

A re-examination of forewing subcosta in Blasticotomidae (Hymenoptera: Tenthredinoidea) with description of new Mesozoic species from northeastern China

Jia-Liang Zhuang^{a,b}, Alexandr P. Rasnitsyn^{c,d}, Chungkun Shih^{a,e}, Dong Ren^a, Mei Wang^{b,*}

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

^b Key Laboratory of Biodiversity Conservation of National Forestry and Grassland Administration, Ecology and Nature Conservation Institute, Chinese Academy of Forestry, Beijing 100091, China

^c Paleontological Institute, Russian Academy of Sciences, 123 Profsoyuznaya ul., 117647 Moscow, Russia

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

^e Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013-7012, USA

Received 5 February 2026; received in revised form 8 April 2026; accepted 22 April 2026

Available online 28 April 2026

Abstract

One new genus *Platyotoma* n. gen., and four new species, *Platyotoma elongata* n. sp., *Platyotoma mirabilis* n. sp., *Pseudoxyla crassa* n. sp. and *Pseudoxyla lata* n. sp., are illustrated and described based on specimens from the Lower Cretaceous Yixian Formation (~125 Ma). The holotypes of blasticotomids, from the Yixian and the Jiulongshan formations in China, are re-examined. Among them, the descriptions of forewing Sc vein morphology in *Abrotoma robusta*, *Synaptotoma limi*, and *Xyelocerus diaphanus* are revised. In addition, a series of new materials of *Dahurotoma linearis* are reported, allowing a revised description of its forewing Sc. Based on a re-evaluation of the forewing Sc morphology within the family, we hypothesize that the presence of Sc stalk is a widespread plesiomorphy in Blasticotomidae. Furthermore, we revised the transformation series of the forewing Sc in Blasticotomidae. These findings not only expand the known fossil species diversity of Blasticotomidae but also provide new evidence on the venation evolution within the Blasticotomidae.

© 2026 Nanjing Institute of Geology and Palaeontology. Published by Elsevier B.V. All rights are reserved, including those for text and data mining, AI training, and similar technologies.

Keywords: sawfly; Yixian Formation; insect fossils; taxonomy; venation evolution

1. Introduction

Blasticotomidae, a small family within Tenthredinoidea, comprises only 14 extant species in two genera and is restricted to the temperate regions of Eurasia (Taeger et al., 2018; Verheyde et al., 2018). Its larvae are specialized borers in fern stems (Wei and Nie, 1999). As one of the ancient groups in Hymenoptera, it occupies a significant

phylogenetic position: it is consistently recovered as sister group to the core tenthredinoids (i.e., tenthredinoids excluding blasticotomids) by both morphological and molecular phylogenetic studies (Ronquist et al., 1999; Vilhelmsen, 2001; Malm and Nyman, 2015; Wutke et al., 2024). Recently, Rasnitsyn and Müller (2023) treated Xyelotomidae, an extinct Mesozoic sawfly family, as a junior synonym of Blasticotomidae based on the morphological similarities observed in adults and larvae. Sun et al. (2024) further divided Blasticotomidae into four subfamilies based on wing venation characteristics:

* Corresponding author.

E-mail address: wangmei@caf.ac.cn (M. Wang).

Blasticotominae Thomson, 1871, Dahurotomidae Sun, Rasnitsyn, Zhuang and Shih in Sun et al., 2024, Pseudoxyelocerinae Sun, Rasnitsyn, Zhuang and Shih in Sun et al., 2024, and Undataminae Sun, Rasnitsyn, Zhuang and Shih in Sun et al., 2024. To date, 16 extinct genera and 27 fossil species of Blasticotomidae have been reported (Table 1).

The subcosta (Sc) of the forewing in Blasticotomidae exhibits a remarkable diversity rarely observed in other hymenopteran lineages. Several types include the bifurcation of the Sc vein; the contraction or absence of its stalk; the complete loss of the Sc vein; the partial loss or reduction of its branches (Sc1, Sc2); and stable additional vein, e.g., the sc+r crossvein (Sun et al., 2024). Together, these

different types of Sc constitute the unique Sc vein morphological patterns in this family. Moreover, Blasticotomidae also displays rare wing venation variations and asymmetries compared to other members in Hymenoptera (Gao et al., 2009a, 2016). As a result, this family represents an essential group for studying the variation and evolution of wing venation in the lower hymenopterans.

Herein, we described one new genus and four new species of Blasticotomidae from the Yixian Formation in Northeast China. To better understand the morphological diversity of vein Sc in the forewing, we systematically reviewed the fossil specimens reported from the Yixian and the Jiulongshan formations, China, based on holotypes and our new materials, and revised the characteriza-

Table 1
List of fossil Blasticotomidae with age, occurrence, and forewing Sc stalk condition. Abbreviations: J1, J2, J3 = Early, Middle, Late Jurassic, respectively; K1 = Early Cretaceous; E2 = Eocene; E3 = Oligocene.

Subfamily	Species	Geological age	Location	Sc stalk
Pseudoxyelocerinae Sun, Rasnitsyn, Zhuang and Shih in Sun et al., 2024	<i>Pseudoxyelocerus bascharagensis</i> Nel, Petrusevičius and Henrotay, 2004	J1	Luxembourg	present
Dahurotominae Sun, Rasnitsyn, Zhuang and Shih in Sun et al., 2024	<i>Dahurotoma linearis</i> Ren in Ren et al., 1995	K1	China	present
	<i>Dahurotoma robusta</i> Rasnitsyn, 1990	K1	Russia	present
	<i>Dahurotoma suni</i> Hong, 1982	K1	China	absent
	<i>Pseudoxyla crassa</i> n. sp.	K1	China	present
	<i>Pseudoxyla heteroclita</i> Rasnitsyn, 1968	J2	Kazakhstan	present
	<i>Pseudoxyla lata</i> n. sp.	K1	China	present
	<i>Aduantoma insolita</i> Sun, Rasnitsyn, Zhuang and Shih in Sun et al., 2024	J2	China	present
	<i>Aethotoma aninomorpha</i> Gao, Shih, Engel and Ren, 2016	J2	China	present
	<i>Apertoma macroclada</i> Gao, Ren and Shih in Gao et al., 2009a	J2	China	present
	<i>Liberitoma tenella</i> Sun, Rasnitsyn, Zhuang and Shih in Sun et al., 2024	J2	China	present
Undataminae Sun, Rasnitsyn, Zhuang and Shih in Sun et al., 2024	<i>Liberitoma compta</i> Sun, Rasnitsyn, Zhuang and Shih in Sun et al., 2024	J2	China	present
	<i>Liberitoma incompleta</i> Sun, Rasnitsyn, Zhuang and Shih in Sun et al., 2024	J2	China	present
	<i>Paradoxotoma tsiaiae</i> Gao, Ren and Shih in Gao et al., 2009a	J2	China	present
	<i>Synaptotoma limi</i> Gao, Ren and Shih in Gao et al., 2009a	K1	China	present
	<i>Undatoma bicolor</i> Rasnitsyn and Jarzembowski in Rasnitsyn et al., 1998	K1	UK	absent
	<i>Undatoma dahurica</i> Rasnitsyn, 1977	J3	Russia	absent
	<i>Undatoma stigmatica</i> Rasnitsyn and Jarzembowski in Rasnitsyn et al., 1998	K1	UK	?
	<i>Undatoma taksha</i> Rasnitsyn, 1990	K1	Russia	?
	<i>Undatoma undurgensis</i> Rasnitsyn, 1990	K1	Russia	?
	<i>Abrotoma robusta</i> Gao, Ren and Shih in Gao et al., 2009a	J2	China	present
	<i>Enspletoma oligocaenica</i> Rasnitsyn and Wedmann in Sun et al., 2024	E3	Germany	absent
	<i>Leridotoma pulcherrima</i> Rasnitsyn and Ansoerge, 2000	K1	Spain	absent
	<i>Leridotoma rudgwickensis</i> Rasnitsyn and Jarzembowski in Rasnitsyn et al., 1998	K1	UK	absent
	<i>Paremphytus ostentus</i> Brues, 1908	E2	USA	absent
Blasticotominae Thomson, 1871	<i>Platyotoma elongata</i> n. gen. n. sp.	K1	China	present
	<i>Platyotoma mirabilis</i> n. gen. n. sp.	K1	China	absent
	<i>Xyelocerus abruptus</i> Sun, Rasnitsyn, Zhuang and Shih in Sun et al., 2024	J2	China	present
	<i>Xyelocerus admirandus</i> Rasnitsyn, 1968	J2	Kazakhstan	absent
	<i>Xyelocerus diaphanus</i> Gao, Ren and Shih in Gao et al., 2009a	J2	China	present
	<i>Xyelotoma nigricornis</i> Rasnitsyn, 1968	J2	Kazakhstan	present

tion of the Sc vein for *Abrotoma robusta* Gao, Ren and Shih in Gao et al., 2009a, *Synaptotoma limi* Gao, Ren and Shih in Gao et al., 2009a, *Xyelocerus diaphanus* Gao, Ren and Shih in Gao et al., 2009a, and *Dahurotoma linearis* Ren in Ren et al., 1995. Upon such, we enriched the fossil records of Mesozoic blasticotomids and re-evaluated the forewing Sc vein morphology in Blasticotomidae, which should facilitate subsequent research on the evolution of wing venation within the family and the basal Hymenoptera.

2. Materials and methods

All compression fossil specimens examined herein were deposited in the Key Laboratory of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University, Beijing (CNU; Dong Ren, Curator). Specimen numbers in this study bear the prefix 'CNU', which refers to the same institution (Capital Normal University). *Platyotoma elongata* n. gen. n. sp. and *P. mirabilis* n. gen. n. sp. were collected from Dawangzhangzi Village, Songzhangzi Township, Lingyuan City, Liaoning Province, China (41°1'N, 119°1'E); *Pseudoxyla crassa* n. sp., *P. lata* n. sp. and new specimens of *Dahurotoma* were collected from Huangbanjigou, Chaomidian Village, Beipiao City, Liaoning Province, China (41°6'N, 120°8'E). Both genera were from the Yixian Formation whose age has been estimated as Early Cretaceous (~125 Ma, Barremian/Aptian) (Wang et al., 2000; Ren et al., 2019).

The specimens were examined and photographed using a Nikon SMZ 25 dissecting microscope equipped with a Nikon DS-Ri2 digital camera system, either dry or wetted with 95% ethanol. The line drawings were prepared using Adobe Illustrator CC 2022 and Adobe Photoshop CC 2021. The measurements of the specimens were taken with a scale bar using ImageJ. The wing venation nomenclature used in this study was modified from Rasnitsyn (1980).

3. Systematic paleontology

Class Insecta Linnaeus, 1758

Order Hymenoptera Linnaeus, 1758

Superfamily Tenthredinoidea Latreille, 1802

Family Blasticotomidae Thomson, 1871

1968 Xyelotomidae – Rasnitsyn, p. 224.

Subfamily Blasticotominae Thomson, 1871

Type genus: *Blasticotoma* Klug, 1834.

Included genera: Type genus, *Abrotoma* Gao, Ren and Shih in Gao et al., 2009a, *Enspeletoma* Rasnitsyn and Wedmann in Sun et al., 2024, *Leridotoma* Rasnitsyn and Ansoerge, 2000, *Paremphytus* Brues, 1908, *Runaria* Malaise, 1931, *Xyelocerus* Rasnitsyn, 1968, *Xyelotoma* Rasnitsyn, 1968 and *Platyotoma* Zhuang, Rasnitsyn, Shih and Wang n. gen.

Genus *Platyotoma* Zhuang, Rasnitsyn, Shih and Wang n. gen.

Etymology: The first part of the generic name is derived from the Greek “Platy-”, meaning straight and referring to the straight vein Cu in cell 1mcu; the second part, “-toma”, refers to the type genus *Blasticotoma* Klug, 1834. Gender feminine.

Type species: *Platyotoma elongata* Zhuang, Rasnitsyn, Shih and Wang n. sp.

Included species: Type species and *P. mirabilis* Zhuang, Rasnitsyn, Shih and Wang n. sp.

Diagnosis: Head and thorax dorsally without punctation. Antenna with first flagellomere slender and longer than, or slightly shorter than, width of head; length of second flagellomere less than twice its width. Forewing with Sc developed and at least present as transverse vein; pterostigma completely sclerotized; 1-Rs short and nearly as long as width of vein R; cell 1mcu quadrilateral and longer than pterostigma, and its apex not widened; M+Cu, 1-Cu and 2-Cu forming a slight angle at junction; cu-a located at middle of cell 1mcu; 3-Cu longer than 1m-cu. Mesothorax with prescutum short and not reaching half length of mesothorax; pseudosternum delimited.

Remarks: *Platyotoma* n. gen. shares the main diagnostic characteristics of the subfamily Blasticotominae, such as the cell 1mcu not widened at the apex and almost aligned with wing axis, and vein Cu nearly straight (weak kinks at M+Cu fork, 1-Cu straight) in forewing. It can be distinguished from *Paremphytus*, *Enspeletoma*, and *Leridotoma* by its elongate forewing cell 1mcu, with an aspect (length-to-width) ratio larger than two (compared to less than two in the other genera, except *Xyelotoma*, *Xyelocerus*, and *Abrotoma*). *Platyotoma* n. gen. could be distinguished from *Abrotoma* and *Xyelocerus* in the surface of head and thorax without punctation (having punctation in *Abrotoma* and *Xyelocerus* except *Xyelocerus admirandus* Rasnitsyn, 1968 without relevant description) and forewing with 1-Rs very short, nearly as long as wide of vein R. Lastly, it differs from *Xyelotoma* in having flagellomeres 6–7 segments and length of thread (flagellomeres excluding the first) shorter than half of the first flagellomeres (in *Xyelotoma*, flagellomeres five-segmented and thread longer than half length of the first flagellomere).

Platyotoma elongata Zhuang, Rasnitsyn, Shih and Wang n. sp.

(Fig. 1)

Etymology: The species name is derived from the Latin word “elongatus”, meaning long, referring to the long 1mcu cell of forewing.

Material: Holotype, CNU-HYM-LL2024201p/c.

Locality and horizon: Dawangzhangzi Village, Songzhangzi Township, Lingyuan City, Liaoning Province, China; Yixian Formation, Lower Cretaceous.

Diagnosis: In addition to generic diagnosis, antenna with the flagellomere ca. 1.6 × as long as width of head, aspect

ratio of second flagellomere approximately two, forewing with Sc stalk present and 1-M longer than Rs+M.

Description: Male. Body length (excluding antenna) 9.41 mm, head 1.57 mm in width and 1.04 mm in length. Color possibly totally dark. Eyes reniform, occupying half length of head. Antenna eight-segmented (Fig. 1F) with the first flagellomere 2.46 mm in length, much longer than the width of head, the total length of remaining flagellomeres 0.60 mm in length; the aspect ratio of the second flagellomere approximately two.

Thorax smooth without any punctation. Mesothorax with prescutum triangular and its length less than half length of mesothorax, median mesoscutal sulcus developed and nearly reaching the posterior of notaulus. Mesoscutellum slightly smaller than mesoprescutum and the distance

from its anterior margin to the posterior margin of notaulus ca. $0.8 \times$ its own length.

Forewing (Fig. 1H) 7.52 mm in length. Pterostigma completely sclerotized and nearly $3.1 \times$ as long as wide. Sc developed and composed of two parts, the basal part relatively long and meeting vein R at half the distance from the origin of 1-Rs (Fig. 1D, E), the distal part sub-perpendicular to vein R and meeting R proximad to origin of 1-Rs; vein R bent at the base of 1-Rs; 1-Rs short and its length similar to width of vein R; 1r-rs ca. $0.6 \times$ length of 2r-rs and the latter inclined towards wing apex; M+Cu slightly curved and forked before level of transverse Sc. Length ratio of 1-M, Rs+M, 2-M, 1m-cu, 1-Cu and 2-Cu nearly $1.1 : 0.8 : 0.6 : 0.6 : 1.2 : 0.9$; angle between 1-M and 1-Cu nearly 49° . Cell 2rm slightly narrow at apex; vein

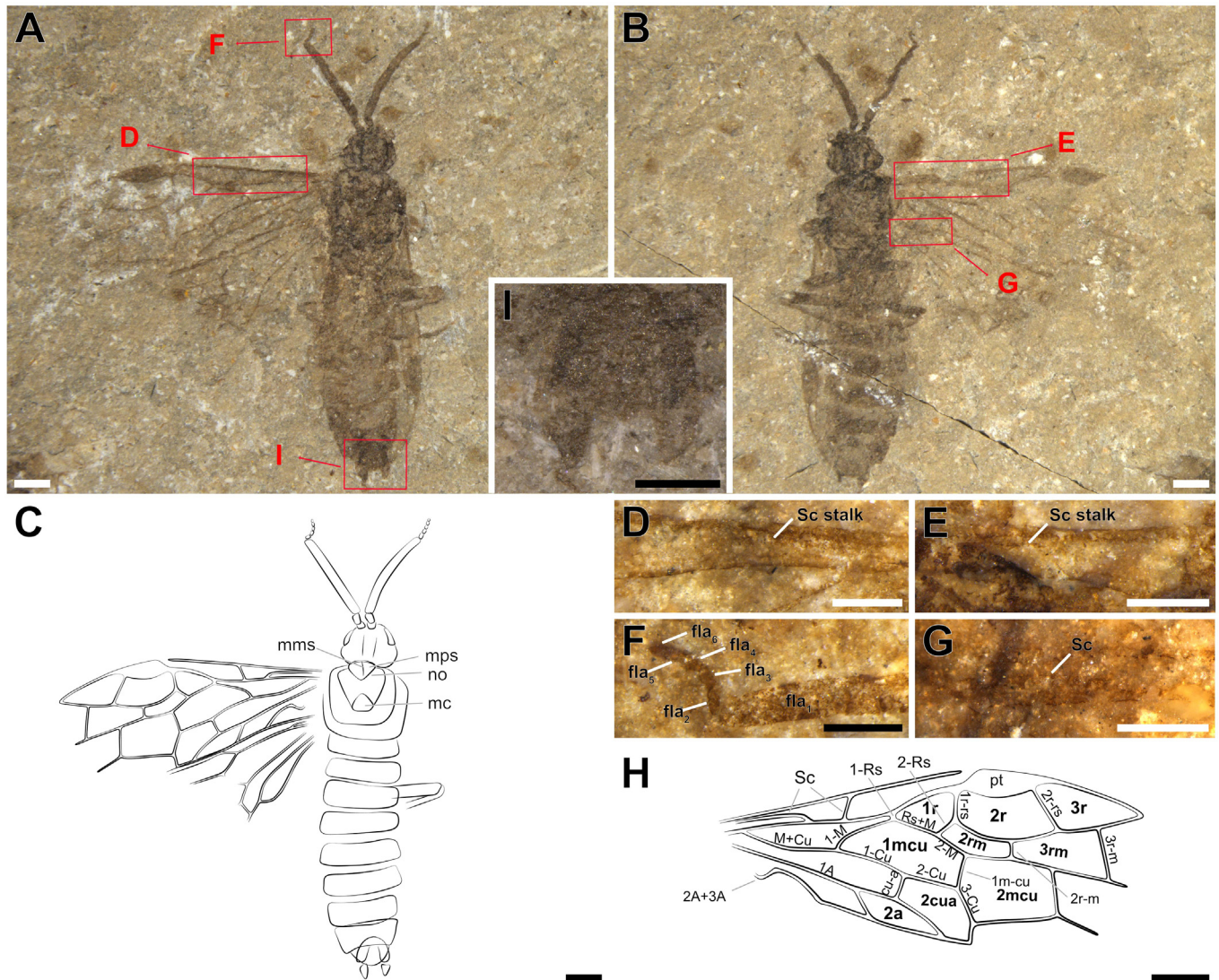


Fig. 1. *Platyotoma elongata* n. gen. n. sp., holotype (CNU-HYM-LL2024201p/c), male. (A) Dorsal view. (B) Ventral view. (C) Line drawing of dorsal view. (D, E) Sc stalk in forewing under alcohol. (F) Partial antenna under alcohol. (G) Sc in hind wing under alcohol. (H) Line drawing of forewing. (I) Male genitalia. Abbreviations: fla_n = nth flagellomere; mc = mesoscutellum; mms = median mesoscutal sulcus; mps = mesoprescutum; no = notaulus; pt = pterostigma. Scale bars = 1 mm (A–C, H) or 0.5 mm (D–G, I).

2-Rs nearly half length of Rs+M; 2r-m ca. $0.3 \times$ length of 3r-m; 3-Cu slightly longer than 1m-cu; cu-a perpendicular to vein 1A and located behind middle of cell 1m-cu; 2A+3A S-shaped curved at the base part; cell 2a ca. $3.9 \times$ as long as wide.

Hind wing with Sc present and meeting vein R at $0.2 \times$ the distance from the origin of 1-Rs (Fig. 1G); 1-Rs ca. $0.6 \times$ the length of 1r-m. Cell a narrow and its apex slightly sharp.

Abdomen narrow and its width similar to that of mesothorax. Male genitalia twisted 180° (Fig. 1I).

Remarks: *Platyotoma elongata* can be distinguished from all other xyelotomids by the following combination of characters: forewing with Sc stalk present, along with a crossvein-like branch, and 1-Rs lost. These characters are otherwise known only from the genera *Synaptotoma* and *Dahurotoma*. Additionally, its forewing cell 1m-cu is quadri-lateral, elongated (at least twice as long as wide) and the apex not widened, which is previously found only in *Xyelocerus*. All above support *Platyotoma elongata* as a new species.

Platyotoma mirabilis Zhuang, Rasnitsyn, Shih and Wang n. sp. (Fig. 2)

Etymology: The species name is derived from the Latin word “mirabilis”, meaning extraordinary, referring to the unique character combination for short 1-Rs and nearly quadrangular cell 1m-cu.

Material: Holotype, CNU-HYM-LL2024202.

Locality and horizon: Dawangzhangzi Village, Songzhangzi Township, Lingyuan City, Liaoning Province, China; Yixian Formation, Lower Cretaceous.

Diagnosis: In addition to the generic diagnosis, antenna with the first flagellomere ca. $0.8 \times$ the width of head, the length-to-width ratio of the second flagellomere approximately 0.9, forewing with Sc stalk absent, 1m-cu almost quadrangular, 1-M short and nearly as long as Rs+M.

Description: Female. Body length (excluding antenna and ovipositor sheath) 11.46 mm, head 1.76 mm in length and 2.31 mm in width. Antenna nine-segmented (Fig. 2E) and the first flagellomere 1.87 mm in length. The length-to-width ratio of the second flagellomere close to 0.9 (Fig. 2E); the ratio of following flagellomeres less than 1.5.

Thorax smooth without any punctation and mesothorax wider than head. Mesothorax with prescutum and scutellum triangular, and their length similar. Gap between mesoprescutum and mesoscutellum more than half length of mesoprescutum; pseudosternum delimited; cenchrus narrow with aspect ratio more than two (Fig. 2C).

Forewing 7.79 mm in length (Fig. 2F). Sc developed as crossvein only, inclined towards the base of forewing; pterostigma slender and completely sclerotized; M+Cu slightly curved, cell 1m-cu slender and longer than pterostigma;

length ratio of 1-M, Rs+M, 2-M, 1m-cu, 2-Cu and 1-Cu nearly $0.8 : 0.6 : 0.7 : 0.6 : 0.9 : 0.8$; 2-Rs ca. $0.7 \times$ length of Rs+M; angle between 1-M and 1-Cu nearly 57° ; 1r-rs parallel to 2r-rs and nearly half length of 2r-rs; 3-Cu ca. $1.4 \times$ length of 1m-cu.

Hind leg at least 7.28 mm in length; femur ca. $0.8 \times$ the length of tibia. Ovipositor 3.08 mm in length and 1.96 mm in width, sheath short and thick nearly 0.87 mm in length.

Remarks: In *Platyotoma* n. gen., species can be easily distinguished by the length of the first flagellomere, which is much longer than the width of head in *P. elongata* n. sp. (ca. $1.6 \times$ the width of head), nearly as long as the width of head in *P. mirabilis* n. sp. In addition, the second flagellomere ca. $2 \times$ as long as wide; basal trunk Sc is developed and 1-M is longer than Rs+M in *P. elongata* n. sp. In contrast, in *P. mirabilis* n. sp., the second flagellomere ca. $0.9 \times$ as long as wide; basal trunk Sc is absent and 1-M is nearly as long as Rs+M. Their synonymy as a male and female of the same species is very unlikely based on the significant differences between their wing venation, which cannot be explained by sexual dimorphism.

Subfamily Dahurotominae Sun, Rasnitsyn, Zhuang and Shih in Sun et al., 2024

Type genus: *Dahurotoma* Rasnitsyn, 1990.

Included genera: Type genus and *Pseudoxyla* Rasnitsyn, 1968.

Genus *Pseudoxyla* Rasnitsyn, 1968

Type species: *Pseudoxyla heteroclita* Rasnitsyn, 1968.

Included species: Besides the type species, *P. crassa* Zhuang, Rasnitsyn, Shih and Wang n. sp. and *P. lata* Zhuang, Rasnitsyn, Shih and Wang n. sp. are also included.

Diagnosis (modified after Rasnitsyn, 1968): Body surface with obvious punctations on head and thorax. Antenna with first flagellomere nearly as long as half head width, combined length of rest flagellomeres nearly equal to length of pedicel. Forewing with Sc developed as basal longitudinal trunk and apical fork proximal to origin of 1-Rs (possibly lost in *P. lata* Zhuang, Rasnitsyn, Shih and Wang n. sp.); 1-Rs inclined towards wing apex and slightly shorter or slightly longer than 1r-rs; cell 3r-m short and its length-to-width ratio nearly 1.1; an additional vein present in cell 3r. Hind leg with femur expanded. Ovipositor with sheath slightly shorter than pterostigma.

Pseudoxyla crassa Zhuang, Rasnitsyn, Shih and Wang n. sp.

(Fig. 3)

Etymology: The species name is derived from the Latin word “crassus”, meaning robust, referring to the strong body of the species.

Material: Holotype, CNU-HYM-LL2024203p/c.

Locality and horizon: Huangbanjigou, Chaomidian Village, Beipiao City, Liaoning Province, China; Yixian Formation, Lower Cretaceous.

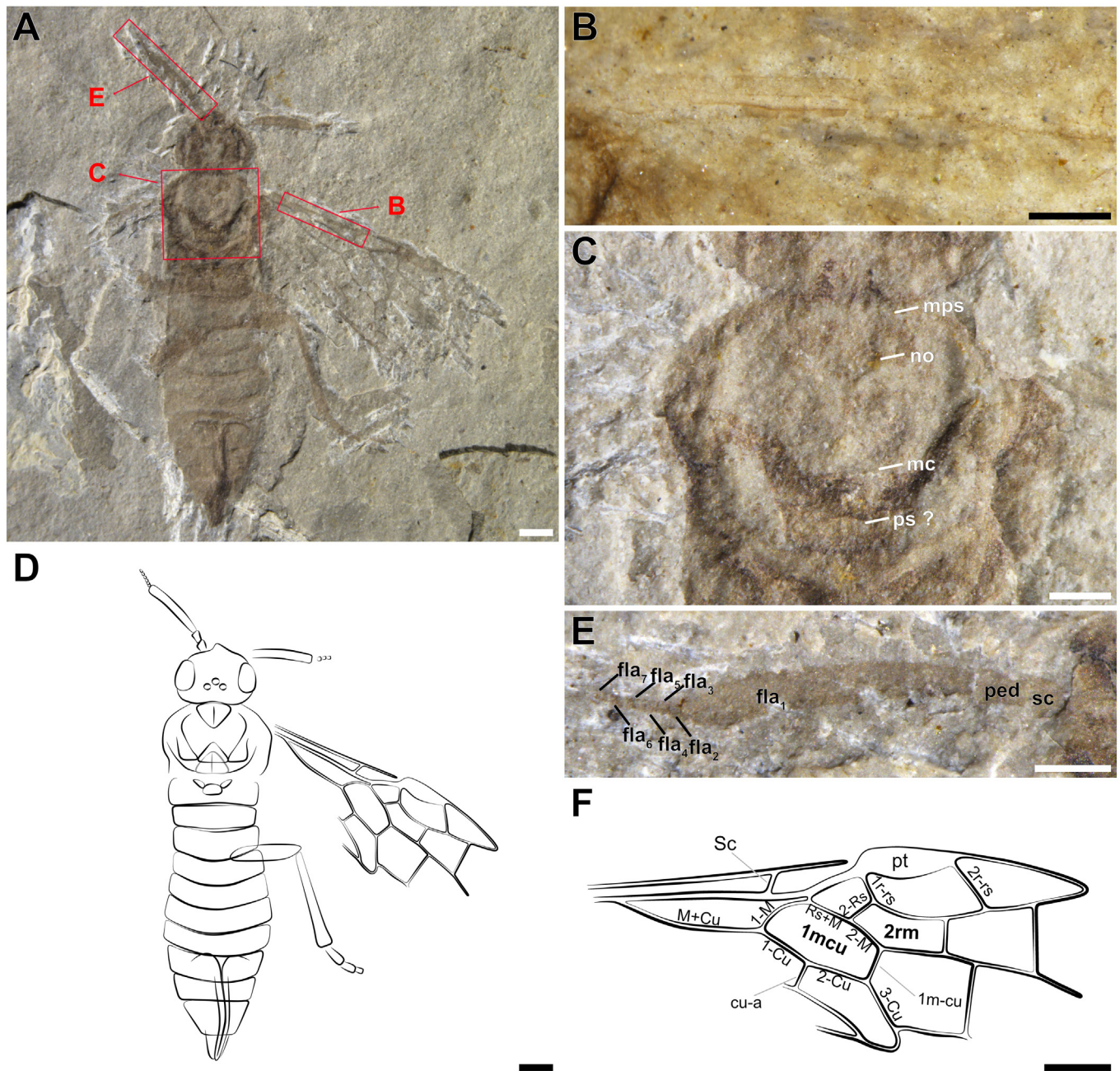


Fig. 2. *Platytoma mirabilis* n. gen. n. sp., holotype (CNU-HYM-LL2024202), female. (A) Dorsal view. (B) Costal area in forewing under alcohol. (C) Thorax. (D) Line drawing of dorsal view. (E) Antenna. (F) Line drawing of forewing. Abbreviations: ped = pedicel; ps = pseudosternum; sc = scape. Scale bars = 1 mm (A, D, F) or 0.5 mm (B, C, E).

Diagnosis: In addition to the generic diagnosis, forewing with pterostigma sclerotized; 1-Rs shorter than Rs+M, additional vein of cell 3r proximal to 3r-m, 1-M nearly perpendicular to 1-Cu, cu-a located at 2/3 of cell 1m-cu. Hind leg with tarsus not modified.

Description: Female. Body length (excluding antenna and ovipositor sheath) 11.63 mm, head 2.54 mm in width and 1.91 mm in length, its surface covered with rough punctations. Ground color dark including antennae basally and

dorsally, hind femora and tarsi, pterostigma and saw sheaths. Antenna with the scape, pedicel, first flagellomere 0.38 mm, 0.30 mm, 1.46 mm in length, respectively; remaining flagellomeres narrower than first, combined length nearly equal to pedicel. Ocellar triangle with anterior angle 120°. Back surface of head apparently with complete occipital carina and with no occipital suture, with wide sclerotized bridge (its identity, either postgenal or hypostomal, is not clear because apparent longitudinal sutures, lateral

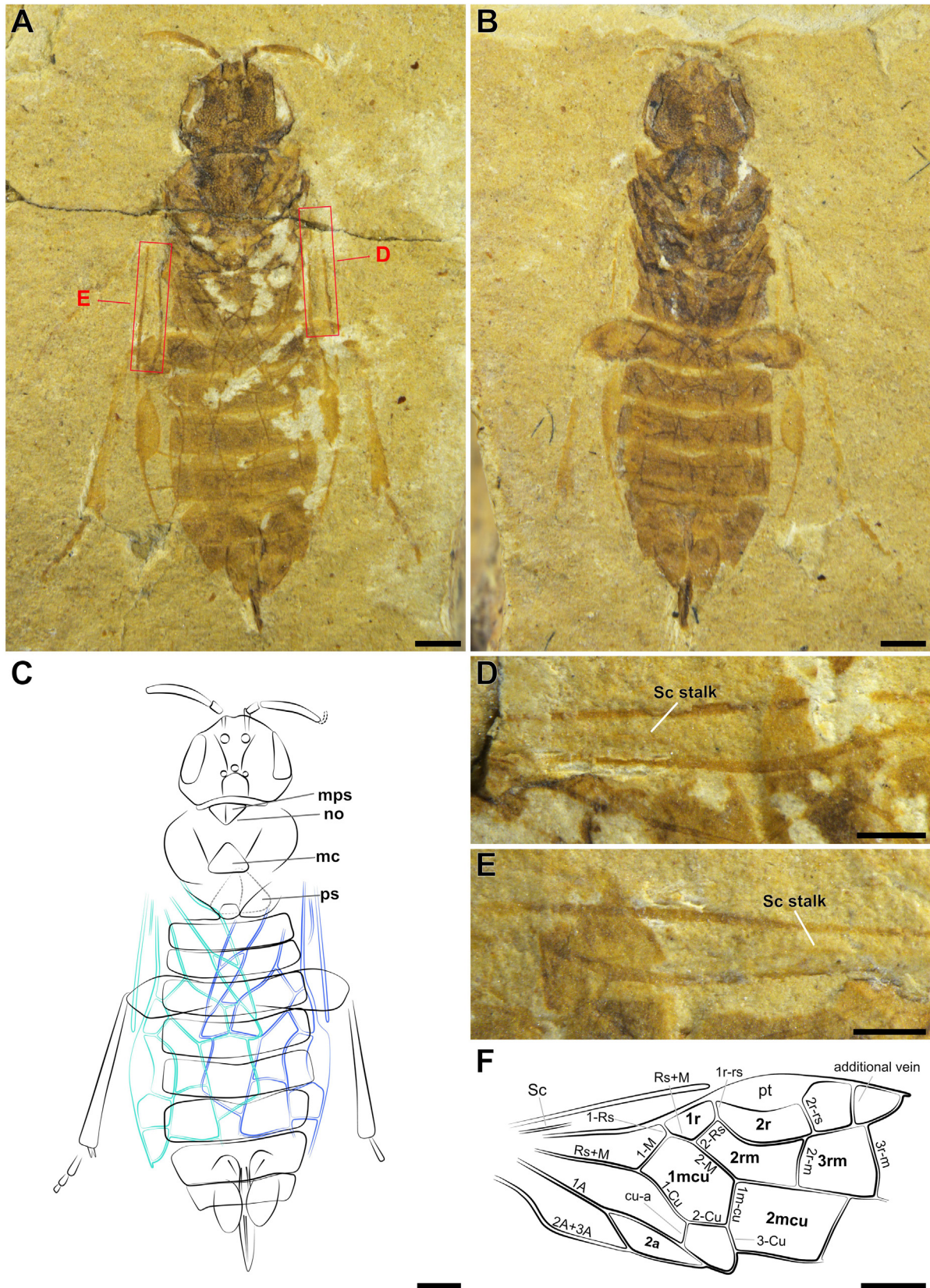


Fig. 3. *Pseudoxyela crassa* n. sp., holotype (CNU-HYM-LL2024203p/c), female. (A) Dorsal view. (B) Ventral view. (C) Line drawing of dorsal view. (D, E) Sc stalk in forewing. (F) Line drawing of forewing. Scale bars = 1 mm in (A–C, F), 0.5 mm (D, E).

and medial ones that might represent hypostomal and interhypostomal sutures, respectively, not sufficiently well developed to be identified unequivocally).

Thorax with punctations on surface, prothorax short with anterior and posterior margins gently curved. Mesothorax with prescutum and scutellum triangular, and later larger than former. Gap between mesoprescutum and mesoscutellum more than half length of mesoprescutum; pseudosternum delimited and larger than mesoscutellum.

Forewing 7.36 mm in length (Fig. 3F). Pterostigma sclerotized; Sc having longitudinal trunk (Fig. 3D, E), 1-Rs shorter than Rs+M, Rs+M ca. $0.8 \times$ as long as 2-Rs, 1-rs ca. $0.6 \times$ as long as 2r-rs, additional vein of cell 3r proximal to 3r-m, M+Cu nearly straight, 1-M nearly perpendicular to 1-Cu; length ratio of 1-M, Rs+M, 2-M, 1m-cu, 2-Cu and 1-Cu nearly $0.7 : 0.4 : 0.9 : 0.7 : 0.6 : 1.1$; cu-a located at $2/3$ of cell 1m-cu, 3-Cu nearly $0.6 \times$ length of 1m-cu; aspect ratio of cell 2a nearly 4.1.

Hind leg at least 7.51 mm in length, with femur very wide, particularly toward apex, with aspect ratio at most 2.6. Basal abdominal terga apparently entire (not split medially). Ovipositor at least 2.53 mm in length, sheath slightly shorter than pterostigma.

Remarks: The new species is assigned to *Pseudoxyla* based on the following characters: antenna with thread short; forewing with 1-Rs present and inclined towards the wing apex; an extra vertical vein present in the middle of cell 3r. It differs from the type species, *P. heteroclita*, by the completely sclerotized pterostigma (marginally sclerotized only in *P. heteroclita*), and from *P. lata*, by the more slender forewing cell 1m-cu.

Pseudoxyla lata Zhuang, Rasnitsyn, Shih and Wang n. sp. (Fig. 4)

Etymology: The species name is derived from the Latin word “latus”, meaning wide, referring to the large and wide cell 1m-cu.

Material: Holotype, CNU-HYM-LL2024204.

Locality and horizon: Huangbanjigou, Chaomidian Village, Beipiao City, Liaoning Province, China; Yixian Formation, Lower Cretaceous.

Diagnosis: In addition to the generic diagnosis, forewing with 1-Rs slightly longer than Rs+M, the additional vein of cell 3r distal to 3r-m, 1-M meeting 1-Cu at the angle of 109° , cu-a located at the middle of cell 1m-cu.

Description: Female. Body length (excluding antenna and ovipositor sheath) 10.24 mm. Ground color dark, appendages paler except dark scape, pedicel, flagellomere 1 dorsally, basally, and saw sheaths; pterostigma, hind tarsi and apices of hind femora and mid and hind tibiae, and hind tarsi infusate. Head 2.52 mm in width and 2.14 mm in length, its surface covered with punctations. Eyes large and short oval-reniform, ocellar triangle with anterior

angle of 103° . Antenna with scape, pedicel, first flagellomere, thread (flagellomeres except the first segment) 0.45 mm, 0.27 mm, 1.34 mm, 0.26 mm in length (Fig. 4D).

Thorax (Fig. 4C) with rough punctations on surface; prothorax short. Mesothorax with mesoprescutum nearly as wide as mesoscutellum, and former shorter than later. Gap between mesoprescutum and mesoscutellum ca. $0.8 \times$ length of mesoprescutum. Cenchrus nearly $2 \times$ as long as wide.

Forewing (Fig. 4H) at least 7.13 mm in length. Sc developed and forked proximal to the origin of 1-Rs, otherwise poorly preserved (Fig. 4F); pterostigma sclerotized, 1-Rs slightly longer than Rs+M, Rs+M ca. $0.7 \times$ length of 2-Rs, 1r-rs ca. $0.4 \times$ length of 2r-rs; additional vein of cell 3r distal to 3r-m, 1-M meeting 1-Cu at angle of 109° ; length ratio of 1-M, Rs+M, 2-M, 1m-cu, 2-Cu and 1-Cu nearly $0.7 : 0.3 : 0.7 : 0.8 : 0.8 : 0.8$; cu-a located at middle of cell 1m-cu; 3-Cu nearly half length of 1m-cu; aspect ratio of cell 2a nearly 5.1.

Hind femur enlarged, hind tarsus short (much shorter than tibia), segments with apical plantulae (Fig. 4E). Basal abdominal terga apparently not split medially. Ovipositor nearly 2.49 mm in length and bearing oblique ridges on surface; sheath slightly shorter than pterostigma (Fig. 4G).

Remarks: The morphology of species of *Pseudoxyla* shows considerable variation, particularly in the sclerotized area of pterostigma, only sclerotized in the basal part and margin in *P. heteroclita*, fully sclerotized in *P. crassa* n. sp. and *P. lata* n. sp. In addition, *P. lata* n. sp. differs from *P. crassa* n. sp. and *P. heteroclita* in having 1-Rs longer than Rs+M (ca. $1.1 \times$, versus, 1-Rs shorter than Rs+M in the other two species), cu-a located at the middle of cell 1m-cu (versus, located distal to the middle part), cell 1m-cu shorter and wider.

4. Discussion

In Hymenoptera, the wing venation exhibits a general trend toward simplification across the order (Rasnitsyn, 1967, 1969; Goulet and Huber, 1993), which is probably driven by miniaturization in most cases (Polilov, 2015). As a key diagnostic character in lower hymenopterans, the evolution of the forewing Sc typically exemplifies a general trend toward venation simplification. For example, in family Xyelidae, vein Sc generally ranges from complex (many branched structures) to gradual simplification and even eventual loss (Gao et al., 2009b). Similarly, the superfamily Tenthredinoidea has undergone a more complex and diversified evolution process in Sc vein morphology (Rasnitsyn, 1980; Sun et al., 2024). This pronounced diversity, coupled with more frequent venation variations compared with other families (Gao et al., 2009a; Sun et al., 2024), underscores the importance of detailed observation based on ample specimens.

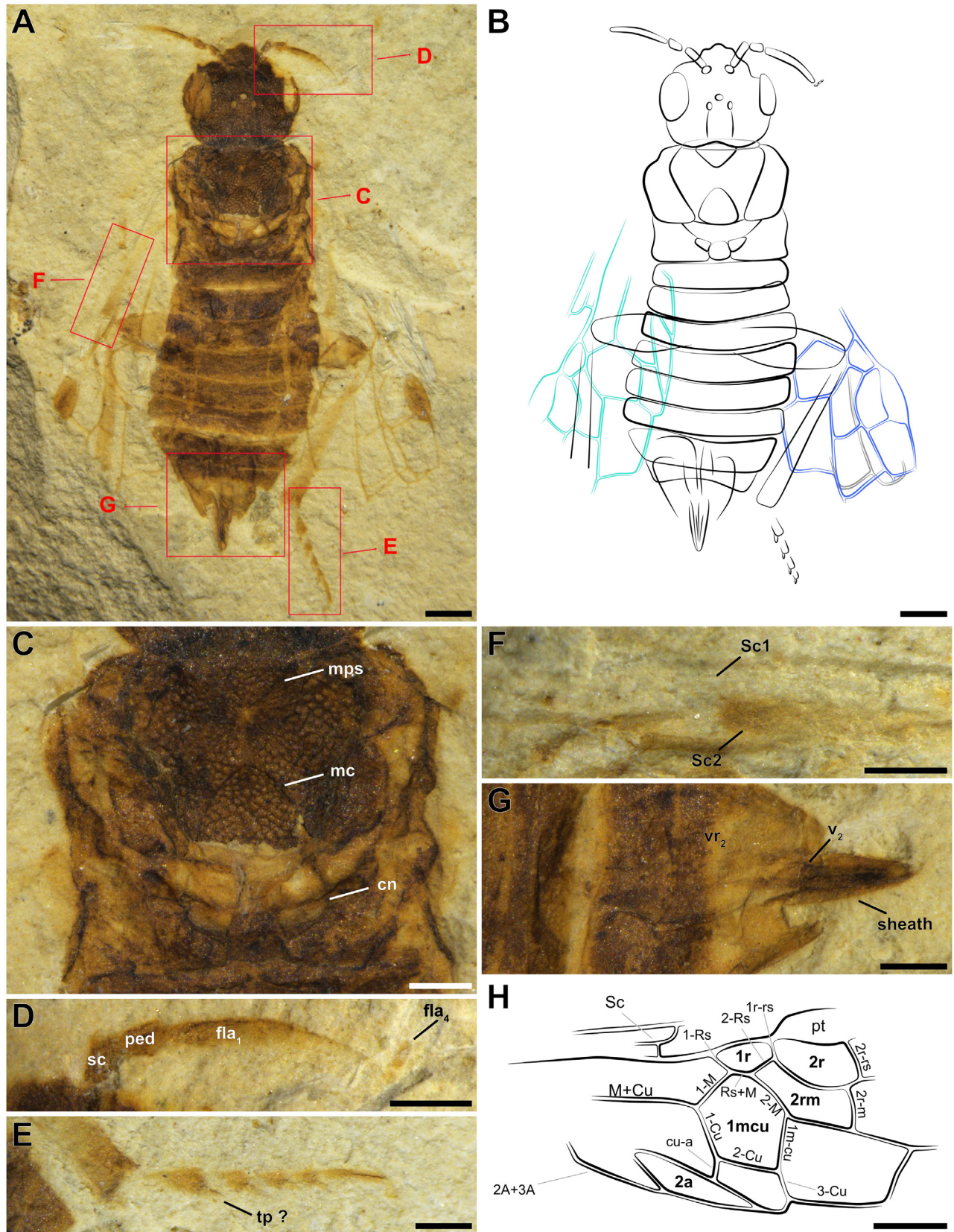


Fig. 4. *Pseudoxyela lata* n. sp., holotype (CNU-HYM-LL2024204), female. (A) Dorsal view. (B) Line drawing of dorsal view. (C) Thorax. (D) Antenna. (E) Tarsus of hind leg. (F) Vein Sc in forewing. (G) Ovipositor. (H) Line drawing of forewing. Abbreviations: cn = cenchrus; tp = tarsal pulvilli. Scale bars = 1 mm (A, B, H) or 0.5 mm (C–G).

4.1. Re-examination of the forewing Sc among all reported species

After examination of all specimens reported and deposited in CNU collections, we found description inaccuracies of the forewing Sc in three species, *Synaptotoma limi*, *Abrotoma robusta*, and *Xyelocerus diaphanus* (Fig. 5 versus figs. 2, 4, 5 in Gao et al., 2009a). Furthermore, most of the new fossil specimens from the Yixian Formation at Huangbanjigou, can be attributed to *Dahurotoma linearis*, but their Sc vein characteristics also contradict previous descriptions (Fig. 6 versus fig. 3.69 in Ren et al., 1995). As a result, the specific results are revised below.

In *Synaptotoma limi* (Fig. 5A), the forewing Sc vein consists of two parts: the basal Sc stalk, which merges into the R at approximately half the distance from the origin of Rs, and a distal crossvein-like Sc, whose distance from the origin of Rs is roughly equal to its own length (Fig. 5B, C). The same forewing Sc is also present in *Dahurotoma robusta* and *Apertoma macroclada* (Rasnitsyn, 1990; Gao et al., 2009a).

For *Abrotoma robusta* (Fig. 5D, E), we identified a forked or V-shaped Sc vein (perhaps Sc2, similar to that of *Xyelocerus abrupta* Sun, Rasnitsyn, Zhuang and Shih in Sun et al., 2024) (Fig. 5F). This structure is visible only under ethanol on one of the paired slabs, which likely led to its initial omission, see Fig. 5G.

The Sc vein in *Xyelocerus diaphanus* (Fig. 5H, I) is also revised. The second junction of Sc and 1-Rs in the forewing is positioned directly after the first, rather than slightly proximal to the base of 1-Rs as previously depicted (Fig. 5J).

Most of the new specimens of *Dahurotoma* Rasnitsyn, 1990 (Fig. 6) can be assigned to *Dahurotoma linearis* based on the forewing with pterostigma only sclerotized at the margins, Rs+M nearly as long as 2-M, cell 1mcu and 2mcu similar in size (Ren et al., 1995). Thorough observation showed that they all have the developed Sc stalk in forewing (Fig. 6G–L) like the type species of the genus, *Dahurotoma robusta* Rasnitsyn, 1990. The stalk part is often partly or faintly preserved, which explains why it was neglected in the original description.

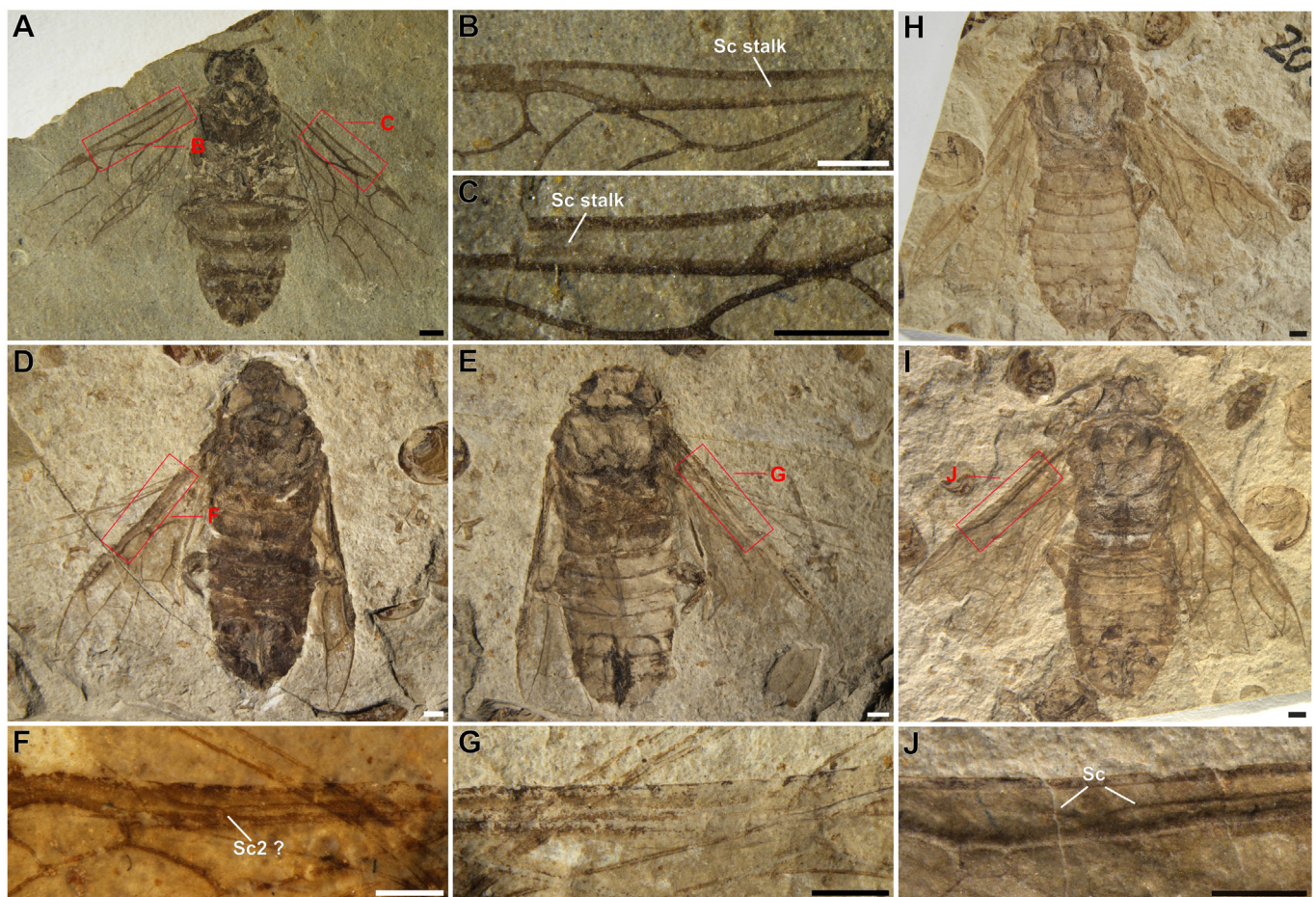


Fig. 5. (A–C) *Synaptotoma limi* Gao, Ren and Shih in Gao et al., 2009a, holotype (CNU-HYM-NN2008012); (A) ventral view; (B, C) Sc stalk in forewing. (D–G) *Abrotoma robusta* Gao, Ren and Shih in Gao et al., 2009a, holotype (CNU-HYM-NN2008014p/c); (D) ventral view; (E) dorsal view; (F) Sc in forewing under alcohol; (G) Sc in forewing. (H–J) *Xyelocerus diaphanus* Gao, Ren and Shih in Gao et al., 2009a, holotype (CNU-HYM-NN2008011p/c); (H) dorsal view; (I) ventral view; (J) Sc in forewing. Scale bars = 1 mm.

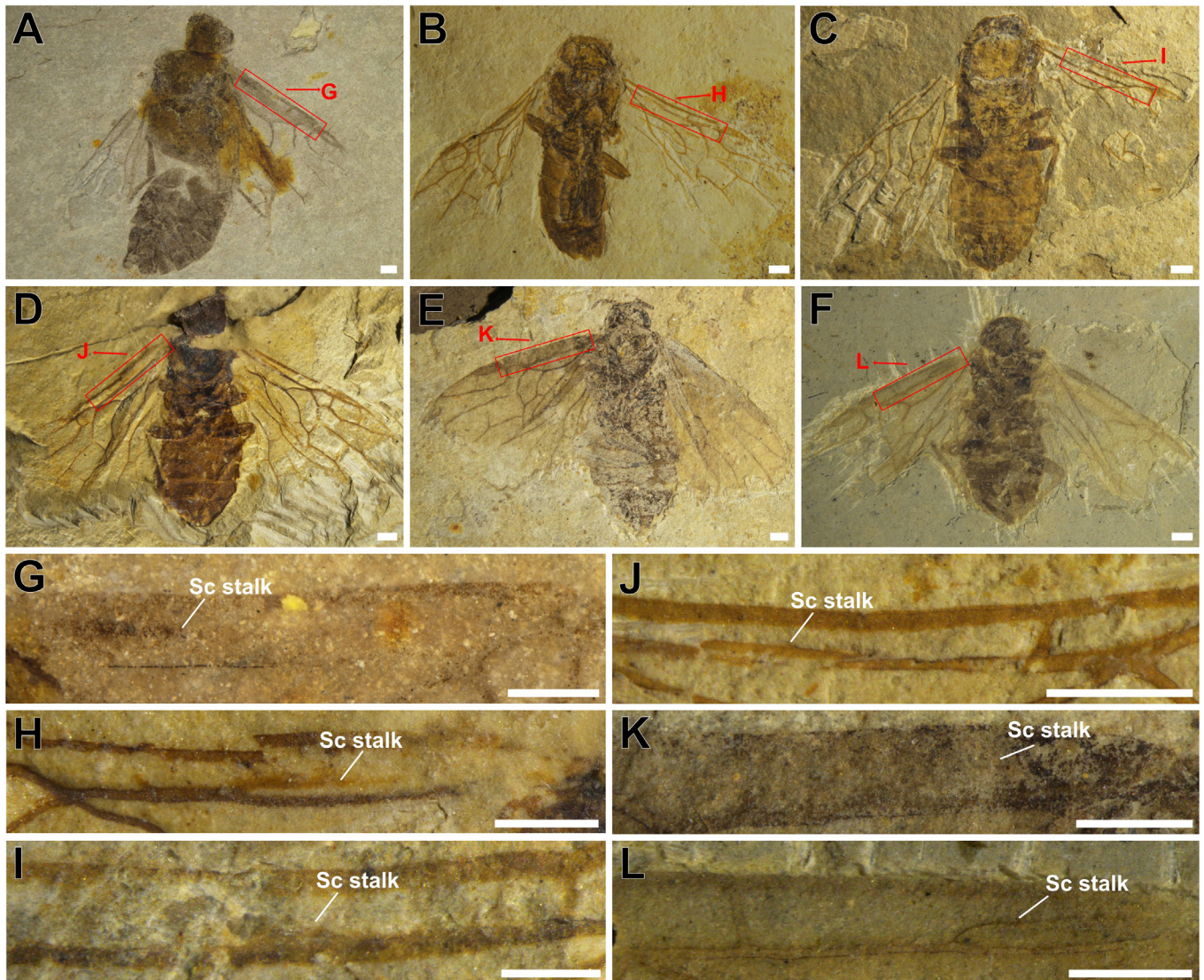


Fig. 6. (A–D, F) *Dahurotoma linearis* Ren in Ren et al., 1995; (A) dorsal view, CNU-HYM-LB2024010; (B) ventral view, CNU-HYM-LB2024011; (C) dorsal view, CNU-HYM-LB2024014; (D) dorsal view, CNU-HYM-LB2024012; (F) ventral view, CNU-HYM-LB2024016. (E) *Dahurotoma* sp., ventral view, CNU-HYM-LB2024015. (G–L) Sc stalk in forewing. Scale bars = 1 mm (A–K, L) or 0.5 mm (I).

4.2. The presence of the Sc stalk in Blasticotomidae

The morphology of the forewing Sc stalk and Sc junction with R, though easily overlooked, is a probable phylogenetically informative character. Herein, we have systematically summarized the Sc stalk of published extinct Blasticotomidae taxa, including the new species in this study (Table 1). Among the 17 extinct genera reported so far, the Sc stalk is only lost in four genera, i.e., *Leridatoma* Rasnitsyn and Ansoerge, 2000, *Undatoma* Rasnitsyn, 1977, *Enspeletoma* Rasnitsyn and Wedmann in Sun et al., 2024, and *Paremphtytus* Brues, 1908, and mainly concentrated in subfamily Blasticotominae Thomson, 1871 (Rasnitsyn, 1977, 1990; Rasnitsyn et al., 1998; Rasnitsyn and Ansoerge, 2000; Sun et al., 2024).

Notably, the latter two genera show closer affinity with extant blasticotomids, as evidenced by the antennae being

3–4 segmented, pterostigma semicircular, 2-Rs absent, cell 1mcu rounded anteriorly in forewing. The Sc vein clearly underwent significant reduction during the evolution of this lineage (*Enspeletoma* + *Paremphtytus* + extant genera *Blasticotoma* and *Runaria*). For *Leridatoma*, although it possesses the typical tenthredinoid trait of a forewing with the oblique crossvein 2r-rs meeting cell 3rm, its precise taxonomic placement requires further research, which is beyond the focus of this article. Additionally, species of *Undatoma* exhibit varying degrees of Sc reduction beyond the loss of the basal stalk (Rasnitsyn, 1977, 1990).

After excluding the above genera, all remaining fossil genera contain at least one species with a developed Sc stalk structure. In view of the above, Sc stalk structure is widespread among members of Blasticotomidae, which may be an important plesiomorphy in ancient groups. However, reduction of Sc — whether complete, partial,

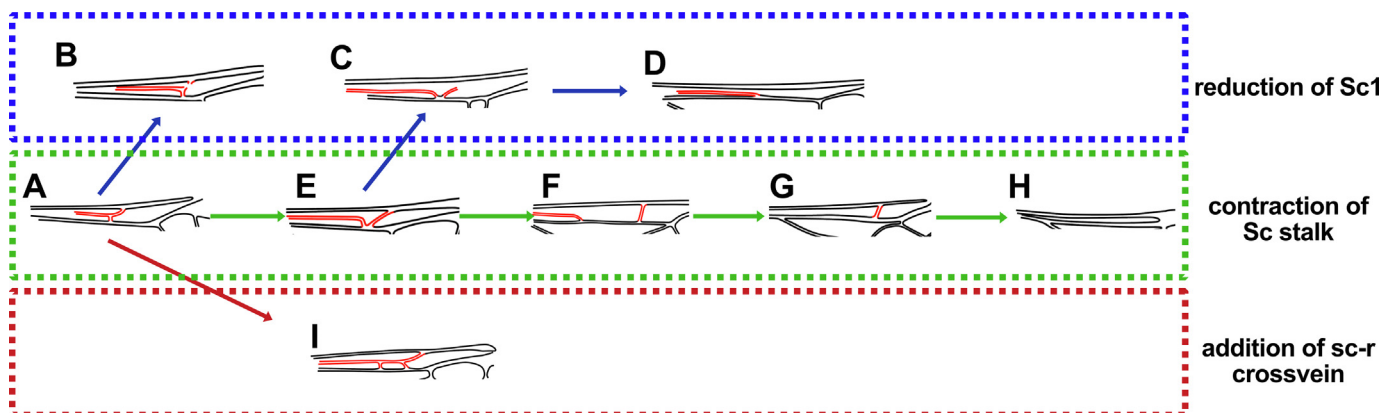


Fig. 7. Different types of transformation of forewing Sc in Blasticotomidae (modified from Sun et al., 2024). (A) *Pseudoxyela heteroclita* Rasnitsyn, 1968. (B) *Paradoxotoma tsaiae* Gao, Ren and Shih in Gao et al., 2009a. (C) *Xyelocerus diaphanus* Gao, Ren and Shih in Gao et al., 2009a. (D) *Aethotoma aninomorpha* Gao, Shih, Engel and Ren, 2016. (E) *Aduantoma insolita* Sun, Rasnitsyn, Zhuang and Shih in Sun et al., 2024. (F) *Dahurotoma linearis* Ren in Ren et al., 1995. (G) *Paremphytus ostentus* Brues, 1908. (H) *Platyotoma mirabilis* n. sp. (I) *Liberitoma incompleta* Sun, Rasnitsyn, Zhuang and Shih in Sun et al., 2024. Note: the Sc vein is marked in red.

or affecting only specific sections such as the fork, stalk or a crossvein-like remnant — has occurred independently in different groups during the evolution of the family.

4.3. A revised evolutionary transformation series in the forewing Sc of Blasticotomidae

Integrating the revisions above with previous work (Sun et al., 2024), the transformation of forewing Sc in Blasticotomidae can be categorized into three main types:

1. Reduction of Sc1 (Fig. 7B–D): This involves the reduction of the Sc1 branch, as illustrated in Fig. 7B–D. The complete or partial loss of the Sc1 segment is rarely observed and has so far been found mainly in Jurassic blasticotomids.
2. Contraction of the Sc stalk (Fig. 7A, E–H): This is another simplification trend unique to Blasticotomidae. The specific form shown in Fig. 7F is particularly prevalent among Cretaceous representatives of this family. It is probable that extant and Cenozoic blasticotomids drifted from this morphological type.
3. Addition of the sc-r crossvein (Fig. 7I): This type of addition is exceptionally rare and might be related to the family's noted propensity for venation variation, similar to the additional veins occasionally observed before 1-Rs or within cell 3r (Gao et al., 2009a, 2016; Sun et al., 2024). Through observation, most specimens of the genus *Liberitoma* deposited in CNU collections exhibit this stable additional crossvein (sometimes asymmetrical), while the remaining show a normal bifurcate Sc or possess sc-r on only one wing.

5. Conclusion

In this work, we report one new genus and four new species of Blasticotomidae — *Platyotoma elongata* n. gen. n.

sp., *Platyotoma mirabilis* n. sp., *Pseudoxyela crassa* n. sp., and *Pseudoxyela lata* n. sp. — from the Lower Cretaceous Yixian Formation (~125 Ma) of northeastern China. Through a detailed re-examination of holotypes and new material, we revise the forewing Sc morphology of several previously described species (*Abrotoma robusta*, *Synaptotoma limi*, *Xyelocerus diaphanus*, and *Dahurotoma linearis*). Our analysis reveals that the presence of a developed Sc stalk is widespread among the Mesozoic blasticotomids and likely represents a plesiomorphic trait for Hymenoptera as a whole. Furthermore, we modify the existing framework for forewing Sc transformation, categorizing it into three types: reduction of the Sc1 branch, contraction of the Sc stalk, and the rare addition of a sc-r crossvein. This work not only expands the taxonomic diversity of the Mesozoic Blasticotomidae but also provides a more solid morphological foundation for understanding wing venation evolution within Hymenoptera.

Declaration of competing interest

All co-authors agree to the content and submission of this manuscript. This paper is new, and it is not being submitted to any other journal. No conflict of interest declared.

Acknowledgments

We are grateful to the two reviewers (Lars Vilhelmsen and Zhi-Wei Liu) for providing us with valuable suggestions and comments to improve this manuscript. In this work, Mei Wang was supported by the Fundamental Research Funds for the Central Non-profit Research Institute of Chinese Academy of Forestry (Grant No. CAFYBB2024QG005). Dong Ren was supported by grants from the National Natural Science Foundation of

China (32020103006). In addition, we would like to give our sincere gratitude to Xiao-tian Liu, Yu Liu and Ning Han (all from Capital Normal University) for their technical support.

References

- Brues, C.T., 1908. New phytophagous Hymenoptera from the Tertiary of Florissant, Colorado. *Bulletin of the Museum of Comparative Zoology, Harvard College* 51, 259–276.
- Gao, T.P., Ren, D., Shih, C.K., 2009a. The first Xyelotomidae (Hymenoptera) from the Middle Jurassic in China. *Annals of the Entomological Society of America* 102, 588–596.
- Gao, T.P., Ren, D., Shih, C.K., 2009b. *Abrotoxyla* gen. nov. (Insecta, Hymenoptera, Xyelidae) from the Middle Jurassic of Inner Mongolia, China. *Zootaxa* 2094, 52–59.
- Gao, T.P., Shih, C.K., Engel, M.S., Ren, D., 2016. A new xyelotomid (Hymenoptera) from the Middle Jurassic of China displaying enigmatic venational asymmetry. *BMC Evolutionary Biology* 16, 155.
- Goulet, H., Huber, J.T., 1993. Hymenoptera of the World: An Identification Guide to Families. Research Branch, Agriculture Canada, Ottawa, 668 pp.
- Hong, Y.C., 1982. Insecta. In: Neimenggol Bureau of Geology and Mineral Resources (Ed.), *Mesozoic Stratigraphy and Paleontology of Guyang Coal-Bearing Basin, Neimenggol Autonomous Region, China*. Geological Publishing House, Beijing, pp. 85–100 (in Chinese).
- Klug, F., 1834. Uebersicht der Tenthredinetae der Sammlung. In: Klug, F. (Ed.), *Jahrbücher der Insektenkunde mit besonderer Rücksicht auf die Sammlung des Königl. Museum in Berlin herausgegeben* 1, 223–253.
- Latreille, P.A., 1802. *Histoire Naturelle, Générale et Particulière des Crustacés et des Insectes*. Dufart, F., Paris, 467 pp. (in French).
- Linnaeus, C., 1758. *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Editio decima, reformata. Laurentius Salvius, Holmiae, 824 pp.
- Malaise, R., 1931. Neue Japanische Blattwespen. *Zoologischer Anzeiger* 94, 201–213.
- Malm, T., Nyman, T., 2015. Phylogeny of the symphytan grade of Hymenoptera: new pieces into the old jigsaw(fly) puzzle. *Cladistics* 31, 1–17.
- Nel, A., Petrulevičius, J.F., Henrotay, M., 2004. New Early Jurassic sawflies from Luxembourg: The oldest record of Tenthredinoidea (Hymenoptera: Symphyta). *Acta Palaeontologica Polonica* 49, 283–288.
- Polilov, A.A., 2015. Small is beautiful: Features of the smallest insects and limits to miniaturization. *Annual Review of Entomology* 60, 103–121.
- Rasnitsyn, A.P., 1967. New Xyelidae (Hymenoptera) from the Mesozoic of Asia. *International Geology Review* 9, 723–737.
- Rasnitsyn, A.P., 1968. New Mesozoic sawflies (Hymenoptera, Symphata). In: Rohdendorf, B.B. (Ed.), *Jurassic Insects of Karatau*. Nauka Press, Moscow, pp. 190–236 (in Russian).
- Rasnitsyn, A.P., 1969. Origin and evolution of lower Hymenoptera. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR* 123, 1–196 (in Russian).
- Rasnitsyn, A.P., 1977. New Hymenoptera from the Jurassic and Cretaceous of Asia. *Paleontologicheskii Zhurnal* 3, 98–108 (in Russian).
- Rasnitsyn, A.P., 1980. The origin and evolution of Hymenoptera. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR* 174, 1–192.
- Rasnitsyn, A.P., 1990. Hymenoptera. In: Ponomarenko, A.G. (Ed.), *Late Mesozoic Insects of Eastern Transbaikalian*. Nauka Press, Moscow, pp. 177–205 (in Russian).
- Rasnitsyn, A.P., Ansoorge, J., 2000. Two new Lower Cretaceous hymenopterous insects (Insecta: Hymenoptera) from Sierra del Montsec, Spain. *Acta Geologica Hispanica* 35, 59–64.
- Rasnitsyn, A.P., Müller, P., 2023. Identity of the insect larva described by Zippel et al. (2022) in the mid-Cretaceous Burmese (Kachin) amber (Hymenoptera, Tenthredinoidea, Blasticotomidae = Xyelotomidae syn. nov.). *Palaeoentomology* 6, 13–16.
- Rasnitsyn, A.P., Jarzembowski, E.A., Ross, A.J., 1998. Wasps (Insecta: Vespida = Hymenoptera) from the Purbeck and Wealden (Lower Cretaceous) of southern England and their biostratigraphical and palaeoenvironmental significance. *Cretaceous Research* 19, 329–391.
- Ren, D., Lu, L.W., Duo, Z.G., Ji, S.A., 1995. *Fauna and Stratigraphy of Jurassic–Cretaceous in Beijing and the Adjacent Areas*. Seismic Publishing House, Beijing, 222 pp. (in Chinese).
- Ren, D., Shih, C.K., Gao, T.P., Wang, Y.J., Yao, Y.Z., 2019. Rhythms of Insect Evolution: Evidence from the Jurassic and Cretaceous in Northern China. Wiley Blackwell, New Jersey, 736 pp.
- 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.
- Sun, C.H., Rasnitsyn, A.P., Wedmann, S., Zhuang, J.L., Shih, C.K., Ren, D., Gao, T.P., 2024. Revisions, new taxa, and venation transformations of the sawfly family Blasticotomidae *sensu lato* (Hymenoptera: Tenthredinoidea) highlight the evolution of the basal Hymenoptera. *Zoological Journal of the Linnean Society* 202, zlae113.
- Taeger, A., Liston, A.D., Prous, M., Groll, E.K., Gehroldt, T., Blank, S.M., 2018. ECatSym – Electronic World Catalog of Symphyta (Insecta, Hymenoptera). Program version 5.0 (19 Dec 2018), data version 40 (23 September, 2018). Available at: <https://www.sdei.de/ecatsym/>.
- Thomson, C.G., 1871. Hymenoptera Scandinaviae. Ohlsson, H., Lundae, 342 pp. (in Swedish).
- Verheyde, F., Alberts, H., Mol, A., 2018. *Blasticotoma filiceti* Klug, 1834 new to Belgium (Hymenoptera: Blasticotomidae). *Bulletin de la Société Royale Belge d'Entomologie* 154, 237–241.
- Vilhelmsen, L., 2001. Phylogeny and classification of the extant basal lineages of the Hymenoptera (Insecta). *Zoological Journal of the Linnean Society* 131 (4), 393–442.
- Wang, X.L., Wang, Y.Q., Zhang, F.C., Zhang, J.Y., Zhou, Z.H., Jin, F., Hu, Y.M., Gu, S., Zhang, H.C., 2000. Vertebrate biostratigraphy of the Lower Cretaceous Yixian Formation in Lingyuan, western Liaoning and neighboring southern Nei Mongol (Inner Mongolia), China. *Vertebrata Palasiatica* 38, 81–99.
- Wei, M.C., Nie, H.Y., 1999. New species of Blasticotomidae (Hymenoptera: Blasticotomorpha) from China with keys to known genera and species of the family. *Entomotaxonomia* 21, 51–59 (in Chinese).
- Wutke, S., Blank, S.M., Boevé, J.-L., Faircloth, B.C., Koch, F., Linnen, C.R., Malm, T., Niu, G.Y., Prous, M., Schiff, N.M., Schmidt, S., Taeger, A., Vilhelmsen, L., Wahlberg, N., Wei, M.C., Nyman, T., 2024. Phylogenomics and biogeography of sawflies and woodwasps (Hymenoptera, Symphyta). *Molecular Phylogenetics and Evolution* 199, 108144.