

New fossils from China elucidating the phylogeny of Praesiricidae (Insecta: Hymenoptera)

MEI WANG¹, ALEXANDR P. RASNITSYN^{2,3}, CHUNGKUN SHIH¹,
MICHAEL J. SHARKEY⁴ and DONG REN¹

¹College of Life Sciences, Capital Normal University, Beijing, China, ²Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia, ³Department of Palaeontology, Natural History Museum, London, U.K. and ⁴Department of Entomology, University of Kentucky, Lexington, KY, U.S.A.

Abstract. A new subfamily of Praesiricidae (Pamphilioidea), Decorisiricinae **subfam.n.**, is erected based on three new genera: *Decorisiricius* **gen.n.**, *Limbisiricius* **gen.n.** and *Brevisiricius* **gen.n.** Two new species – *Decorisiricius patulus* **gen. et sp.n.** and *D. longus* **sp.n.** – from the Lower Cretaceous Yixian Formation and three species – *Limbisiricius aequalis* **gen. et sp.n.**, *Limbisiricius complanatus* **sp.n.** and *Brevisiricius partialis* **gen. et sp.n.** – from the Middle Jurassic Jiulongshan Formation, are described. Based on these well-preserved new fossil specimens and previously published data, the nonmonophyly of Praesiricidae is confirmed and the phylogenetic relationships of species of Praesiricidae are analysed for the first time. Two main clades within Praesiricidae are recognized from the cladistic analysis: Decorisiricinae **subfam.n.** forms a monophyletic lineage, with the remaining members of Praesiricidae plus *Megalodontes* (*Megalodontesidae*) forming its sister group. The two subfamilies Archoxyelydinae and Praesiricinae are discarded with no strong supported synapomorphic characters based on phylogenetic research. A key to all genera of Praesiricidae is provided.

Introduction

Praesiricidae, an extinct family of sawflies, has seven described genera and 15 species to date, which are summarized in Table 1 (Rasnitsyn, 1968, 1969, 1983, 1990). It comprises three subfamilies: Praesiricinae Rasnitsyn; Rudisiricinae Gao, Rasnitsyn, Ren & Shih; and Archoxyelydinae Wang, Rasnitsyn & Ren (Rasnitsyn, 1968; Gao *et al.*, 2010; Wang *et al.*, 2013). However, *Hoplitolyda* Gao, Shih, Rasnitsyn & Ren has not been placed in any subfamily due to its limited number of preserved characters (Gao *et al.*, 2013a). The earliest fossil record of Praesiricidae is *Aulidontes mandibulatus* Rasnitsyn reported from the Upper Jurassic of Southern Kazakhstan (Rasnitsyn, 1983).

Recently, some interesting and enigmatic praesiricid fossils have been described, namely:

- *Rudisiricius*, with only male fossils described, has a thick and long scape, strong and sickle-shaped mandibles, and forewing with dark transverse bands. It is highly diverse in the Yixian

Formation but nowhere else yet (Gao *et al.*, 2010; Wang *et al.*, 2015);

- *Archoxyelyda* has a modified antennal flagellum, consisting of thick and tightly connected flagellomeres, demonstrating flagellar transformation in the lower Hymenoptera (Wang *et al.*, 2013); and
- *Hoplitolyda* is the largest fossil hymenopteran, with a body length estimated at >55.0 mm, and a wing span of >92.0 mm, the genus is the only sawfly with vein SC present in the hind wing but not in the forewing (Gao *et al.*, 2013a).

Phylogenetic relationships among extant pamphilioids have been discussed in several studies (Ronquist *et al.*, 1999, 2012; Sharkey *et al.*, 2012; Klopstein *et al.*, 2013; Malm & Nyman, 2014). The consensus of these results favour the monophyly of Pamphilioidea, with Pamphiliidae and Megalodontesidae as sister groups. However, fossil sawflies have not been incorporated in these studies. Rasnitsyn & Quicke (2002) discussed the interfamilial relationships of the Pamphilioidea including fossil taxa; but the intergeneric relationships of extinct Xyelydidae and Praesiricidae have not been studied.

Recently we collected six specimens of Praesiricidae from northeastern China. Three are from the Lower Cretaceous Yixian

Correspondence: Dong Ren, College of Life Sciences, 105 Xisanhuanbeilu, Haidian District, Capital Normal University, Beijing 100048, China. E-mail: rendong@mail.cnu.edu.cn

Table 1. Summary of known species of Praesiricidae.

Subfamily	Species	Locality	Horizon	Body length (mm)	Wing length (mm)
Praesiricinae	<i>Praesirex hirtus</i> Rasnitsyn	Baissa; Transbaikalia; Russia	Lower Cretaceous	11.0	10.0
	<i>Turgidontes magnus</i> Rasnitsyn	Turga, Transbaikalia, Russia	Lower Cretaceous	21.0	16.0
	<i>Hoplitolyda duolunica</i> Gao, Shih, Rasnitsyn & Ren	Duolun County, Inner Mongolia, China	Lower Cretaceous	>55.0	41.6
Archoxyelydinae	<i>Xyelodontes sculpturatus</i> Rasnitsyn	Bon Tsagan, Bayan-Khongor Aymag, Mongolia	Lower Cretaceous	14.5	10.0 estimated
	<i>Archoxyelyda mirabilis</i> Wang, Rasnitsyn & Ren	Huangbanjigou, Liaoning, China	Lower Cretaceous	9.4	6.5
Rudisiricinae	<i>Aulidontes mandibulatus</i> Rasnitsyn	Karatau, Kazakhstan	Upper Jurassic	<17.0	8.5
	<i>Rudisiricius belli</i> Gao, Rasnitsyn, Shih & Ren	Huangbanjigou, Liaoning, China	Lower Cretaceous	17.5	11.0
	<i>R. crassinodus</i> Gao, Rasnitsyn, Shih & Ren	Huangbanjigou, Liaoning, China	Lower Cretaceous	16.0	11.0
	<i>R. celsus</i> Gao, Rasnitsyn, Shih & Ren	Huangbanjigou, Liaoning, China	Lower Cretaceous	14.2	10.0
	<i>R. validus</i> Wang, Rasnitsyn, Shih & Ren	Huangbanjigou, Liaoning, China	Lower Cretaceous	12.9	9.7
	<i>R. ferox</i> Wang, Rasnitsyn, Shih & Ren	Huangbanjigou, Liaoning, China	Lower Cretaceous	11.9	8.7
	<i>R. ater</i> Wang, Rasnitsyn, Shih & Ren	Huangbanjigou, Liaoning, China	Lower Cretaceous	10.3	6.6
	<i>R. tenellus</i> Wang, Rasnitsyn, Shih & Ren	Huangbanjigou, Liaoning, China	Lower Cretaceous	12.9	8.9
	<i>R. membranaceous</i> Wang, Rasnitsyn, Shih & Ren	Huangbanjigou, Liaoning, China	Lower Cretaceous	13.5	8.8
	<i>R. parvus</i> Wang, Rasnitsyn, Shih & Ren	Huangbanjigou, Liaoning, China	Lower Cretaceous	9.3	6.3
	<i>Decorisiricius patulus</i> gen. et sp.n.	Huangbanjigou, Liaoning, China	Lower Cretaceous	8.9	5.5
	<i>Decorisiricius longus</i> sp.n.	Huangbanjigou, Liaoning, China	Lower Cretaceous	11.0	6.7
Decorisiricinae	<i>Limbsiricius aequalis</i> gen. et sp.n.	Daohugou, Inner Mongolia, China	Middle Jurassic	11.4	7.3
	<i>Limbsiricius complanatus</i> sp.n.	Daohugou, Inner Mongolia, China	Middle Jurassic	11.0	7.4
	<i>Brevisiricius partialis</i> gen. et sp.n.	Daohugou, Inner Mongolia, China	Middle Jurassic	8.6 as preserved	6.4 estimated

Formation near Chaomidian Village belonging to the famous Jehol biota (Ren *et al.*, 1997). The other three are from the late Middle Jurassic Jiulongshan Formation near Daohugou Village belonging to the Yanliao biota (Gao & Ren, 2006). These localities have yielded numerous excellently preserved insect fossils (Ren *et al.*, 2010, 2012), including Embioptera (Huang & Nel, 2009), Mecoptera (Wang *et al.*, 2012), Hymenoptera (Wang *et al.*, 2013), and basal and transitional Siphonaptera (Gao *et al.*, 2012, 2013b; Huang *et al.*, 2012).

A new subfamily, comprising three new genera and five new species, is reported herein, based on a suite of unique characters possessed by all six specimens. The first phylogenetic analysis of intergeneric relationships in Praesiricidae is conducted. The new praesiricids and the phylogenetic results provide new insights into the origin and evolution of Praesiricidae. They also enable us to update the phylogenetic relationships amongst the genera of Praesiricidae and to confirm the monophyly of the new subfamily.

Materials and methods

Examined taxa and terminology

The type material described in this paper is deposited in the Key Lab of Insect Evolution and Environmental Changes,

College of Life Sciences, Capital Normal University, in Beijing, China (CNUB; Ren Dong, Curator). The specimens were examined and photographed, either dry or moistened with 95% ethanol, with a Leica DFC500 digital camera attached to a Leica MZ 16.5 dissecting microscope (Leica, Wetzlar, Germany). Scanning electron micrographs (SEM) were taken using a ESEM (Quanta 200F, FEI) in the Beijing Museum of Natural History.

The colours of fossils described below are not reliably known because of the absence of counterpart fossils, and are simply direct descriptions of the surface of fossils. The line drawings were prepared using Adobe Illustrator CS2 and Adobe Photoshop CS5 software. The wing venation nomenclature used in this paper is modified after Rasnitsyn (1969, 1980). Venation symbols: main (longitudinal) veins = SC, R, RS, RS + M, M, Cu, M + Cu; sections (abscissae) of longitudinal veins = 1-RS, 1-M, etc.; crossveins = 1r-rs, 2r-rs, 2r-m, etc.; cells = 1r, 2rm, 1mcu, etc.

Phylogenetic analysis

A phylogenetic analysis was conducted to elucidate the position of our new subfamily within Praesiricidae and to clarify subfamilial and generic relationships. Many characters, widely used in phylogenetic analyses of extant sawflies (Ronquist *et al.*,

Table 2. Character matrix of 18 characters for the 18 taxa included in this study.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
* <i>Juraphilopotamus lubricus</i> (Trichoptera)	?	2	0	0	1	–	–	–	–	0	0	–	0	1	–	0	0	0
* <i>Anthoxyela orientalis</i> (Xyelidae)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
* <i>Xyelotoma macroclada</i> (Xyelotomidae)	1	0	0	?	0	1	1	2	0	?	0	0	0	0	0	0	1	0
* <i>Scabolyda orientalis</i> (P)	0	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	1
* <i>Prolyda karatavica</i> (X)	0	0	0	0	0	1	0	1	0	1	0	0	0	1	0	0	1	1
* <i>Praesirex hirtus</i> (Pr)	2	1	0	0	0	1	1	?	1	1	?	1	0	1	0	0	1	1
* <i>Turgidontes magnus</i> (Pr)	2	1	0	?	0	1	1	0	1	?	?	1	0	1	0	0	1	1
* <i>Aulidontes mandibulatus</i> (Pr)	2	1	1	1	0	0	0	1	2	1	1	0	0	1	0	0	1	1
* <i>Rudisircius belli</i> (Pr)	2	1	1	?	0	1	1	0	2	1	1	0	0	1	0	0	1	1
* <i>Archoxyelyda mirabilis</i> (Pr)	2	1	0	1	0	1	1	1	1	?	0	0	0	1	0	0	1	1
* <i>Hoplitolyda duolunica</i> (Pr)	2	2	0	?	0	0	1	0	1	0	1	1	0	1	0	0	1	1
* <i>Decorisircius patulus</i> gen. et sp.n. (Pr)	2	1	0	1	0	1	0	0	2	1	0	0	1	1	0	0	1	1
* <i>Limbisircius aequalis</i> gen. et sp.n. (Pr)	2	?	?	?	1	1	0	0	1	1	?	0	1	1	0	0	1	1
<i>Cephalcia semidea</i> (P)	0	1	0	1	0	1	1	0	0	0	0	0	0	0	1	1	1	1
<i>Acantholyda erythrocephala</i> (P)	0	1	0	1	0	1	1	1	0	0	0	0	0	0	1	1	1	1
<i>Neurotoma fasciata</i> (P)	0	2	0	1	0	1	1	0	0	0	0	0	0	0	1	1	1	1
<i>Pamphilus hortorum</i> (P)	0	2	0	1	0	1	1	0	1	0	0	0	0	0	1	1	1	1
<i>Megalodontes capitalatus</i> (M)	2	2	0	1	0	0	1	0	2	1	1	1	0	1	0	0	1	1

* indicates fossil species.

P, Pamphiliidae; X, Xyelydidae; Pr, Praesiricidae; M, Megalodontesidae.

1999, 2012; Schulmeister, 2003), are often poorly preserved in compression fossils. Therefore, only 18 morphological characters, 11 wing characters and seven body characters were employed in our phylogenetic analysis. The character selection was partly based on the characters used by Ronquist *et al.* (1999) in their phylogenetic analysis of the Pamphilioidea and Symphyta. The characters and their states are listed in Appendix.

We chose the following three outgroup species: *Juraphilopotamus lubricus* Wang, Zhao & Ren (Trichoptera, Hydrobiosidae) (Wang *et al.*, 2009), on which the tree was rooted; *Anthoxyela orientalis* Gao & Ren (Xyelidae) (Gao & Ren, 2008); and *Xyelotoma macroclada* Gao, Ren & Shih (Xyelotomidae) (Gao *et al.*, 2009). The ingroup consists of one extinct genus *Scabolyda* (Wang *et al.*, 2014a) and four extant genera *Acantholyda*, *Cephalcia*, *Neurotoma* and *Pamphilus* of Pamphiliidae, one extinct genus *Prolyda* of Xyelydidae (Rasnitsyn, 1983), the extant genus *Megalodontes* of Megalodontesidae, and eight extinct genera of Praesiricidae. Recent species studied here are scored from the literature (Cresson, 1880; Konow, 1904; Benson, 1945; Middlekauff, 1958, 1964; Riou, 1999).

Two genera of Praesiricidae, *Xyelodontes* Rasnitsyn and *Brevisircius* **gen.n.**, were excluded in the matrix due to the lack of key characters preserved on the type specimens. The character matrix is presented in Table 2.

A maximum parsimony analysis of the morphological dataset (Table 2) was conducted in TNT 1.1 (Goloboff *et al.*, 2003) using the traditional search to find most parsimonious trees (MPTs) under the following parameters: memory set to hold 1 000 000 trees; zero random seed, tree bisection reconnection (TBR) branch swapping algorithm with 10 000 replications saving 100 trees per replicate. The characters were mapped in WinClada (Nixon, 2002), all characters were treated as unordered and with equal weight; missing data were coded with question marks.

Results

Analysis of the morphological data matrix by TNT yielded only one most parsimonious tree, with the following characteristics: tree length 41, consistency index (CI) 53 and retention index (RI) 71, which is presented in Fig. 1.

The superfamily Pamphilioidea is confirmed monophyletic by oral and mandibular foramina separated; our target lineage Praesiricidae is paraphyletic, but together with *Megalodontes* (Megalodontesidae) forms a monophyletic group supported by an unambiguous character: SC of forewing absent (character 1-2). This complicated group is split into two major lineages: the monophyly of Decorisircinae is supported by one unambiguous character, namely the ratio of basal 1/3 to 1/2 of costal area to the widest costal area <1/2, very narrow (13-1); and its sister group is supported by one synapomorphy, namely forewing with 1-RS perpendicular to R or reclinal (7-1).

The subfamily Archoxyelydinae is weakly supported by one homoplastic synapomorphy: forewing with 2r-m interstitial (8-1). One synapomorphic character – mandible long and sickle-like (11-1) – supports the Rudisircinae + remaining praesiricids + *Megalodontes*. One unambiguous character – antenna with long, thick scape (3-1) – and one homoplastic character – forewing with 1cu-a distinctly basal to cell 1mcu (9-2) – support the Rudisircinae as a monophyletic group. The remaining genera (*Hoplitolyda*, *Turgidontes*, *Praesirex*) plus *Megalodontes* form a monophyletic group supported by an uniquely derived character: forewing R straight (12-1).

Taxonomy

Superfamily Pamphilioidea Cameron

Family Praesiricidae Rasnitsyn

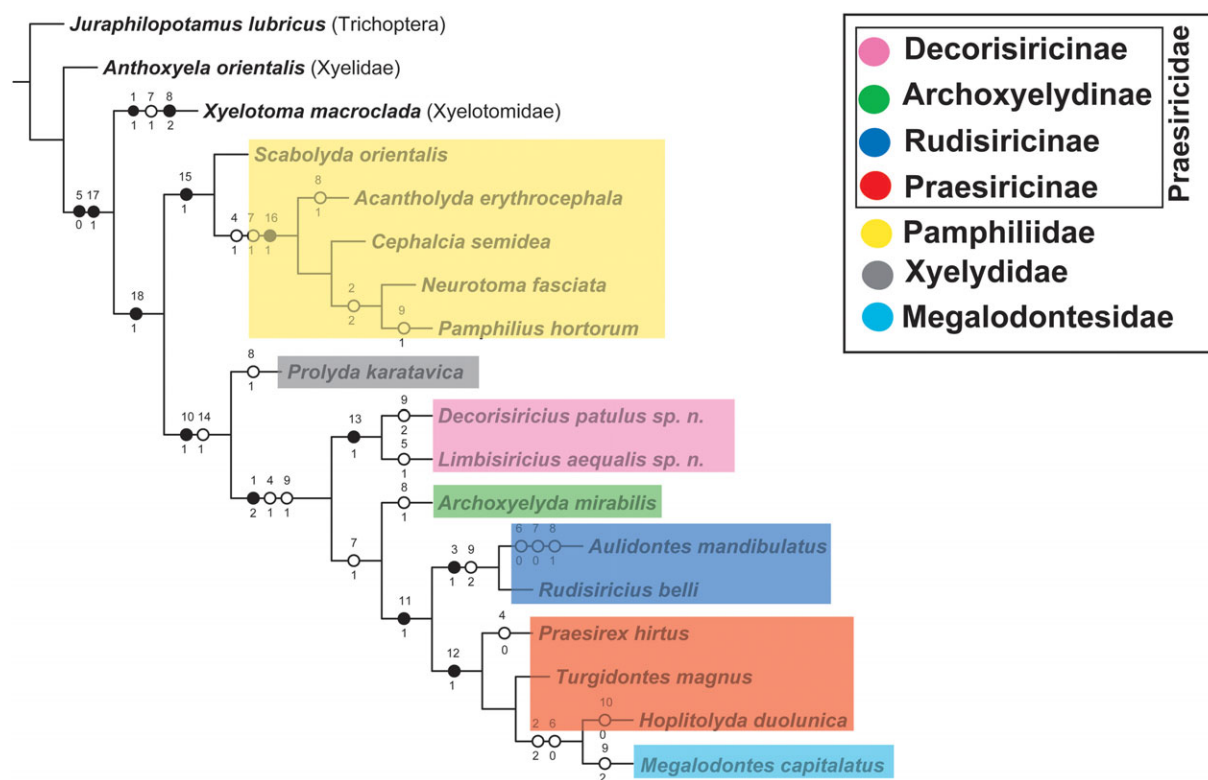


Fig. 1. The strict consensus tree of phylogenetic analysis. (●) Nonhomoplastic; (○) homoplastic.

Subfamily Decorisiricinae subfam.n.

Type genus. *Decorisiricius* gen.n.

Diagnosis. Mandible not very large (almost 0.5× head width). Scape ordinary (much shorter than head length), first flagellomere thicker and much longer than second flagellomere. Forewing with basal $\frac{1}{3}$ to $\frac{1}{2}$ of costal area very narrow; R angled at, or bent near, base of RS; 1-RS proclival; M + Cu nearly straight.

Genera included. *Decorisiricius* gen.n., *Limbisiricius* gen.n. and *Brevisiricius* gen.n.

Decorisiricius gen.n.

Type species. *Decorisiricius patulus* sp.n.

Etymology. The generic name is a combination of the Latin 'decor-', meaning beautiful, referring to the well-preserved fossil and 'siric' from the family Praesiricidae. Gender masculine.

Included species. *Decorisiricius patulus* sp.n. and *Decorisiricius latus* sp.n.

Diagnosis. Head large, rounded, nearly as wide as mesothorax; antenna (incomplete) with 11–15 segments, the first flagellomere $\geq 4.6\times$ as long as wide, thicker than

following segments and about as long as the remaining three segments combined; forewing with pterostigma completely sclerotized; 1-RS about 0.4× as long as 1-M; 1m-cu longer than 0.5× 1-M; 1cu-a basal to the mid-length of cell 1mcu, nearly as long as 2-Cu.

Decorisiricius patulus sp.n. (Fig. 2)

Diagnosis. Forewing: 2-RS present; 2r-m separated from 2r-rs by 0.4× of its own length; 1cu-a distad of the origin of 1-Cu by about 0.5× its own length; 1-Cu nearly 0.5× as long as 2-Cu; 2m-cu angled toward wing base, originating near the middle of cell 3rm.

Etymology. The species name is derived from the Latin word 'patulus', meaning broad, referring to the expanded and complete forewings.

Material. Holotype, No. CNU-HYM-LB-2012127; Paratype: No. CNU-HYM-LB-2012128.

Locality and horizon. Huangbanjigou, Chaomidian Village, Shangyuan Township, Beipiao City, Liaoning Province, China; Early Cretaceous, Yixian Formation.

Description. Holotype: As preserved, body moderately dark; antenna and pterostigma slightly paler than head, thorax and

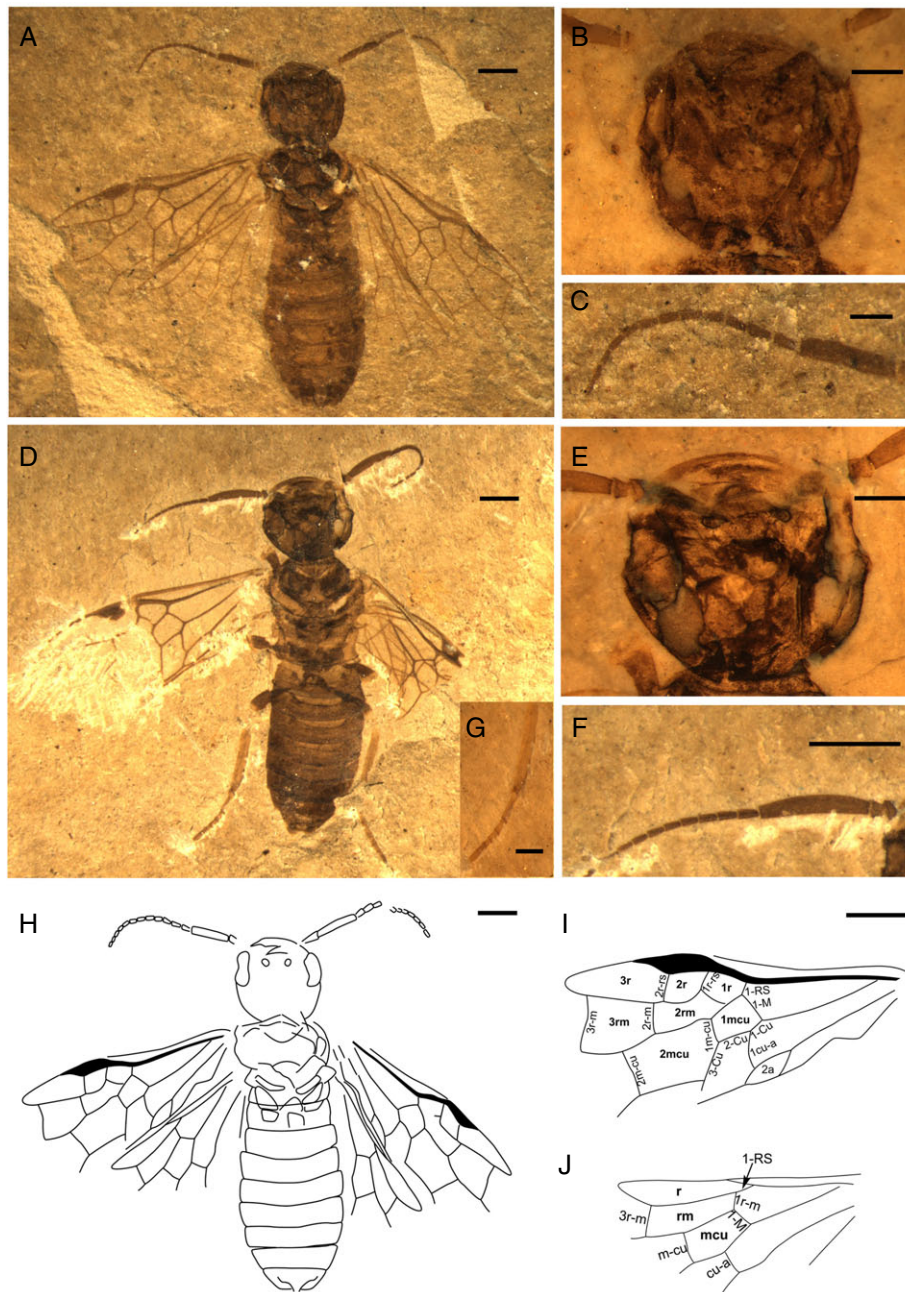


Fig. 2. *Decorisiricius patulus* gen. et sp.n. Holotype (A–C, H–J), CNU-HYM-LB-2012127; Paratype (D–G), CNU-HYM-LB-2012128. (A) Photo of habitus. (B) Head under alcohol. (C) Part of left antenna. (D) Photo of habitus. (E) Head under alcohol. (F) Part of left antenna. (G) Part of left leg under alcohol. (H) Line drawing of holotype. (I) Line drawing of left forewing. (J) Line drawing of left hind wing. Scale bars: 1 mm in (A), (D), (F), (H) and (I); 0.5 mm in (B), (C), (E) and (G). In all figures, cell symbols are bold and vein symbols are thin.

abdomen; forewing somewhat infuscated sub-basally, particularly so in veins in costal area (Fig. 2A).

Head: Head (Fig. 2B) massive and subcircular, about as long as wide, and nearly as wide as mesothorax, with eye relatively large, reniform, situated anteriorly and almost reaching mandibular base; eye length $0.4\times$ head length; right mandible preserved, bent, sickle-shaped, with apical tooth long and

slanting, subapical tooth sharp, situated near mid-length of mandible; antenna (Fig. 2C) nearly $1.5\times$ as long as head width, with 15 segments preserved; pedicel almost $2.3\times$ as long as wide, and $1.2\times$ as wide as the first flagellomere; first flagellomere $4.6\times$ as long as wide, $1.7\times$ as thick as the remaining antennal articles, and about equal to the following four combined; remaining antennal articles elongate and cylindrical.

Thorax: Prothoracic structure poorly known except for pronotum short with wide and shallowly incurved hind margin; mesoscutellum short; dorsal structures posterior to mesoscutellum not observable (Fig. 2A, H).

Abdomen: Abdomen only slightly wider than mesothorax; segments I to II slightly shorter than remaining abdominal segments; genitalia incompletely preserved, structures unknown.

Forewing (Fig. 2H, I): pterostigma completely sclerotized; R distinctly curved at RS base, thickened after origin of RS; 1-RS short and proclival, about $0.36\times$ as long as 1-M; 1r-rs parallel to 1-RS; 2r-rs about $1.3\times$ as long as 1r-rs, with RS between them and arching towards posterior margin of wing; M + Cu almost straight; 2r-m separated from 2r-rs by $0.38\times$ its own length, located distad of the middle of cell 2mcu; 3r-m curved, intersecting cell 3r in apical $1/4$, and nearly twice as long as 2r-m; 1m-cu $0.78\times$ as long as 1-M, 0.74 and $0.59\times$ as long as 2-Cu and 3-Cu, respectively; 1cu-a distinctly bent towards wing apex, nearly as long as 2-Cu, and placed proximad of the middle of cell 1mcu; 1-Cu nearly $0.49\times$ as long as 2-Cu; 2m-cu curved, intersecting middle of cell 3rm; cell 1mcu almost rectangular, $1.43\times$ as long as wide, and $0.9\times$ as long as cell 2rm; cell 2rm almost $0.78\times$ as long as cell 3rm, $0.55\times$ as long as, and $0.52\times$ as wide as, cell 2mcu; cell 3rm widened toward apex; cell 3r $3\times$ as long as cell 2r.

Hind wing (Fig. 2J): vein SC lost; 1-RS slightly shorter than 1-M; crossvein 1r-m distant from bases of both RS and M, and about $0.82\times$ as long as 1-M; 3r-m separated from apex of cell r by a distance slightly longer than its length; crossvein m-cu equal to 3r-m in length, located distad of mid-length of cell rm, and separated from 3r-m by $1.2\times$ of its own length; crossvein cu-a slightly distad of mid-length of cell mcu.

Paratype No. CNU-HYM-LB-2012128 (Fig. 2D–G)

Body moderately dark, including head, antenna, pterostigma, thorax and abdomen, with hind femora slightly paler (Fig. 2D).

Antenna (Fig. 2F) with 11 visible segments, the first flagellomere $5.8\times$ as long as wide, nearly equal to following six flagellomeres combined.

Pronotum short, with slightly waved hind margin; mesoscutum large, occupying nearly half of mesonotum, anterior edge nearly straight; notauli meeting at an angle of 108° , $0.69\times$ as wide as metascutellum; metanotum with cenchri; metascutellum comparatively narrow.

Legs poorly preserved (Fig. 2G); hind tibia comparatively thin and long, $1.9\times$ as wide as hind basitarsus, and nearly as long as the second abdominal segment; length of tarsal segments $1:2:3:4:5 = 4.2:1.9:1.5:1.3:2$. Male genitalia with gonostyle protruding, only apex visible.

Forewing (Fig. 2D) with pterostigma fusiform and widened towards the middle; 1-RS proclival, nearly $0.42\times$ as long as 1-M; 1r-rs bent toward wing apex, and $0.54\times$ as long as 2r-rs; 1m-cu $0.83\times$ as long as 1-M; cell 1mcu $1.4\times$ as long as wide; cell 3rm widened toward apex; cell 3r $3.3\times$ as long as cell 2r.

Measurements (in mm): (Holotype) Body length (excluding antenna) 8.93; head length including mandible 2.22, width 2.03;

forewing length (up to end of cell 3r) 5.48. (Paratype) Body length (excluding antenna) 9.3; head length including mandible 2.2, width 2.4; forewing length (up to end of cell 3r) 6.4.

Decorisiricius longus sp.n. (Fig. 3)

Diagnosis. Forewing: 2-RS lost; 2r-m separated from 2r-rs by its own length; 1cu-a slightly distad of origin of 1-Cu; 1-Cu about $0.3\times$ as long as 2-Cu; and 2m-cu proximad of the middle of cell 3rm.

Etymology. The species name is derived from the Latin word 'longus', meaning long, referring to 2r-m of forewing distant from 2r-rs.

Material. Holotype, No. CNU-HYM-LB-2012126.

Locality and horizon. Huangbanjigou, Chaomidian Village, Shangyuan Township, Beipiao City, Liaoning Province, China; Early Cretaceous, Yixian Formation.

Description. Body infuscated with head, thorax, abdomen and parts of legs; parts of antennae and pterostigma slightly paler (Fig. 3A).

Head: Head (Fig. 3D) relatively large, subcylindrical, length nearly equal to width, and nearly $0.87\times$ as wide as mesothorax; clypeus margin slightly protruding, possibly with slight medial lobe; eyes reniform, $2.3\times$ as long as wide, with ocelli indiscernible; mandible sickle-shaped, long, narrow but not thick; other detailed structures of mouthparts obscure; oral cavity isolated from occipital foramen by hypostomal bridge; occipital foramen nearly rectangular; antenna with only part of the first flagellomere, and remaining two flagellomeres (right antenna) poorly preserved.

Thorax somewhat deformed, structures indiscernible. Abdomen with eight segments as preserved; wider than mesothorax; the fourth segment slightly longer than other segments; sterna narrow, parallel-sided, laterotergites not wide, with medial margin rounded. Genitalia indistinct (sex unknown). Legs poorly preserved, with hind femora wider than fore and mid femora; and mid coxa trapezoidal.

Wings: Forewing (Fig. 3B) with pterostigma completely sclerotized and pterostigma fusiform, widened approaching the middle; R nearly straight, gently bent anteriorly in distal half, thickened before pterostigma; 1-RS slightly proclival, about $0.43\times$ as long as 1-M; crossvein 1r-rs parallel to 2r-rs, inclined to wing apex, with RS between them arching towards wing posterior margin; M + Cu straight; 2r-m on the left forewing bent gently, inclined towards wing apex, and separated from 2r-rs by its own length (Fig. 3C), located distad of the middle of cell 2mcu; 1m-cu about 0.77 and $0.61\times$ as long as 2-Cu and 3-Cu, respectively; crossvein 1cu-a postfurcal, slightly distad of origin of 1-Cu, nearly as long as 2-Cu; 2m-cu slightly inclined, proximad of the middle of cell 3rm; cell 3r $3.63\times$ as long as 2r in length; cell 1mcu $1.42\times$ as long as wide, $0.47\times$ as long as cell 2mcu.

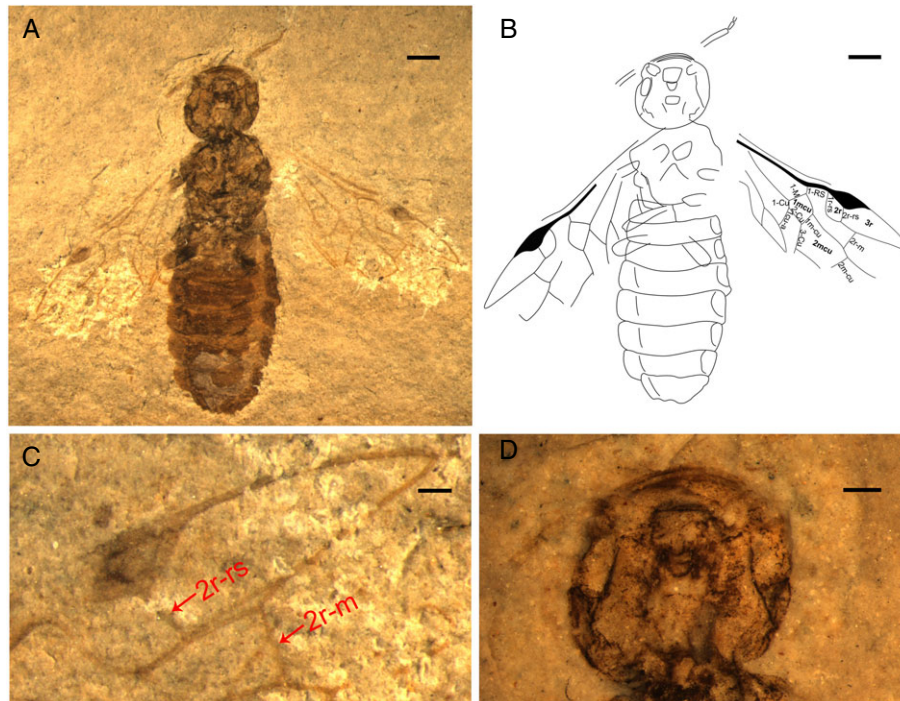


Fig. 3. *Decorisiricius longus* sp.n. Holotype, CNU-HYM-LB-2012126. (A) Photo of habitus. (B) Line drawing. (C) 2r-rs and 2r-m in the right forewing. (D) Head under alcohol. Scale bars: 1 mm in (A) and (B); 0.5 mm in (C) and (D).

Measurement of holotype (in mm). Body length (excluding antenna) 11.0; head length with mandible 2.4; width 2.4; forewing length (up to end of cell 3r) 6.7.

Limbisiricius gen.n.

Etymology. The generic name is a combination of the Latin 'limb-', meaning around, referring to the pterostigma sclerotized around margins, and 'siric' from the family Praesiricidae. Gender masculine.

Type species. *Limbisiricius aequalis* sp.n.

Included species. Type species and *Limbisiricius complanatus* sp.n.

Diagnosis. Head relatively large, rounded and flattened, nearly as wide as or slightly wider than mesothorax; forewing with pterostigma sclerotized around margins, pale medially; 1-RS 0.5–0.7× as long as 1-M; RS + M as long as 2-M; 1r-rs and 2r-rs subvertical to wing anterior margin; crossvein 1m-cu almost as long as 2-Cu; and 1cu-a originating near the middle of cell 1mcu.

Limbisiricius aequalis sp.n. (Fig. 4)

Diagnosis. In addition to the generic diagnosis, head nearly as wide as mesothorax and almost 1.12× as wide as long; 1-RS long, about 0.7× as long as 1-M; cell 3rm shorter than cell 2rm.

Etymology. The species name is derived from the Latin word 'aequalis', meaning equal, referring to 1-RS 0.7× as long as 1-M.

Material. Holotype, No. CNU-HYM-NN-2012129.

Locality and horizon. Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China; Jiulongshan Formation, late Middle Jurassic.

Description. Body including head, thorax, abdomen and legs entirely or predominantly dark, forewing somewhat infuscated sub-basally, particularly so in veins in costal area (Fig. 4A).

Head: Head (Fig. 4C) large and rounded, nearly as wide as mesothorax; almost 1.12× as wide as long; its fore (clypeal) margin slightly waved; eye large and kidney-shaped, about 2.5× as long as wide, 0.46× as long as head; three relatively large ocelli; and foramen occipitalis nearly round; mandible bent inward, when closed reaching opposite side of head, detailed structures indiscernible.

Thorax: Mesothorax deformed, as wide as the second abdominal segment; but with few details preserved. Legs ordinary, hind legs with coxae trapezoid, 2.23× as long as trochanter; hind femora fusiform, not particularly wide (3.5× as long as wide), widest subapically, at least 1.4× as wide as fore and mid femora (Fig. 4A, B).

Abdomen with segments short, the fourth segment wider than others. Ovipositor as preserved, very short, with transverse teeth;

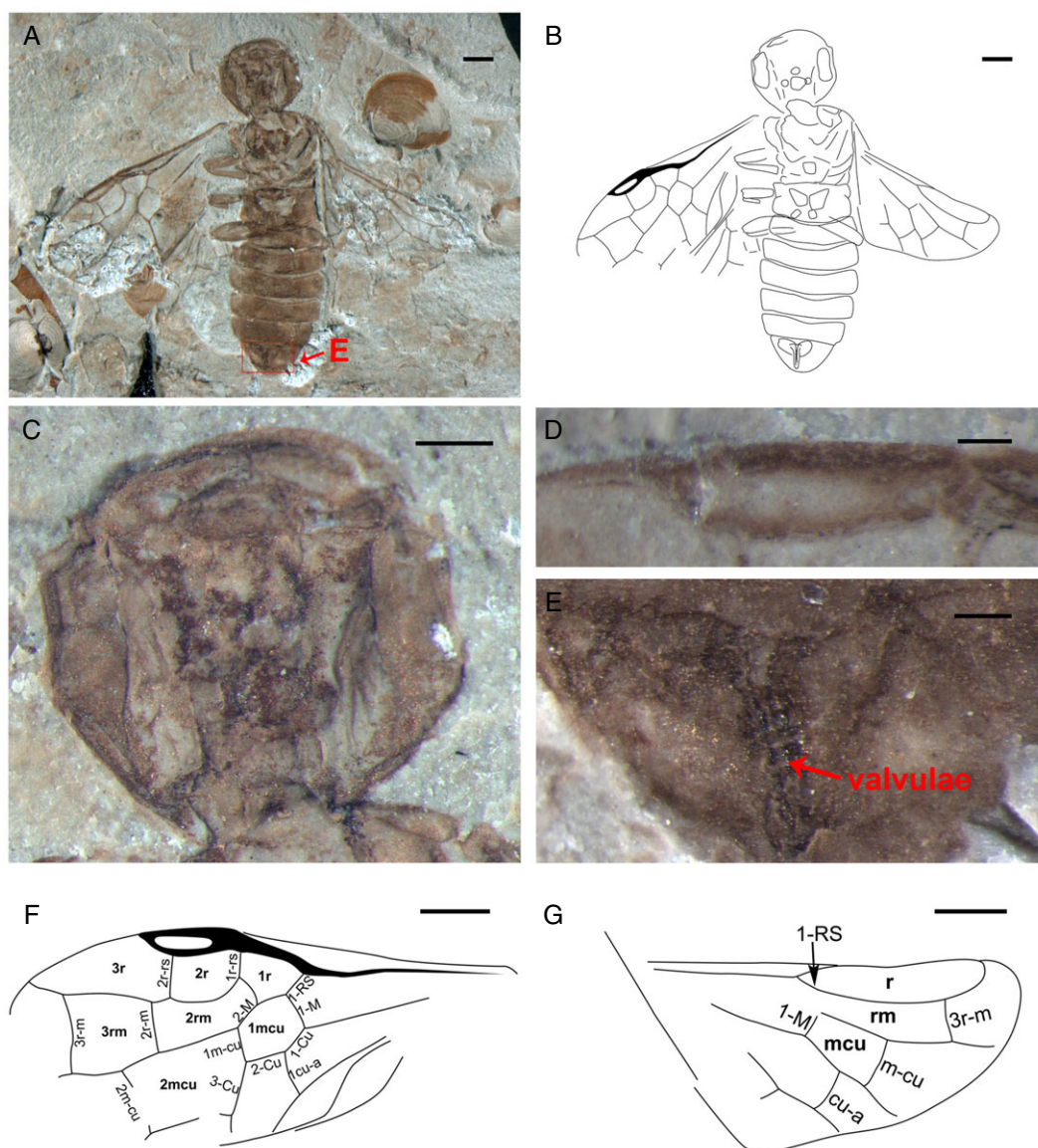


Fig. 4. *Limbisiricius aequalis* gen. et sp.n. Holotype, CNU-HYM-LB-2012129. (A) Photo of habitus. (B) Line drawing. (C) Head. (D) Pterostigma. (E) Ovipositor. (F) Line drawing of left forewing. (G) Line drawing of right hind wing. Scale bars: 1 mm in (A), (B), (F) and (G); 0.5 mm in (C); 0.2 mm in (D) and (E).

stylets widely separated basally and meeting only at apices (Fig. 4E).

Forewing: Forewing (Fig. 4B, F) with pterostigma sclerotized around margins (Fig. 3D); circular-shaped small bumps with a diameter ranging from 0.09 to 0.15 mm present in the area of cells 1cu-a, 2a and 2cu-a (Fig. 5A–D); R becoming thicker and curved gradually slightly proximad of origin of RS; 1-RS proclival, about $0.7\times$ as long as 1-M; vein 1r-rs parallel to 2r-rs, subvertical to wing anterior margin; RS arching gently between 1r-rs and 2r-rs; M + Cu straight; 1cu-a very long, intersecting the middle of cell 1mcu, $1.3\times$ as long as 1-Cu; RS + M nearly as long as 2-M, $0.76\times$ as long as 1-M; vein

1m-cu $0.76\times$ as long as 1cu-a, 0.82 and $0.58\times$ as long as 2-Cu and 3-Cu, respectively, located much proximad of the middle of cell 2rm; 2m-cu slightly proximad of the middle of cell 3rm; 2r-m well separated from 2r-rs by $0.36\times$ its own length, and distad of the middle of cell 2mcu; 3r-m curved, well inclined towards wing base, separated from apex of cell 3r by almost half of its own length; cell 1mcu $1.26\times$ as long as wide, and $0.64\times$ as long as cell 2rm; cell 2rm almost $1.1\times$ as long as cell 3rm, and $0.74\times$ as long as, $0.49\times$ as wide as, cell 2mcu; cell 3r twice as long as cell 2r.

Hind wing: In hind wing (Fig. 4G), vein SC lost; R and M + Cu straight; 1-RS nearly as long as 1-M; 3r-m inclined towards

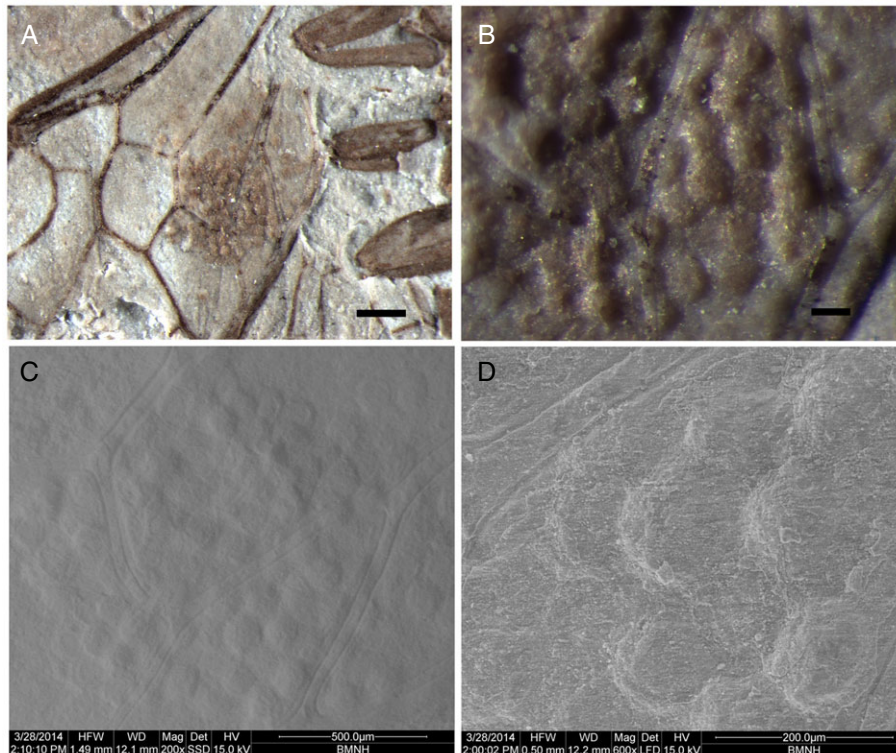


Fig. 5. *Limbisiricius aequalis* gen. et sp.n. (A) Egg-like structure in the posterior margin of left forewing. (B) Magnified egg-like structure; (C, D) SEM views. Scale bars: 0.5 mm in (A); 0.1 mm in (B).

wing base, separated from apex of cell r by $1.47\times$ of its own length; m-cu curved towards wing apex, slightly longer than 3r-m, located slightly distad of mid-length of cell rm, separated from 3r-m by $1.3\times$ its own length; crossvein cu-a distad of mid-length of cell mcu.

Measurement of holotype (in mm). Body length (excluding antenna) 11.4; head length with mandible 2.5; width 2.8; forewing length (up to end of cell 3r) 7.3; hind wing (length up to end of cell 1r) 5.1.

Remarks. *Limbisiricius aequalis* gen. et sp.n. is preserved with small subcircular structures, overlaying its left forewing in the area of cells 1cua, 2a and 2cua (Fig. 5A–D), with diameters ranging from 0.09 to 0.15 mm that may represent eggs. The range of diameters is smaller than those of extant sawfly eggs. The structures may be eggs produced by an unknown aquatic animal when the sawfly corpse was floating in the water or lying on the bottom of an ancient lake. Alternatively, this structure could be a colony of unicellular algae which grew on the corpse. Yet the precise nature of these small circular bumps remains enigmatic.

***Limbisiricius complanatus* sp.n. (Fig. 6)**

Diagnosis. In addition to the generic diagnosis, head nearly $2\times$ as wide as long; 1-RS also proclival, but more inclined; the

angle between 1-RS and 1-M at 107° ; and 1-RS about $0.48\times$ as long as 1-M; cell 3rm equal to cell 2rm in length.

Etymology. The species name is derived from the Latin word ‘complanatus’, meaning flattened, referring to the head shape of this sawfly.

Material. Holotype, No. CNU-HYM-NN-2012130.

Locality and horizon. Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China; Jiulongshan Formation, late Middle Jurassic.

Description. Body, including head, thorax slightly darker than antenna and abdomen (Fig. 6A).

Head: Head (Fig. 6B) massive, $1.97\times$ as wide as long, and $1.3\times$ as wide as mesothorax; clypeal margin with distinct medial lobe; mandible not thick, sickle-shaped, reaching opposite side of head when closed; eyes ovate, nearly $1.5\times$ as long as wide; three relatively large ocelli well preserved, foramen occipitalis rectangular; antenna (Fig. 6C) thin, poorly preserved, segmentations indiscernible.

Thorax: Pronotum short, anterior margin arching forward; mesonotum with mesoscutum relatively large, anterior edge

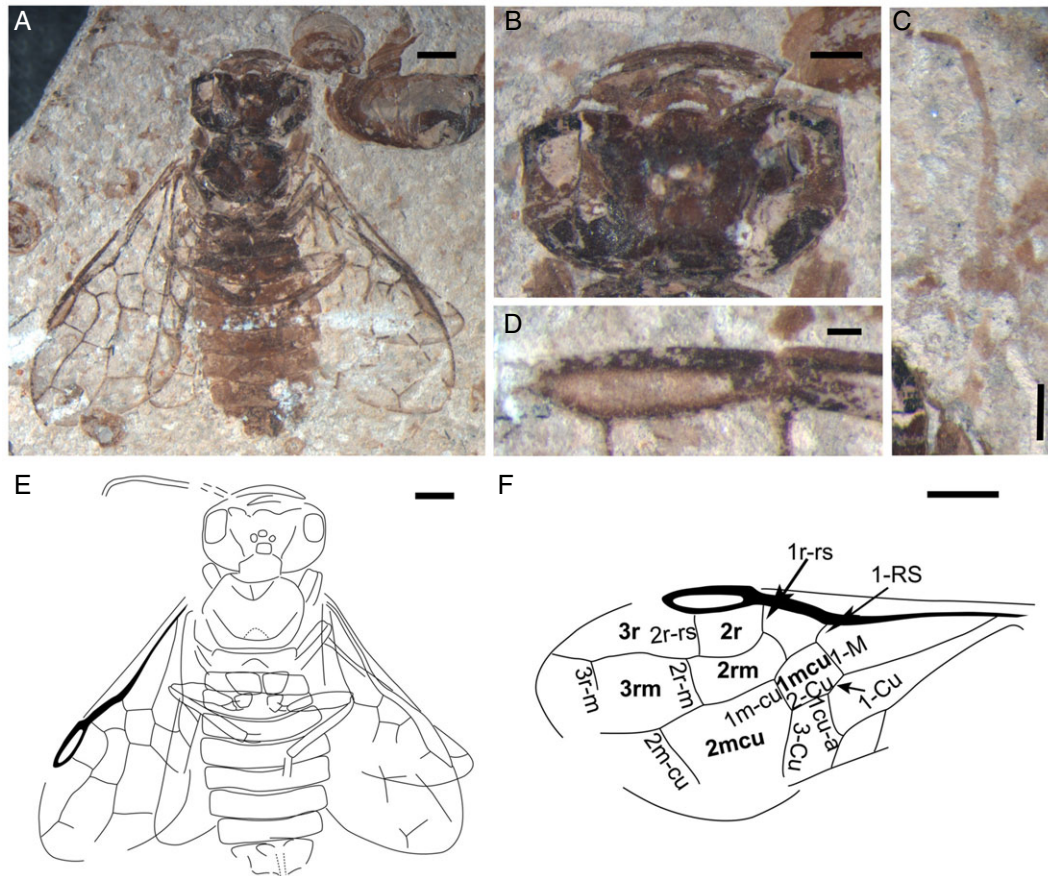


Fig. 6. *Limbisiricius complanatus* sp.n. Holotype, CNU-HYM-NN-2012130. (A) Photo of habitus. (B) Head. (C) Part of left antenna. (D) Pterostigma. (E) Line drawing of habitus. (F) Line drawing of left forewing. Scale bars: 1 mm in (A), (E) and (F); 0.5 mm in (B) and (C); 0.2 mm in (D).

nearly straight, with short notauli forming an angle of 109° ; other structures unknown (Fig. 6A, E).

Legs (Fig. 6A): coxae trapezoid (hind coxae $0.83\times$ as long as wide); trochantellus preserved in hind legs; femora fusiform, about $4.1\times$ as wide as long; hind femora (0.43 mm in wide) shorter than mesothorax; fore and mid femora narrower than hind ones; tibiae comparatively narrow and long; hind tibiae about $1.3\times$ as long as hind femur; tarsi incompletely preserved.

Wings: Forewing (Fig. 6E, F) with pterostigma sclerotized around margins (Fig. 6D); R angular and much thickened before pterostigma; 1-RS proclival, about $0.48\times$ as long as 1-M; vein 1r-rs parallel to 2r-rs, RS arching gently between 1r-rs and 2r-rs; M + Cu straight; 1cu-a very long, intersecting the middle of cell 1mcu, $1.59\times$ as long as 1-Cu; RS + M nearly as long as 2-M, $0.73\times$ as long as 1-M; vein 1m-cu $0.80\times$ as long as 1cu-a, and nearly equal to 2-Cu in length, located well proximad of the middle of cell 2rm; 2m-cu inclined, slightly proximad of the middle of cell 3rm; 2r-m curved toward wing apex, separated from 2r-rs by $0.27\times$ its own length, and distad of the middle of cell 2mcu; 3r-m separated from apex of cell 3r by almost half of its own length; cell 1mcu $1.23\times$ as long as wide, and $0.64\times$ as long as cell 2rm; cell 2rm almost $0.96\times$ as long as 3rm in length,

and $0.74\times$ as long as, $0.59\times$ as wide as, cell 2mcu; cell 3r $2.3\times$ as long as cell 2r.

Measurement of holotype (in mm). Body length (excluding antenna) 10; head length with mandible 2.3; width 3.1; forewing length (up to end of cell 3r) 7.4.

***Brevisiricius* gen.n.**

Etymology. The generic name is a combination of the Latin 'brevi-', meaning short, referring to forewing with RS + M very short, and 'siric' from the family Praesiricidae. Gender masculine.

Type species. *Brevisiricius distortus* sp.n.

Diagnosis. Forewing with pterostigma completely sclerotized; 1-RS $0.65\times$ as long as 1-M; RS + M short, about $0.62\times$ as long as 2-M; 1m-cu shorter than half of 2-Cu; 1cu-a located just slightly proximad of cell 1mcu.

***Brevisiricius partialis* sp.n. (Fig. 7)**

Diagnosis. As for genus due to monotypy.

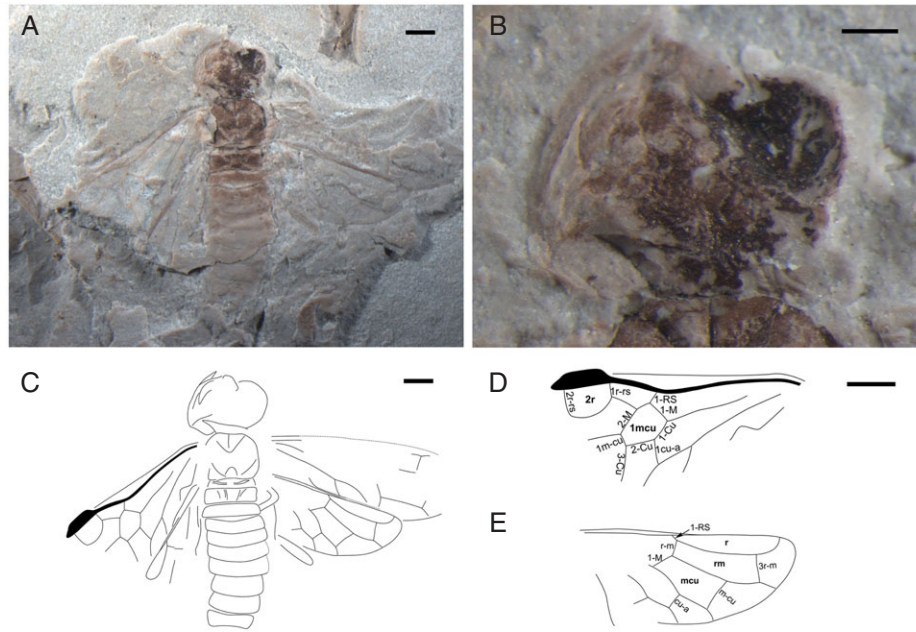


Fig. 7. *Brevisiricius partialis* gen. et sp.n. Holotype, CNU-HYM-NN-2012131. (A) Photo of habitus. (B) Head. (C) Line drawing of habitus. (D) Line drawing of left forewing. (E) Line drawing of right hind wing. Scale bars: 1 mm in (A), (C), (D) and (E); 0.5 mm in (B).

Etymology. The species name is from the Latin word ‘partialis’, referring only to the partly preserved wings.

Material. Holotype, No. CNU-HYM-NN-2012131.

Locality and horizon. Daohugou Village, Shantou Township, Ningcheng County, Inner Mongolia, China; Jiulongshan Formation, late Middle Jurassic.

Description. Body, including head, thorax and part abdomen, dark, with rest abdominal terga, pterostigma moderately pale (Fig. 7A).

Head: Head partly (Fig. 7B) distorted; mandibles sickle-like, and other structures unknown.

Thorax: Mesoscutum relatively large, anterior edge nearly straight, with short notauli forming an angle of 91.3° ; mesoscutellum trapezoidal; metanotum with cenchri comparatively narrow; other structures unknown.

Wings: Forewing (Fig. 7C, D) with pterostigma sclerotized completely; R almost straight, curved at origin of 1-RS; 1-RS proclival, about $0.65\times$ as long as 1-M; vein 1r-rs parallel to 2r-rs, RS arching gently between 1r-rs and 2r-rs; 1cu-a very long, intersecting the middle of cell 1mcu, $1.1\times$ as long as 1-Cu; RS + M 0.69 and $0.62\times$ as long as 1-M, 2-M, respectively; cell 1mcu $1.42\times$ as long as wide; 1m-cu $0.55\times$ as long as 1cu-a, and $0.43\times$ as long as 2-Cu.

Hind wing (Fig. 7E) vein SC lost; 1-RS very short, $0.36\times$ as long as 1-M; 3r-m inclined towards wing apex, separated

from apex of cell 1r by its own length; m-cu curved towards wing base, slightly longer than 3r-m, locating slightly distad of the mid-length of cell rm, separated from 3r-m by its own length; crossvein cu-a just slightly distad of the mid-length of cell mcu.

Measurement of holotype (in mm). Body length (excluding antenna) 8.6, head length with mandible 2.2, width 1.74, forewing length (up to end of pterostigma) 5.7.

Key to genera of Praesiricidae

1. R of forewing straight, not curved or angled. Subfamily Praesiricinae 2
 - R of forewing curved, or angled, near RS base 4
2. Antenna with the first flagellomere not longer than the second flagellomere. Cell 1mcu more than twice as long as wide. Forewing about 40 mm long *Hoplitolyda* Gao, Rasnitsyn, Shih & Ren
 - Antenna with the first flagellomere as long as several following flagellomeres combined. Forewing shorter 3
3. 1-RS inclined toward wing base (reclival) *Praesirex* Rasnitsyn
 - 1-RS inclined slightly toward wing apex, perpendicular to R *Turgidontes* Rasnitsyn
- 4 (1). Forewing with basal $1/3$ to $1/2$ of costal area very narrow. Subfamily Decorisiriciinae 5
 - Forewing with costal area wide throughout 7
5. Pterostigma completely sclerotized 6

Pterostigma sclerotized around margins only	
.....	<i>Limbisiricius</i> gen.n. (Figs 4, 6)
6. 1cu-a intersecting base of cell 1mcu	
.....	<i>Decorisiricius</i> gen.n. (Figs 2, 3)
– 1cu-a intersecting the middle of cell 1mcu	
.....	<i>Brevisiricius</i> gen.n. (Fig. 7)
7 (4). Antenna with scape nearly as long as head length. The first flagellomere distinctly longer and somewhat thicker than following flagellomeres. Subfamily Rudisiriciinae	8
– Antenna with scape much shorter than head length. The first flagellomere forming several tightly connected segments distinctly thicker than following flagellomeres. Subfamily Archoxyelydinae	9
8. 1-RS proclival, nearly as long as 1-M	
.....	<i>Aulidontes</i> Rasnitsyn
– 1-RS perpendicular to R or reclival, much shorter than 1-M	
.....	<i>Rudisiricius</i> Gao, Rasnitsyn, Shih & Ren
9 (7). RS + M longer than 1-M. Eye ordinary. Thorax without coarse sculpture	
.....	<i>Archoxyelyda</i> Wang, Rasnitsyn & Ren
– RS + M shorter than 1-M. Eye small. Mesopleuron coarsely foveolate	<i>Xyelydotes</i> Rasnitsyn

Discussion

Prior to the present paper, *Aulidontes mandibulatus* Rasnitsyn from the Upper Jurassic of Southern Kazakhstan represented the earliest fossil record of Praesiricidae (Rasnitsyn, 1983). The three new praesiricid fossil species of *Limbisiricius* **gen.n.** and *Brevisiricius* **gen.n.**, described here from the late Middle Jurassic Jiulongshan Formation of Inner Mongolia, China, now represent the earliest fossil records, extending Praesiricidae into the late Middle Jurassic.

Xyelydidae, first appeared in the later Early (or earlier Middle) Jurassic (Rasnitsyn, 1969, 1980, 1983, 2006; Grimaldi & Engel, 2005), they have antenna possessing a much enlarged first flagellomere, the same plesiomorphic character as Praesiricidae, representing the hymenopteran ground plan (Rasnitsyn, 1996, 2006; Wang *et al.*, 2013). However, Xyelydidae also have the plesiomorphic character of forewing SC two-branched, which is lost in all Praesiricidae. Based on all reported species of Praesiricidae summarized in Table 1, and the known diversity of Xyelydidae tabulated by Wang *et al.* (2014b), we conclude that praesiricids were most diverse and common during the Lower Cretaceous deposits with 16 species described, in contrast to one species reported from the Upper Jurassic and three from the Middle Jurassic. Conversely, Xyelydidae have only two species from the Lower Cretaceous deposits, eight from the Upper Jurassic and nine from the Middle Jurassic. Comparing the wing lengths of these two extinct families, the average forewing length of Xyelydidae (c. 11.0 mm) is longer than that of Praesiricidae (c. 7.2 mm) during the Jurassic. In the Lower Cretaceous deposits, praesiricid forewings range widely from 5.5 to 16.0 mm, with one exceptional case of 41.6 mm in length; the range of praesiricid forewing lengths shows a strongly increasing trend from the Jurassic (7.3–8.5 mm) to the Early Cretaceous (5.5–16.0 mm).

Gao *et al.* (2013a) reviewed and summarized morphological variation in the family Praesiricidae. With their findings and data from the five new praesiricids described in this study, we summarized new ranges for key morphological characters. The forewing length (up to end of cell 3r) varies greatly, ranging substantially from 5.5 mm in *Decorisiricius patulus* **gen. et sp.n.** to 41.6 mm in *Hoplitolyda duolunica* Gao, Shih, Rasnitsyn & Ren. *Decorisiricius patulus* **gen. et sp.n.** is the smallest praesiricid fossil to date. The pterostigma of forewing is either sclerotized completely (in *Praesirex*, *Rudisiricius*, *Archoxyelyda*) or sclerotized around the margins with the centre unsclerotized or just pale (*Limbisiricius*). The crossvein 1cu-a of forewing is located at the basal part of cell 1mcu (in *Decorisiricius*, *Aulidontes*, *Rudisiricius*) or at the mid-length (in *Limbisiricius*, *Turgidontes*). In addition, the most basal part of costal area is very narrow (in *Decorisiricius*, *Limbisiricius*, *Brevisiricius*) and sometimes broad (*Rudisiricius*, *Archoxyelyda*). And the shape of R of forewing varies from apparently straight (in *Praesirex*, *Turgidontes*, *Hoplitolyda*) to angled at the base of R, and to distinctly curved before base of R (other remaining genera).

Rasnitsyn first considered Praesiricinae as a subfamily of Siricoidea (Rasnitsyn, 1968, 1969), mainly based on one misidentified compression fossil *Praesirex hirtus* with deformed wings, displaced segments of the abdomen and a poorly preserved ovipositor. After this mistake was recognized, Rasnitsyn (1983) raised the taxon to the rank of family and transferred it from Siricoidea to Pamphilioidea. In the same publication, he described three new monotypic genera, *Xyelodontes*, *Aulidontes* and *Turgidontes*, of Praesiricinae. These genera share two synapomorphic characters: forewing SC absent, and the mesopseudosternum almost reaching the anterior margin of the mesothorax, as well as a symplesimorphy in having forewing M + Cu bent. Later, with new records of *Rudisiricius* described from the Early Cretaceous of Yixian Formation in China, Gao *et al.* (2010) reported that the unusual antennal structures and the position of 1cu-a at the basal part of cell 1mcu of *Aulidontes mandibulatus* were similar to those of *Rudisiricius*, and thus transferred *Aulidontes* from Praesiricinae to Rudisiricinae. The poorly preserved fossil of *Xyelodontes sculpturatus* was originally tentatively placed in the subfamily Praesiricinae (Rasnitsyn, 1983). *Archoxyelyda mirabilis* was described later (Wang *et al.*, 2013); it shares with *Xyelodontes* a symplesimorphy in the form of forewing vein R which is angular at the base of RS, but can be distinguished by the basal flagellomeres well discernible but tightly appressed to each other, in contrast to narrower and freely movable distal flagellomeres. This kind of antennal character state is a subfamily synapomorphy according to Rasnitsyn (2006: S706, considerations on *Syntexyela media* whose antenna is similar to *Archoxyelyda* in this respect). Wang *et al.* (2013) established a new subfamily, Archoxyelydinae, to include these two genera, whereas *Turgidontes magnus* and *Praesirex hirtus* remained in the Praesiricinae based on the relatively large cell 1mcu and 1cu-a located at the mid-length of cell 1mcu.

Based on the phylogenetic results presented here, we propose a further refinement of the family structure. Praesiricidae is not a natural group based on our present phylogenetic analyses. Megalodontesidae is a derived branch in Praesiricidae, which is

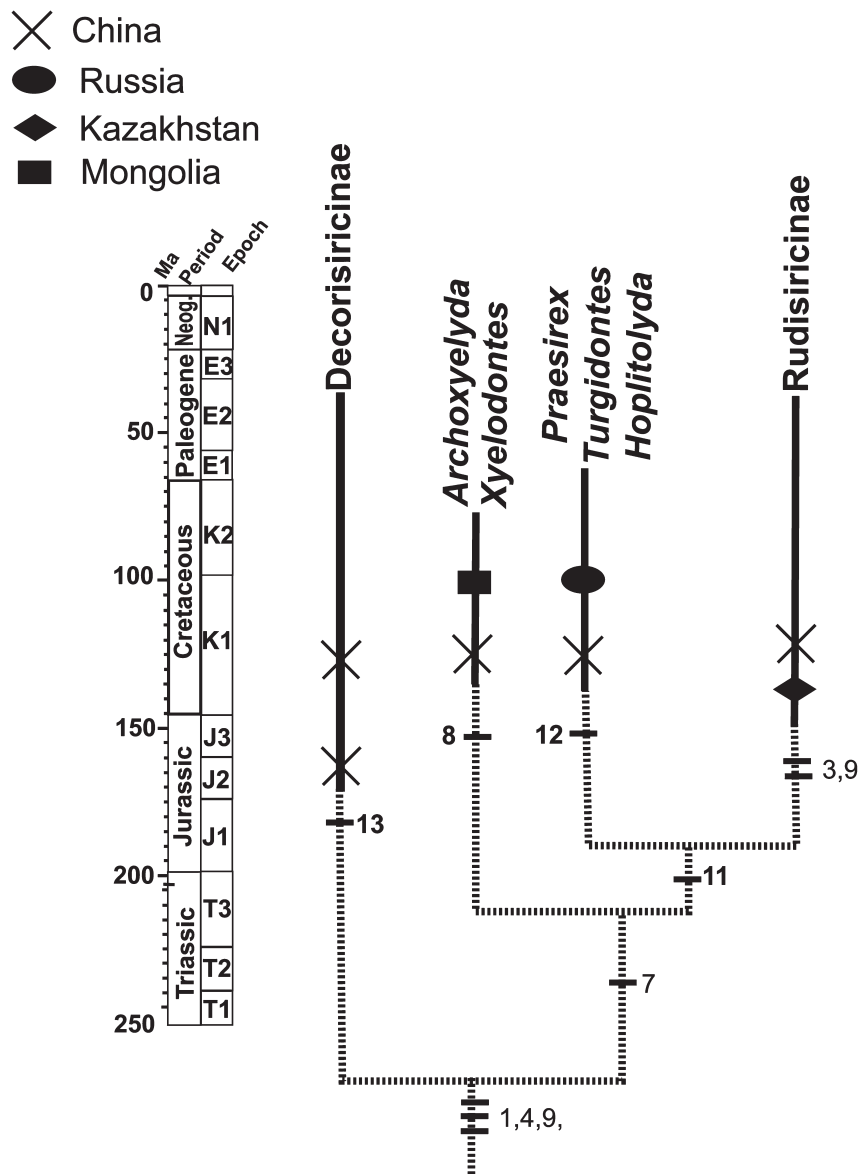


Fig. 8. The phylogenetic relationships of Praesiricidae based on morphological characters, presented in geological time.

consistent with the propositions of Rasnitsyn & Quicke (2002), so the probable solution to date is to include Praesiricidae in Megalodontesidae. However, given the limited information available from preserved fossils, it might be wiser to leave the genera and subfamilies of Praesiricidae alone, hoping that further material in the future might resolve this phylogenetic pending problems. Nevertheless, at present, the new subfamily Decorisiricinae and Rudisiricinae are definitely monophyletic with unambiguous character support; Archoxyelydinae, containing *Archoxyelyda* and *Xyelodontes*, is considered as a monophyly but with a homoplastic character in a very weak support. The remaining three genera *Hoplitolyda*, *Turgidontes* and *Praesirex* are not assigned to any subfamilies for lack of unambiguous synapomorphies.

In summary, the two subfamilies of Praesiricidae and five unassigned species with their respective geological times are presented in Fig. 8. In agreement with both the above phylogenetic results and geological distributions, Decorisiricinae is sister to the remaining praesiricids; it contains the earliest fossil record of Praesiricidae from the late Middle Jurassic of China. More praesiricid fossils are needed to refine our phylogenetic understanding and further enhance our knowledge of praesiricid and pamphilioid evolution.

Acknowledgements

We sincerely thank the editor and two reviewers for their critical reviews of and constructive suggestions for this contribution.

We acknowledge Dr Taiping Gao, Dr Yongjie Wang for their useful advice and discussions on this article. We thank Dr Weiting Zhang and Dr Hu Li for their help using phylogenetic software. This research was supported by the National Basic Research Program of China (973 Program; 2012CB821906), the National Natural Science Foundation of China (No. 31230065, 41272006), Great Wall Scholar of the Beijing Municipal Commission of Education, Program for Changjiang Scholars and Innovative Research Team in University (IRT13081); For APR, the work was additionally supported by the Presidium RAS Program 'Origin and evolution of the geo-biological system'.

References

- Benson, R.B. (1945) Sawflies represented in the mainland of Britain by two races (Hym., Symphyta). *The Entomologist's Monthly Magazine*, Fourth Series, **81**, 103–105.
- Cresson, E.T. (1880) Descriptions of new North American Hymenoptera in the collection of the American Entomological Society. *Transactions of the American Entomological Society*, **8**, 1–52.
- Gao, K.Q. & Ren, D. (2006) Radiometric dating of ignimbrite from Inner Mongolia provides no indication of a post-Middle Jurassic age for the Daohugou Bed. *Acta Geologica Sinica (English Edition)*, **80**, 41–45.
- Gao, T.P. & Ren, D. (2008) Description of a new fossil *Anthoxyela* species (Hymenoptera, Xyelidae) from Yixian Formation of Northeast China. *Zootaxa*, **1842**, 56–62.
- Gao, T.P., Ren, D. & Shih, C.K. (2009) The first Xyelotomidae (Hymenoptera) from the Middle Jurassic in China. *Annals of the Entomological Society of America*, **102**, 588–596. DOI: 10.1603/008.102.0402.
- Gao, T.P., Rasnitsyn, A.P., Ren, D. & Shih, C.K. (2010) The first Praesiricidae (Hymenoptera) from Northeast China. *Annales de la Société Entomologique de France*, **46**, 148–153.
- Gao, T.P., Shih, C.K., Xu, X., Wang, S. & Ren, D. (2012) Mid-Mesozoic flea-like ectoparasites of feathered or haired vertebrates. *Current Biology*, **22**, 732–735.
- Gao, T.P., Shih, C.K., Rasnitsyn, A.P. & Ren, D. (2013a) *Hoplityloda duolunica* gen. et sp. nov. (Insecta, Hymenoptera, Praesiricidae), the Hitherto Largest Sawfly from the Mesozoic of China. *PLoS ONE*, **8**, e62420. DOI: 10.1371/journal.pone.0062420.
- Gao, T.P., Shih, C.K., Rasnitsyn, A.P., Xu, X., Wang, S. & Ren, D. (2013b) New transitional fleas from China highlighting diversity of Early Cretaceous ectoparasitic insects. *Current Biology*, **23**, 1261–1266.
- Goloboff, P.A., Farris, J. & Nixon, K. (2003) TNT, a free program for phylogenetic analysis. *Cladistics*, **24**, 774–786.
- Grimaldi, D. & Engel, M.S. (2005) *Evolution of the Insects*. Cambridge University Press, New York, New York.
- Huang, D.Y. & Nel, A. (2009) Oldest web-spinners from the Middle Jurassic of Inner Mongolia, China (Insecta: Embiodea). *Zoological Journal of the Linnean Society*, **156**, 889–895.
- Huang, D.Y., Engel, M.S., Cai, C.Y., Wu, H. & Nel, A. (2012) Diverse transitional giant fleas from the Mesozoic era of China. *Nature*, **483**, 201–204.
- Klopfstein, S., Vilhelmsen, L., Heraty, J., Sharkey, M.J. & Ronquist, F. (2013) The hymenopteran tree of life: evidence from protein-coding genes and objectively aligned ribosomal data. *PLoS ONE*, **8**, e69344.
- Konow, F.W. (1904) Neue paläarktische [sic!] Chalastogastra. *Zeitschrift für Systematische Hymenopterologie und Dipterologie*, **4**, 226–231.
- Malm, T. & Nyman, T. (2014) Phylogeny of the symphytan grade of Hymenoptera: new pieces into the old jigsaw (fly) puzzle. *Cladistics*, **31**, 1–17.
- Middlekauff, W.W. (1958) The North American sawflies of the genera *Acantholyda*, *Cephalcia* and *Neurotoma* (Hymenoptera, Pamphiliidae). *University of California Publications in Entomology*, **14**, 51–174.
- Middlekauff, W.W. (1964) The North American sawflies of the genus *Pamphilus* (Hymenoptera: Pamphiliidae). *University of California Publications in Entomology*, **38**, 1–84.
- Nixon, K.C. (2002) *WinClada, Version 1.00.08*. Program and documentation. Cornell University, Ithaca, New York.
- Rasnitsyn, A.P. (1968) New Mesozoic sawflies (Hymenoptera, Symphyta). *Jurassic Insects of Karatau* (ed. by B.B. Rohdendorf), pp. 190–236. Nauka Press, Moscow.
- Rasnitsyn, A.P. (1969) Origin and evolution of lower Hymenoptera. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR*, **123**, 1–196 (in Russian).
- Rasnitsyn, A.P. (1980) Origin and evolution of Hymenoptera. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR*, **174**, 1–192.
- Rasnitsyn, A.P. (1983) Fossil Hymenoptera of the superfamily Pamphilioidea. *Paleontological Journal*, **2**, 56–70.
- Rasnitsyn, A.P. (1990) Hymenoptera. *Late Mesozoic Insects of Eastern Transbaikalian*, *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR*, Vol. 239 (ed. by A.G. Ponomarenko), pp. 177–205. Nauka Press, Moscow. (in Russian).
- Rasnitsyn, A.P. (1996) Conceptual issues in phylogeny, taxonomy, and nomenclature. *Contributions to Zoology*, **66**, 3–41.
- Rasnitsyn, A.P. (2006) Ontology of evolution and methodology of taxonomy. *Paleontological Journal*, **40**, 679–737.
- Rasnitsyn, A.P. & Quicke, D.L.J. (eds) (2002) *History of Insects*. Kluwer Academic Publishers, Dordrecht.
- Ren, D., Guo, Z.G., Lu, L.W. *et al.* (1997) A further contribution to the knowledge of the upper Jurassic Yixian Formation in western Liaoning. *Geological Review*, **43**, 449–459.
- Ren, D., Shih, C.K., Gao, T.P., Yao, Y.Z. & Zhao, Y.Y. (2010) *Silent Stories – Insect Fossil Treasures from Dinosaur Era of the Northeastern China*. Science Press, Beijing.
- Ren, D., Shih, C.K., Gao, T.P., Yao, Y.Z. & Zhao, Y.Y. (2012) *Insect Fossil Treasures from the Mesozoic of the Northeastern China*. Science Press, Beijing. (in Chinese).
- Riou, B. (1999) Descriptions de quelques insectes fossiles du Miocène supérieur de la Montagne d'Andance (Ardeche, France). *EPHE Biologie et Evolution des Insectes*, **11–12** [1998–1999], 123–133.
- Ronquist, F., Rasnitsyn, A.P., Roy, A., Eriksson, K. & Lindgren, M. (1999) Phylogeny of the Hymenoptera: a cladistic reanalysis of Rasnitsyn's (1988) data. *Zoologica Scripta*, **28**, 13–50.
- Ronquist, F., Klopfstein, S., Vilhelmsen, L., Schulmeister, S., Murray, D.L. & Rasnitsyn, A.P. (2012) A total-evidence approach to dating with fossils, applied to the early radiation of the Hymenoptera. *Systematic Biology*, **61**, 973–999.
- Schulmeister, S. (2003) Review of morphological evidence on the phylogeny of basal Hymenoptera (Insecta), with a discussion of the ordering of characters. *Biological Journal of the Linnean Society*, **79**, 209–243.
- Sharkey, M.J., Carpenter, J.M., Vilhelmsen, L. *et al.* (2012) Phylogenetic relationships among superfamilies of Hymenoptera. *Cladistics*, **28**, 80–112.
- Wang, M.X., Zhao, Y.Y. & Ren, D. (2009) New fossil caddisfly from Middle Jurassic of Daohugou, Inner Mongolia, China (Trichoptera: Philopotamidae). *Progress in Natural Science*, **19**, 1427–1431.
- Wang, Y.J., Labandeira, C.C., Shih, C.K., Ding, Q.L., Wang, C., Zhao, Y.Y. & Ren, D. (2012) Jurassic mimicry between a hangingfly and a ginkgo from China. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 20,514–20,519.
- Wang, M., Rasnitsyn, P.A. & Ren, D. (2013) New sawfly fossil from the Lower Cretaceous of China enlightens the antennal evolution in

lower Hymenoptera (Pamphilioidea: Praesiricidae: Archoxyelydinae subfam. n.). *Systematic Entomology*, **38**, 577–584.

Wang, M., Rasnitsyn, P.A., Shih, C.K. & Ren, D. (2014a) A new fossil genus in Pamphiliidae (Hymenoptera) from China. *Alcheringa*, **38**, 391–397.

Wang, M., Rasnitsyn, P.A., Shih, C.K. & Ren, D. (2014b) A new Cretaceous genus of xyelydid sawfly illuminating nygmata evolution in Hymenoptera. *BMC Evolutionary Biology*, **14**, 131.

Wang, M., Rasnitsyn, P.A., Shih, C.K. & Ren, D. (2015) Revision of the genus *Rudisircius* (Hymenoptera, Praesiricidae) with six new species from Jehol Biota, China. *Cretaceous Research*, **52**, 570–578.

Accepted 10 April 2015

Appendix

Definition of characters and their states

- 1 Subcosta (SC) of forewing: 0: SC present as longitudinal stem (forked or not); 1: present as crossvein only; 2: absent
- 2 Antenna with the first flagellomere: 0: long, equal to or longer than the rest flagellomeres combined; 1: moderately long, distinctly longer than the second flagellomere; 2: short, subequal to the second flagellomere.
- 3 Antennae with scape: 0: narrow, and shorter than head length; 1: thick and long, more or less equal to head length.
- 4 Posterior of pronotum: 0: nearly straight; 1: curved.
- 5 Forewing with pterostigma: 0: sclerotized (completely or except basally); 1: not sclerotized centrally.
- 6 Forewing with 1-RS length: 0: no shorter than 1-M; 1: shorter than 1-M.
- 7 Forewing with 1-RS inclination: 0: proclival; 1: perpendicular to R or reclival.
- 8 Forewing with 2r-m: 0: postfurcal; 1: interstitial.
- 9 Forewing with 1cu-a: 0: near apex of middle of cell 1mcu; 1: at or very close to middle of cell 1mcu; 2: distinctly basal to cell 1mcu.
- 10 Hind wing with Sc: 0: present; 1: absent.
- 11 Head with mandible: 0: short, not sickle-like; 1: long, sickle-like.
- 12 The form of forewing R: 0: with an angle at RS base and/or distinctly bent before it; 1: straight.
- 13 Ratio of basal $\frac{1}{3}$ to $\frac{1}{2}$ of costal area to widest costal area: 0: wide, $\geq 1/2$; 1 very narrow, $< 1/2$.
- 14 First abdominal tergite: split medially = 0; not split medially = 1.
- 15 M + Cu of forewing: straight, or gently bent = 0; distinctly bent, and in some cases, with an additional crossvein, cu-a or its rudiment = 1.
- 16 Second abdominal tergite: undivided = 0; longitudinally divided = 1.
- 17 Rs of forewings apically: furcate = 0; not furcate = 1.
- 18 Oral and mandibular foramina: confluent = 0; separated = 1.