branches; RA and RP diverging at 12.5 mm distal of wing base, with RA pectinately six-branched and RP eight-branched (right forewing); M + CuA diverging at about one quarter of wing length; stem CuA nearly straight, as long as stem M and fused with CuPaα at about 10.5 mm from wing base; CuA and CuPaα fused for a short interval, with six terminal branches; CuPb strongly curved and Z-shaped; 1A slightly sigmoidal, close to and touching CuPb at one point. Pigmentation present on most of forewing.

Specimen NIGP161450. Male forewing, with preserved length 36.0 mm, width 8.9 mm, ratio of length to maximal width about 4:1. Costal area not visible. ScA sigmoidal, and probably extending to wing mid-length as estimated; ScP nearly straight, ending in anterior margin at four fifths of wing length from base, with nine branches preserved; RA and RP diverging at 12 mm distal of wing base, with RA pectinately five-branched and RP six-branched; M + CuA diverging at about one quarter of forewing length; stem CuA slightly sinuate, as long as stem M and fused with CuPaα at about 10 mm distal of wing base; CuA and CuPaα fused for a short interval, with five terminal branches; CuPb strongly curved and Z-shaped; 1A slightly sigmoidal, close to and touching CuPb at one point. Pigmentation present on most of forewing.

Remarks. Specimens NIGP161448–161450 share almost the same pigmentation as the holotype and the cross-veins between the "handle vein" and CuPaα are regularly arranged and subparallel to the "handle vein". They are, however, different from the holotype in some aspects. In detail, NIGP161448 differs from the holotype in having fewer

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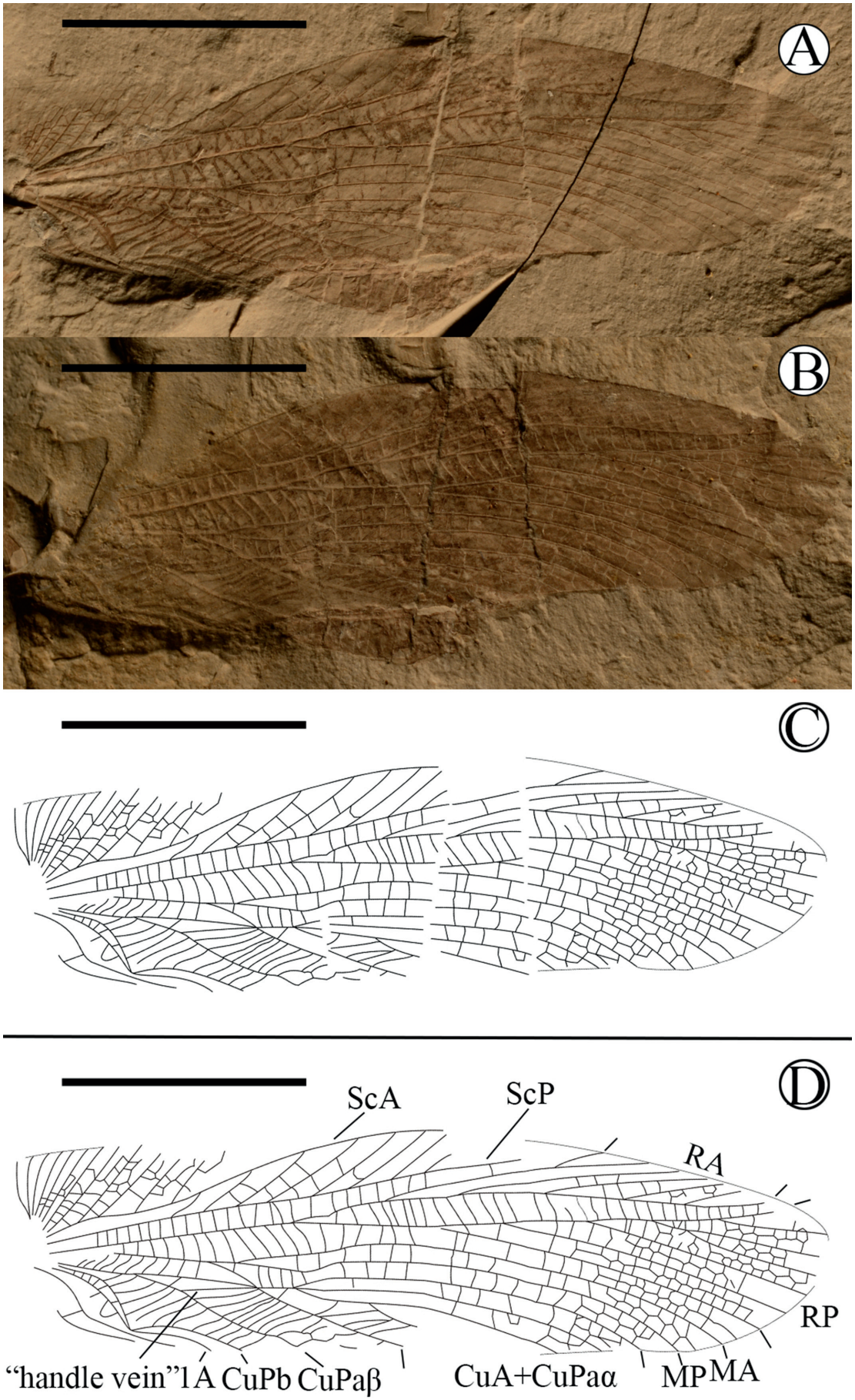

Figure 1 *Sigmaboilus gorochovi* Fang, Zhang, Wang & Zhang, 2007, male forewing: (A) NIGP161451a, part; (B) NIGP161451b, counterpart; (C, D) interpretation based on part and counterpart of specimen NIGP161451. Scale bar = 10 mm.

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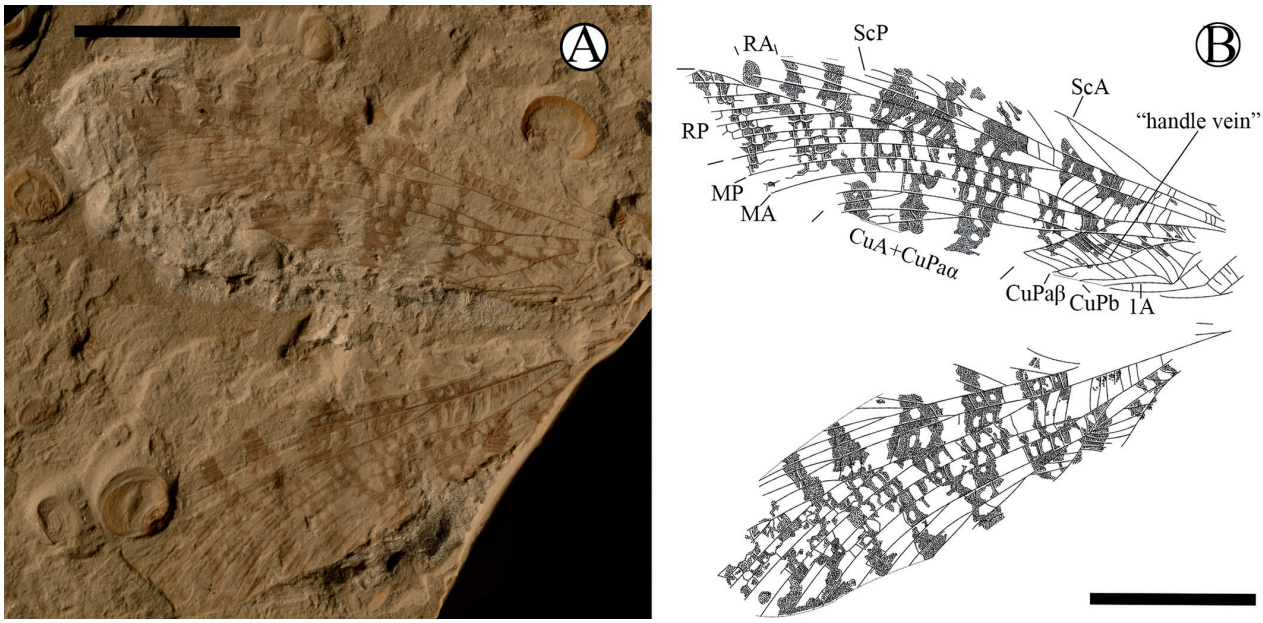

Figure 2 *Sigmaboilus peregrinus* Gu, Zhao & Ren, 2009, male forewing, NIGP161448: (A) Photograph; (B) interpretation. Scale bar = 10 mm.

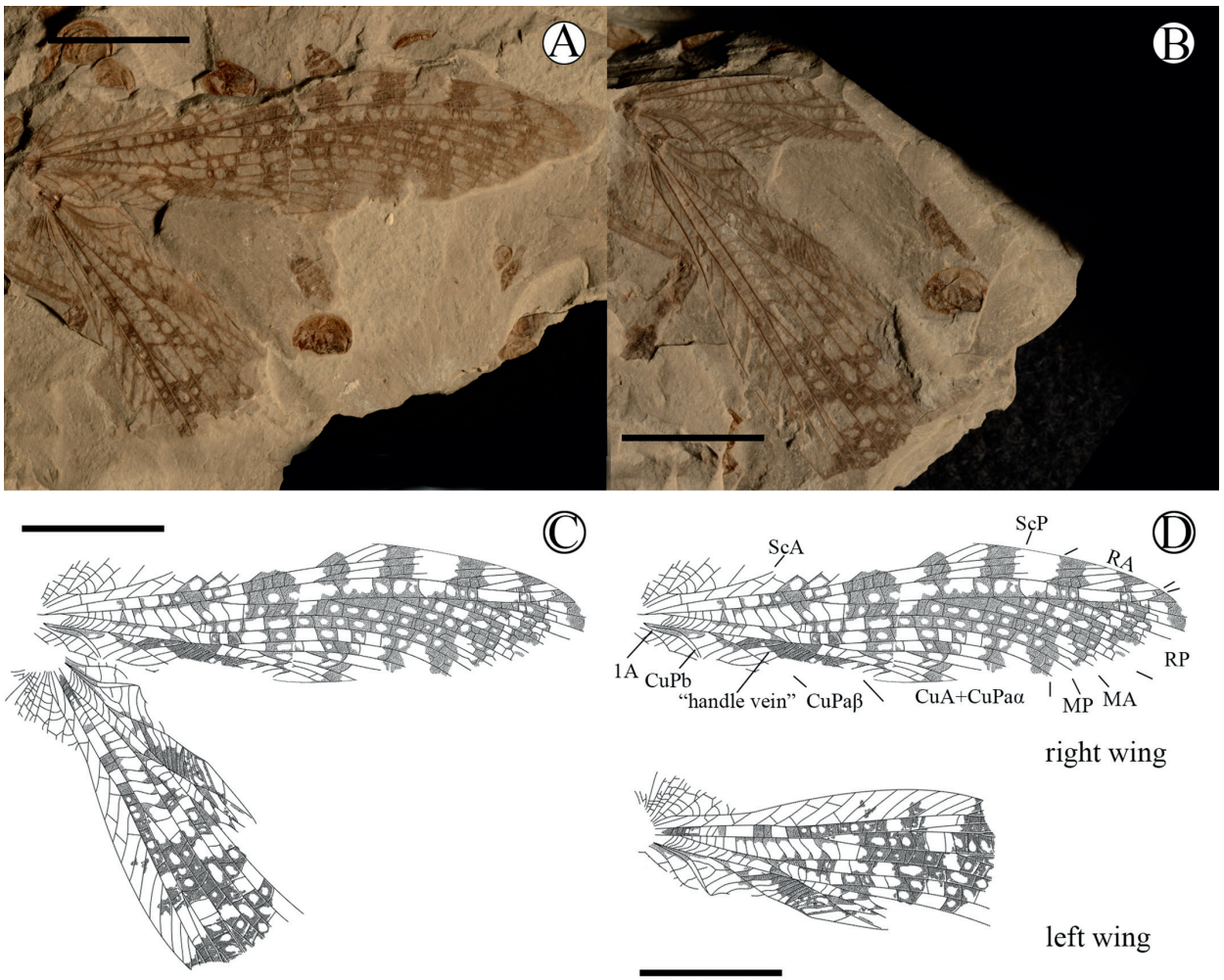

Figure 3 *Sigmaboilus peregrinus* Gu, Zhao & Ren, 2009, male forewing: (A) NIGP161449a, part; (B) NIGP161449b, counterpart; (C, D) interpretation based on part and counterpart of specimen NIGP161449. Scale bar = 10 mm.

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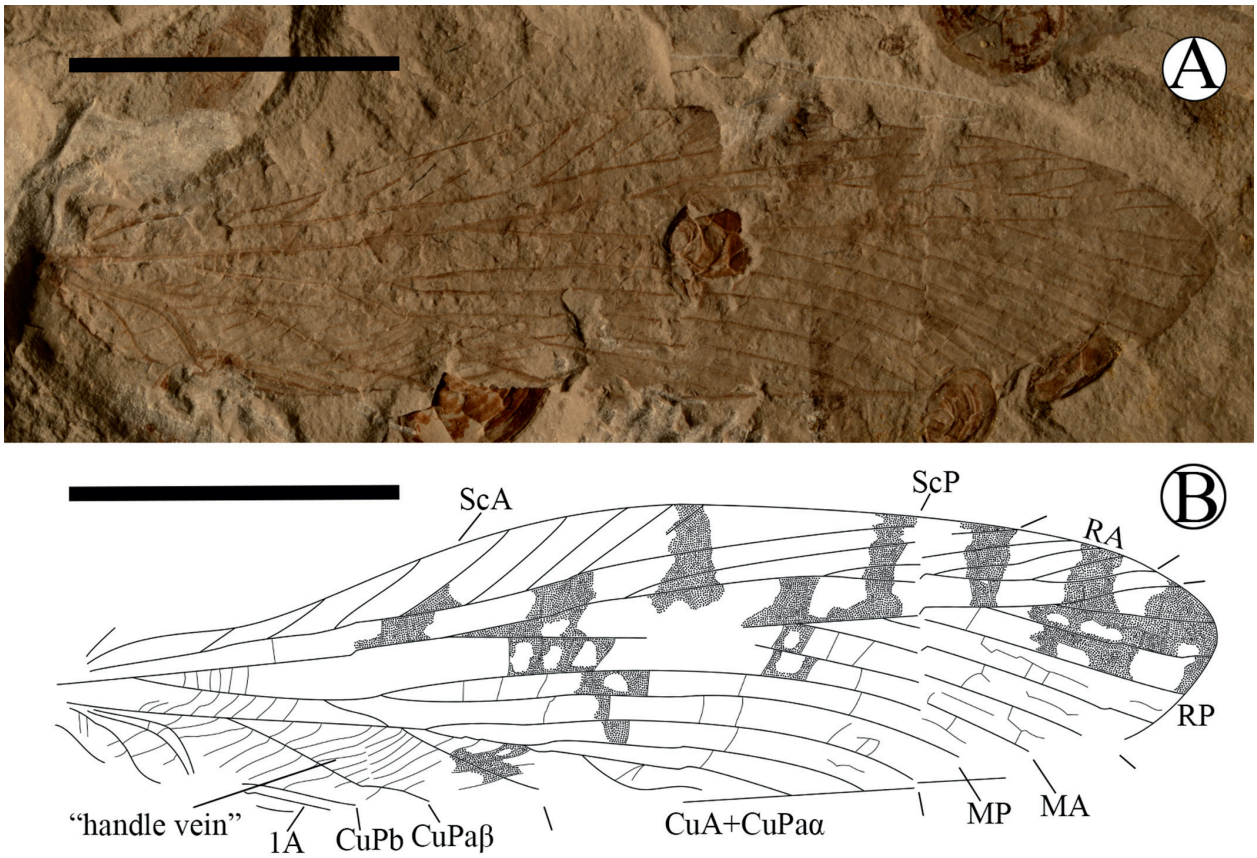

Figure 4 *Sigmaboilus peregrinus* Gu, Zhao & Ren, 2009, male forewing, NIGP161450: (A) Photograph; (B) interpretation. Scale bar = 10 mm.

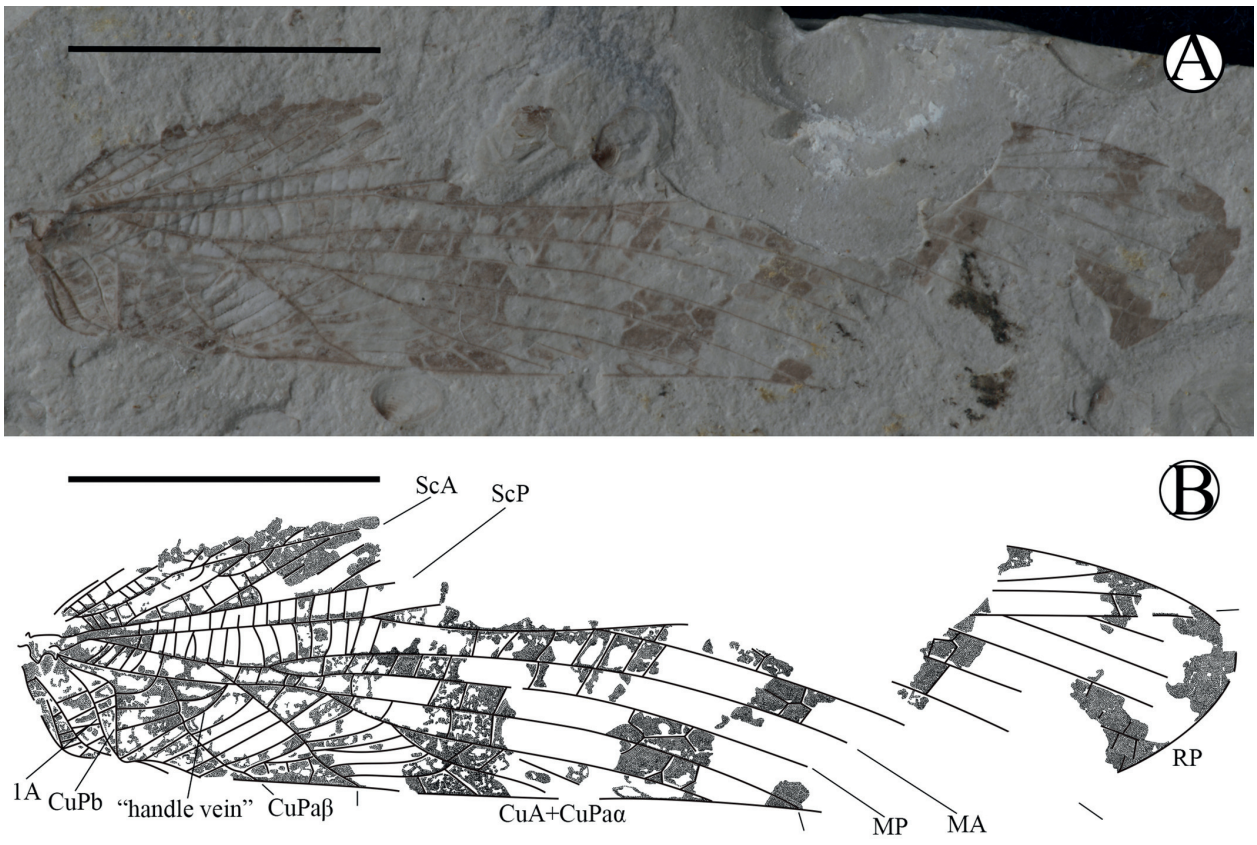

Figure 5 *Sigmaboilus* calophlebius sp. nov., male forewing, holotype, NIGP161447: (A) Photograph; (B) interpretation. Scale bar = 10 mm.

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branches of RA and more branches of CuA + CuPaα; NIGP161449 in having more branches of RP and CuA + CuPaα dividing into two branches, with the anterior one subdividing into three branches and the posterior into two; and NIGP161450 in having fewer branches of RA and RP.

Sigmaboilus calophlebius Wang, Fang & Zhang, sp. nov. (Fig. 5)

Holotype. NIGP161447, incomplete male left forewing with anterior–medial and posterior–apical parts missing.

Etymology. Specific name derived from Latin in reference to the special and beautiful stridulatory vein.

Type horizon and locality. Uppermost Middle–lowermost Upper Jurassic; Daohugou Village, Ningcheng County, Chifeng City, Inner Mongolia, China.

Diagnosis. Based on male forewing. Wing narrow and long; ScA slightly sigmoidal, CuA short, connected to CuPaβ, and forked immediately beyond, with five terminal branches; "handle vein" slightly curved; cross-vein fused with "handle vein" at base of CuA + CuPaα; "oblique veins" (cross-veins between CuPaβ and CuPb) straight or gently curved and regularly arranged; CuPb strongly curved, with middle section perpendicular to posterior wing margin; 1A much less bent than CuPb.

Description. Incomplete male forewing (Fig. 5). Preserved length 39.5 mm, width 9.5 mm as estimated; ratio of length to maximal width 4.2:1. Precostal area incomplete; ScA with only basal section preserved just before R fork (into RA and RP) and slightly sigmoidal; ScP straight, with distal part missing and reaching anterior margin at three quarters of wing length from base (estimated), four branches preserved, with cross-veins between them reticulated. Area between ScP and R very narrow, and cross-veins in this area almost straight. R slightly oblique anteriorly; RA and RP diverging at about one quarter of wing length from base, with RP pectinately seven-branched, and only two branches of RA preserved; cross-veins between branches of RP reticulated. M + CuA diverging at about one sixth of wing length; stem M short, 2 mm long, forking into MA and MP at 8 mm distal of wing base; both MA and MP very long, simple and slightly arched; area between R and MA broad, cross-veins between M + CuA and R, RP and MA, MA and MP almost straight and simple and regularly spaced. Stem CuA shorter (about 1.0 mm) than stem M and fused with CuPaα at 8.5 mm distal of wing base; stem CuA nearly straight; CuPaα diverging from CuPa at 5.0 mm distal of forewing base; CuA connected to CuPaα at 2.0 mm distal of origin of CuPaβ and dividing immediately beyond, with five terminal branches. Stridulatory vein strong; cross-veins between M + CuA and CuPa, "oblique veins" (cross-veins between CuPaβ and CuPb) and "handle vein" slightly curved; cross-vein fused with "handle vein" at base of CuA + CuPaα; cross-veins between last branch of CuA + CuPaα and CuPaβ slightly curved. CuPb strongly curved and Z-shaped; 1A slightly sigmoidal. Area between 1A and 2A slightly broader than between CuPb and 1A. Pigmentation present on most of forewing.

Remarks. The new species is confidently referable to *Sigmaboilus*, based on the following features: forewing narrow and long, ratio of length to maximal width about 4; ScA sigmoidal; CuPb slightly Z-shaped, touching 1A at one point close to hind margin. It differs from all congeners by the following forewing features: the stridulatory vein is strongly curved and perpendicular to the posterior margin; CuPb ends on the posterior margin much closer to the wing base; the cross-vein between the "handle vein" and CuPaα is fused with the former at the base of CuA + CuPaα; and the anal area is nearly square in shape.

3. Discussion

The phenomenon of sexual dimorphism is common in forewings of the Jurassic Hagloidea (in which most males have an acoustic mating system) and the Middle Jurassic is an important period for the evolution of the stridulatory apparatus in Hagloidea (Fang *et al*. 2010). The stridulatory apparatus (part of CuPb) and the area between the "handle vein" and CuPaα are of great significance in evolution in association with sound production. Two opposite trends, improvement and reduction, were considered by Gorochov (2003) to be present in the evolution of the stridulatory apparatus of Hagloidea. One of the most common ways of improving the stridulatory apparatus is a widening of the stridulatory area in the middle of the tegmina (up to occupying most of the tegmina), and one of way of reduction is decreasing the stridulatory area in the middle part of the tegmina, whilst increasing the proximal part (Gorochov 2003).

The genus *Sigmaboilus* is considered transitional between the improvement and reduction models and is probably closer to the latter because of the inconspicuous "handle vein". It is difficult to identify females of this genus (which is only based on forewings), due to their lack of stridulatory apparatus. It is reasonable to suppose that the differentiation of the stridulatory apparatus in Prophalangopsidae originated in the late Middle Jurassic, or even earlier. Intraspecific variation in the forewing venation is a universal feature of prophalangopsids (Gu *et al*. 2009). So it is questionable, at least sometimes, to use the number of branches of RA, RS and CuA + CuPaα as diagnostic characters, especially in species of *Sigmaboilus*. Here, a new key to the species of this genus is proposed, based on male tegmina, especially their stridulatory apparatus and its related veins (or cross-veins); the genus shows a nearly uniform "handle vein".

Although specimens NIGP161448–161450 (Figs 2–4) are assigned to *S. peregrinus* and NIGP161451 (Fig. 1) to *S. gorochovi*, there are some differences between these specimens and the holotypes that are considered as intraspecific variations herein. Furthermore, some differences are recognised between the left and right forewings in the same individual, as shown in specimen NIGP161448 (differences in the position of RP branches, the position of the MA + MP fork and the cross-veins between CuA and M) and specimen NIGP161449 (differences in the cross-veins between CuA and M, and between CuPb and CuPaβ, and the length of CuA). These all add to our understanding of natural variation in these extinct prophalangopsids.

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