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# A new cnemidolestodean stem-orthopteran insect from the Late Carboniferous of China

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Gu, J.-J., Béthoux, O., and Ren, D. 2014. A new cnemidolestodean stem-orthopteran insect from the Late Carboniferous of China. *Acta Palaeontologica Polonica* 59 (3): 689–696.

A new Late Carboniferous cnemidolestodean insect *Xixia huban* gen. et sp. nov., is described from the Xiaheyan locality (Zhongwei City, Ningxia, China; Tupo Formation). Its combination of character states and observed variants on the wing venations are indicative of homologies shared with more derived members of the order. In particular it is ascertained that MP runs fused with CuA and CuA + CuPa, but is not usually visible as a distinct vein. The new genus exhibits previously unknown coloration pattern composed of dark patches distributed over the whole forewing (as opposed to regular stripes or rows of spots, previously documented in the group). The comparatively abundant sample makes it one of the best documented cnemidolestodeans to date.

Key words: Insecta, Archaeorthoptera, Cnemidolestodea, *Aetophlebia singularis*, Pennsylvanian, Xiaheyan locality, Ningxia, China.

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## Introduction

Grasshoppers, crickets, and katydids compose the diverse order Orthoptera. Recent revisions have demonstrated that the group had numerous stem-representatives in Late Carboniferous faunas (e.g., Béthoux and Nel 2005a, b). Together with crown-Orthoptera, they compose the super-ordinal taxon Archaeorthoptera. Some of these Archaeorthoptera were placed by Béthoux (2005) in the order Cnemidolestodea Handlirsch, 1937. A list of genera assigned to this order was proposed in the latter publication and was complemented by Béthoux (2007a). Cnemidolestodeans are known from several Late Carboniferous localities, such as Mazon Creek (IL, USA), Commentry (France), and Radstock (UK). The genus *Tococladus* Carpenter, 1966, reported from various Permian localities (Carpenter 1966; Novokshonov 1999; Béthoux et al. 2003), is considered to be the only representative of the group after the Late Carboniferous. The vast majority of the corresponding species are documented based on a single specimen (with the noticeable exception of *Narkemina angustiformis* Sharov, 1961; Aristov 2012), and the diagnostic characters of the order are based on forewing venation.

The diverse fauna of the Late Carboniferous Xiaheyan locality (Ningxia Province, China) is currently being studied based on abundant samples. Among stem-Orthoptera, in addition to the archaeorthopteran *Sinopteron huangheense* Prokop and Ren, 2007, *Chenxiella liuae* Liu, Ren, and Prokop, 2009, and *Heterologus duyiwuer* Béthoux, Gu, and Ren, 2012, material of several Cnemidolestodea species was collected (Prokop and Ren 2007; Liu et al. 2009; Béthoux et al. 2012). Besides *Longzhua loculata* Gu, Béthoux, and Ren, 2011, which is a putative "basal" member of the order, a new and easily identifiable species was sampled (Gu et al. 2011). Documentation of its intra-specific variability has shed new light on the evolution of derived wing morphologies observed in Cnemidolestodea.

*Institutional abbreviations.*—CNU, Key Lab of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.

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*Other abbreviations.*—ScP, posterior Subcosta; R, Radius; RA, anterior Radius; RP, posterior Radius; M, Media; CuA, anterior Cubitus; CuP, posterior Cubitus; CuPa, anterior branch of CuP; CuPb, posterior branch of CuP; AA, anterior Analis; AA1, first anterior Analis; AA2, second anterior Analis; LFW, left forewing; LHW, left hind wing; RFW, right forewing; RHW, right hind wing.

# Material and methods

Specimens were examined using a Leica DCF 500 dissecting microscope and illustrated with the aid of a drawing tube. Photographs were taken using a Canon EOS 450D digital camera coupled to a Canon 50 mm macro lens (and an extension tube as appropriate), or a Canon MP-E 65 mm macro lens (all lenses equipped with polarizing filters). Photographs reproduced on Figs 1 and 2 are a combination of photographs of a specimen both dry and immersed in ethanol. The photograph indicated as light-mirrored is the product of an optical effect aiming to present a positive view of a negative imprint (for details see Béthoux and Briggs 2008; Béthoux et al. 2004).

In several cases the exact number of branches of a given vein is difficult to estimate because forks occurring near the wing margin give rise to veinlets that could simplybe cross-veins. In addition to this distinctions between veins, veinlets, and cross-veins might be artificial to some extent (Béthoux and Schneider 2010), or assignment of a distal vein to a vein sector can often be ambiguous. In specimen descriptions we provide a range for such cases (e.g., RP pectinate with 7–8 branches in the specimen CNU-NX1-392).

The wing venation nomenclature used in this paper is based on conjectures of topological homology proposed by Béthoux and Nel (2002) for Archaeorthoptera, itself based on that proposed for Orthoptera (Béthoux and Nel 2001). These conjectures were challenged by Gorochov (2005) in favor of those followed by Sharov (1968, 1971; and some earlier authors), but these comments were addressed by Béthoux (2007a). Subsequent comments by Rasnitsyn (2007), supporting the alternative conjectures proposed by Gorochov and Rasnitsyn in Gorochov and Rasnitsyn (2002), have been discussed by Béthoux (2008). In agreement between the authors, the traditional nomenclatural procedure is followed herein. This does not imply support for this approach on the part of OB.

# Systematic palaeontology

Superorder Archaeorthoptera Béthoux and Nel, 2002

Order Cnemidolestodea Handlirsch, 1937

Family incertae sedis

Genus *Xixia* nov.

*Etymology:* From the Chinese *Xixia*, referring to an ancient name of the area, where the material was collected.

*Type species*: *Xixia huban* sp. nov.; designated herein, see below; monotypic.

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

*Remarks.*—Assignment of the new genus to the taxon Archaeorthoptera is straightforward, as it exhibits a basic diagnostic character of this taxon, namely the fusion of CuA (diverging from M + CuA) with the anterior branch of CuP (Béthoux and Nel 2002, Béthoux 2007b). The new genus exhibits typical characters of the order Cnemidolestodea, such as ScP reaching RA, and MP diverging obliquely from M and reaching the stem of CuA + CuPa (Béthoux 2005). The connection of anterior veinlet(s) from (MP +) CuA + CuPa with the posterior branch of MA is also a distinctive cnemidolestodean feature.

For comparison with the new material, data on most representatives of the order Cnemidolestodea are available and referenced in Béthoux and Nel (2005a), Béthoux (2005), Gu et al. (2011), and Aristov (2012). *Xixia* differs from *Cnemidolestes* Handlirsch 1906, *Ischnoneura* Brongniart, 1893, and *Protodiamphipnoa* Brongniart, 1885 by its distinct fusion of the most anterior veinlet from MP + CuA + CuPa with the posterior branch of MA. It also differs from *Bouleites* Lameere, 1917, *Protodiamphipnoa*, *Cnemidolestes*, *Ischnoneura*, *Amphiboliacridites* Langiaux and Parriat, 1974, and *Paranarkemina* Pinto, 1990 (and closely related species from the Parana basin assigned to various genera, the validity of many of which might be dubious; Béthoux 2007b), by its comparatively distal origin of RP. Among taxa sharing this derived condition, the type species of *Xixia* differs from most of them (such as *Narkemina* Martynov, 1930; see Sharov [1961], Storozhenko [1998], Aristov [2012]) by its low number of MP + CuA + CuPa branches. This trait is shared with *Narkeminopsis* species (see Béthoux and Nel [2005a], Brauckmann and Herd [2006]). However, the branching pattern of MP + CuA + CuPa, viz. not clearly internally pectinate, is unique to *Xixia*. Notice that this trait is shared with *Longzhua* Gu, Béthoux, and Ren, 2011, but this taxon has a much more basal origin of RP.

There is a wide variety of forewing coloration patterns within Cnemidolestodea. For example, forewings of *Cnemidolestes woodwardi* (Brongniart, 1893) and *Narkeminopsis eddi* Whalley, 1979, among others, are covered by parallel and transverse dark stripes. *Protodiamphipnoa gaudryi* Brongniart, 1885 has dark forewings with an "eye-spot" color pattern near wing mid-length in addition to small spots in basal part. *Ischnoneura oustaleti* (Brongniart, 1885) and *Amphiboliacridites joanesi* Langiaux and Parriat, 1974 have several dark and round spots in forewings. The new genus exhibits a coloration pattern previously unknown, composed of dark patches distributed over the whole forewing, without regular stripes or rows of spots.

The distinctive combination of characters exhibited by the type species of *Xixia*, and the unique coloration pattern, justify the erection of a new genus.

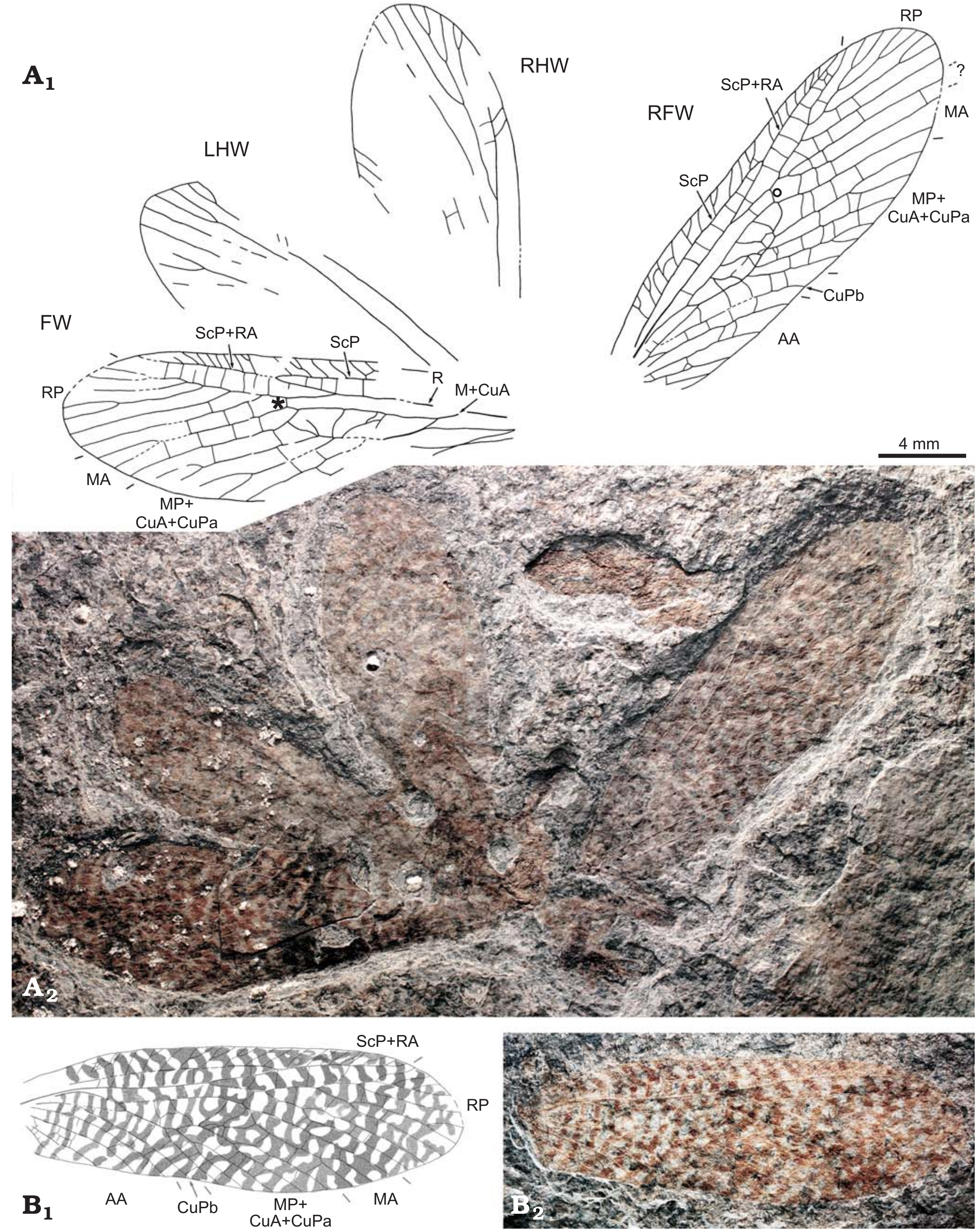

Fig. 1. Late Carboniferous cnemidolestodean insect *Xixia huban* gen. et sp. nov. from Xiaheyan, China. **A**. Holotype specimen CNU-NX1-381; drawing ($A_1$), asterisk indicates a cross-vein, open circle—the anterior branch of MA fusing with RP; photograph ($A_2$), LFW, RFW, and LHW as positive imprints, RHW as negative imprint. **B**. Specimen CNU-NX1-380; drawing ($B_1$); photograph ($B_2$), left forewing, positive imprint, flipped horizontally.

### *Xixia huban* sp. nov.

Figs. 1, 2.

*Etymology*: From Chinese *huban*, tiger's stripes; referring to the forewing coloration of the species.

*Holotype*: CNU-NX1-381 (Fig. 1A), well preserved individual, with almost complete wing pairs and undistinguishable thoracic remains.

*Type locality*: Near Xiaheyan Village, Zhongwei City, Ningxia Hui Autonomous Region, China.

*Type horizon*: Namurian, Late Carboniferous; Tupo Formation (Lu et al. 2002).

*Material*.—Holotype and 11 additional specimens: CNU-NX1-380 (Fig. 1B), -382 (Fig. 2A), -383 (Fig. 2B), -384 (Fig. 2C), -385, -387 (Fig. 2D), -388 to -391, and -392 (Fig. 2E).

*Diagnosis*.—Forewing: distal origin of RP (closer to wing mid-length than to wing base); MP + CuA + CuPa with few branches (usually 6, ranging from 5 to 8–9); anterior veinlet(s) from MP + CuA + CuPa fused with posterior branch of MA; dark patchy coloration.

*Description*.—*Forewing*: length 17.9–21.8 mm, best width (opposite second third of wing length) 5.9–7.0 mm; ScP reaching RA, with anterior oblique veinlets; RA and RP diverging near wing mid-length; ScP + RA simple, with strong anterior veinlets; first fork of RP nearly opposite to the fusion of ScP with RA; RP usually with 7 to 8 branches reaching apex, exceptionally 6 or more than 8, rarely with a single veinlet reaching ScP + RA; RP without consistent branching pattern; basal stem of M + CuA close to R for some distance, then directed towards posterior wing margin; M + CuA usually separating into MA and MP + CuA; first fork of MA distal to the origin of RP but basal to the fusion of ScP with RA; MA usually with 3 branches, rarely 2 (?); most anterior branch of MA close to RP but distinct from it (at least in 2 of the observed forewings), shortly connected to it (at least in 1 of the observed forewings), or fused with it for some distance (at least in 2 of the observed forewings); free portion of MP + CuA short; area between MA and anterior branch of MP + CuA + CuPa broad, with long and curved cross-veins, rarely with a distinct portion of MP (diverging from MP + CuA + CuPa; if so, it re-fuses with CuA + CuPa); MP + CuA + CuPa with a main anterior stem from which diverge posterior branches, commonly with 5–7 terminal branches, usually 6, occasionally more than 7, in addition to the most anterior veinlet(s), usually fused with posterior branch of MA, rarely fused at the branching point of MA; CuPb weak, strongly concave and simple; AA1 strongly convex, simple, rarely fused with another AA branch; cross-veins reticulated only in broad areas, otherwise distinct and simple.

*Holotype specimen CNU-NX1-381* (Fig. 1A): well preserved individual, almost complete wing pairs and undistinguishable thoracic remains, positive imprint (with right hind wing in ventral view); right forewing: length 21.0 mm, broadest width 6.6 mm; RP without consistent branching pattern, with 7 (8?) branches reaching wing apex; most anterior branch of MA fused with RP for 0.6 mm, forked close to its divergence from RP; MA with a total of 3 (2?) terminal branches; no evident portion of free MP; MP + CuA + CuPa with 6 terminal branches; left forewing: basal part missing, preserved length ~21 mm; RP posteriorly pectinate, with 7 branches reaching wing apex; MA with 3 branches reaching posterior margin, without fusion with RP (see discussion); CuA + CuPa with 6 terminal branches preserved; hind wings: RP originating near or distal to wing mid-length; right hind wing: preserved wing length 13.8 mm; RP with 6 preserved branches; left hind wing: preserved wing length 15.7 mm; RP probably with 5 or 6 preserved branches.

*Specimen CNU-NX1-380* (Fig. 1B): well preserved, complete, isolated left forewing, positive and negative imprints; length 20.1 mm, broadest width 6.4 mm; RP without consistent branching pattern, with 10 branches reaching wing apex; MA with 3 terminal branches; no evident portion of free MP; MP + CuA + CuPa with 5 terminal branches, with two anterior veinlets (stronger than cross-veins) fused with the posterior branch of MA.

*Specimen CNU-NX1-382* (Fig. 2A): well preserved and almost complete; isolated right forewing, positive and negative imprints; length about 22 mm, broadest width 6.5 mm; RP with at least 7 branches (assuming that MA has 2 terminal branches); most anterior branch of MA briefly connected to RP; occurrence of strong "veinlet" between MA and CuA + CuPa, possibly being MP reaching CuA + CuPa; CuA + CuPa with 6 terminal branches, with a strong and straight veinlet fused with MA at the point of branching of MA.

*Specimen CNU-NX1-383* (Fig. 2B): well preserved isolated left forewing, apex missing, positive and negative imprints; estimated length about 20 mm, broadest width 6.5 mm; RP without consistent branching pattern, with 5 preserved branches, and an anterior veinlet reaching Sc + RA; MA with 3 terminal branches, most anterior branch briefly connected to RP, then forked; no evident portion of free MP; CuA + CuPa with 4–5 terminal branches; AA1 and AA2 connected by a strong veinlet/fused.

*Specimen CNU-NX1-384* (Fig. 2C): well preserved, complete, isolated left forewing, positive imprint; length 20.3 mm, broadest width 6.6 mm; RP without consistent branching pattern, with 7 (8?) branches reaching wing apex, and a veinlet reaching RA (assuming a 3-branched MA); most anterior branch of MA fused with RP for 1.3 mm; distinct portion of MP visible in the area between MA and (MP +) CuA + CuPa, diverging from MP + CuA + CuA and re-uniting with it further; CuA + CuPa with 6–7 terminal branches.

*Specimen CNU-NX1-387* (Fig. 2D): well preserved, complete, isolated right forewing, negative imprint; length 17.9 mm, broadest width 5.9 mm; RP without consistent branching pattern, with 8 (9?) branches reaching wing apex (assuming a 3/4-branched MA); most anterior branch of MA fused with RP for 1.1 mm; no evident distinct portion of MP; CuA + CuPa with 9 terminal branches.

*Specimen CNU-NX1-392* (Fig. 2E): well preserved, complete, isolated left forewing, positive imprint; length 21.3 mm, broadest width 7.0 mm; RP without consistent branch-

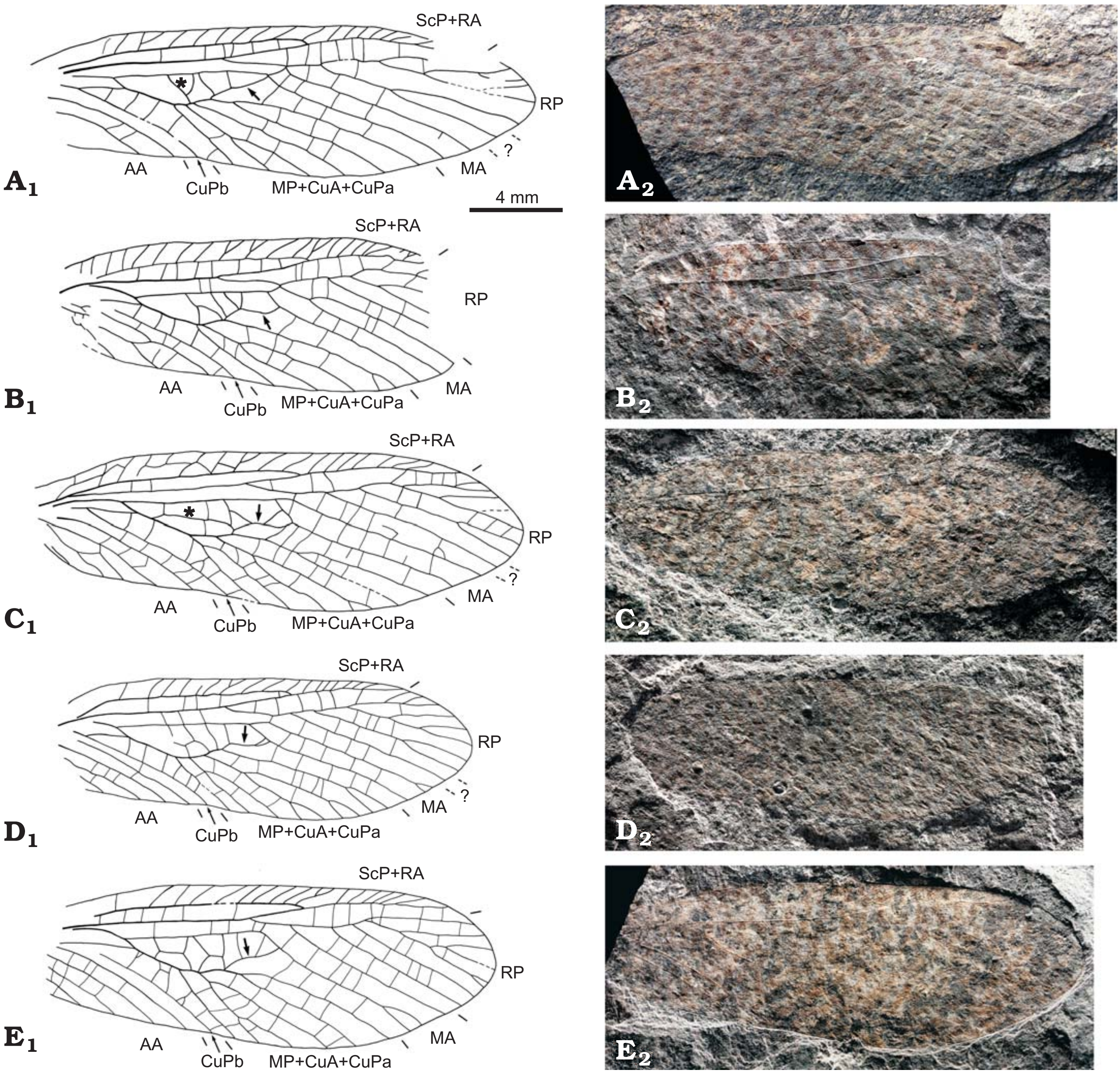

Fig. 2. Late Carboniferous cnemidolestodean insect *Xixia huban* gen. et sp. nov. from Xiaheyan, China; coloration omitted in all drawings; arrows indicate the anterior veinlet from MP + CuA + CuPa fusing with the posterior branch of MA; all figures at the same scale. **A**. Specimen CNU-NX1-382, drawing (A$_1$), asterisk indicates a putative free portion of MP, and photograph (A$_2$), right forewing, positive imprint. **B**. Specimen CNU-NX1-383, drawing (B$_1$) and photograph (B$_2$), left forewing, positive imprint, flipped horizontally. **C**. Specimen CNU-NX1-384, drawing (C$_1$), asterisk indicates a putative portion of MP, and photograph (C$_2$), left forewing, positive imprint, flipped horizontally. **D**. Specimen CNU-NX1-387, drawing (D$_1$) and photograph (D$_2$), right forewing, negative imprint, light-mirrored, flipped horizontally. **E**. Specimen CNU-NX1-392, drawing (E$_1$) and photograph (E$_2$), left forewing, positive imprint, flipped horizontally.

ing pattern, with 7–8 branches reaching wing apex (assuming a 3-branched MA); most anterior branch of MA fused with RP for 1.1 mm; no evident distinct portion of MP; CuA + CuPa with 6 terminal branches reaching posterior margin.

*Remarks*.—In several cases, distinguishing actual fusion of the anterior branch of MA with RP from a mere connection of MA and RP by a short cross-vein is not evidently possible. This is exemplified by the holotype specimen (Fig. 1A). Based on the observation that MA is 3-branched in the specimen with obvious lack of fusion (Fig. 1B), and provided that the 3 distal branches that can be assigned to MA have no connection with RP in the left forewing of the holotype,

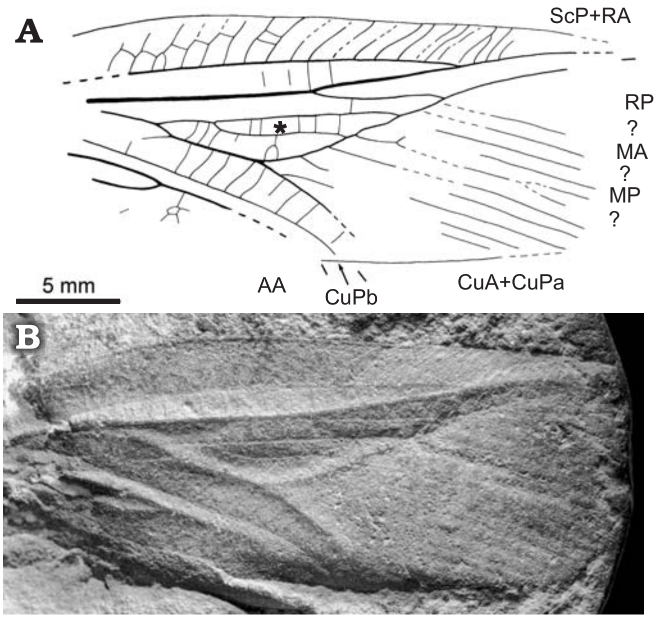

Fig. 3. Late Carboniferous cnemidolestodean insect *Aetophlebia singularis* Scudder, 1885 from Mazon Creek, USA. Holotype specimen USNM 038147, drawing (**A**), asterisk indicates MP; and photograph (**B**), left forewing, positive imprint, flipped horizontally.

we assume that no fusion occurs in this wing (therefore the asterisk on Fig. 1A indicates a cross-vein). In contrast, in the right forewing, only one distal branch attributable to MA has an origin distinct from RP. However, if a fusion is assumed (via the element indicated by the open circle on Fig. 1A), 1 or 2 additional branches can be attributed to MA, which is more consistent with the condition observed in the left forewing. It must be emphasized that the number of MA branches might vary between 2 and 3, rendering several isolated forewings difficult to interpret. A similar range of variation is documented in *Narkemina angustiformis* (see Aristov 2012).

Apart from this variation, which is definitely of intra-specific significance, the specimens we assign to the new species exhibit limited differences. Variation in size is negligible, compared with that observed in extant relatives (e.g., Ciplak et al. 2008; Picaud and Petit 2008; Adis et al. 2008). Variation in aspect ratio can be explained by plastic deformation, known to have affected the material from the Xiaheyan locality (Cui et al. 2011; Gu et al. 2011; Guo et al. 2013). Such deformation also amplified size differences. Other variations are minimal with respect to those documented in *Longzhua loculata*, a related species (see original description). Therefore we found no ground to presume that several species compose the set of selected specimens. The coloration pattern observed in forewings of *Xixia huban* allows the species to be easily distinguished from any other related species, and from all species occurring in the same locality.

*Stratigraphic and geographic range*.—Type locality and horizon only.

# Discussion

Various aspects of the wing venation of *X. huban* are worth being discussed. Observations made in *Protodiamphipnoa gaudryi* (see Béthoux and Nel 2005a), *Longzhua loculata* (see Gu et al. 2011), and *Aetophlebia singularis* Scudder, 1885 (Fig. 3), among others, have shown that MP fuses with CuA + CuPa in Cnemidolestodea species. In the above-mentioned species MP occurs as a distinct vein, diverging from M (itself diverging from M + CuA). In turn it has been assumed that, in more derived Cnemidolestodea species, MP diverges from M + CuA at the point of divergence of CuA (Béthoux 2005). In other words M + CuA separates into MA and MP + CuA (instead of into M and CuA), and MP no longer occurs as a distinct vein.

In *X. huban*, the specimen CNU-NX1-384 was observed to have a vein diverging from (MP +) CuA + CuPa, and then re-uniting with it (asterisk on Fig. 2C). This vein is likely MP. In the specimen CNU-NX1-382 (Fig. 2A) the first visible "cross-vein" in the area between MA and CuA + CuPa is comparatively strong and might belong to MP. In other specimens of *X. huban* no evidence on the location of MP was found. These observations indicate that MP is usually completely fused with CuA and CuA + CuPa, corroborating previous assumptions.

The species *X. huban* exhibits a more or less distinct connection of the anterior veinlet(s) of MP + CuA + CuPa with the posterior branch of MA (arrows on Fig. 2). This connection occurs in many cnemidolestodean insects. A "predating" condition was documented in a rare variant of *L. loculata*, a species putatively considered a basal relative of other Cnemidolestodea. In this species most specimens have the most anterior branch of (MP +) CuA + CuPa directed towards the anterior wing margin, but lack the fusion with MA. However, one specimen exhibits an actual fusion of the most anterior branch of (MP +) CuA + CuPa with the posterior branch of MA (Gu et al. 2011: fig. 5.3). Provided the assumed course of MP in *X. huban*, it is not unlikely that the "connection" is actually composed of MP. However, we found no decisive evidence for such interpretation: it could equally be a composed of (a set of) strong cross-vein(s). Therefore we propose to refer to the element indicated by arrows on Fig. 2 as "MP + CuA + CuPa veinlet(s)".

# Conclusion

Based on the comparatively abundant sample at hand, composed of 12 well identified specimens, data on the wing venation variability of derived members of the order Cnemidolestodea is significantly augmented. In particular variants departing from the average morphology were used to ascertain earlier conjectures of primary homologies. This information, combined with similar data on *Longzhua loculata*, means that our knowledge of the forewing venation "transformation series" of Cnemidolestodea is becoming more complete and accurate. It is anticipated that data on other related species occurring at the Xiaheyan locality and remaining to be described (research in progress) will allow the systematics of the Cnemidolestodea to be refined in the near future. In turn the composition and evolution of Late Carboniferous insect faunas will be better appreciated. This paper and others tend to indicate that Archaeorthoptera composed a highly diverse group at the time (possibly even dominant), in contrast to younger faunas.

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## References

Adis, J., Sperber, C.F., Brede, E.G., Capello, S., Franceschini, M.C., Hill, M., Lhano, M.G., Marques, M.M., Nunes, A.L., and Polar, P. 2008. Morphometric differences in the grasshopper *Cornops aquaticum* (Bruner, 1906) from South America and South Africa. *Journal of Orthoptera Research* 17: 141–147.

Aristov, D.S. 2012. Members of the genus *Narkemina* Martynov (Insecta: Eoblattida: Cnemidolestidae) from the Carboniferous of Siberia *In*: A.Y. Rozanov, A.V. Lopatin, and P.Y. Parkhaev (eds.), *Modern Paleontology: Classical and New Methods*, 37–48. Eighth All-Russian School, Moscow.

Béthoux, O. 2005. Cnemidolestodea (Insecta): an ancient order reinstated. *Journal of Systematic Palaeontology* 3: 403–408.

Béthoux, O. 2007a. Archaeorthoptera wing venation nomenclature: a reply to Gorokhov. *Paleontological Journal* 41: 338–340.

Béthoux, O. 2007b. Cladotypic taxonomy applied: titanopterans are orthopterans. *Arthropod Systematics & Phylogeny* 65: 135–156.

Béthoux, O. 2007c. Ordinal assignment of the genus *Tococladus* Carpenter, 1996 (Insecta: Archaeorthoptera). *Alavesia* 1: 3.

Béthoux, O. 2008. Groundplan, nomenclature, homology, phylogeny, and the question of the insect wing venation pattern. *Alavesia* 2: 219–232.

Béthoux, O. and Briggs, D.E.G. 2008. How *Gerarus* lost its head: stem-group Orthoptera and Paraneoptera revisited. *Systematic Entomology* 33: 529–547.

Béthoux, O. and Nel, A. 2001. Venation pattern of Orthoptera. *Journal of Orthoptera Research* 10: 195–198.

Béthoux, O. and Nel, A. 2002. Venation pattern and revision of Orthoptera sensu nov. and sister groups. Phylogeny of Palaeozoic and Mesozoic Orthoptera sensu nov. *Zootaxa* 96: 1–88.

Béthoux, O. and Nel, A. 2005a. Some Palaeozoic "Protorthoptera" are "ancestral" orthopteroids: major wing braces as clues to a new split among the "Protorthoptera". *Journal of Systematic Palaeontology* 2: 285–309.

Béthoux, O. and Nel, A. 2005b. Some Palaeozoic "Protorthoptera" are "ancestral" orthopteroids: major wing braces as clues to a new split among the "Protorthoptera", corrigendium. *Journal of Systematic Palaeontology* 3: 223.

Béthoux, O. and Schneider, J.W. 2010. Description of a hind wing of a new basal Archaeorthoptera (Mazon Creek, IL; Pennsylvanian). *Alavesia* 3: 81–85.

Béthoux, O., Gu, J.-J., and Ren, D. 2012. A new Upper Carboniferous stem-orthopteran (Insecta) from Ningxia (China). *Insect Science* 19: 153–158.

Béthoux, O., Nel, A., and Lapeyrie, J. 2004. The extinct order Caloneurodea (Insecta, Pterygota, Panorthoptera): wing venation, systematics, and phylogenetic relationships. *Annales Zoologici* 54: 289–318.

Béthoux, O., Nel, A., Galtier, J., Lapeyrie, J., and Gand, G. 2003. A new species of Tococladidae Carpenter, 1966 from the Permian of France (Insecta: Archaeorthoptera). *Geobios* 36: 275–283.

Brauckmann, C. and Herd, K.J. 2006. Insekten-Funde aus dem Westfalium D (Ober-Karbon) des Piesberges bei Osnabrück (Deutschland). Teil 2: Neoptera. *Osnabrücker naturwissenschaftliche Mitteilungen* 30/31 (for 2005): 19–65.

Brongniart, C. 1885. Les Insectes fossiles des terrains primaires. Coup d'oeil rapide sur la faune entomologique des terrains paléozoïques. *Bulletin de la Société des Amis des Sciences naturelles de Rouen* 1885: 50–68.

Brongniart, C. 1893. Recherches pour servir à l'histoire des insectes fossiles des temps primaires précédées d'une étude sur la nervation des ailes des insectes. *Bulletin de la Société d'Industrie Minérale de Saint-Etienne* 3 (7): 124–615.

Carpenter, F.M. 1966. The Lower Permian insects of Kansas. Part 11: The orders Protorthoptera and Orthoptera. *Psyche* 73: 46–88.

Ciplak, B., Sirin, D., Taylan, M.S., and Kaya, S. 2008. Altitudinal size clines, species richness and population density: case studies in Orthoptera. *Journal of Orthoptera Research* 17: 157–163.

Cui, Y., Béthoux, O., and Ren, D. 2011. Intraindividual variability in Sinonamuropteridae forewing venation (Grylloblattida; Late Carboniferous): taxonomic and nomenclatural implications. *Systematic Entomology* 36: 44–56.

Gorochov, A.V. 2005. Review of Triassic Orthoptera with descriptions of new and little known taxa. Part 1. *Paleontological Journal* 39: 178–186.

Gorochov, A.V. and Rasnitsyn, A.P. 2002. Superorder Gryllidea Laicharting, 1781 (= Orthopteroidea Handlirsch, 1903). *In*: A.P. Rasnitsyn and D.L.J. Quicke (eds.), *History of Insects*, 293–303. Kluwer Academic Publishers, Dordrecht.

Gu, J.-J., Béthoux, O., and Ren, D. 2011. *Longzhua loculata* n. gen. and n. sp., one of the most completely documented Pennsylvanian Archaeorthoptera (Insecta; Ningxia, China). *Journal of Paleontology* 85: 303–314.

Guo, Y., Béthoux, O., Gu, J.-J., and Ren, D. 2013. Wing venation homologies in Pennsylvanian "cockroachoids" (Insecta) clarified thanks to a remarkable specimen from the Pennsylvanian of Ningxia (China). *Journal of Systematic Palaeontology* 11: 41–46.

Handlirsch, A. 1906 (1908). *Die fossilen Insekten und die Phylogenie der rezenten Formen. Ein Handbuch für Paläontologen und Zoologen*. 1430 pp. Wilhelm Engelmann, Berlin.

Handlirsch, A. 1937. Neue Untersuchungen über die fossilen Insekten mit Ergänzungen und Nachträgen sowie Ausblicken auf phylogenetische, palaeogeographische und allgemein biologische Probleme. I Teil. *Annalen des Naturhistorischen Museums in Wien* 48: 1–140.

Lameere, A. 1917. Révision sommaire des insectes fossiles du Stéphanien de Commentry. *Bulletin du Museum National d'Histoire Naturelle, Paris* 23: 141–200.

Langiaux, J. and Parriat, H. 1974. Faune entomologique du bassin de Blanzy-Montceau. *"La Physiophile", Société d'Etude des Sciences Naturelles et Historique de Montceau-les-Mines* 81: 62–74.

Liu, Y., Ren, D., and Prokop, J. 2009. Discovery of a new Namurian archaeorthopterid from Ningxia, China (Insecta: Archaeorthoptera). *Zootaxa* 2032: 63–68.

Lu, L., Fang, X., Ji, S., and Pang, Q. 2002. A contribution to the knowledge of the Namurian in Ningxia. *Acta Geoscientia Sinica* 23: 165–168.

Martynov, A.V. 1930. Palaeozoic insects from the Kuznetsk basin [in Russian with English summary]. *Izvetiâ Glavnogo Geologorazvedočnogo Upravleniâ* 49: 1221–1248.

Novokshonov, V.G. 1999. New fossil insects (Insecta: Hypoperlida, Panorpida, ordinis incertis) from the Chekarda locality. *Paleontological Journal* 33: 54–57.

Picaud, F. and Petit, D.P. 2008. Body size, sexual dimorphism and ecological succession in grasshoppers. *Journal of Orthoptera Research* 17: 177–181.

Pinto, I.D. 1990. A new Upper Carboniferous paraplecopteran insect from South Brazil. *Pesquisas, Zoologia, Porto Alegre* 17: 7–10.

Prokop, J. and Ren, D. 2007. New significant fossil insects from the Upper Carboniferous of Ningxia in northern China (Insecta: Palaeodictyoptera, Archaeorthoptera). *European Journal of Entomology* 104: 267–275.

Rasnitsyn, A.P. 2007. On the discussion of the wing venation of (Archae) Orthoptera (Insecta). *Paleontological Journal* 41: 341–344.

Scudder, S.H. 1885. Palaeodictyoptera: on the affinities and classification of Paleozoic Hexapoda. *Memoirs of the Boston Society of Natural History* 3 (12): 319–351.

Sharov, A.G. [Šarov, A.G.] 1961. Order Paraplecoptera in Paleozoic insects from Kuznetsk basin [in Russian]. *Trudy Paleontologičeskogo Instituta, Akademiâ Nauk SSSR* 85: 164–224.

Sharov, A.G. [Šarov, A.G.] 1968. Phylogeny of orthopteroid insects [in Russian]. *Trudy Paleontologičeskogo Instituta, Akademiâ Nauk SSSR* 118: 1–216.

Sharov, A.G. 1971. *Phylogeny of the Orthopteroidea*. vi + 251 pp. Israel Program for Scientific Translations, Jerusalem.

Storozhenko, S.Y. [Storoženko, S.Y.] 1998. *Sistematika, filogeniâ i évoluciâ grilloblattidovyh nasekomyh (Insecta: Grylloblattida)*. 207 pp. Dal'nauka, Vladivostok.

Whalley, P.E.S. 1979. New species of Protorthoptera and Protodonata (Insecta) from the Upper Carboniferous of Britain, with a comment on the origin of wings. *Bulletin of the British Museum (Natural History), Geology* 32: 85–90.