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Early Pennsylvanian aykhalids from Xiaheyan, northern China and their palaeogeographical significance (Insecta: Megasecoptera)

Les aykhalidés du Pennsylvanien inférieur de Xiaheyan, Nord de la Chine et leur signification paléogéographique (Insecta : Megasecoptera)

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ABSTRACT

The first members of the Palaeozoic insect family Aykhalidae (Megasecoptera) to be described were discovered in Siberia. Two new genera and three species from the Early Pennsylvanian (Namurian) Tupo Formation at Xiaheyan in northern China (Ningxia Hui Autonomous Region) are described on the basis of the patterns of their wing venation. An emended diagnosis of the Aykhalidae is provided based on the larger sample of specimens now available. *Sinopalaeopteryx* gen. nov. is established with two described species (*S. olivieri* sp. nov. and *S. splendens* sp. nov.). Monotypic *Namuroptera* gen. nov. is established for *N. minuta* sp. nov., a species that is markedly smaller in size, has a pointed connection between MA and RP, and very long brace m-cua well aligned with a short rp-m brace compared to *Aykhal* and *Sinopalaeopteryx*. All these newly described taxa extend our knowledge of the morphological disparity within the Aykhalidae. Due to the number of shared characters in wing venation, we consider Aykhalidae to be closely related to Sphecopteridae, with a broad distribution across Euramerica, Siberia and North China. In addition, this study documents individual and intraspecific variability in wing venation in the Aykhalidae and Sphecopteridae.

Mots clés :
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Gen. nov. et sp. nov.
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RÉSUMÉ

Les premiers représentants de la famille d'insectes paléozoïques Aykhalidae (Megasecoptera) décrits ont été découverts en Sibérie. Sur la base de leur nervation alaire, deux nouveaux genres et trois espèces sont décrits dans le Pennsylvanien inférieur (Namurien) de la formation Tupo dans la localité Xiaheyan, dans le Nord de la Chine (région autonome Ningxia Hui). Une diagnose amendée des Aykhalidae est proposée sur la base de ces nouvelles découvertes. *Sinopalaeopteryx* gen. nov. est établi avec deux espèces, *S. olivieri* sp. nov. et *S. splendens* sp. nov. Le genre monotypique *Namuroptera* gen. nov. est établi pour *N. minuta* sp. nov., une espèce de taille particulièrement petite. Ces taxons diffèrent nettement d'*Aykhal* et de *Sinopalaeopteryx* par leur plus petite taille, la connexion à angle aigu entre

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MA et RP, et une très longue nervure transverse m-cua bien alignée avec une courte nervure transverse rp-m. Toutes les espèces nouvellement décrites augmentent nos connaissances sur la disparité morphologique chez les Aykhalidae. En raison du nombre de caractères partagés dans la nervation alaire, nous considérons les Aykhalidae comme étroitement apparentés aux Sphecopteridae, famille à large distribution en Euramérique, Sibérie et Chine du Nord. En outre, notre étude nous permet de souligner la variabilité individuelle et intraspécifique de la nervation alaire chez les Aykhalidae et les Sphecopteridae.

1. Introduction

Palaeodictyopteroida Bechly, 1996 (= Palaeodictyopterida) has been conventionally considered to be a member of Palaeoptera, which includes four orders: Palaeodictyoptera, Megasecoptera, Permothemistida and Diaphanopterodea, the relationships among which are unresolved. Sroka et al. (2014) recently proposed Palaeodictyopterida as a sister group of Neoptera based on a cladistic analysis of palaeopteran groups including fossil and recent taxa, which was also previously suggested by Willmann (2004).

Rohdendorf (1962) proposed the concept Megasecopteroidea comprising Megasecoptera with wings permanently spread in the resting position, Diaphanopterodea with roof-like folded wings and Campylopterodea. The latter group was later rejected by Nel and Huguet (2002), who transferred the monotypic Campylopteridae to Odonataoptera. Several authors doubt the monophyly of Megasecoptera due to the lack of clear autapomorphy. Kukalová-Peck (1975) presented a list of characters for Megasecoptera and stated that each feature can occur also in Palaeodictyoptera. Riek (1976) proposed a key to the Megasecoptera with a division into two suborders, the Eumegasecoptera with the following characters "costal and subcostal spaces relatively broad, with stem of Cu diverging more or less regularly from wing base", and the Protohymenoptera with "costal and subcostal spaces very narrow, with Sc and R crowded close to costal margin and with basal sections of stems of main veins, with exception of anal vein, all crowded close to fore margin". Carpenter (1992) considered the Megasecoptera a palaeopterous order, which is likely to be transferred to the Palaeodictyoptera in the future because they share many characters. Sinitshenkova (2002: 120) established the order Mischopterida based on a fusion of Megasecoptera Brongniart, 1893 and Archodonata Martynov, 1932. Several families formerly included in the Megasecoptera were transferred to the order Dictyoneurida (= Palaeodictyoptera) and the status of suborders Eubleptina (∼ Eubleptoidea Laurentiaux, 1953), Mischopterina (∼ Eumegasecoptera), Aspidothoracina (∼ Protohymenoptera), Permothemistina (∼ order Permothemistida = Archodonata) were changed by the same author. Grimaldi and Engel (2005) proposed three lineages of Megasecoptera, with Eubleptoptera a sister group of Eumegasecoptera + Protohymenoptera mainly based on the different widths of their costal areas and other characteristics of their venation.

The present study deals with new members of Megasecoptera, which have wings that are usually markedly narrow at the base, frequently petiolate, generally reduced wing venation with branches on the main veins, narrow anal area, loss of archedictyon, few cross veins and long multisegmented cerci. The most obvious characteristic of megasecopteran wings is the form and shape of the anal area. There are two main types of anal area (Fig. 1). The first with two or more anal veins emerging from one point at the bases of the wings is present in Brodiopteridae and Xenopteridae (Fig. 1a) (Pinto, 1986; Pecharová et al., 2015). It is proposed that the latter family name be changed to Xenopteraidae (Ross et al., 2013). The second with one usually pectinate anal vein, which runs more or less parallel to the posterior wing margin, is present in the remaining families e.g., Sphecopteridae and Protohymenidae (Fig. 1b and c). Another frequently used character in the diagnosis of many families is the connection between veins RP-MA and M-CuA, which is rather variable in some families like the Brodiopteridae and Sphecopteridae, and very stable in others, e.g., Mischopteridae (see Fig. 1d–g).

The first published reference to the Namurian entomofauna in China is by Hong and Peng (1995). They presented a paper at the 18th Pacific Science Congress in Beijing. Hong (1998), proposed the name Qilianshan entomofauna for insects from Namurian C in the Qilianshan Mountains, and indicated they were the oldest entomofauna known from the North China palaeocontinent. Subsequent research resulted in several studies that focused on members of the following insect groups: Palaeodictyoptera, Odonatoptera, stem-Grylloblattodea, stem-Dictyoptera, stem-Orthoptera (Archaeorthoptera) and stem-Plecoptera (e.g., Béthoux et al., 2011; Li et al., 2013a; Liu et al., 2009; Prokop and Ren, 2007; Ren et al., 2008). Pecharová et al. (2015) briefly reviewed the previous studies on fossil insects and focused on describing the megasecopteran *Brodioptera sinensis* Pecharová, Ren and Prokop, 2015 based on an evaluation of more than 50 specimens. Such an extensive dataset for a single species is the source of our knowledge about intraspecific variability, which is rarely documented for Early Bashkirian insects.

The results presented here were partially previously elaborated during the preparation of the masters' thesis of the first author (Pecharová, 2013).

2. Material and methods

All specimens are deposited in the collection of Key Laboratory of Insect Evolution and Environmental Changes at Capital Normal University (prefix CNU-) in Beijing (China). Material consists of 14 compressed fossils mainly of fragments or complete wings. Due to the distortion of some

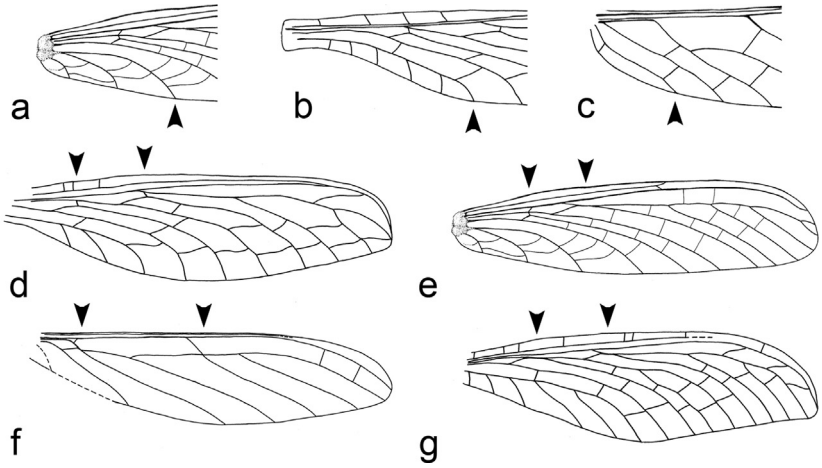


Fig. 1. Drawings of the wing venation of Megasecoptera with particular emphasis on main diagnostic characters (colour patterns omitted). **a**: *Brodioptera sinensis* Pecharová, Ren and Prokop, 2015 (Brodiopteridae); **b**: *Sphecoptera brongniarti* Meunier, 1908 (Sphecopteridae); **c**: *Permohymen schucherti* Tillyard, 1924 (Protohymenidae); **d**: *Foriria maculata* Meunier, 1908 (Foririidae); **e**: *B. sinensis* Pecharová, Ren and Prokop, 2015 (Brodiopteridae); **f**: *Scytohymen extremus* Martynov, 1937 (Scytohymenidae); **g**: *Corydaloides scudderi* Brongniart, 1885 (Corydaloididae). Abbreviations: **a–c**: arrangement of anal veins, A1 indicated by arrow; **d–g**: various types of connection between RP and MA (apical connection), M and CuA (basal connection) in the form of a brace or pointed fusion, positions indicated by arrows (drawings adopted or modified based on a personal re-examination by the authors).

Fig. 1. Dessins de nervations alaires de Megasecoptera, l'accent étant mis particulièrement sur les principaux caractères diagnostiques (les schémas en couleur ont été omis). **a** : *Brodioptera sinensis* Pecharová, Ren et Prokop, 2015 (Brodiopteridae) ; **b** : *Sphecoptera brongniarti* Meunier, 1908 (Sphecopteridae) ; **c** : *Permohymen schucherti* Tillyard, 1924 (Protohymenidae) ; **d** : *Foriria maculata* Meunier, 1908 (Foririidae) ; **e** : *B. sinensis* Pecharová, Ren et Prokop, 2015 (Brodiopteridae) ; **f** : *Scytohymen extremus* Martynov, 1937 (Scytohymenidae) ; **g** : *Corydaloides scudderi* Brongniart, 1885 (Corydalolididae) Abréviations : **a–c** : arrangement des veines anales, Al indiqué par des flèches ; **d–g** : types variés de connexion entre RP et AP (connexion apicale), M et CuA (connexion basale), sous forme d'une attache ou d'un point de fusion, positions indiquées par des flèches (dessins adoptés ou modifiés sur la base d'un réexamen par les auteurs).

of the fossils, we selected only seven for the description. The seven poorly preserved specimens (Nos. CNU-NX1-640, CNU-NX1-645a, b, CNU-NX1-648, CNU-NX1-668a, b, CNU-NX1-669a, b, CNU-NX1-670a, b, CNU-NX1-673) are considered therefore to have an uncertain systematic attribution. The main problem with these fossils is that it is difficult to interpret the basal part of the wing, which bears numerous diagnostic characters such as the connection of CuA with M. Therefore, we decided only to record these specimens because extensive field research at Xiaheyan is still ongoing and the discovery of additional material is anticipated.

Xiaheyan is situated in Zhongwei County in the Ningxia Hui Autonomous Region in northwestern China. The paralic development of the Tupo Formation with intercalated coal seams is biostratigraphically correlated with the Carboniferous strata in Europe, North America and Russia (Li et al., 1993, 2003; Wang, 2010). Zhang et al. (2013) provide the most comprehensive summary of the stratigraphy of the Tupo Formation correlated with Namurian B/C (Bashkirian) in Europe on the basis of occurrences of the following ammonoids (*Reticuloceras reticulatum*, *Gastrioceras listeri*, *G. montgomeryense*) and conodonts (*Declingnathodus noduliferous*, *Neognathodus symmetricus*). Insects are preserved as compressed fossils in greyish or black shales accompanied by plants, fish and bivalves (Zhang et al., 2013). Xie et al. (2004) indicate that the depositional environment was marine-lagoonal with tidal flats and marshlands.

The specimens were viewed using Leica MZ12.5 and Nikon SMZ 645 stereomicroscopes in a dry state and under a film of ethyl alcohol. Line drawings were made using a stereomicroscope with a camera lucida attachment. Photographs of fossils in a dry state or under a film of ethyl alcohol were taken using a Canon D550 digital camera equipped with MP-E 65 mm and EF 50 mm macro-lenses. Original photographs were processed using the image editing software Adobe Photoshop CS4 and some were also carefully processed using the stacking software Helicon Focus Pro.

The higher systematics of Megasecoptera is not satisfactorily resolved. The present work generally follows Riek (1976) and Carpenter (1992), and takes into consideration the comments of Sinitshenkova (2002) on this concept. Wing venation nomenclature generally follows the scheme of Kukalová-Peck (1991). Wing venation abbreviations: A1: first anal vein; CuA/CuP: cubitus anterior/posterior; MA/MP: media anterior/posterior; RA/RP: radius anterior/posterior; ScP: subcosta posterior; cross veins (braces) indicate veinal connections rp-ma, rp-m and m-cua.

3. Systematic palaeontology

Class INSECTA Linnaeus, 1758
Superorder PALAEODICTYOPTEROIDA Bechly, 1996
Order MEGASECOPTERA Brongniart, 1885
Suborder EUMEGASECOPTERA *sensu* Riek, 1976
Family AYKHALIDAE Sinitshenkova, 1993

Included genera. ***Aykhal*** Sinitshenkova, 1993 (type genus), *Sinopalaeopteryx* gen. nov., *Namuroptera* gen. nov.

Emended diagnosis. Wings elongate, petiole not obvious, costal area basally wide with several cross veins, widest part of costal area near wing base, ScP slightly longer than half the wing length and ending into RA before

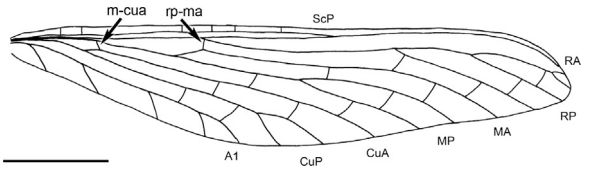


Fig. 2. *Sinopalaeopteryx splendens* gen. nov. et sp. nov., holotype CNU-NX1-641a (Capital Normal University, Beijing, China), line drawing of hindwing. Scale bar = 5 mm.
Fig. 2. *Sinopalaeopteryx splendens* gen. nov. et sp. nov., holotype CNU-NX1-641a (Capital Normal University, Pékin, Chine), dessin au trait d'aile arrière. Barre d'échelle = 5 mm.

first branching of RP, pterostigma slightly expressed or not obvious, RP multibranched, MA connected to RP at one point or by cross vein rp-ma (brace), MA simple, MP deeply forked, CuA simple, few simple cross veins arranged in a steplike pattern along posterior margin of the wing, single anal vein pectinate with at least four branches.

Genus ***Sinopalaeopteryx*** gen. nov.

Type species. *Sinopalaeopteryx splendens* sp. nov.

Etymology. Composite name after Sinae (China), palaeo (ancient) and pteryx (wing), masculine in gender.

Diagnosis. Based on wing venation. Wing basally narrow, broadest at about midwing, with stems of main veins basally close to each other, costal margin nearly straight, costal area widest at basal third gradually narrowing to midwing, ScP ending on RA proximal to the first branching of RP, RP with three branches, the first one simple or with terminal twig, MA connected by brace rp-ma with RP near the point where RA and RP divide, simple CuA connected by cross vein m-cua to M, first anal vein runs gradually parallel to the posterior wing margin.

Sinopalaeopteryx splendens sp. nov. (Figs. 2–4)

Etymology. Named in Latin after the brilliant state of its preservation.

Material. Holotype. CNU-NX1-641a, b (a) nearly a complete counter-imprint of a well-preserved insect wing; (b) rather fragmentary imprint of posterior part of the wing.

Supplementary material. CNU-NX1-667a, b, (isolated wing lacking apical third), CNU-NX1-672 (isolated wing lacking basal part).

Type stratum and locality. Tupo Formation, Carboniferous, Lower Pennsylvanian, Bashkirian, (equivalent to Namurian B–C), Xiaheyan Village, Zhongwei County, Ningxia Hui Autonomous Region, China.

Diagnosis. Wing of triangular shape, widest at about midwing, wing width markedly decrease from midwing to ending of MA, costal area with at least six perpendicular cross veins, ScP terminating on RA well before the first division of RP, CuP with terminal twig.

Description. Based on Holotype specimen No. CNU-NX1-641a, b.

Nearly complete wing of triangular shape, broadest at about midwing, membrane hyaline, several simple straight or oblique cross veins present between main longitudinal veins; costal margin raised basally forming a broad costal area with four perpendicular cross veins, concave ScP nearly straight ending on RA behind midwing, 15.5 mm from the wing base; RA + RP basally close to stem of M, separation of RA from RP about 1/3 along the wing length, RA simple reaching costal margin 1.1 mm from wing apex, RP pectinate ending in three main terminal branches that cover the apex of the wing, first branch with short terminal twig; division of MA and MP 1.4 mm basal of separation of RA and RP, simple convex MA diverging to RP with short connection by cross vein (brace) rp-ma just behind the separation of RA and RP; concave MP distally branched, ending in two branches on posterior wing margin; stem of Cu basally separated from RA + RP and M, division of CuA and CuP 4.5 mm from wing base, simple CuA diverging to M, shortly connected to M by cross vein (brace) m-cua; concave CuP with short terminal twig; anal area strongly reduced, single anal vein pectinate with 5 short branches.

Dimensions. *Holotype*. CNU-NX1-641a, b: Wing length 27.3 mm, maximum width 5.6 mm, distance from division CuA/CuP to first branch of RP 14.5 mm; CNU-NX1-667a, b: Preserved wing length 19.0 mm (estimated total wing length similar to the holotype), maximum width 5.4 mm, distance from division CuA/CuP to first branch of RP 14.2 mm; CNU-NX1-672: Length of preserved part of wing 17.7 mm (estimated total length 20.0 mm), maximum width 4.5 mm, distance from division CuA/CuP to first branch of RP 9.3 mm.

Discussion. *Sinopalaeopteryx* gen. nov. is attributed to the monotypic family Aykhalidae based on the following combination of wing venation characteristics:

- wing elongate without basal petiole;
- presence of rather broad costal area;
- ScP ending on RA slightly behind the midwing;
- RP multibranched;
- stems of M and Cu not fused at base of the wing;
- MP ends with two long branches (Sinitshenkova, 1993).

Aykhalidae were established for genus *Aykhal* with *A. helenae* Sinitshenkova, 1993 based on an isolated forewing from the Yakutia-Sakha deposits in Russia close to the boundary between Late Pennsylvanian and Early Permian (Zherikhin, 2002: 337). *Sinopalaeopteryx* gen. nov. differs from *Aykhal* in having a nearly straight costal margin (both fore- and hindwings), cross veins in costal area are sparsely arranged, brace rp-ma close to the point of division of RP and RA, brace m-cua is equal or longer than the part of CuA that emerges from CuP (in *Aykhal* this brace is shorter), first anal vein runs nearly parallel to the posterior wing margin. The lack of a pterostigma as in *Aykhal* could be considered as a variable character for Aykhalidae, due to its weak sclerotization in the holotype *A. helenae* Sinitshenkova, 1993, and therefore cannot be used as a significant character for separation (see Fig. 5). Due to the lack of prominent oblique cross veins between RA and RP distally and the aforementioned characters we propose separating *Sinopalaeopteryx* from the genus *Aykhal*. Moreover, we should noticed the Namurian age of *Sinopalaeopteryx* in contrast to the Gzhelian/Asselian age of *Aykhal*. Therefore, the designation of the genus *Sinopalaeopteryx* is well grounded and *Aykhal* is probably a closely related genus. Based on the triangular wing shape of *S. splendens* sp. nov. and its slightly reduced

Fig. 3. (Color online.) *Sinopalaeopteryx splendens* gen. nov. et sp. nov., holotype CNU-NX1-641a (Capital Normal University, Beijing, China), photograph of hindwing. Scale bar = 5 mm.
Fig. 3. (Couleur en ligne.) *Sinopalaeopteryx splendens* gen. nov. et sp. nov., holotype CNU-NX1-641a (Capital Normal University, Pékin, Chine), photographie d'aile arrière. Barre d'échelle = 5 mm.

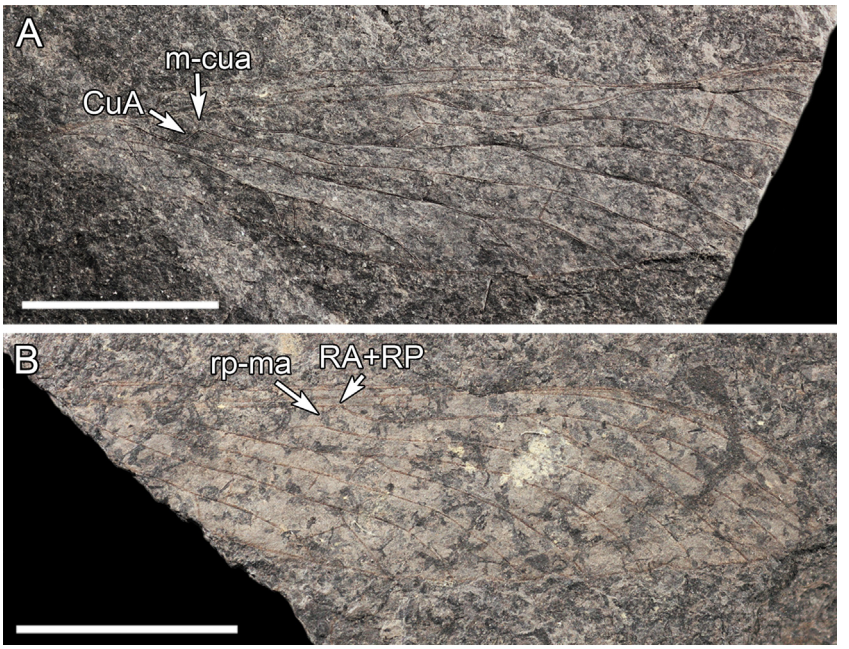


Fig. 4. (Color online.) *Sinopalaeopteryx splendens* gen. nov. et sp. nov. **A**. Photograph of specimen No. CNU-NX1-667a (Capital Normal University, Beijing, China). **B**. Photograph of specimen No. CNU-NX1-672 (Capital Normal University, Beijing, China). Scale bars = 5 mm.
Fig. 4. (Couleur en ligne.) *Sinopalaeopteryx splendens* gen. nov. et sp. Nov. **A**. Photographie du spécimen nº CNU-NX1-667a (Capital Normal University, Pékin, Chine). **B**. Photographie du spécimen nº CNU-NX1-672 (Capital Normal University, Pékin, Chine). Barre d'échelle = 5 mm.

costal area and costal margin without prominent serration, we consider that it is most probably a hindwing.

On the other hand, *Sinopalaeopteryx* gen. nov. shares a number of diagnostic characters with the genera *Sphecoptera* Brongniart, 1893 and *Cyclocelis* Brongniart, 1893, both placed in the family Sphecopteridae as they differ mainly in having petiolate wings (Carpenter, 1951: 345). However, petiolate wings in Megasecoptera is a rather

Fig. 5. (Color online.) *Aykhal helenae* Sinitshenkova, 1993. Photograph of holotype PIN No. 3838/1 (Palaeontological Institute of RAS coll., Moscow, Russia). Scale bar = 5 mm.
Fig. 5. (Couleur en ligne.) *Aykhal helenae* Sinitshenkova, 1993. Photographie de l'holotype PIN nº 3838/1 (Palaeontological Institute of RAS coll., Moscou, Russie). Barre d'échelle = 5 mm.

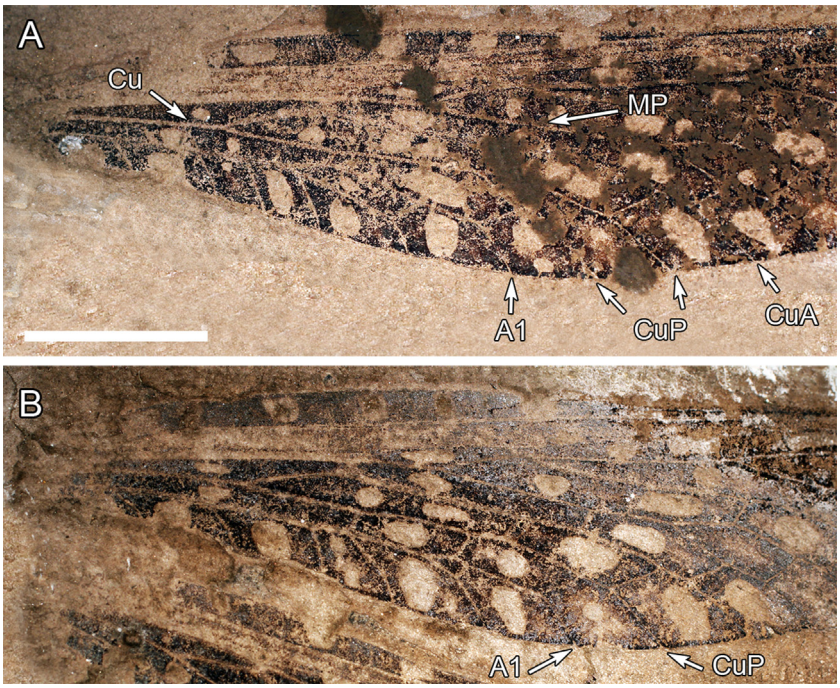


Fig. 6. (Color online.) *Cyclocelis chatini* Brongniart, 1893, syntype, No. R51136 (Muséum national d'histoire naturelle, Paris, France). **A**. Photograph of left forewing horizontally flipped over. **B**. Photograph of right forewing. Scale bar = 10 mm.
Fig. 6. (Couleur en ligne.) *Cyclocelis chatini* Brongniart, 1893, syntype, nº R51136 (Muséum national d'histoire naturelle, Paris, France). **A**. Photographie d'aile avant gauche, horizontalement basculée. **B**. Photographie d'aie avant droite. Barre d'échelle = 10 mm.

variable character and therefore difficult to use in systematics, e.g., family Bardohymenidae includes genera such as *Bardohymen* Zalessky, 1937 with clearly petiolate wings, but also other taxa that lack petioles, like *Calohymen* Carpenter, 1947. Sinitshenkova (2002: 121) has already recorded that the wings in both suborders of Mischopterida (Mischopterina and Aspidothoracina) of various taxonomic ranks are petiolate. Therefore, we consider this character to be variable as can be seen for instance in the Sphecopteridae, in which the wings of *Sphecoptera* spp. are generally more petiolate than those of *Cyclocelis* (Carpenter, 1951). Thus, in the future Aykhalidae is likely to be synonymized with Sphecopteridae due to the lack of significant diagnostic features with exception of that in all Sphecopteridae

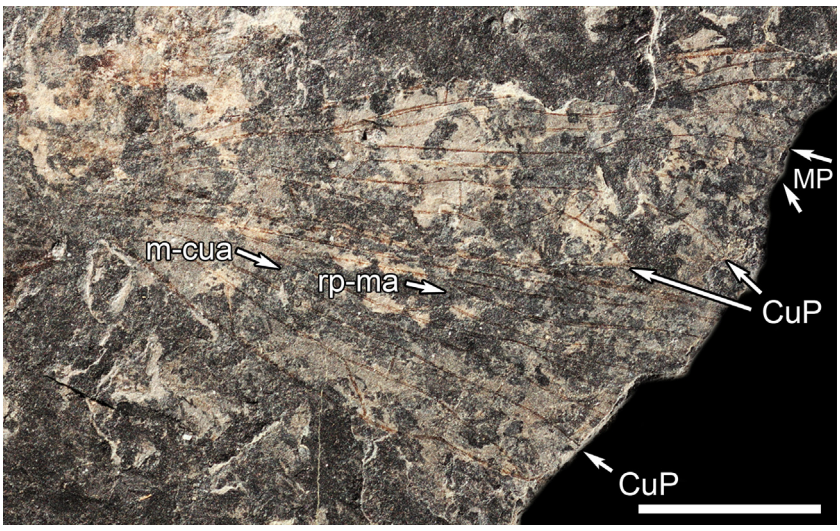
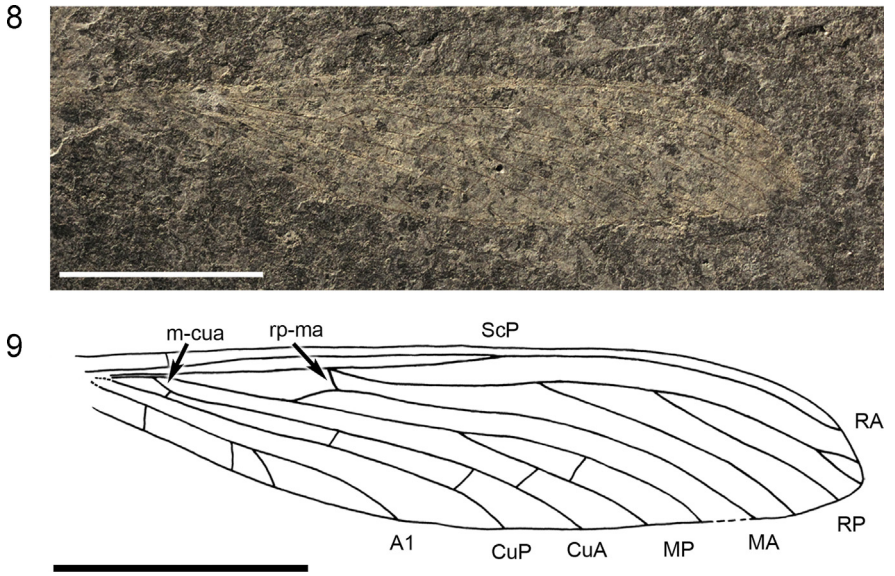


Fig. 7. (Color online.) *Sinopalaeopteryx olivieri* gen. nov. et sp. nov., specimen CNU-NX1-644b (Capital Normal University, Beijing, China), photograph of basal parts of fore- and hindwing with indication of branched CuP on forewing (horizontally flipped). Scale bar = 3 mm.
Fig. 7. (Couleur en ligne.) *Sinopalaeopteryx oliveri* gen. nov. et sp. nov., spécimen CNU-NX1-644b (Capital Normal University, Pékin, Chine), photographie des parties basales d'aile avant et arrière, avec indication de CuP branché sur l'aile avant (horizontalement basculé). Barre d'échelle = 3 mm.



Figs. 8 and 9. (Color online.) *Sinopalaeopteryx olivieri* gen. nov. et sp. nov., holotype CNU-NX1-642a (Capital Normal University, Beijing, China), photograph and line drawing of wing. Scale bar = 5 mm.
Figs. 8. (Couleur en ligne.) *Sinopalaeopteryx olivieri* gen. nov. et sp. nov., holotype CNU-NX1-642a (Capital Normal Université, Pékin, Chine), photographie et dessin au trait d'aile. Barre d'échelle = 5 mm.

vein ScP ending well behind the first branching of RP, unlike in Aykhalidae where ScP ending before this point. Nevertheless, for consistency with current systematics we prefer to maintain Aykhalidae and Sphecopteridae as separate families until the discovery of more complete material resolves this problem.

Note. The family Sphecopteridae comprise two genera, *Sphecoptera* and *Cyclocelis* both known from Gzhelian of Commentry (France), a famous locality for exceptionally fine insect preservation. Supporting their possible relationship the genus *Cyclocelis* and *Sinopalaeopteryx* share a deeply branched MP vein and less petiolate wings among other characters. Nevertheless, re-examination of one of three syntypes of *Cyclocelis chatini* Brongniart, 1893 (all four wings preserved, No. R51136 housed in the Muséum national d'histoire naturelle, Paris) by one of us (MP) revealed variation in the venation in the basal part of the wing with CuP on the left forewing (and also right hindwing) either simple or with terminal twig. This difference is associated with a different arrangement of the first anal vein of the corresponding wing (see Fig. 6). Similar individual variability in CuP occurs in *Sinopalaeopteryx olivieri* sp. nov., where CuP has terminal twig only on one forewing (specimen CNU-NX1-644a, b) (Fig. 7). These examples of individual plasticity in some wing vein characteristics, which are commonly used in taxonomy, indicate that the careful selection of proper diagnostic characters is essential for stable systematics.

Sinopalaeopteryx olivieri sp. nov. (Figs. 7–10A)

Etymology. Named after the palaeoentomologist Dr. Olivier Béthoux who is also studying insect material from Xiaheyan.

Material. *Holotype*. CNU-NX1-642a, b (formerly 91NZ4033 and 91NZ1029): (a) imprint of four insect wings, one completely preserved, two lacking basal parts and one folded and deformed in medial part (b) counter-imprint poorly preserved.

Supplementary material. CNU-NX1-644a, b (fragmentary preserved head, two pairs of wings incompletely preserved, abdomen with sclerotized ovipositor ventrally preserved, cerci). CNU-NX1-647a, b: (a) partially preserved head with short incomplete mouthparts, two nearly completely preserved wings, two fragmentary preserved wings, fragmentary preserved male genitalia, (b) apical parts of two wings.

Type stratum and locality. Tupo Formation, Carboniferous, Lower Pennsylvanian, Bashkirian, (equivalent to Namurian B–C), Xiaheyan, Zhongwei County, Ningxia Hui Autonomous Region, China.

Diagnosis. Wings homonomous, wing widest at about midwing, posterior margin evenly curved, from midwing to ending of MA nearly straight, ScP terminating on RA near the level of the first branching of RP, CuP simple or with terminal twig, brace m-cua almost three times longer than the short oblique CuA emerging from CuP.

Description. Based on Holotype specimen No. CNU-NX1-642a, b.

Both pairs of homonomous wings basally slender, membrane probably originally hyaline without a colour pattern; length of wing about 17.0 mm, width 3.6 mm at widest part; irregular cross veins sparsely distributed along posterior part of wing; anterior margin of wing slightly basally convex forming costal area with at least one perpendicular cross vein; ScP slightly bowed and terminating on RA beyond midwing, about 6.9 mm from wing apex; division RA and RP at about 1/3 of the wing length; simple RA

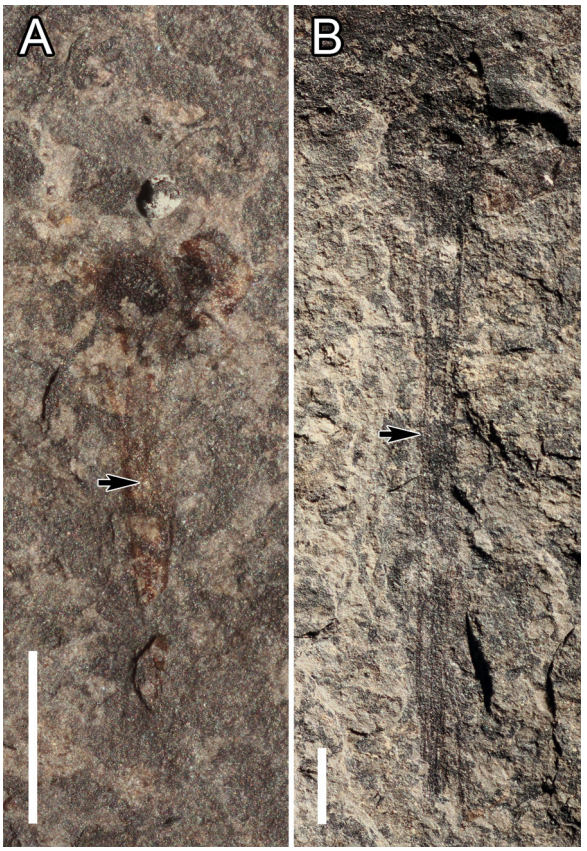


Fig. 10. (Color online.) Two types of rostrum-like mouthparts from Xiaheyan (China). **A**. *Sinopalaeopteryx olivieri* gen. nov. et sp. nov. (Aykhalidae), specimen CNU-NX1-647a (Capital Normal University, Beijing, China), detailed photograph of head with stout rostrum. **B**. *Brodioptera sinensis* Pecharová, Ren and Prokop, 2015, specimen CNU-NX1-609b (Capital Normal University, Beijing, China), detailed photograph of head with slender elongate rostrum, arrows indicate rostrum. Scale bars = 1 mm.
Fig. 10. (Couleur en ligne.) Deux types de parties de la bouche de type rostre en provenance de Xiaheyan (Chine). **A**. *Sinopalaeopteryx olivieri* gen. nov. et sp. nov. (Aykhalidae), spécimen CNU-NX1-647a (Capital Normal University, Pékin, Chine), photographie de détail de la tête avec un rostre robuste. **B**. *Brodioptera sinensis* Pecharová, Ren et Prokop, 2015, spécimen CNU-NX1-609b (Capital Normal University, Pékin, Chine), photographie de détail de la tête avec un rostre allongé mince ; les flèches indiquent le rostre. Barre d'échelle = 1 mm.

running parallel to anterior margin of wing reaches it close to apex; RP pectinate with three main branches, first branch simple or with terminal twig; M basally adjacent to radius, division of MA and MP based of separation of RA and RP; convex MA simple, basally connected by a short cross vein (brace) to division point of RA + RP; concave MP distally branched ending with two branches on posterior margin of wing; stem of Cu basally separated from RA + RP and M, division of CuA and CuP 3.2 mm from wing base, simple CuA diverging to M, shortly connected to M by cross vein (brace); simple CuP; anal area formed by single pectinate anal vein with four branches.

Dimensions. Holotype CNU-NX1-642a, b: Wing length 17.0 mm, maximum width 3.5 mm, CNU-NX1-644a, b: Length of best-preserved wing 16.5 mm, maximum width 3.4 mm, CNU-NX1-647a, b: Length of head including mouthparts 2.6 mm, forewing length 18.0 mm, maximum width 4.9 mm, hindwing length 18.6 mm, maximum width 4.9 mm.

Discussion. This fossil clearly belongs to the genus *Sinopalaeopteryx* as it has all of the diagnostic characters. Holotype of *S. olivieri* sp. nov. has four wings in various states of preservation, but it is impossible to distinguish between fore- and hindwings. Wings are homonomous without any sign of triangular shape as occurs in *S. splendens* sp. nov. Several differences in wing venation can be used to separate *S. olivieri* sp. nov. from *S. splendens* sp. nov.:

- ScP ends closer to the point of separation of the first branch of RP;
- brace m-cua distinctly much longer;
- wings markedly smaller in comparison to the latter species.

Cross veins are rather sparse in *S. olivieri* and numerous in *S. splendens*. However, this can be due to poor preservation.

The most apical branch of RP in *S. olivieri* is either simple or with short terminal twig. This example indicates possible problems associated with using "short terminal twig" as a diagnostic character in taxonomy.

Partly preserved head with mouthparts in form of stylets (No. CNU-NX1-647a) is discussed below (Chapter 4).

Genus ***Namuroptera*** gen. nov.

Type species. *Namuroptera minuta* sp. nov. here designated.

Etymology. Composite name after Namurian age and -ptera, feminine in gender.

Diagnosis. Based on wing venation; costal area with at least three perpendicular cross veins, ScP ending on RA beyond the midwing, near the level of the first branching of RP; MA connected at one point to RP; RP with three branches, the first one simple or with terminal twig, m-cua brace longer than a short oblique part of CuA emerging from CuP, aligned with a short brace rp-m; CuP simple; the first anal vein runs gradually parallel to posterior wing margin.

Namuroptera minuta sp. nov. (Figs. 11 and 12)

Etymology. Name based on its small size, in Latin.

Material. *Holotype*. CNU-NX1-646a, b (male), (a) counter-imprint of insect with partly preserved head with antenna, both pairs of wings with distinct wing venation markedly deformed, distal part of abdomen with gonopods and incomplete cerci; (b) imprint of fragmented head and a well-preserved set of wings.

Type stratum and locality. Tupo Formation, Carboniferous, Lower Pennsylvanian, Bashkirian, (equivalent to Namurian B–C), Xiaheyan, Zhongwei County, Ningxia Hui Autonomous Region, China.

Description. Based on Holotype specimen No. CNU-NX1-646a, b (male).

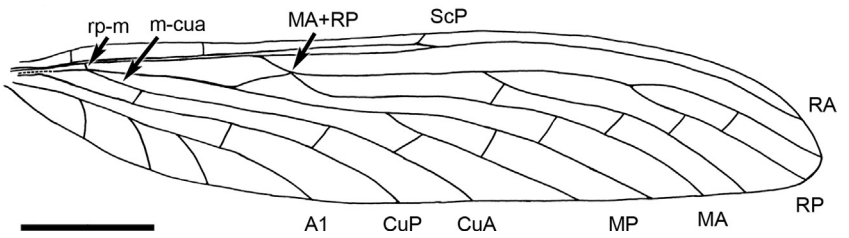


Fig. 11. *Namuroptera minuta* gen. nov. et sp. nov., holotype CNU-NX1-646b (Capital Normal University, Beijing, China), line drawing of the best preserved wing. Scale bar = 2 mm.
Fig. 11. *Namuroptera minuta* gen. nov. et sp. nov. holotype CNU-NX1-646b (Capital Normal University, Pékin, Chine), dessin au trait de l'aile la mieux préservée. Barre d'échelle = 2 mm.

Caput. Poorly preserved with possible internal structures (endoskeleton) and multisegmented long antennae.

Thorax. Fragmentarily preserved, prothorax markedly elongated.

Wings. Both pairs basally broad, membrane hyaline, forewing and hindwing nearly homonomous with broader costal area in forewings; venation slightly distorted (corresponding measurements given for right hindwing); costal margin slightly convex; ScP reaching RA well beyond midwing, 5.8 mm from wing apex, short cross vein present between ScP and anterior wing margin 0.2 mm before tip of ScP; costal area basally broad with several oblique or perpendicular cross veins present in basal half of wing area; radius slightly basally bowed, separation of RA from RP in basal third of the wing, 4.2 mm from wing base, RA reaching anterior wing margin well before wing apex, RP pectinate ending in three branches that cover wing apex, first branch simple or with terminal twig; stem of M running basally close to radius, division of MA and MP 3.8 mm from the wing base, convex simple MA strongly diverging to RP and connected at one point; concave MP ending with two long branches on posterior wing margin, division of CuA and CuP 2.1 mm from wing base, convex simple CuA connected with M by very long brace m-cua (0.8 mm long) aligned with short brace rp-m; concave CuP simple, single anal vein pectinate reaching posterior wing margin with four simple branches.

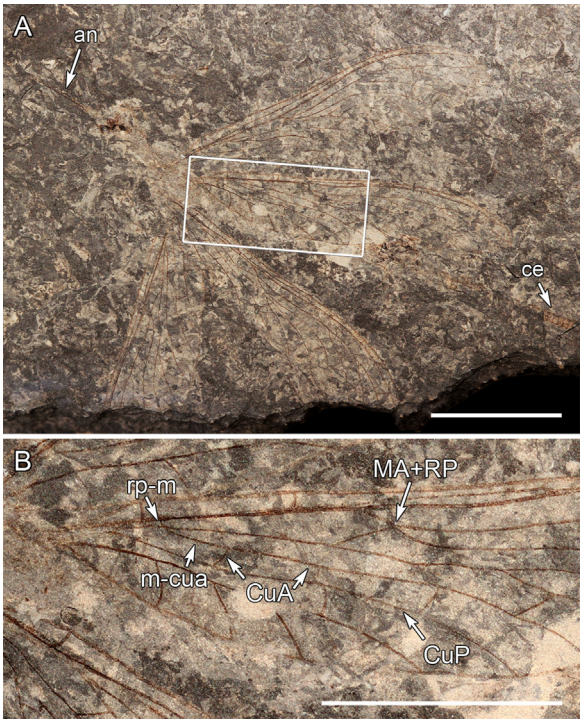


Fig. 12. (Color online.) *Namuroptera minuta* gen. nov. et sp. nov., holotype CNU-NX1-646b (Capital Normal University, Beijing, China). **A**. Photograph of habitus with marked part in detail, [an: antenna; ce: cerci]. **B**. Detail of basal part of hindwing. Scale bars = 5 mm (A), 3 mm (B).
Fig. 12. (Couleur en ligne.) *Namuroptera minutra* gen. nov. et sp. nov., holotype CNU-NX1-646b (Capital Normal University, Pékin, Chine). **A**. Photographie de l'habitus avec la partie encadrée pour le détail [an : antenne ; ce : cerci]. **B**. Détail de partie basale d'aile arrière. Barres d'échelle = 5 mm (A), 3 mm (B).

Abdomen. Male gonopods present, the terminal abdominal segment with a pair of segmented stout cerci bearing dense setation.

Dimensions. Holotype CNU-NX1-646a, b: estimated body length 13.5 mm, wing length 12.5 mm (the most complete without visible distortion), maximum width 2.5 mm.

Discussion. First, this fossil has the same pattern of venation as the family Sphecopteridae but differs mainly in having basally broader wings and an RA that does not reach the apex of the wing. The combination of the following characters:

- elongate nearly homonomous wings not petiolate basally;
- costal area basally broad with several cross veins;
- ScP ending on RA beyond midwing;
- RP with several branches;
- stems M and Cu basally well separated;
- MP branched,

support the placement of this fossil in the Aykhalidae (Sinitshenkova, 1993).

Namuroptera gen. nov. differs in the presence of a pointed connection between MA and RP and very long brace m-cua and well aligned short brace rp-m, unlike in *Aykhal* and *Sinopalaeopteryx*. In addition, *Namuroptera* markedly differs in the smaller size of its wings, which are about 12 mm long compared to a range of 17 to 27 mm for *Aykhal* and *Sinopalaeopteryx*. Nevertheless, *Namuroptera* provides evidence for a disparity in the pattern of venation in Aykhalidae.

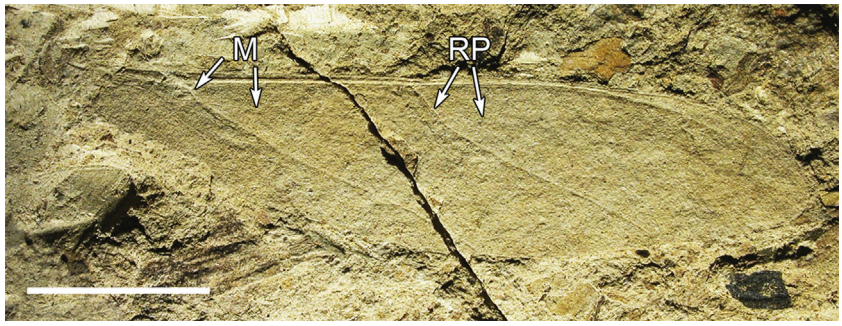


Fig. 13. *Scytohymen extremus* Martynov, 1937, holotype No. 2/99 (Palaeontological Institute of RAS coll., Moscow, Russia), photograph of wing. Scale bar = 10 mm.
Fig. 13. *Scytohymen extremus* Martynov, 1937, holotype nº 2/99 (Palaeontological Institute of RAS coll., Moscou, Russie), photographie d'aile. Barre d'échelle = 10 mm.

In particular, the course of vein CuA beyond its separation from CuP, markedly changes at the level of brace m-cua from strongly convex (proximal part) to neutral or concave (distal part). We suspect this is similar to the course of vein RP at the point of contact with MA as can be seen in *Scytohymen extremus* Martynov, 1937 (Fig. 13).

Note. The fossils from Ningxia are often badly distorted with hardly identifiable veinal splits. This can be seen on the right hindwing of CNU-NX1-646a, b (Fig. 12), where vein RA seems to run over ScP, which is not the case on the other wings. This is a result of postmortal distortion.

4. Morphology of the mouthparts of Aykhalidae

The head and mouthparts of Aykhalidae are only preserved in *S. olivieri* (suppl. spec. No. CNU-NX1-647a), which clearly show rather short and basally stout stylets and fragmentarily preserved other parts, possibly the eyes (see Fig. 10A). However, the lengths of the stylets are half the length of those of *B. sinensis* (Brodiopteridae), in which the stylets are half the length of the body (see Fig. 10B) (Pecharová et al., 2015). The occurrence of both types at the same locality suggests probable adaptation to feeding on a different plant, if these insects are herbivorous. Variation in size of stylets among Palaeodictyopteroida is rather broad and associated with their specialization for feeding on particular plants or tissues of plants (Shear and Kukalová-Peck, 1990). Labandeira and Phillips (1996) described palaeodictyopteran piercing-and-sucking damage to the phloem and xylem of the marattialean tree fern *Psaronius chasei* from the Late Pensylvanian in the Illinois Basin. Shcherbakov et al. (2009) report Cordaite seeds with punctures made by palaeodictyopteroids (?Megasecoptera) in the Early Permian of Russky Island, South Primorye in Russian Far East. So far, the palaeobotanical record for Xiaheyan has revealed a fascinating fructification of *Nudasporestrobus ningxicus* with *in situ* megaspores possibly attributed to a lycopsid *Sigillaria* sp. The large cylindrical strobilus has an incomplete peduncle with sporophylls arranged in ascending spirals, each bearing a sporangium with megaspores *in situ* (Feng et al., 2008). Such plants are a rich food source for sucking insects, but so far, there is no evidence of piercing or sucking damage to these plants.

5. Conclusions

Early Namurian insects are currently the oldest unambiguous records of Pterygota or winged insects, a novelty undoubtedly responsible for their success (Engel et al., 2013; Nicholson et al., 2014). Megasecopterans are among the groups with members already known since the Namurian B from deposits in Europe and North America (Brauckmann et al., 2003; Nelson and Tidwell, 1987). The recent discovery of the Chinese locality at Xiaheyan revealed an unexpected diversity of insects. The presence of *B. sinensis* Pecharová, Ren and Prokop, 2015 (Megasecoptera: Brodiopteridae) supports relationships with species known from Europe [*B. pintoi* (Brauckmann et al., 2003)] and North America (*B. cumberlandensis* Copeland, 1957 and *B. stricklani* Nelson and Tidwell, 1987) of a similar age (Pecharová et al., 2015). Moreover, there are many megasecopterans along with the odonatopterans, archaeorthopterans and grylloblattodenans discovered at this locality. At least, it seems that they are the most abundant group of palaeodictyopteroids after the scarce Palaeodictyoptera, for which there are two described species (Li et al., 2013b; Prokop and Ren, 2007).

Two new genera and three species of megasecopteran Aykhalidae, *S. olivieri* gen. nov., sp. nov., *S. splendens* sp. nov. and *Namuroptera minuta* gen. nov., sp. nov. from Xiaheyan, together with known *A. helenae* from Gzhelian/Asselian of Yakutia-Sakha deposits in Siberia reveal unique links with the family Sphecopteridae known from the Gzhelian in Europe (Commentry, France). This close relationship is based on a number of shared characteristics of wing venation, which is also supported by the time span and broad distribution. This discovery also reveals that pattern in wing venation of some related megasecopteran families remained stable during the Pennsylvanian.

In addition, we document intraspecific (and individual) variability in the veins RP and CuP of members of the family Aykhalidae (*S. olivieri* gen. nov., sp. nov.) and Sphecopteridae (*C. chatini* Brongniart, 1893). Finally, the polarity of the course of vein CuA in *N. minuta* gen. nov., sp. nov. beyond its separation from CuP changes markedly at the level of brace m-cua from strongly convex to neutral or concave. We suspect this is comparable to the course of vein RP at

the point of contact with MA as can be seen in *S. extremus* Martynov, 1937.

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