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The smallest Palaeodictyoptera (Insecta) discovered at Xiaheyan (Late Carboniferous, China)

Le plus petit Palaeodictyoptera (Insecta) découvert à Xiaheyan (Carbonifère tardif, Chine)

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ABSTRACT

Fossil insects of the Late Carboniferous have been popularized as lost giants of the past. However, their small contemporaries are very poorly known. In this paper, we report the discovery of the smallest known member of the Palaeodictyoptera, an extinct group of sap-feeders including some of the largest insects ever known. The new representative, *Tytthospilaptera wangae*, collected at the Xiaheyan locality (Ningxia, China; early Late Carboniferous), belongs to the Spilapteridae and had a wing span of only about 2 cm. Observed veins elevation is best explained by a simple (convex) MA with a (concave) branch of MP translocated onto it. This pattern is congruent with the one involving a series of 'simple anterior sectors and branched posterior sectors', observed in many Palaeodictyoptera families. We compiled size data on the corresponding superfamily (viz., the Spilapteroidea). The available sample is found insufficient to adequately test the hypothesis of a global effect of an elevated atmospheric p_{O_2} on the size of these insects during the late Late Carboniferous *vs.* that of a lineage-specific trend possibly driven by an arms race in size. More intensive sampling appears necessary to address such evolutionary questions.

RÉSUMÉ

Les insectes fossiles du Carbonifère tardif ont été popularisés comme des géants du passé disparus. Néanmoins, leurs contemporains de petite taille sont encore très mal connus. Dans cet article, nous rapportons la découverte du plus petit Palaeodictyoptera, un groupe éteint de suceurs de sève incluant des insectes parmi les plus grands. Le nouveau représentant, *Tytthospilaptera wangae*, récolté dans la localité de Xiaheyan (Ningxia, Chine ; Carbonifère tardif précoce), appartient aux Spilapteridae et avait une envergure de seulement 2 cm environ. Le patron de nervation qui prend le mieux en compte l'élévation observée des

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nervures implique une MA (convexe) simple, sur laquelle une branche de MP (concave) est transposée. Ce *pattern* est cohérent avec celui impliquant une série de «secteurs antérieurs simples et secteurs postérieurs branchés», observé chez de nombreuses familles de Palaeodictyoptera. Nous avons compilé des données de taille sur la superfamille correspondante (viz., les Spilapteroidea). L'échantillonnage disponible s'avère insuffisant pour tester de manière adéquate l'hypothèse d'un effet global d'une p_{O_2} atmosphérique élevée sur la taille des insectes durant le Carbonifère tardif par rapport à celle d'une tendance spécifique à certaines lignées liée à une course à la grande taille. Un effort d'échantillonnage accru apparaît comme une nécessité pour aborder de telles questions évolutives.

1. Introduction

The discovery of gigantic Pennsylvanian insects at the Commentry locality (France) at the end of the 19th century (Brongniart, 1885, 1893) resulted in long-lasting sketches of forests populated by nightmarish dragonfly-like Odonata (griffen-, dragon- and damselflies). Insects affected by gigantism also include the less popular Palaeodictyopteroidea, a group of exclusively Paleozoic insects (see Shcherbakov, 2011 or Béthoux et al., 2010) provided with a piercing-and-sucking rostrum; and, to a lesser extent, relatives of grasshoppers, crickets and katydids (Archaeorthoptera). Investigations of the factors that regulated insect size since the Palaeozoic were prompted by these discoveries. Recent studies, mainly focused on the physiology of extant insects under hyper- or hypoxia, have provided indirect support for the hypothesis of a positive effect of the high level of atmospheric p_{O_2} at the time (Chown and Gaston, 2010; Dudley, 1998; Harrison et al., 2010; Kaiser et al., 2007). A recent fossil-based contribution on the topic (Clapham and Karr, 2012) relied on maximum wing sizes, the largest Palaeozoic species being populated by the Odonata. However the hypothesis that gigantism affected only a few lineages could not be tested. Indeed, it cannot be excluded that territoriality, a mating regime common among Odonata and favouring large males (relative to female size) through male-male contests (Corbet, 2004; Serrano-Meneses et al., 2008; Tsubaki and Ono, 1987; although factors other than size influence fitness) could have triggered a 'size race' specific to the group during the Palaeozoic (Li et al., 2013a).

A common caveat of such investigations is that the smallest and the largest species of a given group often remain unknown (Blackburn and Gaston, 1994). This is especially true for fossil insects: the largest ones were probably represented by very small populations, and therefore had a depleted likelihood of being fossilized, and the smallest ones are likely to be overlooked during sampling (in particular for imprints – as opposed to amber). Here we report the discovery of the smallest Palaeodictyoptera ever, recovered from the Xiaheyan locality (early Late Carboniferous; China). Its wing morphology has implications for the accepted topological homologies of wing venation for the family it belongs to (the Spilapteridae), and its size allows some considerations of a presumed 'age of giant insects'.

2. Material and methods

We follow the serial insect wing venation groundplan (Lameere, 1922, 1923). The corresponding wing venation nomenclature is repeated for convenience: ScP, posterior Subcosta; RA, anterior Radius; RP, posterior Radius; M, Media; MA, anterior Media; MP, posterior Media; Cu, Cubitus; CuA, anterior Cubitus; CuP, posterior Cubitus; AA: anterior analis. On figures right and left forewings are indicated as RFW and LFW respectively, and right and left hind wings as RHW and LHW.

The new fossil specimen was collected from the Pennsylvanian strata near Xiaheyan village (Zhongwei City, Ningxia Hui Autonomous Region, China). It is housed in the Key Lab of Insect Evolution and Environmental Changes, College of Life Science, Capital Normal University, Beijing, China (CNU; Dong Ren, Curator). Observations and draft drawings were performed using a Leica MZ12.5 dissecting microscope and a drawing tube. Final drawing was prepared based on both draft drawings and photographs using Adobe Illustrator CS6.

Photographs were taken using a Canon EOS 5D Mark III digital camera coupled to a MP-E 65 mm macro lens. Resulting photographs were optimized using Adobe Photoshop CS6. Photographs reproduced on Fig. 1 are 'dry-ethanol composites' (*i.e.* they are a combination of photographs of a specimen both dry and immersed in ethanol).

3. Systematic Palaeontology

Class: INSECTA Linnaeus, 1758
Order: PALAEODICTYOPTERA Goldenberg, 1877
Superfamily: SPILAPTEROIDEA Brongniart, 1893
Family: SPILAPTERIDAE Brongniart, 1893 (nom. correct. Handlirsch, 1906)

Remarks. By virtue of the principle of coordination (ICZN, 1999) Brongniart (1893) must be granted authorship for this taxon (and, incidentally, those of the same group), as he stated (p. 344): "*Ici s'arrête la première sous-famille de ces Platypterida, que nous pourrons désigner sous le nom de SPILAPTERIDA*" [Here ends the first sub-family of these *Platypterida*, which we can designated under the name SPILAPTERIDA], *contra* previous accounts (Carpenter, 1992; Li et al., 2013b; among others).

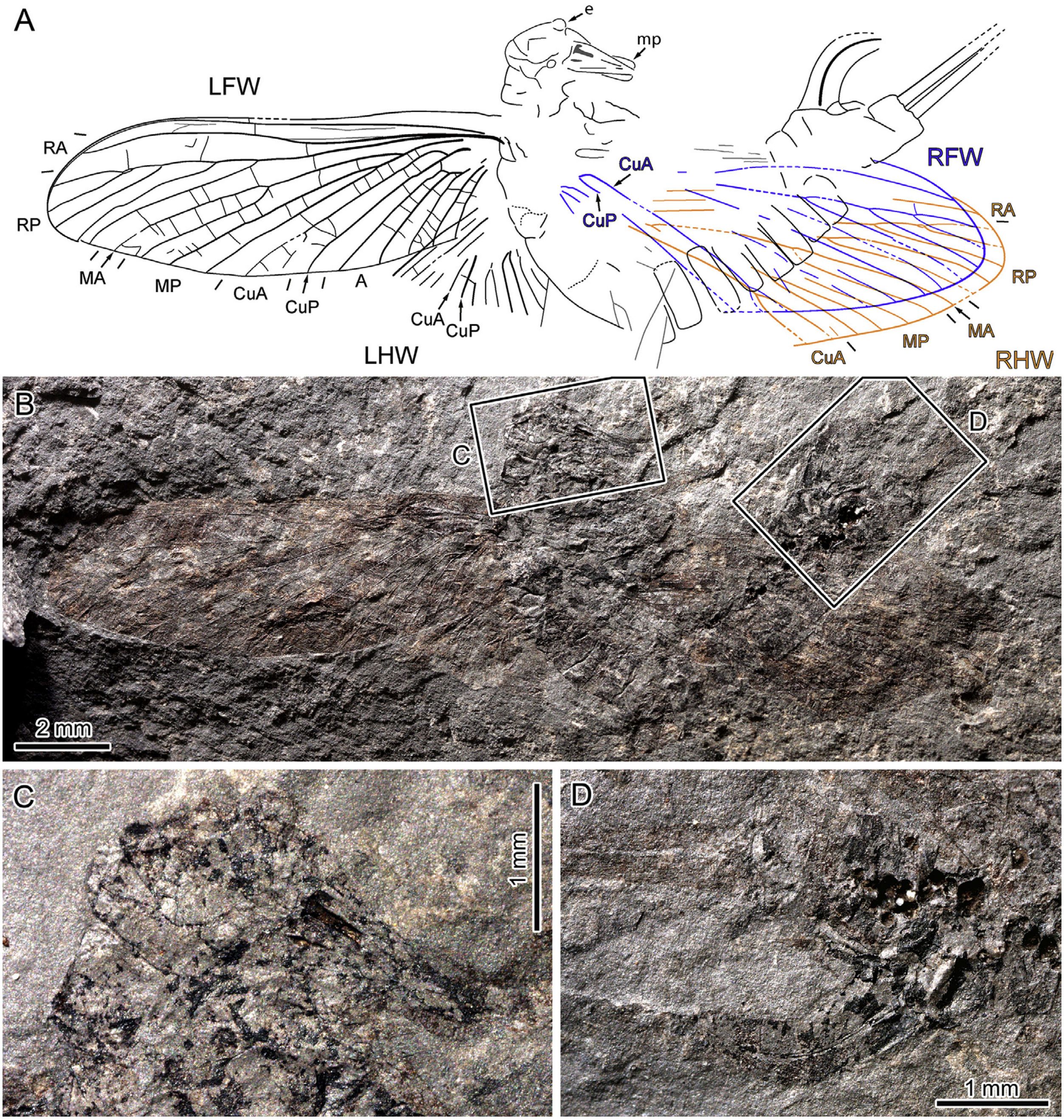

Fig. 1. (Color online). *Tytthospilaptera wangae* Liu, Béthoux, Yin & Ren, gen. et sp. n. (early Late Carboniferous; Xiaheyan Village, Tupo Formation, Ningxia, China), holotype CNU-NX1-165. A. Habitus drawing (wings and wing venation abbreviations, see text; e: eye; mp: maxillary palp). B. Habitus photograph; C, detail of head, photograph as located on B; D, detail of terminalia, photograph as located on B (for interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Fig. 1. (Couleur en ligne). *Tytthospilaptera wangae* Liu, Béthoux, Yin & Ren, gen. et sp. n. (Carbonifère tardif précoce ; village de Xiaheyan, formation Tupo, Ningxia, Chine), holotype CNU-NX1-165. A. Dessin d'habitus (pour les abréviations relatives aux ailes et à la nervation alaire, voir texte ; e : œil ; mp : palpe maxillaire). B. Photographie d'habitus. C. Détail de la tête, agrandissement du cadre en B. D. Détail des terminalia, agrandissement du cadre en B (pour l'interprétation des références faites à la couleur dans cette légende, le lecteur est prié de se référer à la version en ligne de cet article).

Tytthospilaptera Liu, Béthoux, Yin & Ren, gen. n.

Type species. *Tytthospilaptera wangae* Liu, Béthoux, Yin & Ren sp. n.

Etymology. From the Ancient Greek 'tytthos' (little, small), and '*Spilaptera*', type-genus of the corresponding family.

Diagnosis. By monotypy, that of the type species.

Remark. Because of monotypy, the assignment of the new genus at the familial level is discussed under the species heading.

Tytthospilaptera wangae Liu, Béthoux, Yin & Ren sp. n. (Fig. 1)

Etymology. In honor of Ms Qi Wang, who unearthed the available specimen of the species.

Locus typicus and stratum typicum. Xiaheyan locality ('Phoenix 1' trench – exact location of this trench will be published elsewhere). Ningxia Hui Autonomous Region, China; Tupo Formation; Namurian, early Late Carboniferous (Lu et al., 2002; Zhang et al., 2012).

Material. Holotype specimen: CNU-NX1-165 (one side only; veins in inverted elevation; female), collected by Qi Wang during 2013 excavations.

Diagnosis. Both wing pairs: CuA with a very distal fork (located in the distal third of this vein length).

Description: Female specimen moderately well preserved, abdomen bent and partly dislocated, rostrum and terminalia well visible; right wings overlapping, overlapped by abdomen; left forewing very well preserved; only base of left hind wing preserved: body stout, about 13 mm long (from head to the last segment of abdomen); abdomen twisted/disrupted at the level of the terminalia; **head**: rostrum about 1.4 mm long, lumen exposed (Fig. 1C); on each side of the rostrum, two rounded red-brown areas, interpreted as the distal parts of the maxillary palps, as long as the rostrum; **thorax**: segments and legs not discernible; no prothoracic winglets; **forewing** (essentially based on left forewing; veins elevation as if viewed dorsally): length 10.0 mm, max. width 3.4 mm; ScA not visible; simple and straight ScP running parallel to anterior margin, reaching apex; convex RA undulated, simple; area between ScP and RA with vein remains of uncertain origin (twin imprints of disjointed epidermic layers?); area between RA and RP broadest in its distal part; RP pectinate, with five branches covering whole apical area; MA convex, simple, fused for 3.0 mm with the anterior-most branch of MP (itself concave distal to its divergence from MA); free stem of MP forked 0.6 mm distal to its origin (*i.e.* MP with 3 concave branches; probably 4 in the right forewing); CuA/CuP fork about 1.3 mm distal to wing base: origin of CuA very oblique; CuA convex, with a very distal fork; CuP concave, simple; all veins posterior to CuP (anal area) concave, with a total of 5 branches; CuP and the anterior-most branch of the anal area connected by a strong cross-vein; cross-venation scalariform except along the posterior margin, where it is reticulated where visible; **hind wing** (essentially based on right hind wing): similar to forewing; length about 9.6 mm; MP with 4 distal branches; CuA fork more basal than in forewing; **abdomen**: rounded cavities distributed along the ventral? side; ovipositor exposed laterally, a robust and curved valve visible, with a median ridge, about 2 mm long; cerci incomplete, elongate, covered with microtrichia (segmentation not discernible), preserved length about 2.1 mm.

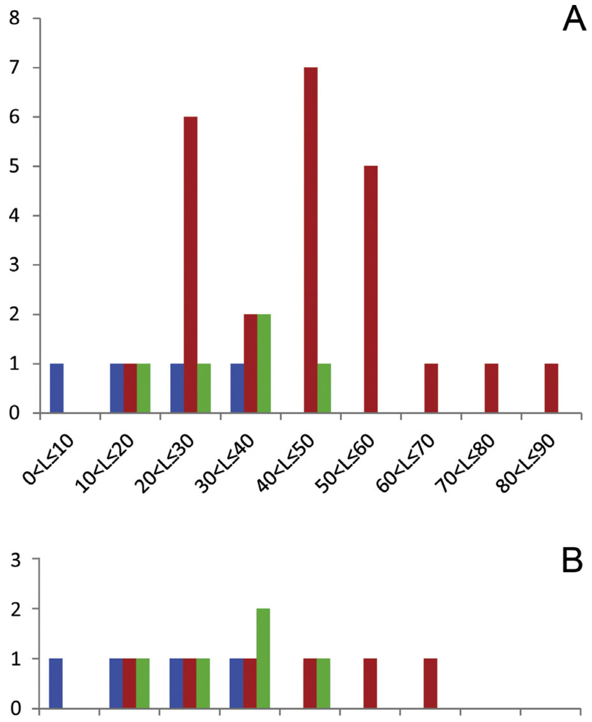

Fig. 2. Size distribution of Spilapteroidea in the early and late Late Carboniferous, and Early Permian. A. Abundance per size (blue: early Late Carboniferous; red: late Late Carboniferous; green: Early Permian). B. The same analysis excluding species from the Commentry locality (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Fig. 2. Distribution de taille des Spilapteroidea durant le Carbonifère tardif précoce, Carbonifère tardif tardif, et le Permien précoce. A. Abundance par taille (bleu : Carbonifère tardif précoce ; rouge : Carbonifère tardif tardif ; vert : Permien précoce). B. La même analyse excluant les espèces du gisement de Commentry (Pour l'interprétation des références faites à la couleur dans cette légende, le lecteur est prié de se référer à la version en ligne de cet article).

Remarks. The assignment of the new specimen (and, incidentally, the new species and genus) to the order Palaeodictyoptera is straightforward: the occurrence of the piercing and sucking rostrum (Fig. 2C) is a diagnostic and derived condition of the taxon. Assignment to the Spilapteridae is straightforward as well: as it possesses a concave anterior wing margin, a branch of MP translocated onto MA (interpreted as the posterior branch of MA by previous authors – see below). Li et al. (2013b) attribute the genus *Sinodunbaria* to the Spilapteridae based on additional characters, some of which occur in the new species (such as 'MA [herein MA + MP *partim*] and MP [herein MP *partim*] [each] with two branches'), but which do not occur in all Spilapteridae. The new species notably differs from other Spilapteroidea families by its moderately developed cross-venation (abundant in Fouqueidae), and the very basal origin of RP (more distal in Eubleptidae).

The very distal position of the CuA fork, and the low number of CuA branches (two) allows us to distinguish the new specimen from any other Spilapteridae species (in which the fork is located more basally, and the number of CuA branches is rarely below 5 and never below 3; e.g. *Baeoneura* has 3). This trait alone justifies the erection of a new species and a new genus.

4. Discussion

4.1. The Media in Spilapteroidea

As occurring in several other Spilapteridae, the first anterior branch of the Media exhibits two branches in *T. wangae* gen. et sp. n. This led previous workers to assume a forked anterior Media (MA) in these insects (Carpenter, 1992; Kukalová, 1969; Li et al., 2013b; Sharov and Sinitshenkova, 1977; among others). However, in the left forewing of the new specimen (negative view) we observed that the stem of this vein and its anterior branch are both concave, as expected of an anterior sector viewed ventrally, but that its posterior branch is convex, as are branches of the genuine MP. This configuration is best explained by a translocation of a branch of MP onto MA. If so, the branching pattern of M would conform the 'simple anterior sector and branched posterior sector' observed in many Palaeodictyoptera families (Béthoux et al., 2007).

We gathered additional evidence of the occurrence of this peculiar vein elevation pattern in Spilapteroidea. The photograph composing the fig. 4 in Sharov and Sinitshenkova (1977) shows, in an isolated wing of *Dunbaria quinquefasciata* (Spilapteridae), 'MA' with a main stem and anterior branch (herein considered the genuine MA) convex, and a posterior branch concave (herein considered MP *partim*). The same pattern is also visible on the photograph composing the fig. 14A.11 in Carpenter (1997), illustrating a specimen of *Eubleptus danielsi*, (Eubleptidae; veins elevation visible in right wings), and the photograph composing the fig. 1 in Beckemeyer and Byers (2001; in *Dunbaria fasciipennis*, Spilapteridae). It must be emphasized here that the corresponding pattern requires suitable orientation of the light source to be rendered visible.

Vein translocation is a transformation type that has now been reported in lineages of total-Orthoptera (Béthoux, 2007, 2012) and of total-Dictyoptera (Béthoux and Wieland, 2009; Guo et al., 2013). There is no documented occurrence in palaeopteran insects, but the Megasecoptera species *Anomalohymen dochmus*, distinguishable from related ones by a 'branched MA', might actually be a rare variant of a known species in which a branch of RP was translocated onto MA. According to the available photographs of this species (Beckemeyer and Engel, 2009) the 'anterior branch of MA' is concave, a feature expected for a branch of RP (which, unusually, is simple rather than branched, corroborating the translocation hypothesis). Given these data, it is therefore reasonable to assume that a translocation of a branch of MP, or several, onto MA, occurred in Spilapteridae.

4.2. An "Age of Giant Insects"?

There are few localities (if any) sufficiently sampled to provide a reference point for the size distribution of Pennsylvanian insects. The famous Commentry insects (late Late Carboniferous; France) were recovered partly by miners and then gathered by engineers, and partly by students (Brongniart, 1883), almost certainly using tools and methods nowadays considered inappropriate. This is evidenced by damage caused to the most complete specimen of the gigantic *Meganeura monyi*: five centimeter-long grooves produced with a centimeter-wide conical scissors (or a small pickaxe) cross the specimen. It implies that this very large specimen was still overlooked after four hits into it. It is then sound to assume that small insects went unnoticed. Furthermore the nodule-type of preservation, common in the Pennsylvanian (e.g. Mazon Creek, Coseley, and Montceau-les-Mines localities, among others), has rarely provided small insects (except a few Miomoptera; Oudard, 1980). Indeed the 'hammering' or 'freeze-thawing' techniques are improper to ideally expose remains without large flat surfaces. In summary, there is a dearth of data on small-sized insects of the Pennsylvanian (Nel et al., 2013). Such data would allow a more decisive testing of the hypothesis of a positive effect of high atmospheric p_{O_2} on insect size during the Pennsylvanian (Clapham and Karr, 2012; among others): were only a few lineages affected by gigantism, other macro-ecological causes such as particular mating regimes, or a comparatively low level of predation pressure, might have to be considered (Bechly, 2001; Li et al., 2013a, b).

To illustrate the limitations of the current data to conclusively address this question we conducted a size distribution analysis based on all species of Spilapteroidea sufficiently known for a robust estimation of their wing length, and using three time intervals (early Late Carboniferous, $n = 4$; late Late Carboniferous, $n = 24$; Early Permian, $n = 5$; Fig. 2). *T. wangae* occupies the left part of the distribution. When taking all species into account (Fig. 2A), the survey shows that large to very large species are concentrated during the second interval, suggestive of an 'age of giant insects' at this time (Gzhelian to Early Artinskian?; 304 to *ca.* 288 Myr; there is a significant difference between sample medians: $H(\text{Chi}^2)$: 8.677, $P = 0.01302$). However, these data are largely dominated by a single sample, namely the Commentry locality ($n = 18$). The trend is no longer apparent if this sample, clearly biased towards large species if compared to others, is discarded [Fig. 2B; there is no significant difference between sample medians: $H(\text{Chi}^2)$: 3.981, $P = 0.1362$]. This result suggests that the conclusions are highly dependent on particular samples and, given the small number of samples, easily biased. Our data tend to indicate that early Late Carboniferous forms were comparatively smaller, but this trend would require more exhaustive data to be appreciated, especially

Table 1
Data on species of Spilapteroidea for which wing length is available; species from *Homaloneura elegans* Brongniart, 1885 to *Mecynostomata dohrni Brongniart, 1893* (top to bottom) have been recovered from the Commentry locality (France, Late Pennsylvanian).
Tableau 1
Données sur les espèces de Spilapteroidea, pour lesquelles la longueur de l'aile est disponible ; les espèces d'*Homaloneura elegans* Brongniart, 1885 à *Mecynostomata dohrni Brongniart, 1893* (de haut en bas) ont été récoltées à Commentry, France (Pennsylvanien supérieur).

Species name and notes	Familial affiliation	Wing length (mm) (forewing unless specified)	Age	Data collected from
Paradunbaria pectinata Sinitshenkova & Sharov, 1977	Spilapteridae	22.0	Early Permian	Original description
Dunbaria borealis Sinitshenkova & Sharov, 1977	Spilapteridae	34.0	Early Permian	Original description
Dunbaria quinquefasciata (Martynov, 1940)	Spilapteridae	34.0	Early Permian	Sinitshenkova & Sharov, 1977
Dunbaria fasciipennis Tillyard, 1924 (average of 6 specimens)	Spilapteridae	17.3	Early Permian	Kukalová-Peck, 1971
Spilaptera splendens Prokop, Roques & Nel, 2014	Spilapteridae	43.0	Early Permian	Original description
Homaloneura elegans Brongniart, 1885	Spilapteridae	33.0	late Late Carboniferous	Kukalová, 1969
Homaloneura bonnieri Brongniart, 1893	Spilapteridae	43.0	late Late Carboniferous	Kukalová, 1969
Homaloneura punctata Brongniart, 1893	Spilapteridae	28.0	late Late Carboniferous	Kukalová, 1969
Homaloneura joannae Brongniart, 1893	Spilapteridae	22.5	late Late Carboniferous	Kukalová, 1969
Homaloneura lehmani Kukalová, 1969	Spilapteridae	23.0	late Late Carboniferous	Original description
Homaloneura bucklandi Brongniart, 1893	Spilapteridae	29.0	late Late Carboniferous	Kukalová, 1969
Spilaptera packardi Brongniart, 1885	Spilapteridae	53.0	late Late Carboniferous	Kukalová, 1969
Spilaptera libelluloides Brongniart, 1885	Spilapteridae	57.0	late Late Carboniferous	Kukalová, 1969
Spilaptera venusta Brongiart, 1893	Spilapteridae	>40	late Late Carboniferous	Original description
Becquerelia superba Brongniart, 1893 (hind wing)	Spilapteridae	85.0	late Late Carboniferous	Kukalová, 1969
Becquerelia tincta Brongniart, 1893	Spilapteridae	24.0	late Late Carboniferous	Kukalová, 1969
Epitethe meunieri (Brongniart, 1893)	Spilapteridae	48.0	late Late Carboniferous	Kukalová, 1969
Spiloptilus ramondi (Brongniart, 1893)	Spilapteridae	60.0	late Late Carboniferous	Kukalová, 1969
Lamproptilia grandeuryi Brongniart, 1885	Spilapteridae	75.0	late Late Carboniferous	Kukalová, 1969
Fouquea lacroixi Brongniart, 1893	Fouqueidae	49.0	late Late Carboniferous	Kukalová, 1969
Fouquea superba (Meunier, 1909)	Fouqueidae	50.0	late Late Carboniferous	Kukalová, 1969
Fouquea needhami Lameere, 1917	Fouqueidae	55.0	late Late Carboniferous	Kukalová, 1969
Mecynostomata dohrni Brongniart, 1893	Mecynostomatidae	50.0	late Late Carboniferous	Kukalová, 1969
Baeoneura obscura Sinitshenkova in Sinitshenkova & Sharov, 1977	Spilapteridae	25.0	late Late Carboniferous	Original description
Spilaptera americana Carpenter & Richardson, 1971	Spilapteridae	> 40	late Late Carboniferous	Original description
Bojoptera colorata Kukalová, 1958	Spilapteridae	51.0	late Late Carboniferous	Original description
Neuburgia altaica Martynov, 1931	Spilapteridae	32.0	late Late Carboniferous	Sinitshenkova & Sharov, 1977
Eubleptus danielsi Handlirsch, 1906	Eubleptidae	14.0	late Late Carboniferous	Carpenter, 1983
Neofouquea suzannae Carpenter, 1967	Fouqueidae	> 65	late Late Carboniferous	Original description
Severinopsis vetusta Kukalová, 1958	Spilapteridae	> 30	early Late Carboniferous	Original description
Sinodunbaria jarmilae Li, Ren, Pecharová & Prokop, 2013	Spilapteridae	21.6	early Late Carboniferous	Original description
Tytthospilaptera qiae gen. et sp. nov.	Spilapteridae	9.8	early Late Carboniferous	Original description
Delitzschala bitterfeldensis Brauckmann & Schneider, 1996	Spilapteridae	11.0	early Late Carboniferous	Original description

given the comparatively high palaeolatitude of the Xiaheyan locality (Table 1).

5. Conclusions

The Xiaheyan locality is a privileged window to investigate insect evolution at an early stage (Late Namurian/Early Bashkirian; ca. 318 Myr). Predating a putative 'insect giant age', the fossiliferous layers have embedded the most exhaustive Pennsylvanian insect fauna known to date, including species in the range of *ca.* 20 mm wingspan, such as *Sinonamuropteris ningxiaensis* (stem-Grylloblattodea; Cui et al., 2011), *Gulou carpenteri* (stem-Plecoptera; Béthoux et al., 2011), and, now, *T. wangae*. Continuing excavations will provide a sample critical to evaluate the actual impact of high atmospheric p_{O_2} on insect size during the Late Carboniferous and the Early Permian.

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