

New xyelydid sawflies from the Lower Cretaceous of China

Mei Wang^a, Alexandr P. Rasnitsyn^{b,c}, Chungkun Shih^a, Dong Ren^{a,*}

^a College of Life Sciences, Capital Normal University, 105 Xisanhuanbeilu, Haidian District, Beijing 100048, China

^b Palaeontological Institute, Russian Academy of Sciences, Moscow 117997, Russia

^c Department of Palaeontology, Natural History Museum, Cromwell Road, London SW7 5BD, UK

ARTICLE INFO

Article history:

Received 18 August 2014

Accepted in revised form 11 December 2014

Available online

Keywords:

Sawfly

Xyelydidae

Fossil insect

Yixian Formation

Jehol Biota

ABSTRACT

One new genus and three new species, *Fissilyda compta* gen. et sp. nov., *F. alba* sp. nov., and *F. parilis* sp. nov., and a new species, *Novalyda decora* sp. nov., are described and figured on the basis of five well-preserved fossils from the Lower Cretaceous Yixian Formation of China. All of these well-preserved new fossil specimens have a desclerotized pterostigma which is pale at the base, while *F. alba* sp. nov. has the crossvein cu-a linearly aligned with vein a in the hind wing, both are rather unusual and important characters in Hymenoptera. These new taxa broaden the diversity of Xyelydidae in the Early Cretaceous and their new morphological characters enhance our understanding of the evolution and relationships of this small extinct family.

© 2014 Elsevier Ltd. All rights reserved.

1. Introduction

The superfamily Pamphilioidea comprises four families: that is, Pamphiliidae, Megalodontesidae, Xyelydidae and Praesiricidae (Rasnitsyn, 1969, 1983). It was believed that the first two extant families are monophyletic and are as sister groups in the phylogeny of Pamphilioidea (Rasnitsyn and Quicke, 2002; Ronquist et al., 2012; Sharkey et al., 2012). However, the monophyly of extinct families Xyelydidae and Praesiricidae is questionable (Grimaldi and Engel, 2005). Recently, Wang et al. (M. Wang, personal information, Aug. 2014) demonstrated that Praesiricidae is not a natural group and its two subfamilies (Decorisiricinae and Rudisiricinae) are well segregated. But the phylogenetic status of Xyelydidae, monophyletic or paraphyletic, needs further study.

So far, there are seven genera and twenty species assigned to Xyelydidae, mostly distributed in Kyrgyzstan, China, Siberia and Kazakhstan from the Middle Jurassic to the Lower Cretaceous (vide Table 1 in Wang et al., 2014a). Nonetheless, among all the reported species, only two genera with two species are from the Lower Cretaceous, viz, one is from the Yixian Formation of Huangbanjigou, Liaoning, China (Gao et al., 2013a) and the other from the Yixian Formation of Duolun, Inner Mongolia, China (Wang et al., 2014a). Based on five well-preserved fossil xyelydids collected recently

from the Yixian Formation of Huangbanjigou, we describe a new genus with three new species and a new species of a previously erected genus *Novalyda*. These new taxa broaden the diversity of xyelydid sawflies in the Cretaceous. In addition, we discuss the palaeodiversity of the Xyelydidae in two main localities and horizons.

2. Materials and methods

The specimens studied here were collected from the Lower Cretaceous Yixian Formation of Huangbanjigou, Beipiao City, Liaoning Province, China. A location map of the locality at Huangbanjigou is shown in Fig. 1. The age of Yixian Formation is about 125 Ma, and is associated with the famous Jehol Biota (Ren et al., 1995). Excavations of this area have yielded a variety of excellently preserved insects (Ren et al., 2010, 2012; Wang et al., 2013, 2014a, 2015), which have made significant contributions to the understanding of early evolution and diversity of insects during the mid Mesozoic (Zhang et al., 2010).

All of these five type specimens (four with part and counterpart) described herein are housed at the Key Laboratory of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China (CNUB; Dong Ren, Curator).

The specimens were examined and photographed, either dry or moistened with 95% ethanol, under Leica MZ 16.5 dissecting microscope (Leica, Wetzlar, Germany) with attached Leica DFC500

* Corresponding author. Tel.: +86 10 68901757; fax: +86 10 68980851.

E-mail address: rendong@mail.cnu.edu.cn (D. Ren).

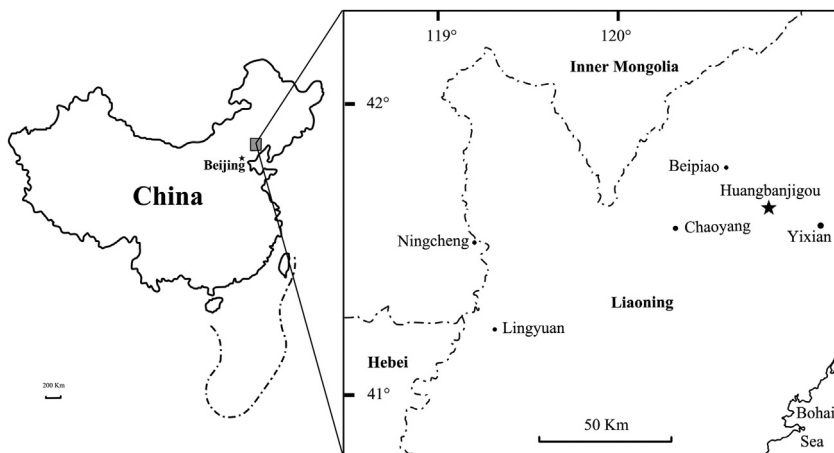


Fig. 1. A location map of the locality at Huangbanjigou with geographic coordinates (41.6°N, 120.8°E).

digital camera. The line drawings were prepared using Adobe Illustrator CS2 and Adobe Photoshop CS5 software.

The wing venation nomenclature used in this study is modified from Rasnitsyn (1969, 1980). Venation symbols: SC, R, RS, RS + M, M, Cu, M + Cu – main (longitudinal) veins; 1-RS, 1-M etc. – sections of these veins; 1r-rs, 2r-rs, 2r-m, etc. – crossveins; 1r, 2rm, 1m-cu, etc. – cells (Wang et al., 2014a).

3. Systematic paleontology

Order: Hymenoptera Linnaeus, 1758
Suborder: Symphyta Gerstaecker, 1867
Superfamily: Pamphilioidea Cameron, 1890
Family: Xyelidae Rasnitsyn, 1968

Genus *Novalyda* Gao, Engel, Shih & Ren, 2013

Type species. *Novalyda cretacea* Gao, Engel, Shih & Ren, 2013

Emended diagnosis. Forewing with SC two branched, SC1 much closer to C, apparently parallel to it, and meeting C near the origin of 1-RS; SC2 oblique; M + Cu very straight; 1-RS extremely short, at least 1/6 of 1-M; 1-M vertical to 1-Cu, and RS + M; 3r-m oblique and long, about 1.6 times as long as 2r-m, and 2m-cu just at the middle of cell 3rm.

Remarks. Since *Novalyda* was erected based on only one specimen, the diagnosis of this genus is relatively limited. The new species *N. decora* reported herein (without preserved head) has 1-RS short, about 1/5 of 1-M, and 1m-cu as long as 2-M, which are different from the original generic diagnosis. However, these two species share some synapomorphic characters, thus we emend the generic diagnosis by supplementing some new venational characters.

Included species. Type species and *N. decora* sp. nov.

Novalyda decora sp. nov.

(Figs. 2 and 3)

Derivation of name. The specific name is derived from the Latin word “decorus” referring to the beautiful posture of this sawfly.

Type Material. Holotype, No. CNU-HYM-LB-2012139 (p/c)

Horizon and locality. Lower Cretaceous, Yixian Formation; Huangbanjigou, Chaomidian Village, Shangyuan Township, Beipiao City, Liaoning Province, China.

Diagnosis. Forewing with pterostigma pale at base, 2r-m interstitial, 2-M as long as 1m-cu.

Description (Figs. 2 and 3).

Holotype (part and counterpart): Body, as preserved, moderately brown, including part of pterostigma, mesothorax and legs slightly darker than abdomen (Fig. 2A and B).

Head not preserved. Pronotum short; mesoscutum large, anterior margin nearly straight, mesoprescutum occupying 0.3 times of mesothorax, with short notauli at an angle of 106°, mesoscutellum trapezoidal, nearly the same size as the metascutellum, the latter oval (Figs. 2C and 3A).

Part of mid legs and hind legs preserved, hind coxae trapezoid, relatively large, 1.3 times as wide as long, femora fusiform, hind femur 1.72 times as wide as mid femora, tibia comparatively thin and long (length of hind tibia equal to the width of mesothorax), hind tibia (Fig. 2E) 2.1 times as long as, 1.5 times as wide as the mid one; mid basitarsus 0.52 times as wide as mid femur, slightly longer than remaining tarsomeres combined, length of tarsal segments 1:2:3:4:5 = 5.4:1.87:1.47:1:1.2; hind tibia with basitarsus long, about as long as remaining three tarsomeres combined, 2nd and 3rd triangle, 4th subquadrate, and 5th elongate, length of tarsal segments 1:2:3:4:5 = 3.6:1.55:1.25:1:1.2.

Abdomen only slightly wider than mesothorax, the first fourth segments slightly wider than rest of abdominal segments, abdominal segments split into some parts, and genital segments not preserved.

Forewing (Fig. 3B) with pterostigma membranous and pale basally, otherwise sclerotized completely (Fig. 2D); SC two branched, SC1 very close to vein C, merging into C near to the origin of RS, SC2 oblique, meeting R prior to separation of RS from R, probably equal to 1-M in length, vein R markedly thickening before pterostigma. Vein 1-RS very short, nearly 1/5 times as long as that of 1-M; 1r-rs parallel to 2r-rs, and the latter about 1.58 times as long as the former one, with RS between them arching towards wing posterior margin; M + Cu slightly bent, and nearly straight, 2r-m slightly antefurcal, located distal to the middle of cell 2mcu, 3r-m oblique, slightly wavy separated from apex of cell 3r by nearly half of its length, and 1.65 times as long as 2r-m; 1m-cu as long as 2-M, 0.6 times and 0.3 times as long as 2-Cu and 3-Cu, respectively; 1cu-a bent distinctly towards wing apex, placed apparently distal to the middle of cell 1m-cu, 1-Cu nearly 1.4 times as long as 2-Cu; 2m-cu

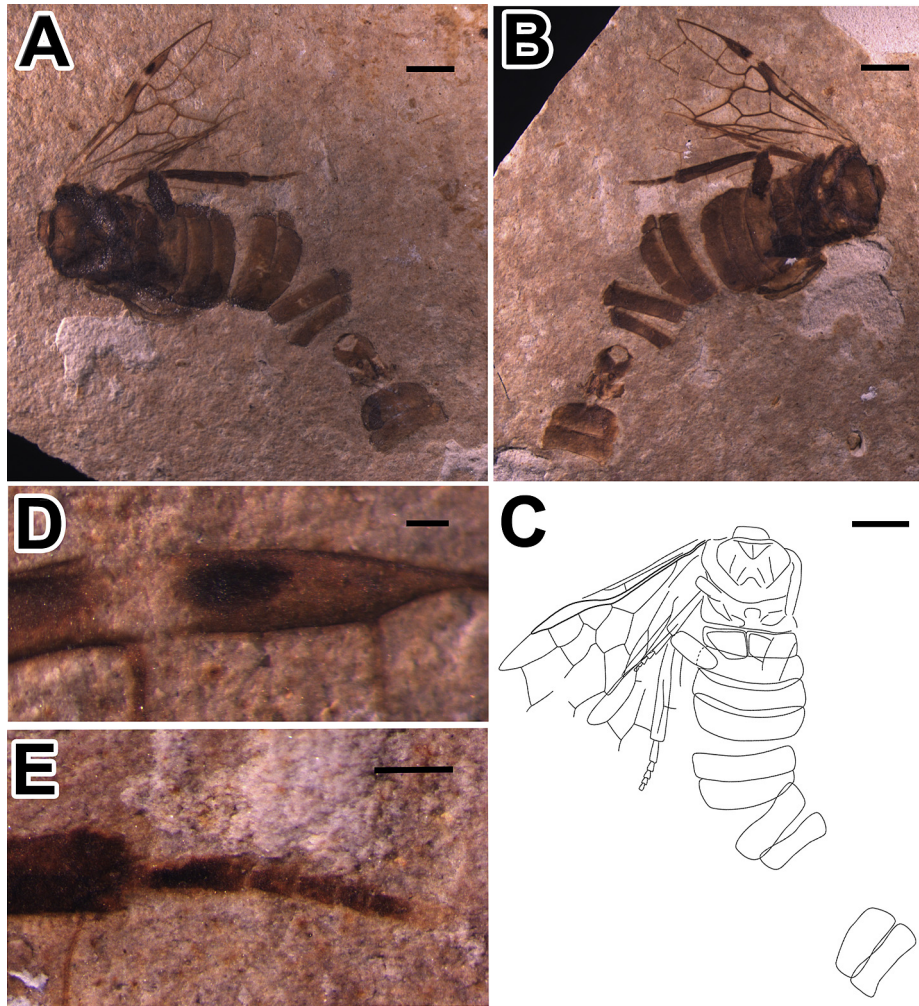


Fig. 2. *Novalyda decora* sp. nov. Holotype, CNU-HYM-LB-2012139 (p/c). A, Photo of part. B, Photo of counterpart. C, Line drawing of counterpart. D, Pterostigma. E, Part of hind tibia. Scale bars: 2 mm in A–C; 0.2 mm in D; 0.5 mm in E.

distal to the middle of cell 3rm. Cell 1r relatively small, the same as cell 2r in length; cell 1mcu approaching pentagonal, 1.52 times as long as wide, and 0.78 times as long as cell 2mcu. Cell 2rm almost 0.73 times as long as 3rm, 0.64 times as long as and 0.46 times as wide as, cell 2mcu; cell 3rm widening toward apex, cell 3r 1.8 times as long as cell 2r.

Hind wing with 3r-m separated from apex of cell r by a distance slightly longer than its length, crossvein m-cu located distal to midlength of cell rm.

Dimensions (in mm). Body length at most 17.3, forewing length up to end of cell 3r 8.5.

***Fissilyda* gen. nov.**

Derivation of name. The new generic name is a combination of the Latin word “Fissus-” meaning split and break, referring to the pterostigma which is just pale at the base, while otherwise sclerotized completely, and -lyda (a common suffix among xyelydid genera). The gender is feminine.

Type species. *Fissilyda compta* sp. nov.

Species included. Type species, *Fissilyda alba* sp. nov. and *Fissilyda parilis* sp. nov.

Diagnosis. Antenna with at least 20 segments, forewing with pterostigma pale at base, and otherwise sclerotized completely;

SC two branched; 1-RS short, at least 0.3 times as long as 1-M; 2r-m far from 2r-rs by at least 0.5 times of its own length; and cell 1mcu relatively large, almost from 1.35 times to 1.9 times as long as wide.

***Fissilyda compta* sp. nov.**

(Figs. 4–6)

Derivation of name. The specific name is derived from the Latin word “comptus”, referring to this beautifully well-preserved fossil sawfly.

Type Material. Holotype, No. CNU-HYM-LB-2012142 (p/c); Paratype, No. CNU-HYM-LB-2012138.

Horizon and locality. Lower Cretaceous, Yixian Formation; Huangbanjigou, Chaomidian Village, Shangyuan Township, Beipiao City, Liaoning Province, China.

Diagnosis. SC2 very short, vertical; R straight before origin of RS. In hind wing, M + Cu straight, and 1-Cu in line with 2-Cu; crossvein a proximal to cu-a, and the latter at the middle of cell mcu.

Description.

Holotype (part and counterpart): As preserved, body moderately brown, including antennae, head, thorax, abdomen and legs (Fig. 4A and B).

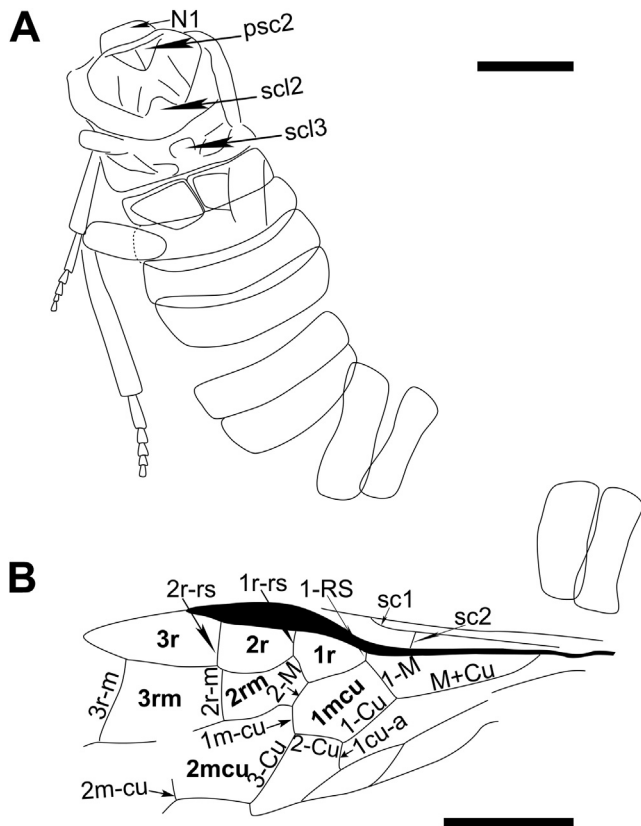


Fig. 3. Interpretation of *Novalyda decora* sp. nov. Holotype. A, Body. B, Left forewing of counterpart. Cell symbols are bold and vein symbols are thin. N1, pronotum; psc2, mesoprescutum; scl2, mesoscutellum; scl3, metascutellum. Scale bars: 2 mm.

Head (Fig. 4G) large, nearly round-shaped, 0.85 times as wide as mesothorax, with eyes narrow and long, reniform, occupied about 0.48 times as long as head; clypeal margin waved, mandible relatively short, sickle-shaped and bent inward, with apical tooth long and slanting. Antenna nearly 2.2 times as long as head width, with at least 20 segments preserved (Fig. 4C). Scape almost as wide as, and 0.59 times as long as, the 3rd antennal segment; pedicel small, subquadrate (Fig. 4D); 3rd antennal segment about as long as the following four segments combined, and the remaining segments growing shorter and narrower toward the apex, elongate and rectangle. Occipital foramen normal size, almost at the middle of head.

Thorax with pronotum relatively short, posterior margin nearly straight; mesonotum with median mesoscutal sulcus and notauli present, metanotum with two small cenchri present (Fig. 4H). For further detail and discussion of the head and thorax morphology see Fig. 5A.

Femora fusiform, not particularly wide (hind femur 3.4 times as long as wide), three pairs of femora of the same wide. Hind tibia, about 1.67 times as long as hind femora, and 0.79 times as long as length of sternum 3.

Abdomen with eight segments preserved, the 2nd–4th segments widest, almost 3.8 times as wide as long, and growing narrower toward apex.

Forewing with pterostigma (Fig. 4E) pale at base, otherwise sclerotized completely. SC two branched, anterior branch of SC meeting C distal to posterior of SC merging into R, SC2 very short, subvertical (Fig. 4F); R nearly straight and thickened after

origin of RS, 1-RS short and proclival, inclined toward wing apex, about 0.33 times as long as 1-M. Crossvein 1r-rs parallel to 1-RS, 2r-rs about 1.66 times as long as 1r-rs, with RS between them arching towards wing posterior margin; M + Cu curved gently, 2r-m separated from 2r-rs by 0.51 times its own length, located distal to the middle of cell 2mcu, 3r-m oblique towards wing apex, separated from apex of cell 3r by 0.71 times of its length, and nearly 1.63 times as long as 2r-m; 1m-cu 0.5 times as long as 1-M, 0.47 times and 0.34 times as long as 2-Cu and 3-Cu, respectively; 1cu-a long, nearly as long as 2-Cu, and placed almost at the middle of cell 1mcu, 1-Cu nearly equal to 2-Cu in length; 2m-cu straight, just at the middle of cell 3rm, and the latter widened toward apex; cell 1mcu 1.85 times as long as wide, and 0.91 times as long as cell 2rm. Cell 2rm almost 1.17 times as long as 3rm, 0.79 times as long as and 0.45 times as wide as, cell 2mcu; cell 3rm widened toward apex, cell 3r 2.04 times as long as cell 2r (Fig. 5B).

Hind wing (Fig. 5C) with SC absent, 1-RS long, almost as long as 1-M, crossvein 1r-m distant from bases of both RS and M; 3r-m separated from apex of cell r by its own length; crossvein m-cu oblique towards wing base, slightly longer than 3r-m, distal to the middle of cell rm, and separated from 3r-m by 0.82 times of its own length. Crossvein cu-a nearly at the middle of cell mcu. Vein M + Cu straight, and 1A arched.

Paratype CNU-HYM-LB-2012138 (Fig. 6 (in the web version)): Colour not reliably known because of absence of counterpart fossil, as preserved, similar to holotype except that head dark near its anterior (Fig. 6A).

Head almost circular, eyes large, about half of head length. Occipital foramen relatively small, located distal to the middle of head. Antenna only part of 3rd segment preserved, thinner and narrower than that of holotype, nearly as wide as scape, remaining antennal segments indiscernible (Fig. 6B).

Thorax slightly wider than head, pronotum short, anterior margin nearly straight, and posterior margin arched forward; mesonotum with median mesoscutal sulcus and notauli present, metanotum with one cenchri observable, metascutellum nearly as large as mesoscutellum, the former triangle and latter trapezoidal.

Abdomen with eight segments and the first one split in the middle; genitals not preserved.

Coxae trapezoid, hind femur relatively wide, 2.8 times as long as wide, and 1.4 times as wide as fore and mid ones. Hind tibia comparatively long and narrow, 9.2 times as long as wide, about 1.7 times as long as hind femora, and almost as long as the width of sternum 5 (Fig. 6D).

Forewing with pterostigma pale at base, otherwise sclerotized completely. SC two branched, and SC2 very short, almost as long as 1-RS, vertical; R nearly straight before origin of 1-RS and thickened after origin of RS, an additional thickened area existed in costal area distal to 1-RS (Fig. 6C); M + Cu bent smoothly; 1-RS about 0.38 times as long as 1-M, 2r-m separated from 2r-rs by 0.51 times its own length, and 3r-m separated from apex of cell 3r by 0.6 times of its length; 1m-cu 0.7 times as long as 1-M, as long as 2-Cu and 0.42 times as long as 3-Cu; 2m-cu curved towards wing apex, at the middle of cell 3rm, and the latter widened toward apex. Cell 1mcu 1.42 times as long as wide and 0.69 times as long as cell 2rm, and cell 2rm as long as cell 3rm (Fig. 6D).

Dimensions (in mm). CNU-HYM-LB-2012142 (p/c): Body length (excluding antenna) 12.5, head length with mandible 2.72,

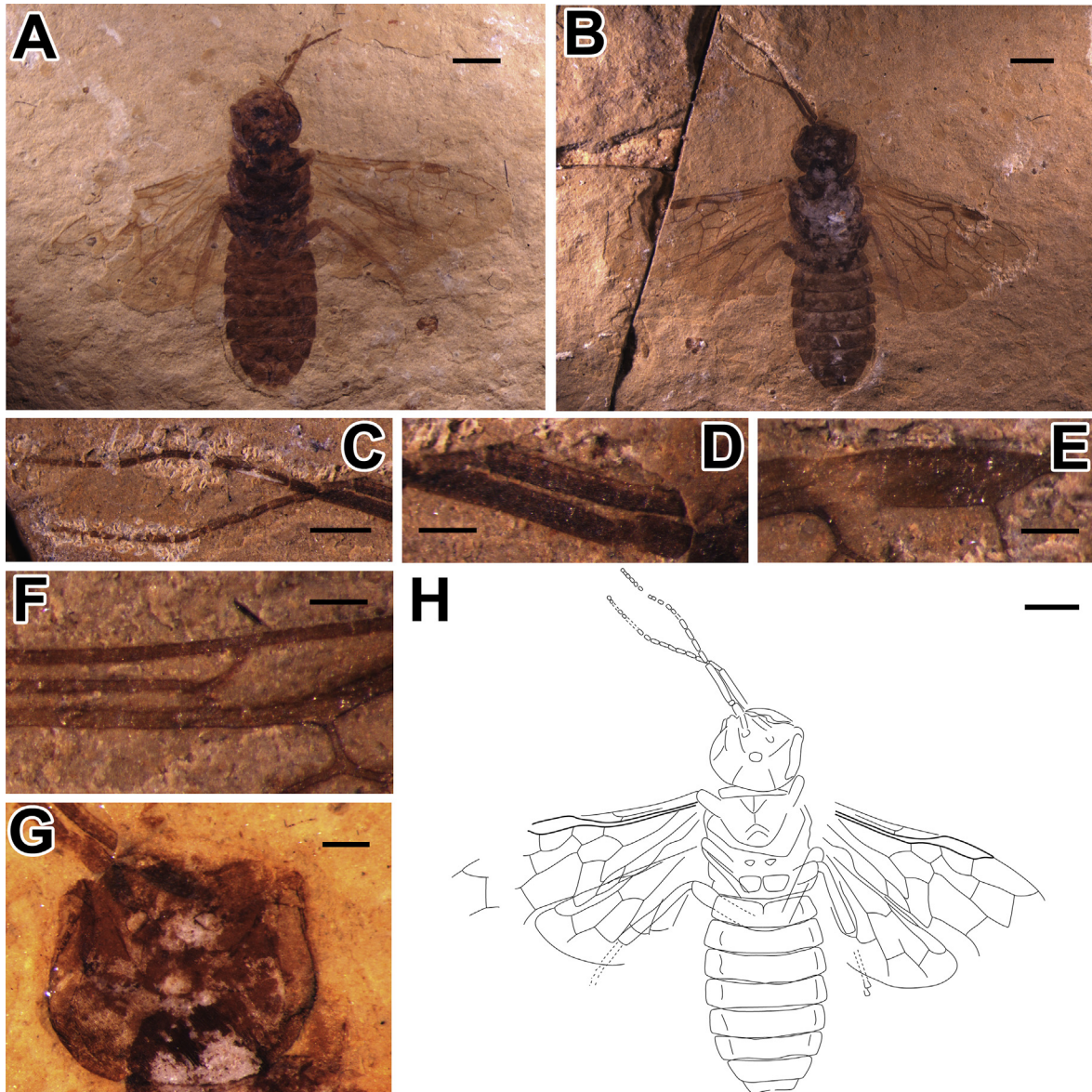


Fig. 4. *Fissilyda compta* gen. et sp. nov. Holotype, CNU-HYM-LB-2012142 (p/c). A, Photo of part. B, Photo of counterpart. C, Flagellomeres of counterpart. D, The first three antennomeres of counterpart. E, Pterostigma. F, Vein SC in the forewing of counterpart. G, Head of counterpart under alcohol. H, Line drawing of counterpart. Scale bars: 2 mm in A, B and H; 0.5 mm in C and G; 0.2 mm in D, E and F.

width 2.9, forewing length up to end of cell 3r 8.0, hind wing length up to end of cell r 5.3; CNU-HYM-LB-2012138: Body length (excluding antenna) 12.3, head length without mandibles about 2.2, width 3.0, forewing length up to end of cell 3r 8.4.

***Fissilyda alba* sp. nov.**

(Fig. 7)

Derivation of name. The specific name is derived from the Latin word “*albus*”, referring to the pterostigma of this sawfly which is completely pale.

Type Material. Holotype, No. CNU-HYM-LB-2012140 (p/c)

Horizon and locality. Lower Cretaceous, Yixian Formation; Huangbanjigou, Chaomidian Village, Shangyuan Township, Beipiao City, Liaoning Province, China.

Diagnosis. Most part of pterostigma pale; SC2 oblique and nearly as long as 1r-rs; cell 1mcu relatively large, about 1.8 times as long as wide; 2r-m distal to 2r-rs by 0.84 times of its own length,

and 3r-m equal to 2r-m in length. Hind wing with crossveins cu-a and a almost linearly aligned.

Description.

Holotype (part and counterpart): Only the first abdominal segment, wings and parts of its pronotum, and mesonotum are well preserved in this fossil specimen. Body, as preserved, moderately dark with pale pterostigma (Fig. 7A and B).

Pronotum short with wide and straight hind margin, nearly 11.8 times as wide as length; mesoprescutum small, nearly 0.17 times as long as mesonotum, with short notauli at an angle of 120°, mesoscutellum almost trapezoidal, other dorsal structures posterior to mesoscutellum not observable (Fig. 7C).

Abdomen with first segment about as wide as mesothorax.

Forewing with pale, unsclerotized pterostigma (Fig. 7D); SC two branched, anterior branch of SC relatively long and merging into C slightly distal to posterior of SC meeting R. Vein R becoming thickened but the extent not so much. 1-RS subvertical, about

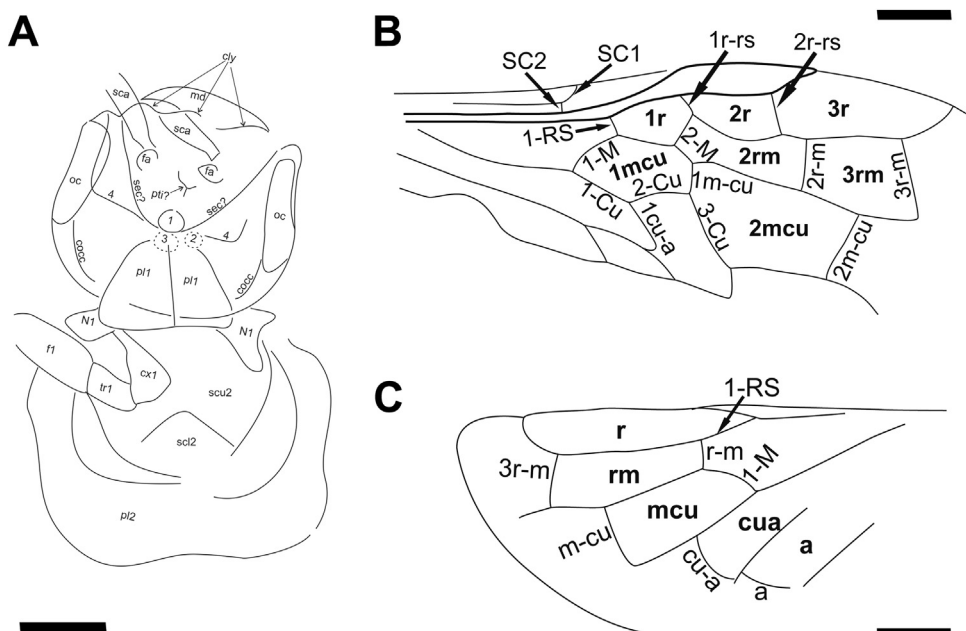


Fig. 5. Interpretation the wings of *Fissilyda compta* gen. et sp. nov. Holotype. A, Interpretation of head and part of thorax (tentative because of non-standard morphology and confusing mixture of dorsal and ventral structures preserved); cly – clypeus; cocc – occipital carina (ventral); cx1 – fore coxa (ventral); f1 – fore femur (ventral); fa – antennal foramen (dorsal); md – mandible; N1 – pronotum; oc – eye (ocular foramen) (dorsal); pl1 – fore pleura; pti? – lower tentorial bridge (characteristic of Pamphilioidea) or possibly hypostomal bridge (ventral); sca – scape (dorsal); scl2 – scutellum (dorsal); scu2 – mesoscutum (dorsal); sec? – possibly (if dorsal) epicranial suture, atypical in that it runs towards head fore margin and does not stop next to antennal orifice; if ventral, no clear homologue is available; tr1 – fore trochanter (ventral); 1–4 – structures of questionable identity: 1 – either fore ocellus (if dorsal) of fore half of occipital foramen (before tentorial bridge; if ventral); 2 – ill-preserved lateral ocellus (if dorsal); 3 – ill preserved rear half of occipital foramen (if ventral); 4 – suture or carina of obscure homology, undoubtedly ventral as crossing eye margin which is dorsal. B, Right forewing of counterpart. C, Left hind wing of counterpart. Cell symbols are bold and vein symbols are thin. Scale bars: 1 mm.

0.3 times as long as 1-M, the latter curved distinctly towards anterior wing margin; 2r-rs curved towards wing apex, about 1.95 times as long as 1r-rs; M + Cu slightly bent, 2r-m oblique, separated from 2r-rs by 0.84 times its own length, located distal

to the middle of cell 2mcu, 1m-cu almost as long as 2-M, 0.57 times as long as 1-M, 0.54 times and 0.32 times as long as 2-Cu and 3-Cu, respectively; 1cu-a straight, nearly as long as M + Cu, and placed apparently proximal to the middle of cell 1mcu, 2m-

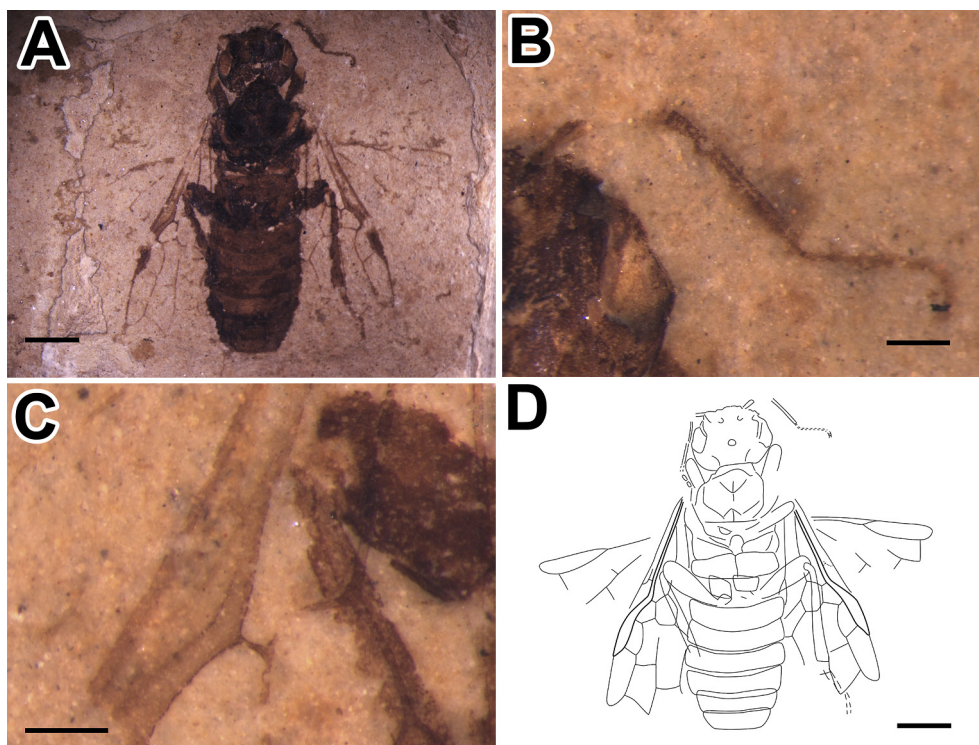


Fig. 6. *Fissilyda compta* gen. et sp. nov. Paratype, CNU-HYM-LB-2012138. A, Habitus. B, Antenna. C, Vein SC and the additional thickened area in costal area of the forewing. D, Line drawing. Scale bars: 2 mm in A and D; 0.5 mm in B and C.

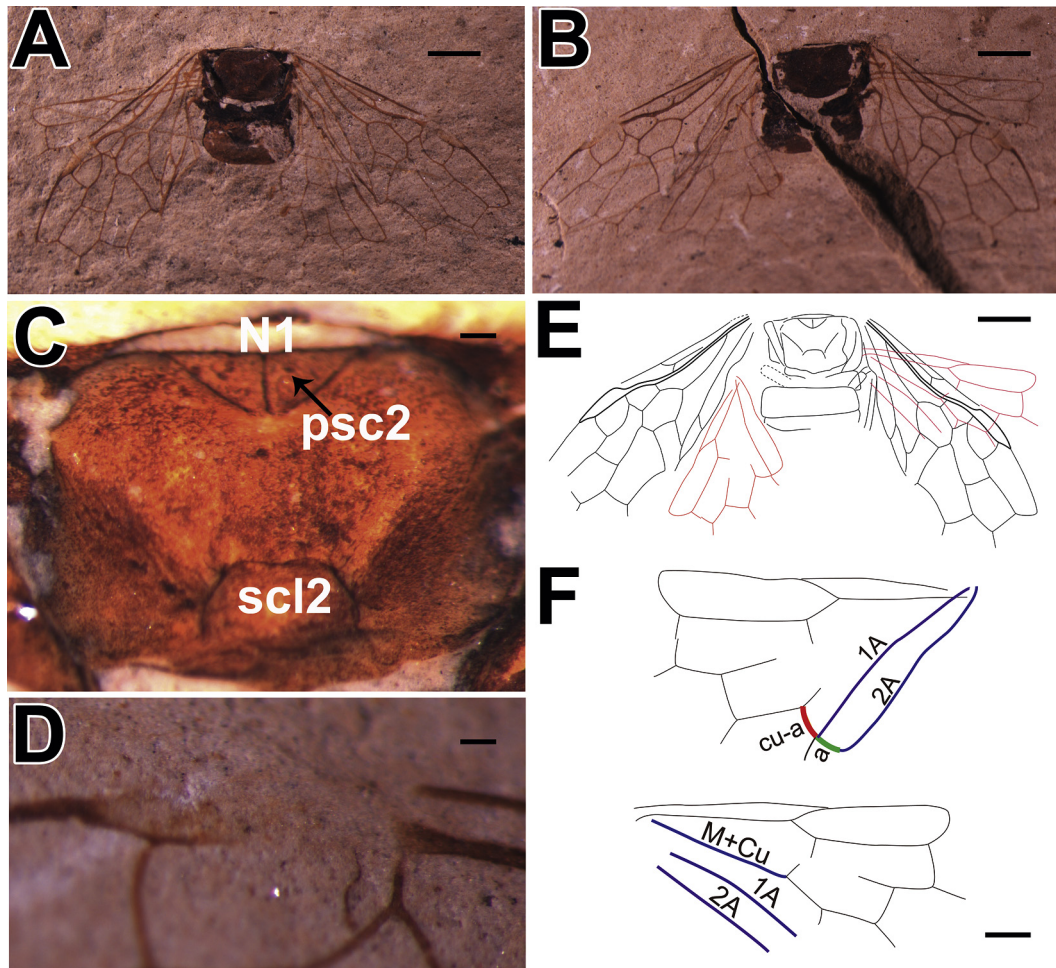


Fig. 7. *Fissilyda alba* sp. nov. Holotype, CNU-HYM-LB-2012140 (p/c). A, Photo of part. B, Photo of counterpart. C, Thorax of part under alcohol. D, Pterostigma. E, Line drawing of counterpart. F, Interpretations of left and right hind wings of counterpart. Scale bars: 2 mm in A, B and E; 0.2 mm in C and D; 1 mm in F. N1, pronotum; psc2, mesoprescutum; scl2, mesoscutellum.

cu almost at the middle of cell 3rm. Cell 1mcu 1.8 times as long as wide, and 0.89 times as long as cell 2rm. Cell 2rm almost 1.13 times as long as 3rm, 0.78 times as long as and 0.54 times as wide as, cell 2mcu (Fig. 7E).

Hind wing (Fig. 7F) with SC not discernible, 1-RS almost as long as 1-M, crossvein 1r-m distant from bases of both RS and M, about 0.59 times as long as 1-M; cell r widely rounded apically. 3r-m separated from apex of cell r by a distance slightly shorter than its length, crossvein m-cu equal to 3r-m in length, located distal to midlength of cell rm, separated from 3r-m by its own length. Crossvein cu-a slightly proximal to the middle of cell mcu. Vein M + Cu straight, 1A and 2A curved near midlength. Cells cua and a truncated before midlength of cell mcu.

Dimensions (in mm). Body length as preserved 4.2, forewing length up to end of cell 3r 9.5, hind wing length up to the end of cell r 6.35.

***Fissilyda parilis* sp. nov.**
(Fig. 8)

Derivation of name. The specific name is derived from the Latin word “parilis”, referring to the forewing with SC1 equal to SC2 in length.

Type Material. Holotype, No. CNU-HYM-LB-2012141 (p/c)

Horizon and locality. Lower Cretaceous, Yixian Formation; Huangbanjigou, Chaomidian Village, Shangyuan Township, Beipiao City, Liaoning Province, China.

Diagnosis. Forewing with sclerotized pterostigma pale at base, and widening toward apex; SC1 as long as SC2; 1m-cu equal to 2-Cu in length, and hind wing with crossvein a proximal to cu-a.

Description.

Holotype (part and counterpart): As preserved, body, including antenna, head, thorax and abdomen infuscated, legs much paler (Fig. 8A and B).

Head nearly trapezoid, widest slightly distal to the middle of head length, 1.5 times as wide as long, 0.97 times as wide as mesothorax, its fore (clypeal) margin slightly waved; mandibles relatively thin and gentle; antennae (Fig. 8C) with only part of the scape and 3rd antennal segment preserved, and detailed structures indiscernible.

Pronotum short, mesonotum with notauli present, mesoprescutum occupied 0.38 times as long as mesonotum; mesopseudosternum triangular, almost as large as mesoprescutum, and well distant of the fore margin of mesoventropleuron (Fig. 8A, B, and G).

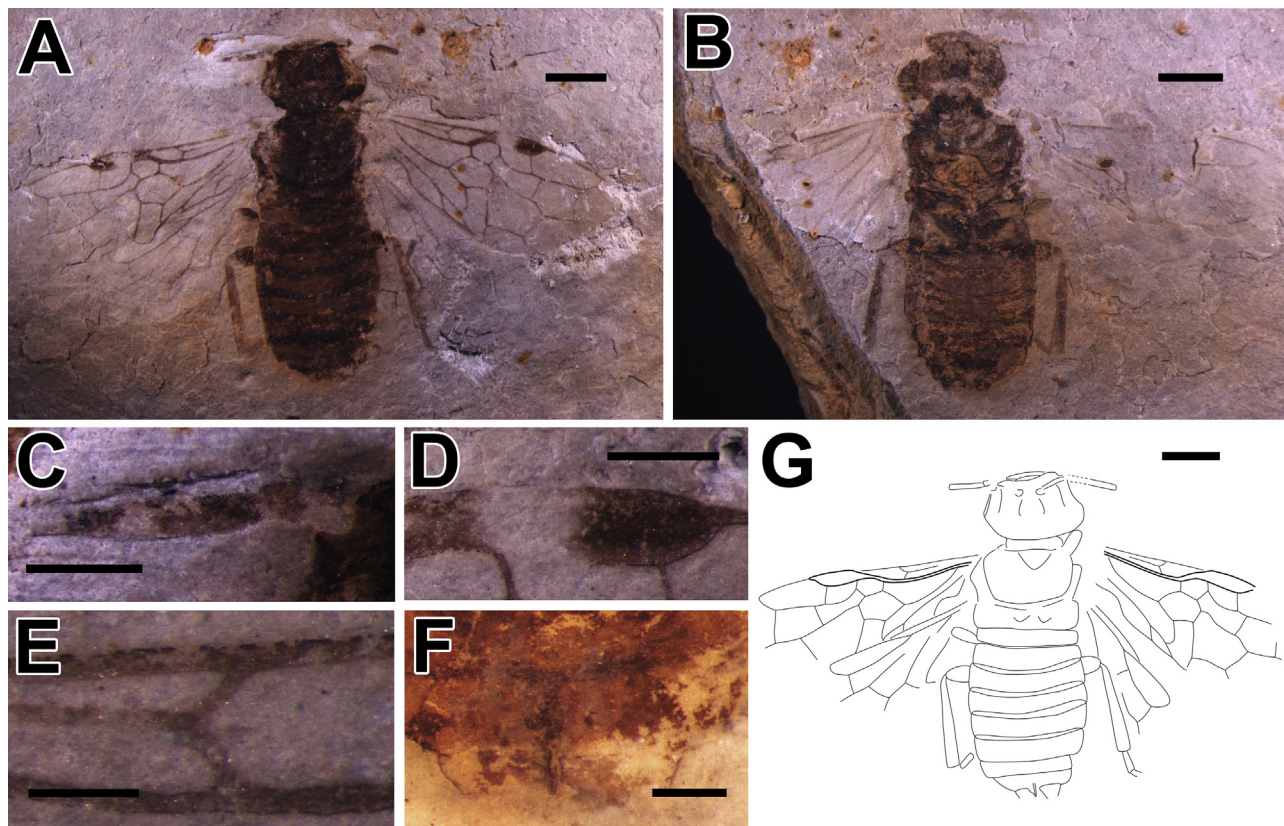


Fig. 8. *Fissilyda parilis* sp. nov. Holotype, CNU-HYM-LB-2012141 (p/c). A, Photo of part. B, Photo of counterpart. C, Antenna of part. D, Pterostigma. E, Vein SC in right forewing of part. F, Genitals under alcohol of part. G, Line drawing of holotype. Scale bars: 2 mm in A, B and G; 0.5 mm in C–F.

Abdomen with eight segments preserved, but genostyle poorly preserved (Fig. 8F).

Legs (Fig. 8G) with hind coxae trapezoid, small, nearly twice as wide as long, femora short (hind femur almost 0.62 times as long as mesopleuron wide), not particularly wide (hind femur about three times as long as wide), with fore and mid femora narrower than the hind. Tibia relatively narrow and long, covered with thick setae, hind tibiae about 7.4 times as long as wide, 1.4 times as long as hind femur. Tarsi incompletely preserved.

Forewing with pterostigma place at base, otherwise sclerotized apically (Fig. 8D). SC two branched, anterior branch of SC equal to the posterior branch of SC in length (Fig. 8E); R bent smoothly and thickening before pterostigma, 1-RS proclival, almost as long as SC2, 0.38 times as long as 1-M; vein 1r-rs inclined towards wing apex, parallel to 2r-rs, RS between 1r-rs and 2r-rs arching gently towards wing hind margin. M + Cu curved gently, 1-M almost as long as 1-Cu; 2r-m oblique towards wing base, separated from 2r-rs by 0.56 times its own length, located distal to the middle of cell 2mcu; 3r-m inclined towards wing apex, 1.6 times as long as 2r-m, separated from cell 3r apex by 0.67 times its own length. Crossvein 1m-cu 1.39 times as long as 2-M, 0.77 times and 0.37 times as long as 2-Cu and 3-Cu, respectively; 1cu-a long, nearly as long as 2-Cu, and slightly distal to the middle of cell 1mcu, and 2m-cu almost at the middle of cell 3rm. Cell 1mcu 1.35 times as long as wide, and 0.89 times as long as cell 2rm. Cell 2rm almost 0.98 times as long as 3rm, 0.73 times as long as and 0.5 times as wide as, cell 2mcu. Cell 3r 2.24 times as long as cell 2r.

Hind wing (Fig. 8G) with 1-RS long, 1.25 times as long as 1-M, crossvein 1r-m distant from bases of both RS and M; cell r

widely rounded apically; 3r-m separated from apex of cell r by a distance slightly longer than its length; crossvein m-cu oblique towards wing base, slightly longer than 3r-m, located far from the middle of cell rm, and separated from 3r-m by 0.74 times of its own length. Crossvein cu-a slightly distal to the middle of cell mcu. Vein M + Cu straight, and 1A curved gently. Cell cua truncated slightly distal to midlength of cell mcu.

Dimensions (in mm). Body length (excluding antenna) 11.2, head length with mandible 2.32, width 3.47, forewing length up to end of cell 3r 7.8, hind wing length up to end of cell r 5.38.

4. Discussion

Characters of pterostigma are important diagnostic features for sawflies. For example, the three subfamilies of xyelids, Archexyelinae, Xyelinae and Macroxyelinae often exhibit variation in their pterostigma. Rasnitsyn described how they sometimes have a completely sclerotized pterostigma, or a basally desclerotized pterostigma, or a pterostigma that is only sclerotized around the bordering veins (Rasnitsyn, 1967, 1969, 1980; Wang et al., 2012; Lara et al., 2014). However, in the extinct family Xyelydidae, the pterostigma is relatively stable. Most have pterostigma completely sclerotized (for example: *Xyelyda excellens*, *Rectilyda sticta*, *Sagulyda magna*, *Mesolyda sibirica*, *Prollyda karatavica*) (Rasnitsyn, 1968, 1983; Wang et al., 2014a), and only a few have a pterostigma sclerotized just around bordering veins (e.g. *Strophandria moderata*, *Ferganolyda cubitalis*, *F. sogdiana*, *Prollyda depressa*) (Rasnitsyn, 1968, 1969, 1983). In addition, Gao et al. (2013a) described the first Cretaceous xyelydid *Novalyda cretacea*, from the Lower Cretaceous Yixian Formation at Huangbanjigou, which

has pterostigma sclerotized widely around the margins but with a membranous central portion, similar to that in *Prolyda xylocera*.

Occasionally, the pterostigma of the same taxa can be desclerotized or completely sclerotized due to fossilisation and/or preservation. Hence, the colour and structure of the pterostigma sometimes can be ambiguous. However, all four new species described in this paper have pterostigma desclerotization and pale at base, but usually sclerotized completely near apex (except *F. alba* sp. nov.). The consistency character indicates that it is not caused by uncertainty in fossilization and/or preservation. It is the first time that this unique pterostigma is reported in Xyelidae, which only occurred in the Cretaceous, based on our current knowledge.

Wang et al. (2014a) summarized the reported data of wing lengths for all species of xyelids. Herein, after we add new data in Table 1 by Wang et al., 2014a, the list shows that there are nine species in the Middle Jurassic, eight species discovered in the Upper Jurassic, and six in the Lower Cretaceous to date, indicating that xyelids are comparatively diverse in the Jurassic period. While comparing the wing lengths of Xyelidae in this two epochs, the average lengths of forewings in Jurassic (ca. 13.0 mm) is usually larger than those in Cretaceous (ca. 8.0 mm) (excluding the relatively exaggerated *Rectilyda sticta* from statistical calculation).

Furthermore, the wing venation of Xyelidae in the two epochs is relatively stable, with the forewing with SC two branched, elementary longitudinal veins and crossveins all present, without additional unusual veins. It can be best differentiated from the other Cretaceous genus of *Novalyda*, *Fissilyda* gen. nov. can be best differentiated from it by having a longer 1-RS, at least 1/3 that of 1-M, and SC in the middle of the costal area, rather than SC1 being much closer to C and parallel to it, M + Cu bent smoothly, and 2r-m distal of 2r-rs remotely.

Nevertheless, a significant feature in *F. alba* is worth mentioning. Its hind wing has the crossvein cu-a linearly aligned with a, and nearly of the same length (Fig. 7F). The cells cua and a are truncated before midlength of cell mcu, forming crossvein cu-a in line with a. The same phenomenon can also be observed in *Hoplitolyda duolunica* (Praesiricidae; Gao et al., 2013b); whereas crossvein a is usually slightly proximal to cu-a among most of xyelids, pamphilids and megalodontesids (viz. *Onycholyda amplexa*, *Prolyda xylocera*, etc).

However, in Xyelidae, the most basal group in Hymenoptera (Rasnitsyn, 1969, 1980; Rasnitsyn and Quicke, 2002; Wang et al., 2012, 2014b), we find that most, either extinct or extant subfamilies, also have crossvein a proximal to cu-a. The only exceptions are *Megaxyela petrefacta* and *Macroxyela ferruginea* which have crossvein cu-a linearly aligned with a, but cu-a is longer, almost 1.5 times as long as crossvein a. While in Tenthredinidae, Xyelotomidae and Xiphidriidae, their hind wings have cu-a and a present, and crossvein a proximal to cu-a (viz. *Athalia rosae*, *Blennallantus compressicornis*, *Paradoxotoma tsaiiae*, *Xiphidria camelus*). The same is shown in *Cephus pygmeus*, but the latter has two crossveins of cu-a present. In contrast, some other representatives, such as *Heteroperreyia hubrichi* (Pergidae), *Tremex columba* (Siricidae), *Orussus abietinus* (Orussidae), have crossvein cu-a and longitudinal vein 1A present, but lacking crossvein a.

As aforementioned, based on our observation of extinct and extant sawflies, we can tentatively draw a conclusion that this trait (crossvein cu-a linearly aligned with a in hind wing) could be traced to the most basal group of Hymenoptera and persists in some of its extant species. Meanwhile, this character occurs in the extinct families Xyelidae and Praesiricidae as well, but not present in other families of Symphyta. As a result, our preliminary conclusions are that the aforementioned character, cu-a in line with a in the hind wing, is an ancient trait, and that was stably inherited in

Xyelidae, but was either lost and or changed in other superfamilies, such as Pamphilioidea.

5. Conclusions

Fissilyda compta gen. et sp. nov., *F. alba* sp. nov., and *F. parilis* sp. nov., and a new species, *Novalyda decora* sp. nov., are described from the Lower Cretaceous Yixian Formation of China, broadening the diversity of xyelid sawflies in the Cretaceous. Some of these specimens exhibit the unusual character of pterostigma desclerotized and pale at the base. This is the first time that this unique pterostigma is reported in Xyelidae. In addition we describe how *F. alba* has crossvein cu-a linearly aligned with vein a in hind wing. This venation is similar to that in Xyelidae, indicating that it may represent an ancient trait in the Symphyta.

Acknowledgements

We sincerely thank the editor and two anonymous reviewers for their critical reviews and constructive suggestions. We acknowledge Dr. Victoria G. Pook (University of Kentucky, USA) for her copyediting and improving of this article. We thank Dr. Taiping Gao for his kind help. 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 and KEY project of the Beijing Municipal Commission of Education (KZ201310028033), 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 geological system".

References

- Gao, T.P., Engel, M.S., Ortega-Blanco, J., Shih, C.K., Ren, D., 2013a. A new xyelid sawfly from the Lower Cretaceous of China (Hymenoptera: Xyelidae). *Journal of the Kansas Entomological Society* 86 (1), 78–83.
- Gao, T.P., Shih, C.K., Rasnitsyn, A.P., Ren, D., 2013b. *Hoplitolyda duolunica* gen. et sp. nov. (Insecta, Hymenoptera, Praesiricidae), the hitherto largest sawfly from the Mesozoic of China. *PLoS One* 8 (5), e62420. <http://dx.doi.org/10.1371/journal.pone.0062420>.
- Grimaldi, D., Engel, M.S., 2005. *Evolution of the Insects*. Cambridge University Press, New York, p. 755.
- Lara, M.B., Rasnitsyn, A.P., Zavattieri, A.M., 2014. *Potrilloxyela menendezii* gen. et sp. nov. from the late Triassic of Argentina: the oldest representative of Xyelidae (Hymenoptera: Symphyta) for Americas. *Paleontology Journal* 48 (2), 182–190.
- Rasnitsyn, A.P., 1967. New Xyelidae (Hymenoptera) from the Mesozoic of Asia. *International Geology Review* 9 (5), 723–737.
- Rasnitsyn, A.P., 1968. New Mesozoic sawflies (Hymenoptera, Symphyta). In: Rohdendorf, B.B. (Ed.), *Jurassic insects of Karatau*. Nauka Press, Moscow, pp. 190–236.
- 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., Quicke, D.L.J. (Eds.), 2002. *History of Insects*. Dordrecht etc. Kluwer Academic Publishers, 517.
- Ren, D., Lu, L.W., Guo, Z.G., Ji, S.A., 1995. *Fauna and stratigraphy of Jurassic-Cretaceous in Beijing and the adjacent areas*. Seismic Publishing House, Beijing, China, p. 43.
- Ren, D., Shih, C.K., Gao, T.P., Yao, Y.Z., Zhao, Y.Y., 2010. Silent story - insect fossil treasures from dinosaur era of the northeastern China. Science Press, Beijing, p. 332.
- 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, p. 409 (in Chinese).
- 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.
- Sharkey, M.J., Carpenter, J.M., Vilhelmsen, L., Heraty, J.M., Liljeblad, J., et al., 2012. Phylogenetic relationships among superfamilies of Hymenoptera. *Cladistics* 28, 80–112. <http://dx.doi.org/10.1111/j.1096-0031.2011.00366.x>.

- Wang, M., Shih, C.K., Ren, D., 2012. *Platyxyela* gen. nov. (Hymenoptera, Xyelidae, Macroxyelinae) from the Middle Jurassic of China. *Zootaxa* 3456, 82–88.
- 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 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.
- Wang, M., Rasnitsyn, P.A., Ren, D., 2014b. Two new fossil sawflies (Hymenoptera, Xyelidae, Xyelinae) from the Middle Jurassic of China. *Acta Geologica Sinica (English Edition)* 88 (4), 1801–1840.
- Zhang, H.C., Wang, B., Yan, F., 2010. Evolution of insect diversity in the Jehol Biota. *Science China Earth Sciences* 53 (12), 1908–1917.