

Original Article

Revisions, new taxa, and venation transformations of the sawfly family Blasticotomidae *sensu lato* (Hymenoptera: Tenthredinoidea) highlight the evolution of the basal Hymenoptera

Chenhui Sun¹, Alexandr P. Rasnitsyn^{2,3,*}, Sonja Wedmann⁴, Jialiang Zhuang¹, Chungkun Shih^{1,5}, Dong Ren^{1, }, Taiping Gao^{1,* }

¹College of Life Sciences, Capital Normal University, Beijing 100048, China

²Paleontological Institute, Russian Academy of Sciences, 123, 117647 Moscow, Russia

³Department of Palaeontology, Natural History Museum, Cromwell Road, London SW7 5BD, UK

⁴Senckenberg Forschungsinstitut Grube Messel, Senckenberg Forschungsinstitut und Naturmuseum Frankfurt am Main, 64409 Messel, Germany

⁵Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013-7012, USA

*Corresponding authors. Alexandr P. Rasnitsyn, Paleontological Institute, Russian Academy of Sciences, 123, 117647 Moscow, Russia. E-mail: alex.rasnitsyn@gmail.com; Taiping Gao, College of Life Sciences, Capital Normal University, 105 Xisanhuanbeilu, Haidian District, Beijing 100048, China. E-mail: tpgao@cnu.edu.cn

ABSTRACT

Wing venation pattern is particularly important in the taxonomy and classification of insects, especially for fossil material. There are recognized transformation series that apparently often represent a mainstream in the evolutionary trend of the wing venation of Hymenoptera. One notable instance is the gradual reduction of the subcosta veins from multiple branches to their total absence. Herein, we place four new genera and six new species in the family Blasticotomidae (=Xyelotomidae) of Hymenoptera. They are *Xyelocerus abruptus* sp. nov., *Liberitoma tenella* gen. et sp. nov., *Liberitoma compta* sp. nov., *Liberitoma incompleta* sp. nov., *Aduantoma insolita* gen. et sp. nov., and *Apertoma* gen. nov. from the Middle Jurassic of China, and *Enspletoma oligocaenica* gen. et sp. nov. from the Upper Oligocene of Germany. The newly discovered species of *Liberitoma* from China possessed a supernumerary hind branch of vein Sc in its forewing, which has apparently never been recorded before in other hymenopterans, and the unique venation pattern of *Aduantoma* suggests the possibility of two additional steps of vein Sc transformation before its complete loss. Based on the new findings, Blasticotomidae are proposed to be divided into four subfamilies: Blasticotominae Thomson 1871, Dahurotominae subfam. nov., Pseudoxyelocerinae subfam. nov., and Undatominae subfam. nov.

Keywords: sawfly; Jiulongshan Formation; Mesozoic; Tertiary; fossil; venation; biogeography

INTRODUCTION

The former family Xyelotomidae are a small extinct family of Tenthredinoidea within Hymenoptera erected by Rasnitsyn (1968), with 13 genera and 20 species described so far from the Lower Jurassic to the Lower Cretaceous in Kazakhstan, France, England, Spain, and China. Xyelotomidae have been regarded as a basal lineage of Tenthredinoidea (Rasnitsyn 1968, 1980, Nel *et al.* 2004). In a recent study, Xyelotomidae were synonymized under Blasticotomidae owing to the similarity between their larva and adult (Rasnitsyn and Müller 2023). Blasticotomidae in this new and broad understanding can be identified by the xyelid-like antenna, characterized by a basal flagellomere that is

composite, long, and thick, typically accompanied by a thread of normal, short, and thin flagellomeres. Additionally, they exhibit a special wing venation, with 2r-rs entering cell 3rm instead of 2rm, and with Rs being always simple. The resulting morphological diversity of Blasticotomidae *s.l.* grows significantly, leading to a taxonomic structure that appears entangled and obscure, particularly when considering the new and abundant fossil specimens presented in this study.

In Hymenoptera, their comparatively simple patterns of wing venation are important classification characters to distinguish different taxa, which show a trend of simplification across the Order (Rasnitsyn 1967, 1969, Goulet and Huber 1993).

Starting from basal taxa of Hymenoptera, wing venation forms a long transformation series, and the trend of these changes is often traceable and stable. Thereby, a conventionally accepted pattern for the evolution of wing venation has already been established as a mainstream model.

Different from the stable morphology generally found in hymenopterans, vein Sc varies particularly widely among Blasticotomidae *s.l.* It ranges from almost maximum richness in branching known in the whole order, as is exemplified by some Xyelidae (e.g. *Gigantoxyla quadrifurcata* Rasnitsyn, 1966 and *Abrotoxyla lepida* Gao, Ren & Shih 2009; cf. [Rasnitsyn 1966](#), [Gao *et al.* 2009a](#)) up to its complete loss. Details of the diversity pattern of Sc in both forewings and hind wings provide valuable insights into the evolution of the wing venation in the lower Hymenoptera, warranting further detailed examination.

Herein, we report four new genera and six new species of Blasticotomidae from the Jiulongshan Formation of Daohugou, Ningcheng County, Inner Mongolia, China, and from the Upper Oligocene of the Enspel crater lake deposits in Westerwald, Germany. We have organized the taxonomic diversity of the family with its 19 genera into four subfamilies and developed a key to all genera (excluding the one known solely as a larva). We also discuss and illustrate the diversity and transformations of the subcostal veins (Sc) in both forewings and hind wings of Blasticotomidae. We put forth a hypothesis regarding their transformation series as possible proxies for the future phylogenetic analyses of the group.

MATERIALS AND METHODS

The 16 Jurassic specimens described in this study were collected from the Jiulongshan Formation, Daohugou Village, Ningcheng County, Inner Mongolia, China. All the specimens reported here are housed in the Key Laboratory of Insect Evolution & Environmental Changes, Capital Normal University of Beijing in China (CNUB; Curator: Dong Ren). Over the last two decades, numerous species of exceptionally preserved fossil insects have been documented in the Middle Jurassic Yanliao Entomofauna of Northeastern China, with particular focus on the Daohugou area ([Ren *et al.* 2002, 2009, 2019](#), [Gao *et al.* 2016, 2021](#)). These specimens were examined using a Nikon SMZ 25 dissecting microscope and an attached Nikon DS-Ri2 digital camera system. The wing venation nomenclature used in this study is modified from [Rasnitsyn \(1980\)](#). For some images, we covered the specimens in 95% ethanol to obtain clearer results.

One specimen from the Oligocene was collected in a former crater lake near the village Enspel, in the Westerwald, southwest Germany ([Schindler and Wuttke 2010](#)). Thousands of insects were discovered from this Fossil-Lagerstätte between 1990 and 2015 ([Wedmann 2000](#), [Wedmann *et al.* 2010](#)). The bituminous sediments were dated as the late Oligocene ([Mertz *et al.* 2007](#)) and yielded a highly diverse biota (e.g. [Poschmann *et al.* 2010](#)). The investigated specimen is a part of the State Collection of Natural History Rhineland-Palatinate and is accessible via the Museum of Natural History Mainz (NHMMZ) in Germany. The specimen is stored in a plastic box filled with glycerin. It was examined with a Leica MZ12.5 stereomicroscope with an attached camera lucida, and the photographs were taken with an attached Nikon D300 digital camera.

RESULTS

Class Insecta Linnaeus, 1758

Order Hymenoptera Linnaeus, 1758

Superfamily Tenthredinoidea Latreille, 1802

Family Blasticotomidae Thomson, 1871 (=Xyelotomidae Rasnitsyn, 1968)

Type genus: Blasticotoma Klug, 1834.

Diagnosis: Antenna with the first flagellomere several times longer and much thicker than following thread segments (reduced to one or no segments in Cenozoic Blasticotominae). Wing venation characteristically tenthredinoid (with 2r-rs joining cell 3rm rather than 2rm) and complete (except for forewing with vein 2-RS lost in Cenozoic Blasticotominae). Larva endophytic (feeding within fern stems), with stemma touching antennal base dorsally, antenna setiform and consisting of six or seven segments. Legs setiform and six-segmented, with no prolegs present. Abdominal sterna dissected with transverse, oblique and longitudinal folds. Posterior terga sclerotized, concave and furnished with marginal processes.

Composition: The family is composed of four subfamilies: Blasticotominae Thomson, 1871, Dahurotomidae subfam. nov., Pseudoxyelocerinae subfam. nov., and Undatominae subfam. nov., and the unplaced genus *Zippelia* Rasnitsyn & Müller, 2023, known only from a larva.

Remarks: The reasons to synonymize Xyelotomidae under Blasticotomidae are explained by [Rasnitsyn and Müller \(2023\)](#). In short, it is because of the high similarity of adult and particularly of larval morphology of the Mesozoic Xyelotomidae and Cenozoic Blasticotomidae. Under the resulting broader understanding of the family, it differs from other tenthredinoid families in having its flagellum differentiated into a long and thick basal segment and a thin segmented thread, except for some Cenozoic genera that have lost the thread-like antennal segments in Argidae and Zenargidae (for the latter, cf. [Malagón-Aldana *et al.* 2021 a, b](#), [Malagón-Aldana *et al.* 2022](#)). However, Blasticotomidae differ from Argidae and Zenargidae in having a more complete wing venation and particularly in the forewing crossvein 2r-rs is always present (*vs.* lost in Argidae).

Subfamily Blasticotominae Thomson, 1871, stat. nov.

Blasticotomina [Thomson 1871](#): p. 294.

Blasticotomidae [André 1881](#): p. 464.

Blasticotominae [Dalla Torre 1894](#) CA†. Hym. 1: 399.

Xyelotomidae [Rasnitsyn 1968](#): p. 224.

Type genus: Blasticotoma Klug, 1834.

Diagnosis: Forewing with Cu straight at M+Cu fork or with very weak kinks there; cell 1mcu short, scarcely widened or not widened at all towards the distal end, almost aligned with wing axis; 1-Cu straight.

Composition: Besides the type genus, *Runaria* Malaise, 1931, *Paremphtus* Brues, 1908, *Xyelotoma* Rasnitsyn, 1968, *Xyelocerus* Rasnitsyn, 1968, *Abrotoma* Gao, Ren & Shih, 2009, *Leridotoma* Rasnitsyn & Ansoerge, 2000 (including *Undatoma rudgwickensis* Rasnitsyn & Jarzembowski, 1998), *Enspeletoma* Rasnitsyn & Wedmann, gen. nov.

Remarks: For diagnostics of all subfamilies and genera considered, see the key below.

Genus *Xyelocerus* Rasnitsyn, 1968

Type species: *Xyelocerus admirandus* Rasnitsyn, 1968.

Diagnosis: Pterostigma narrow, often pale centrally. Vein Sc with stalk distant from R; Sc₁ crossvein-like (Sc₂ lost or at most dot-like small) or lost (in type species). Cell 1m-cu wide, with Rs+M and 2-M aligned and parallel to 1-Cu,

Composition: Besides the type species, *Xyelocerus diaphanous* Gao, Ren & Shih, 2009 and *Xyelocerus abruptus* Sun, Rasnitsyn, Zhuang & Shih, sp. nov.

Xyelocerus abruptus Sun, Rasnitsyn, Zhuang & Shih, sp. nov.

(Fig. 1)

<http://zoobank.org/urn:lsid:zoobank.org:act:4F22E9A3-FA40-459D-A8EE-A21B31CEE004>

Diagnosis: Forewing with pterostigma sclerotized. Vein Sc present, forming kink to R and touching it in a point at level of 1-M base, or preserving dot-like short Sc₂, and with Sc₁ oblique crossvein-like. 1-M bent before 1-Rs, five times as long as 1-Rs. Rs+M, 1m-cu, and 2-Cu of subequal length.

Etymology: The species name is derived from the Latin word 'abruptus', meaning suddenly steep, referring to the kink of Sc before touching R.

Material: Holotype, CNU-HYM-NN2022311. Paratypes: CNU-HYM-NN2022312; CNU-HYM-NN2022313; CNU-HYM-NN2022314; CNU-HYM-NN2022315 (poorly preserved, sex unknown); CNU-HYM-NN2022316 (poorly preserved, sex unknown).

Locality and horizon: Latest Middle Jurassic (late Callovian), Jiulongshan Formation; Daohugou Village, Wuhua Township, Ningcheng County, Chifeng City, Inner Mongolia, China.

Description (Fig. 1A–C): Holotype, CNU-HYM-NN2022311. Very incompletely preserved. Sex unknown. Body length 12.8 mm, with abdomen partly preserved.

Head: Temples convex, extending lateral beyond eyes. Antenna incompletely preserved.

Forewing: Left forewing length 11.4 mm as preserved. Pterostigma fully sclerotized. Sc forming kink and touching R in a point at level of 1-M base; Sc₁ oblique (Fig. 1C). Two

adventitious '1-Rs' present before true one in left forewing, forming two small cells. 1-M (1.88 mm) straight and ~6.2 times as long as 1-Rs (0.30 mm). Vein M+Cu slightly bent. Crossvein 1r-rs shorter than 2-RS. Cell 1r small, 1m-cu large, Rs+M, 1m-cu and 2-Cu of subequal length.

Legs: Left hind tibia narrow, 5.3 mm long.

Paratype CNU-HYM-NN2022312 (Fig. 1D, E)

Sex unknown. Very incompletely preserved, preserved similar to holotype.

Paratype CNU-HYM-NN2022313 (Fig. 1F, G)

Female. Generally similar to holotype. Head and thorax dorsally coarsely punctated. Adventitious '1-Rs' present before true one in right forewing (Fig. 1G), forming a small cell. Body length 19.9 mm, right forewing length 15.6 mm, ovipositor length 3.4 mm.

**Paratype CNU-HYM-NN2022314 p/c
(part and counterpart) (Fig. 1H, I)**

Sex unknown. Body and wings very incompletely preserved. As preserved, similar to holotype. Adventitious '1-Rs' present before true one in right forewing (Fig. 1I), forming a small cell. Right forewing length 14.8 mm as preserved.

Enspeletoma Rasnitsyn & Wedmann gen. nov.

Type species: *Enspeletoma oligocaenica* Rasnitsyn & Wedmann gen. et sp. nov.

<http://zoobank.org/urn:lsid:zoobank.org:act:C92A60A4-F156-4903-BCCE-07644EE4140C>

Etymology: The first part of the genus name is derived from the type locality Enspel; the second part, '-toma', refers to the type genus *Blasticotoma* Klug, 1834. Gender feminine.

Included species: Type species only (Fig. 2A–C).

Diagnosis: Pterostigma almost as long and wide as cell 1m-cu; cell 3rm with veins 2r-rs and 2m-cu opposite each other; vein 2r-m about as long as vein 2r-rs; cell 2m-cu relatively short, about as long as cell 1r+2rm.

Remarks: Although known from a fragmentary fossil (Fig. 2A), the new genus demonstrates diagnostic characters of the subfamily Blasticotominae as defined above and in the key below. It differs clearly from other genera and particularly from the only other Cenozoic fossil, *Paremphtus ostentus* Brues, 1908 (Fig. 2D, E), in having a huge pterostigma and a very short cell 2m-cu (Fig. 2B, C).

Enspeletoma oligocaenica Rasnitsyn & Wedmann gen. et sp. nov.

(Fig. 2A–C)

<http://zoobank.org/urn:lsid:zoobank.org:act:B0B4637E-607D-4B87-A3C5-4F842B05C035>

Diagnosis: As for genus (see above).

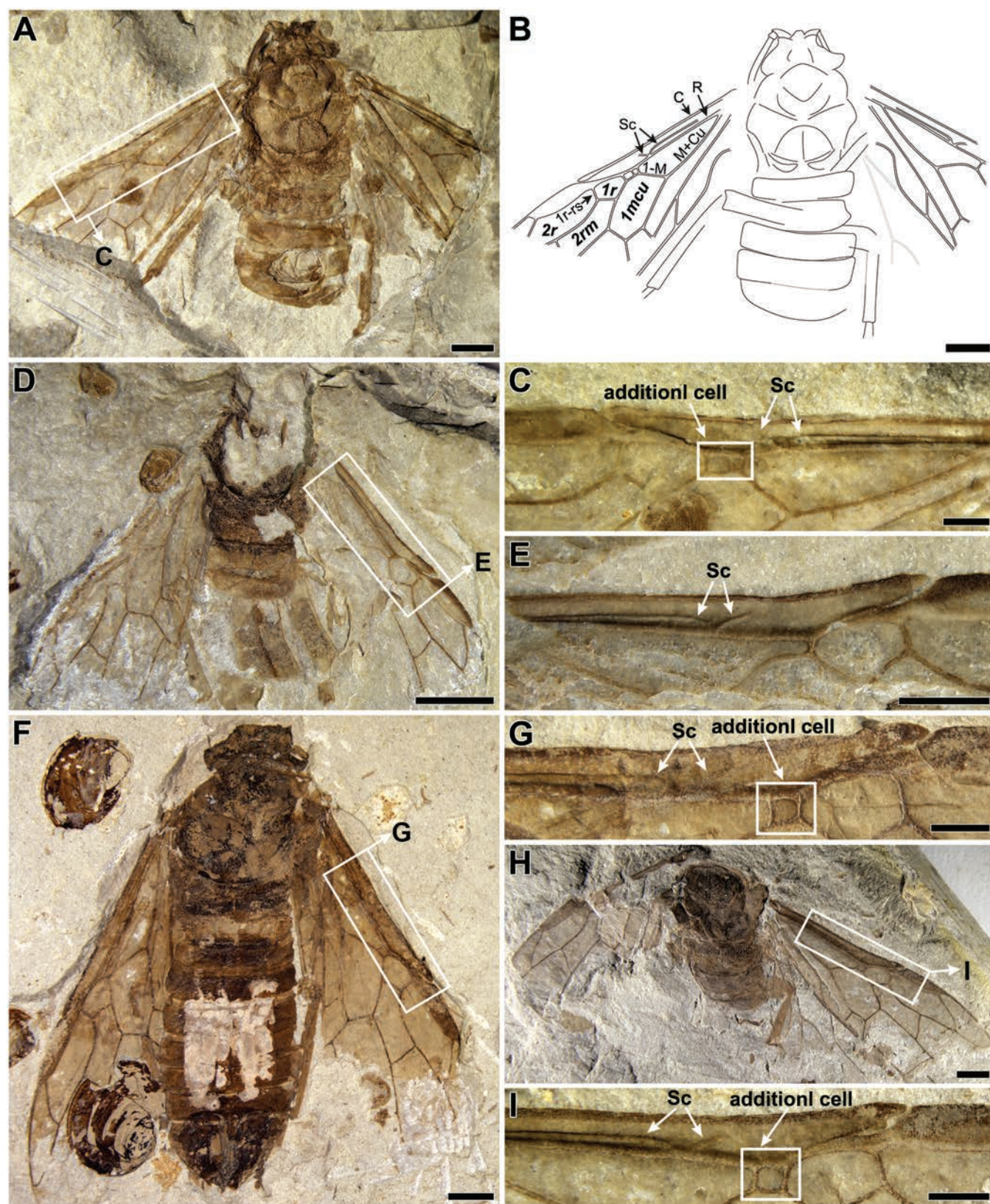


Figure 1. *Xyelocerus abruptus*. A–C, dorsal view (A), line drawing (B), and vein Sc in left forewing (C) of the holotype of CNU-HYM-NN2022311, sex unknown. D, E, dorsal view (D) and vein Sc in right forewing (E) of the paratype of CNU-HYM-NN2022312, sex unknown. F, G, ventral view (F) and vein Sc in right forewing (G) of the paratype of CNU-HYM-NN2022313, female. H, I, ventral view (H) and vein Sc in right forewing (I) of the paratype of CNU-HYM-NN2022314p. Scale bars: 2 mm in A, B, F, H; 1 mm in C–E, G, I.

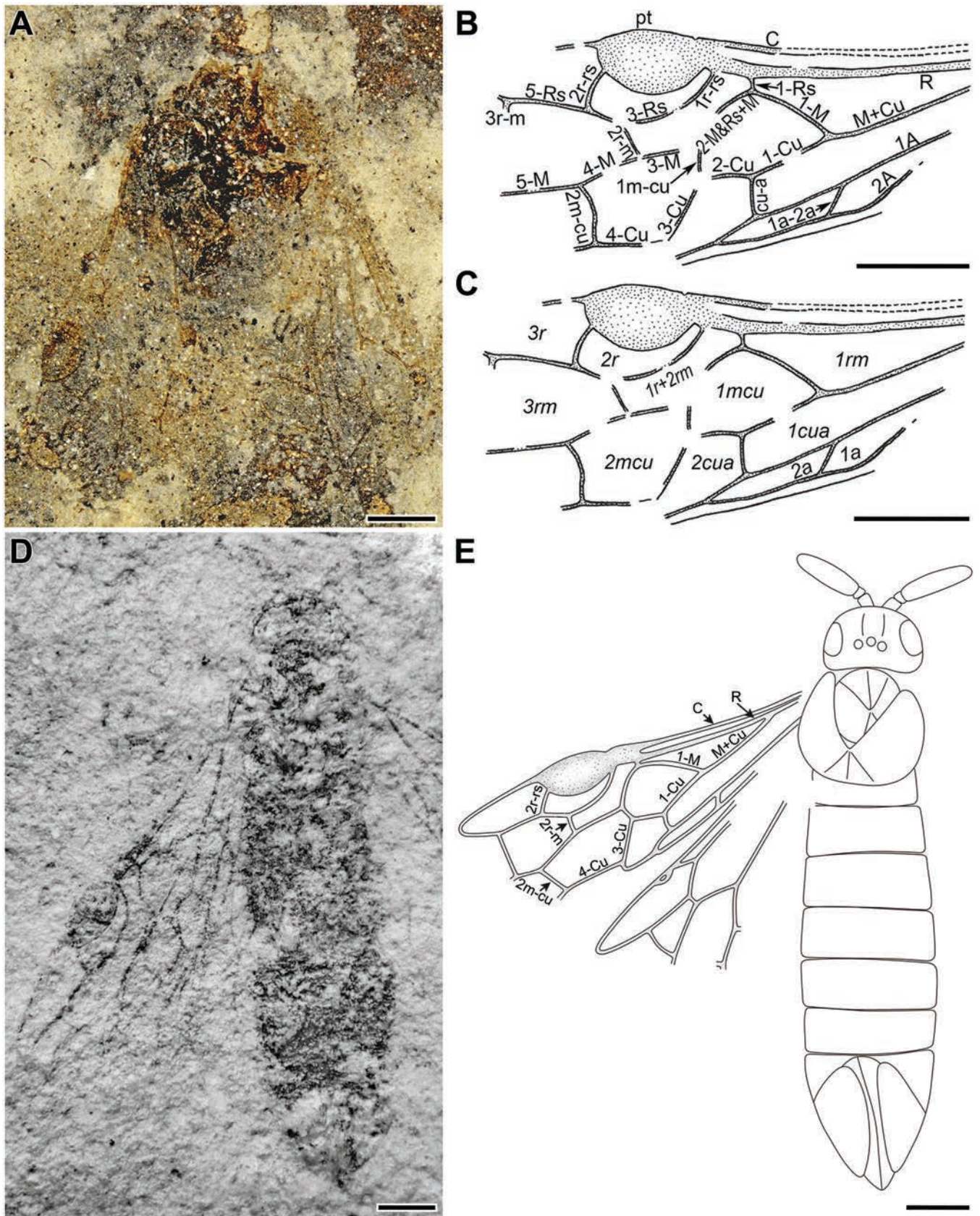


Figure 2. Cenozoic extinct Blasticotominae. A–C, *Enspeletoma oligocaenica*. Holotype, NHMMZ PE 1995/9108-LS, sex unknown, Upper Oligocene of Enspel, Germany. A, dorsal view. B, C, line drawings of forewing, reconstructed from both preserved wings, with veins labelled (B) and with cells labelled (C). D, E, *Paremphytus ostentus*. Holotype No. 2042, Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA; female, uppermost Eocene, Colorado, USA. D, dorsal view. E, line drawing (Zhelekhovtzev and Rasnitsyn 1972). Scale bars: 1 mm.

Etymology: The species is named after the Oligocene, the geological epoch when it was fossilized.

Material: Holotype, coll. no. NHMMZ PE 1995/9108-LS, only one plate. Dorsoventrally embedded, parts of thorax, large parts of left forewing and basal parts of right forewing preserved (Fig. 2A); forewing venation can be reconstructed with combined information from both wings (Fig. 2B, C).

Locality and horizon: Enspel, Westerwald, Germany; Digging site 5, Local horizon 16 (Wedmann 2000); Upper Oligocene, 24.9–24.5 Mya; Mammal Palaeogene zone MP 28 (Storch et al. 1996, Mertz et al. 2007).

Description: Holotype, NHMMZ PE 1995/9108-LS. Sex unknown. Thorax 3.7 mm long as preserved. Pterostigma dark, very large, ~1.1 mm long, 0.6 mm wide. Costal space narrow as preserved, with no traces of Sc visible. Vein 1-Rs distinct, short. 1-M, 1-Cu, and 2-M & RS+M (upper side of cell 1mcu) of almost equal lengths. Rs between 2r-rs and 2r-m much shorter than 2r-rs and slightly longer than 1m-cu. Vein 2r-m about as long as vein 2r-rs, and 2r-m equidistant from 1m-cu and 2m-cu. Cell 2mcu relatively short, about as long as cell 1r+2rm. Cell 1r+2rm as long as cell 3rm. Distal part of cell 3rm apparently very high (higher than distal part of cell 2mcu). 1m-cu about half as long as 3-Cu and 4-Cu. 2-Cu ~0.6 times as long as 1-Cu and ~1.4 times as long as 1m-cu.

Subfamily Dahurotominae Sun, Rasnitsyn, Zhuang & Shih subfam. nov.

= Protenthredinidae Hong, 1982 (invalid name because of synonymy of type genus name, cf. ICZN #39)

Type genus: *Dahurotoma* Rasnitsyn, 1990 [= *Protenthredo* Hong, 1982 (nom. preocc.), = *Davidsmithia* Pagliano & Scaramozzino, 1990 (nom. nov. for *Protenthredo* Hong, 1982), = *Liaotoma* Ren, 1995].

Diagnosis: Forewing Cu with distinct kinks at M+Cu fork and at 1m-cu; cell 1mcu short, scarcely or not at all widened distally and oriented strongly oblique with wing axis.

Composition: Type genus and *Pseudoxyela* Rasnitsyn, 1968.

Subfamily Pseudoxyelocerinae Sun, Rasnitsyn, Zhuang & Shih subfam. nov.

Type genus: *Pseudoxylocerus* Nel, Petrulevicius & Henrotay, 2004.

Diagnosis: Cu with kinks at M+Cu fork and at 1m-cu distinct but not strong; cell 1mcu long, scarcely or not at all widened distally and oriented moderately oblique with wing axis.

Composition: Type genus only.

Subfamily Undatominae Sun, Rasnitsyn, Zhuang & Shih subfam. nov.

Type genus: *Undatoma* Rasnitsyn, 1977.

Diagnosis: Cu with no distinct kink at M+Cu fork; 1-Cu distinctly bent; cell 1mcu long, usually distinctly widened apically, oriented moderately oblique with wing axis.

Composition: Besides type genus, *Paradoxotoma* Gao, Ren & Shih, 2009, *Synaptotoma* Gao, Ren & Shih, 2009, *Liberitoma* Sun, Rasnitsyn, Zhuang & Shih, gen. nov., *Aduantoma* Sun, Rasnitsyn, Zhuang & Shih, gen. nov., *Apertoma* Sun, Rasnitsyn, Zhuang & Shih, gen. nov.

Liberitoma Sun, Rasnitsyn, Zhuang & Shih gen. nov.

Type species: *Liberitoma tenella* Sun, Rasnitsyn, Zhuang & Shih sp. nov.

<http://zoobank.org/urn:lsid:zoobank.org:act:470D88B3-89FE-45AF-937E-41D9D4A49581>

Etymology: The generic name is a combination of the Latin 'liber-', meaning free and unfettered, referring to the unique triple-branched Sc in the forewing, and '-toma' from the type genus *Undatoma* Rasnitsyn, 1977. Gender feminine.

Included species: Besides the type species, *Liberitoma compta* Sun, Rasnitsyn, Zhuang & Shih sp. nov. and *Liberitoma incompleta* Sun, Rasnitsyn, Zhuang & Shih sp. nov.

Diagnosis: Antenna with thread four-segmented as preserved, at least one-third as long as first flagellomere. Forewing with pterostigma wide, sclerotized; Sc complete (with stalk and apical fork) and additionally with secondary hind branch basal to Sc₂, all branches ending before 1-Rs separation; 1-Rs developed; 1-M longer than 2-Cu. Hind wing with Sc two-branched and with series of basal hamuli.

Remarks: The most important character supporting the new genus at a generic level is the unique presence of an additional hind branch of Sc, a characteristic seemingly unparalleled in any other hymenopterans. Yet we consider it as a stabilized character of diagnostic value rather than an individual variation because it is visible in all specimens available with the respective wing part preserved.

Liberitoma tenella Sun, Rasnitsyn, Zhuang & Shih gen. et sp. nov. (Fig. 3)

<http://zoobank.org/urn:lsid:zoobank.org:act:5896464E-D0A3-480B-8E32-EB0477BAC53F>

Diagnosis: Antenna with the remaining filament part at least half as long as the first flagellomere; length-to-width ratio of each segment ~4:1. Forewing with the basal branch of Sc and Sc₂ short, vertical, and the basal branch joining with R far from 1-M base; Sc₁ long, curved; Sc₂ meeting R slightly before 1-M base.

Etymology: The species name is derived from the Latin word 'tenellus', meaning weak, referring to the slim flagellum.

Material: Holotype, CNU-HYM-NN2022301.

Locality and horizon: Latest Middle Jurassic (late Callovian), Jiulongshan Formation; Daohugou Village, Wuhua Township, Ningcheng County, Chifeng City, Inner Mongolia, China.

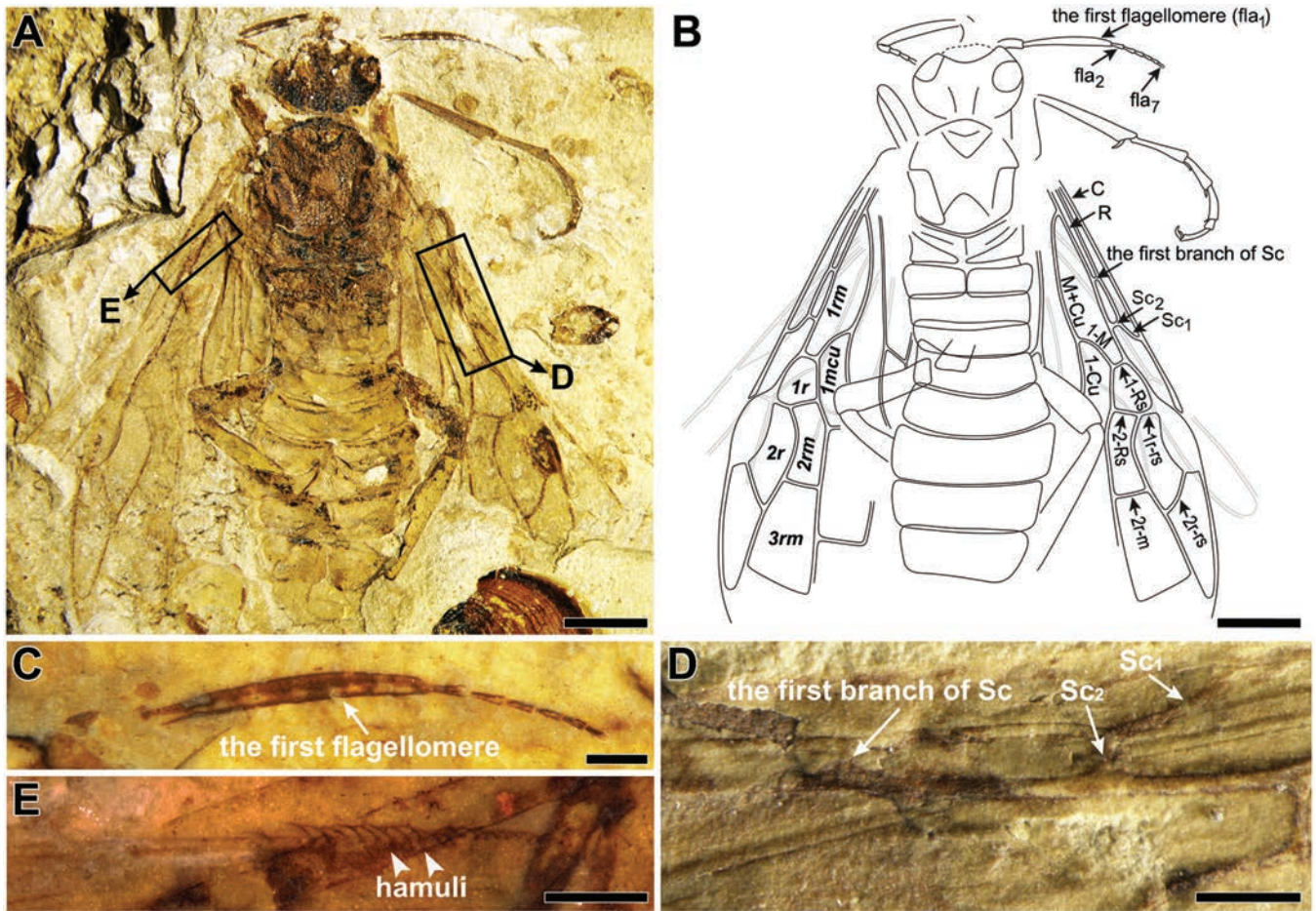


Figure 3. *Liberitoma tenella*. Holotype, CNU-HYM-NN2022301, sex unknown. A, dorsal view. B, line drawing. C, right antenna under alcohol. D, vein Sc of forewing. E, hamuli of left hind wing under alcohol. Abbreviations: fla₁, fla₂, fla₃, fla₇ = first, second, third, and seventh flagellomere. Scale bars: 2 mm in A, B; 0.5 mm in C–E.

Description: Holotype, CNU-HYM-NN2022301 (Fig. 3A, B). Sex unknown. Body length (excluding antenna) 13.9 mm; forewing nearly complete, head, thorax, part of legs, and antennae preserved. Surface sculpture coarsely punctated, especially on head, thorax, and the first abdominal segment. Abdomen with eight segments preserved.

Head: Short, ovate, with eyes small, roundish, not bulging, placed near to head fore margin.

Antenna: The right antenna well preserved; the first flagellomere (fla₁, 2.1 mm) slightly shorter than the width of head (2.6 mm), gradually thickening towards apex, and about two times as long as thread. Thread with six segments preserved, length (in millimetres) of each flagellomere: 0.31, 0.26, 0.22, 0.20, and 0.17 (the length of the last flagellomere was not measured owing to partial preservation), and length to width ratio of each flagellomere ~4:1 (Fig. 3C).

Forewing: Length 12.3 mm as preserved; vein Sc sub-parallel to R, with basal branch and Sc₂ vertical, very short; Sc₁ curved, much longer; basal branch joining with R prior to 1-M base almost for the length of cell 1r; Sc₂ merging into R a short distance after 1-M base; Sc₁ much longer than 1-Rs (Fig. 3D). Pterostigma wide, fully sclerotized. Vein M+Cu bent, Cu with no distinct

kink at M+Cu fork. Vein 1-M (1.1 mm) ~3.5 times as long as 1-Rs (0.3 mm) and weakly arching towards anterior margin. 1-Cu distinctly bent. Cell 1mcu distinctly widened apically, oblique and long. Crossvein 2r-rs (1.1 mm) about three times as long as 1r-rs (0.3 mm), oblique and meeting pterostigma only near its apex. Cell 2r receiving 2r-m at about two-thirds of its length. Cell 1r large, 2r and 2rm narrow and equal in width, 2rm wide and shaped like a regular quadrangle, 1mcu long.

Hind wing: Partly preserved, with a row of basal hamuli (Fig. 3E). Sc with two branches ending well before end of costal space; Sc₁ long, bent; Sc₂ short, vertical.

Legs: Right foreleg and both hind legs partly preserved; all surfaces of legs covered by numerous fine setae. Protibia 2.7 mm long, with only one spur visible; tarsus very long, lengths (in millimetres) of tarsomeres: 1.37, 0.87, 0.65, 0.37, and 0.69, respectively; tarsal claw strongly bent. Hind femora moderately thick, hind tibia rather thick, 3.9 mm long.

***Liberitoma compta* Sun, Rasnitsyn, Zhuang & Shih sp. nov.**

(Figs 4, 5)

<http://zoobank.org/urn:lsid:zoobank.org:act:6E1D3226-993D-4E53-9672-53DEB11C4A8C>

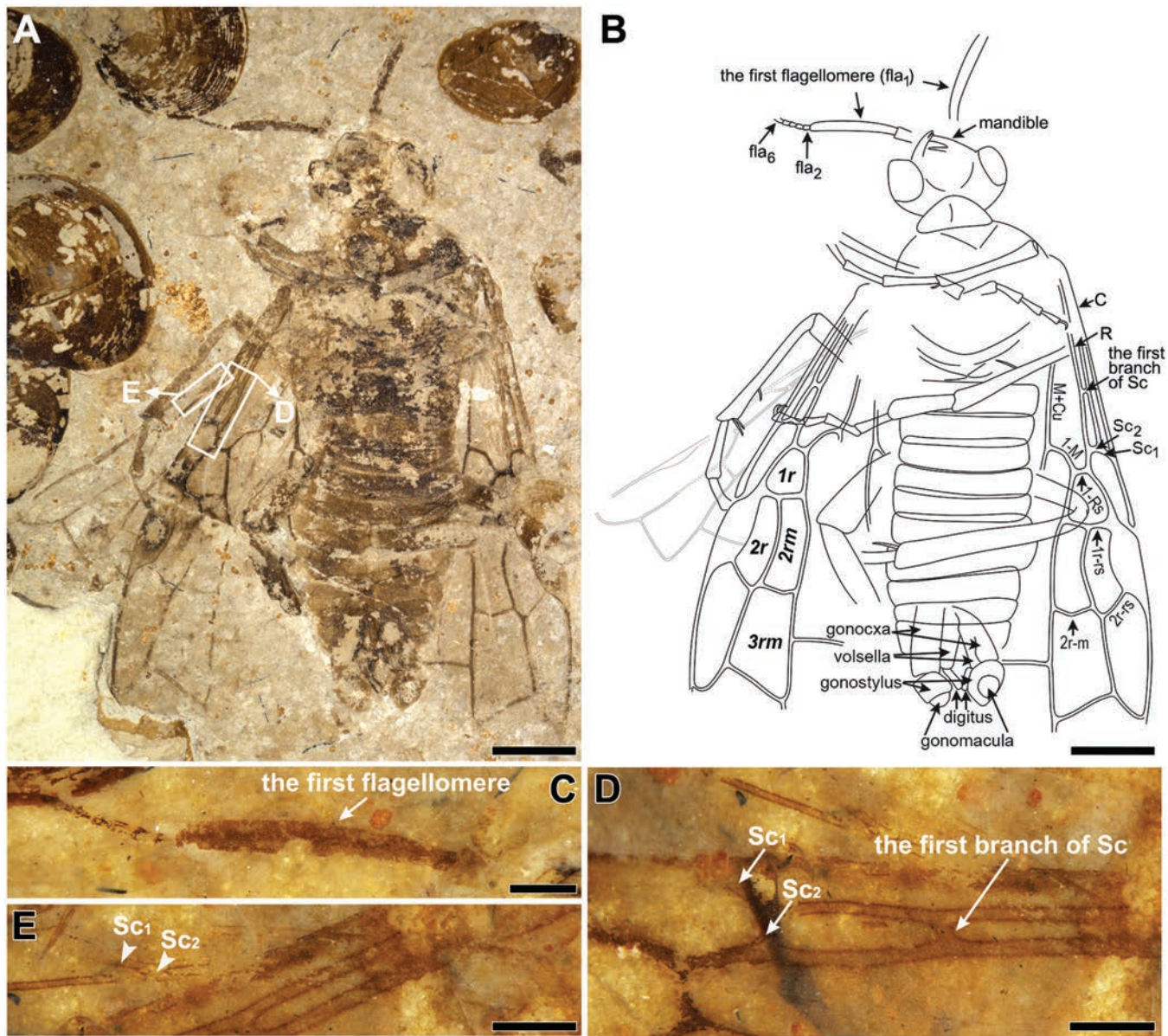


Figure 4. *Liberitoma compta*. Holotype, CNU-HYM-NN2022302, male. A, ventral view. B, line drawing. C, left antenna under alcohol. D, vein Sc of left forewing. E, vein Sc and hamuli of left hind wing under alcohol. Abbreviations: fla_1 , fla_2 , fla_3 , fla_6 = first, second, third, and sixth flagellomere. Scale bars: 2 mm in A, B; 0.5 mm in C–E.

Diagnosis: Antenna with thread at least one-third of first flagellomere, with five preserved segments, each with length to width ratio $\sim 2:1$. Forewing with Sc basal branch short, vertical, meeting R prior to 1-M base; Sc_2 short, slightly proclined, merging into R at level of 1-M base; Sc_1 proclined and short (about as long as Sc_2).

Etymology: The species name is derived from the Latin word ‘comptus’, meaning ornamented, adorned, referring to this sawfly being preserved in good condition.

Material: Holotype, CNU-HYM-NN2022302. Paratypes: CNU-HYM-NN2022303; CNU-HYM-NN2022304; CNU-HYM-NN2022305; CNU-HYM-NN2022306.

Locality and horizon: Latest Middle Jurassic (late Callovian), Jiulongshan Formation; Daohugou Village, Wuhua Township, Ningcheng County, Chifeng City, Inner Mongolia, China.

Description: Holotype, CNU-HYM-NN2022302 (Fig. 4). Male. Body length 13.4 mm as preserved (excluding antennae). Surface coarsely punctated, especially on head, thorax, and the first abdominal segments (Fig. 4A, B).

Head: Short, ovate, with eyes not small, roundish, apparently bulging, placed near the fore margin of head. Mandibles with two teeth visible.

Antenna: First flagellomere (2.1 mm) shorter than width of head (2.8 mm), and about three times as long as thread. Thread with five segments preserved, thicker than those of type species, length (in millimetres) of each flagellomere: 0.16, 0.15, 0.15, and 0.13 (the last flagellomere was not measured owing to partial preservation), length to width ratio $\sim 2:1$ (Fig. 4C).

Forewing: Sc with basal branch short, vertical; Sc_2 short, slightly proclining; Sc_1 short, oblique, basal branch meeting R well basal



Figure 5. *Liberitoma compta*. A, B, dorsal view (A) and vein Sc of left forewing (B) of the paratype of CNU-HYM-NN2022303, sex unknown. C–E, ventral view (C), mandible under alcohol (D), and vein Sc of left forewing (E) of the paratype of CNU-HYM-NN2022304, sex unknown. F, G, dorsal view (F) and vein Sc of right forewing (G) of the paratype of CNU-HYM-NN2022305, female. H–J, ventral view (H), mandible under alcohol (I), and vein Sc of right forewing (J) of the paratype of CNU-HYM-NN2022306, male. Scale bars: 2 mm in A–C, F, H; 0.5 mm in B, E, G, J.

to 1-M base; Sc_2 merging into R basal to 1-Rs for more than 1-Rs length; Sc_1 curved, about as long as Sc_2 (Fig. 4D). Pterostigma fully sclerotized. Vein M+Cu slightly bent; 1-M (0.9 mm) obviously curved, about three times as long as 1-Rs (0.3 mm). Crossvein 2r-rs (0.8 mm) roughly two times as long as 1r-rs (0.3 mm), oblique and intersecting with pterostigma near its apex; 2r-m connecting with cell 2r almost at the end of the cell, and distinctly bent towards apex of wing at middle. Cell 1r large; 2r and 2rm narrow and equal in lengths and widths.

Hind wing: Sc two-branched, forking far from apex of costal space, with hind branch very short and fore one longer, oblique (Fig. 4E). Basal hamuli visible in left hind wing.

Legs: Long and narrow, fore tibia 3.0 mm long, tarsus relatively shorter than that in type species, tarsus with two segments present; tarsomere I (1.42 mm) longer than tarsomere II (0.83 mm), claw strongly bent. Middle tibia 3.4 mm long, with two apical spurs visible.

Abdomen: Male genitalia apparently not reverted, with gonocoxa and gonostylus massive, gonostylus apparently with gonomacula, volsella with stick-like digitus, cuspis and penis valves not distinct.

Remarks: Gonomacula has not been recorded in other Tenthredinoidea yet including extant Blasticotomidae.

Paratype CNU-HYM-NN2022303 (Fig. 5A, B)

Sex unknown. Generally similar to the holotype as preserved. Antenna well preserved and complete. First flagellomere (1.9 mm) obviously shorter than width of head (2.6 mm), approximately two times as long as thread, and a total of seven thread segments preserved; length to width ratio of each flagellomere about two (Fig. 5A). Only left forewing partly preserved. Vein Sc three-branched, the first branch uniquely running into R very close to separation of 1-M from M+Cu; Sc_1 preserved incompletely; Sc_2 oblique, meeting R before origin of 1-Rs (Fig. 5B).

Paratype CNU-HYM-NN2022304 (Fig. 5C–E)

Sex unknown. Similar to the holotype. Mandibles incompletely preserved, thick and curved (Fig. 5D). Legs partly well preserved, all with vaguely visible numerous fine spines. Right foreleg: tibia (2.2 mm) with two apical spurs present, almost equal in length; tarsus with four segments present, tarsomere I longer than tarsomeres II and III combined; lengths of individual tarsomeres (in millimetres): 1.01, 0.43, 0.36, and 0.34. Right middle tibia length 2.8 mm, tarsomeres I and V longer than tarsomeres II, III, and IV combined; lengths of individual tarsomeres (in millimetres): 1.24, 0.49, 0.42, 0.27, and 0.55. Right hind tibia 4.4 mm long, with no spur preserved. Left hind tibia (4.2 mm) with two apical spurs preserved, one long and one short; tarsus with five tarsomeres and one tarsal claw preserved, tarsomere I approximately equal to tarsomeres II, III, and IV combined; lengths of individual tarsomeres (in millimetres): 1.24, 0.51, 0.40, 0.35, and 0.67. Body length 9.9 mm, forewing length 12.7 mm.

Paratype CNU-HYM-NN2022305 (Fig. 5F, G)

Female. Forewings both partly preserved. Vein Sc triple-branched, shaped like an inverted 'Y'; the first branch intersecting

with R before separation of 1-M from M+Cu; Sc_1 and Sc_2 both oblique in different directions; Sc_1 (0.28 mm) ~1.7 times as long as Sc_2 (0.16 mm), merging into C a short distance before separation of 1-Rs from R; Sc_2 meeting R before origin of 1-Rs (Fig. 5G). M+Cu slightly bent; 1-M (1.1 mm) curved and about three times more than 1-Rs (0.3 mm). Crossvein 1r-rs obviously shorter than 1r-m; 2r-rs (1.3 mm) roughly three times as long as 1r-rs (0.4 mm), oblique and intersecting with pterostigma near its apex. Cell 1r large; cell 2r and cell 2rm narrow. Body length 16.9 mm, right forewing length 13.3 mm, ovipositor length 3.0 mm.

Paratype CNU-HYM-NN2022306 (Fig. 5H–J)

Male. Body length 16.5 mm (excluding antennae). Mandible paired preserved, bent like a sickle (Fig. 5I). Forewings partly preserved, Vein Sc with three branches (Fig. 5J), the first branch merging into R before separation of 1-M from M+Cu; Sc_1 (0.31 mm) short, ~1.9 times as long as Sc_2 (0.16 mm), and inclining towards apex of the wing, merging into C before separation of 1-Rs from R; Sc_2 slightly oblique, meeting R before origin of 1-Rs. M+Cu slightly bent, 1-M (1.1 mm) arcuately, and approximately three times more than 1-Rs (0.3 mm). Cell 1r large; 1mcu long and lengthening to posterior margin. Male genitalia different from holotype, with gonocoxa longer, gonostylus shorter and much narrower. Body length 16.7 mm, right forewing length 10.3 mm, genitalia length 2.2 mm.

***Liberitoma incompleta* Sun, Rasnitsyn, Zhuang & Shih sp. nov.**

(Figs 6, 7)

<http://zoobank.org/urn:lsid:zoobank.org:act:ACA2BD6F-3B75-4160-9321-ADE470B52CCE>

Diagnosis: Forewing with basal branch of Sc vertical, meeting R distinctly before level of 1-M base; Sc_2 obviously proclined and short, meeting R distinctly behind level of 1-M base; and Sc_1 curved and long.

Etymology: The species name is derived from the Latin word 'incompletus', meaning incomplete and referring to fragmentary preservation of this fossil sawfly.

Material: Holotype, CNU-HYM-NN2022307. Paratypes: CNU-HYM-NN2022308; CNU-HYM-NN2022309.

Locality and horizon: Latest Middle Jurassic (late Callovian), Jiulongshan Formation; Daohugou Village, Wuhua Township, Ningcheng County, Chifeng City, Inner Mongolia, China.

Description: Holotype, CNU-HYM-NN2022307 (Fig. 6). Female. Body length 14.3 mm as preserved (excluding antennae). Head, thorax, and the first abdominal segment coarsely punctated.

Head: Eye big, flat, occupying most of head side, distant from fore margin of head. Antenna not preserved.

Forewing: Only left forewing partly preserved. Vein Sc with basal branch vertical, short; Sc_2 proclined, short; Sc_1 curved, long; basal branch of Sc meeting R slightly before level of 1-M base;

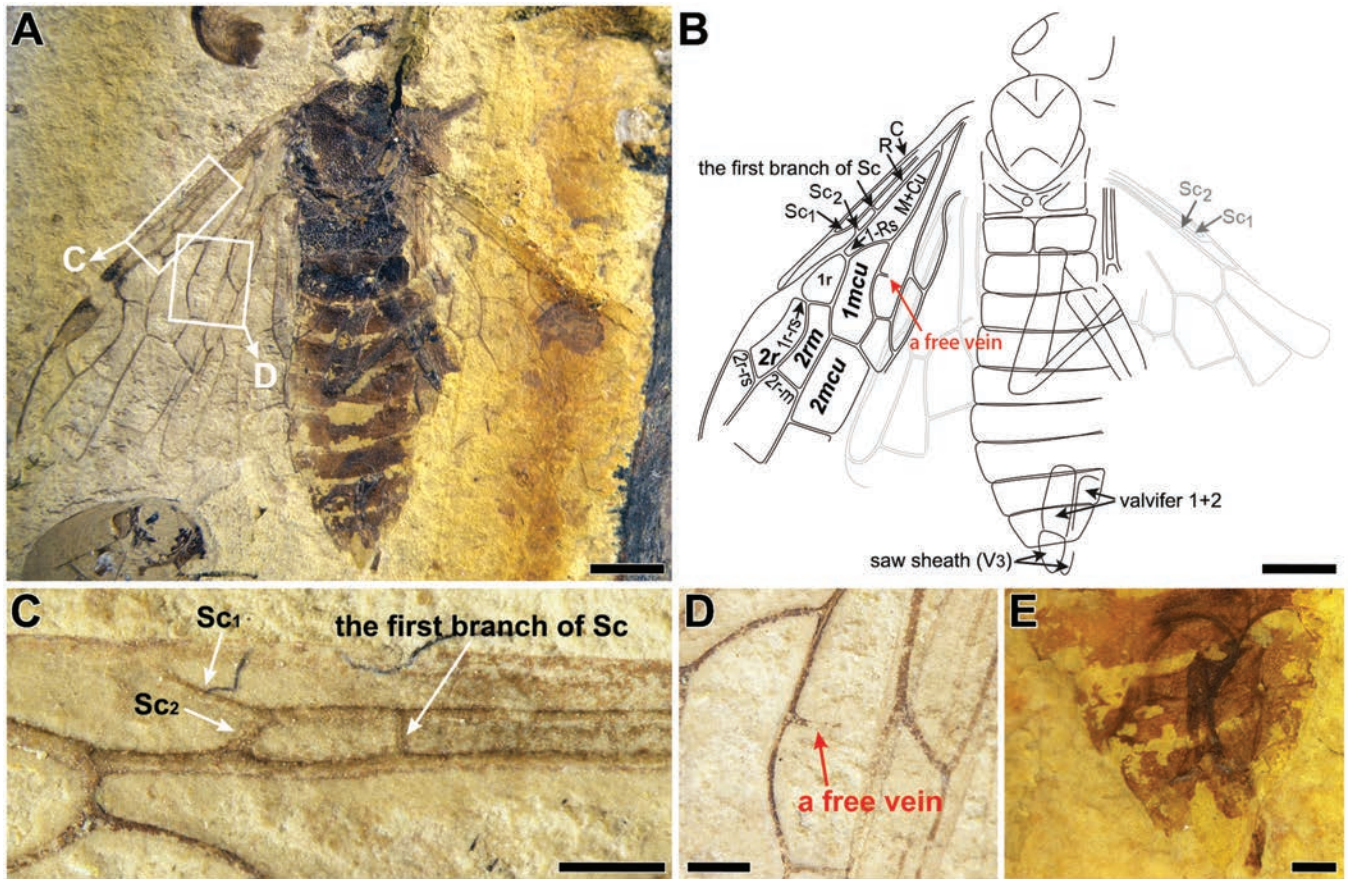


Figure 6. *Liberitoma incompleta*. Holotype, CNU-HYM-NN2022307, female. A, ventral view. B, line drawing. C, vein Sc of left forewing. D, a free vein of left forewing. E, ovipositor under alcohol. Abbreviation: v₂, second valvula. Scale bars: 2 mm in A, B; 0.5 mm in C–E.

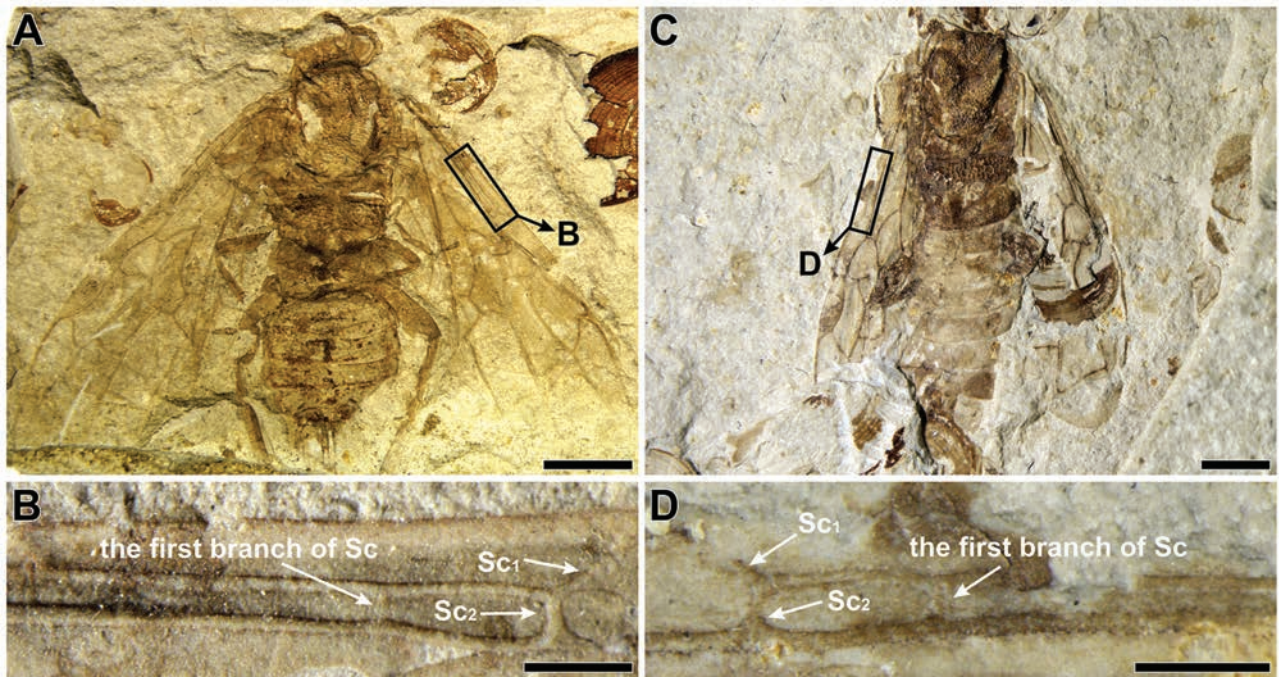


Figure 7. *Liberitoma incompleta*. A, B, dorsal view (A) and vein Sc of right forewing (B) of the paratype of CNU-HYM-NN2022308, sex unknown. C, D, dorsal view (C) and vein Sc of left forewing (D) of the paratype of CNU-HYM-NN2022309, sex unknown. Scale bars: 2 mm in A, C; 0.5 mm in B, D.

Sc₂ merging into R at midway between basal branch of Sc and 1-Rs; Sc₁ almost reaching level of 1-Rs (Fig. 6C). Pterostigma fully sclerotized. M+Cu slightly bent, 1-M (1.1 mm) bent, about five times as long as 1-Rs (0.2 mm) (Fig. 6C). 1-Cu bent, with short adventitious veinlet within cell 1cu (Fig. 6D). Cell 1mcu distinctly widened apically, oblique and long. Crossvein 1r-rs obviously shorter than 2-RS; 2r-rs (0.9 mm) about two times as long as 1r-rs (0.4 mm), oblique and meeting with pterostigma near its apex; 2r-m connecting with 2r roughly at three-quarters of its length. Cells 1r large, 2r and 2rm narrow and nearly equal in width, 1mcu long, and 2mcu wide.

Hind wing: Sc with two branches, forking far from apex of costal space, with hind branch very short and fore one longer, oblique.

Legs: Poorly preserved, except for hind femora and tibiae 4.1 mm and 3.7 mm long, respectively.

Abdomen: Ovipositor short (Fig. 6E), 2.3 mm long; saw sheaths wide, subtriangular, slightly longer than wide.

Paratype, CNU-HYM-NN2022308 (Fig. 7A, B)

Female: Body length 12.6 mm as preserved (Fig. 7A). Vein Sc three-branched in forewing, the first branch of Sc running into R much prior to separation of 1-M from M+Cu; Sc₁ (0.43 mm) relatively extended compared with Sc₂ (0.17 mm), ~2.5 times as long as Sc₂, and inclining to apex of the wing, merging into C a short distance before separation of 1-Rs from R, shorter than holotype; Sc₂ vertical, sub-parallel to the first branch, meeting R before origin of 1-Rs (Fig. 7B). M+Cu slightly bent; 1-M (1.0 mm) with curvature about three times more than 1-Rs (0.3 mm). Crossvein 1r-rs obviously shorter than 1r-m; 2r-rs (1.0 mm) about two times more than 1r-rs (0.4 mm), oblique and meeting with pterostigma nearly its apex; 2r-m connecting with cell 2r at three-quarters of its length, and slightly bent towards apex of wing at middle. Cell 1r large, 2r narrow. Body length 12.6 mm, forewing length 11.0 mm, ovipositor length 1.7 mm.

Paratype, CNU-HYM-NN2022309 (Fig. 7C, D)

Sex unknown: Body length 10.4 mm, with head not preserved and abdomen partly preserved (Fig. 7C). Forewings partly preserved. Vein Sc with three branches, the first branch intersecting with R a short distance before separation of 1-M from M+Cu; Sc₁ (0.33 mm) relatively extended compared with Sc₂ (0.12 mm), ~2.7 times as long as Sc₂ and bent to apex of the wing, merging into C before separation of 1-Rs from R; Sc₂ marginally oblique and meeting R before origin of 1-Rs (Fig. 7D). M+Cu slightly bent; 1-M (1.1 mm) curved, and about four times as long as 1-Rs (0.26 mm). Crossvein 2r-rs (0.9 mm) about two times as long as 1r-rs (0.4 mm), oblique and intersecting with pterostigma near its apex; 2r-m adjoining with cell 2r at three-quarters of its length, and bent towards apex of wing at middle. Cell 1r large, 2r and 2rm narrow and equal in width. Body length 10.4 mm, right forewing length 10.5 mm.

***Aduantoma* Sun, Rasnitsyn, Zhuang & Shih gen. nov.**

<http://zoobank.org/urn:lsid:zoobank.org:act:F2C9AEB7-D2BA-4CC8-A48A-E6724C7657D7>

Type species: *Aduantoma insolita* Sun, Rasnitsyn, Zhuang & Shih **sp. nov.**

Etymology: The generic name is a combination of the Latin 'Aduant-', meaning associated, and referring to the Sc in forewing, and '-toma' from the type genus *Undatoma* Rasnitsyn, 1977. Gender feminine.

Included species: Type species only.

Diagnosis: Forewing with pterostigma wide. Vein Sc with stalk distant from R, making a kink to touch R and leaving Sc₁ oblique crossvein-like. 1-Rs present, single. 1-M shorter than 2-Cu. Cell 1mcu long, with its upper side three times as long as 1m-cu.

***Aduantoma insolita* Sun, Rasnitsyn, Zhuang & Shih gen. et sp. nov.**

(Fig. 8)

<http://zoobank.org/urn:lsid:zoobank.org:act:0041EF57-E06D-4083-A47D-26F6EC9D8DD3>

Diagnosis: As for genus (see above).

Etymology: The species name is derived from the Latin word 'insolitus', meaning unusual, rare, and referring to the posture of this sawfly preserved gracefully.

Material: Holotype, CNU-HYM-NN2022310 p/c (part and counterpart).

Locality and horizon: Latest Middle Jurassic (late Callovian), Jiulongshan Formation; Daohugou Village, Wuhua Township, Ningcheng County, Chifeng City, Inner Mongolia, China.

Description: Holotype, CNU-HYM-NN2022310 (Fig. 8A–C). Male. Body length (excluding antennae) 8.4 mm. Forewing nearly complete, head, thorax, and part of legs preserved.

Head: Transverse, somewhat narrowed forwards, with eyes occupying most of head sides, flat. Antennae not preserved.

Forewing: Length 6.5 mm as preserved. Pterostigma wide, sclerotized basally. Sc with stalk free (distant from R), with kink to touch R at level of 1-M base, leaving Sc₁ as oblique crossvein intersecting with C behind level of 1-Rs (Fig. 8D). 1-Rs distinct, single. 1-M (0.48 mm) 3.4 times as long as 1-Rs (0.14 mm), gently arching, shorter than 2-Cu. Cell 1r large; Rs+M more than twice as long as 2-M. M+Cu bent. Crossvein 2r-rs (0.5 mm) nearly equal to 1r-rs (0.4 mm), oblique, and meeting with pterostigma only near its apex. 1m-cu longer than 2-Cu.

Leg: Left hind leg well preserved. Protibia 2.0 mm long, with no spurs visible; tarsomere I longer than tarsomeres II, III, and IV combined; tarsomere lengths (in millimetres): 0.76, 0.32, 0.26, and 0.16, respectively; last segment not fully preserved.

Abdomen: Male genitalia (Fig. 8E) with gonocoxa comparatively small, gonostylus long, penis long and wide.

***Apertoma* Sun, Rasnitsyn, Zhuang & Shih gen. nov.**

Xyelotoma Gao, Ren & Shih, 2009; Ann. Entomol. Soc. Am. 102(4), p. 589, fig. 1 (partim, only for *Xyelotoma macroclada* Gao, Ren & Shih, 2009).

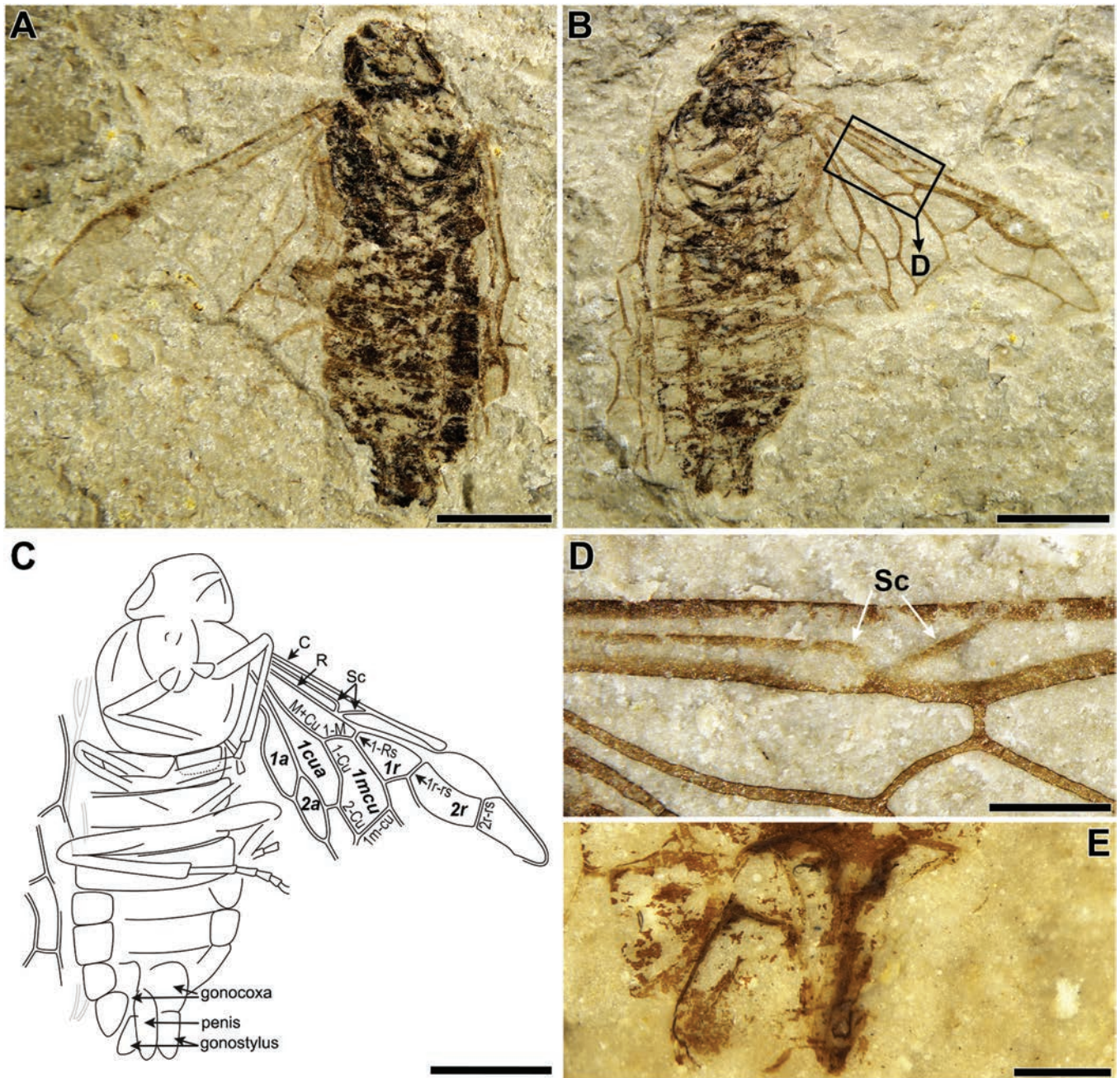


Figure 8. *Aduantoma insolita*. Holotype, CNU-HYM-NN2022310 p/c (part and counterpart), male. A, dorsal view. B, ventral view. C, line drawing. D, vein Sc in right forewing. E, male genitalia under alcohol. Scale bars: 2 mm in A–C; 0.5 mm in D, E.

Type species: *Apertoma* (*Xyelotoma*) *macroclada* Gao, Ren & Shih, 2009.

Etymology: The generic name is a combination of the Latin 'Aper-', meaning discrete, referring to the unique triple-branched Sc in the forewing, and '-toma' from the type genus *Undatoma* Rasnitsyn, 1977. Gender feminine.

Included species: Type species only.

Diagnosis: Forewing with pterostigma medium wide, sclerotized. Sc with stalk distant from R, ending at R well before free Sc, the latter forming oblique crossvein. 1-Rs present, short. 1-M much

longer than 2-Cu. Cell 1m-cu long, with its upper side three times as long as 1m-cu.

Remarks: Under the present concept of Blasticotomidae, the type species cannot be included in *Xyelotoma* and is assigned to *Apertoma* gen. nov. in the subfamily Undatominae because of 1-Cu bent and cell 1m-cu long and widened apically. These characters, together with M+Cu aligned with 1-Cu, are characteristic of Undatominae. Within that subfamily, the new genus is unique in the form of Sc splitting into stalk ending to R, and crossvein-like Sc, well distant from the stalk. For additional details, see the key below.

Key to genera of Blasticotomidae by forewing venation (excluding *Zippelia engeli* Rasnitsyn & Müller, 2023, known from a larva only)

1. Cu without distinct kink at fork M+Cu 2
- Cu with distinct kink at fork M+Cu..... 16
2. 1-Cu straight; cell 1mcu scarcely or not at all widened distally and almost streamlined with wing axis, usually short ($\leq 2:1$). (Subfamily Blasticotominae Thomson, 1871) 3
- 1-Cu distinctly bent; cell 1mcu usually distinctly widened apical, oriented oblique, usually long ($> 2:1$). (Subfamily **Undatominae subfam. nov.**) 10
3. 2-Rs lost, Sc lost, pterostigma wide, antennal thread (flagellum behind composite first segment) with one or no segments...4
- 2-Rs present, Sc rarely lost, pterostigma variable, antennal thread with several segments 7
4. 2r-rs and 2m-cu on about one level. Cell 1mcu as long as cell 2mcu 5
- 2r-rs more basal than 2m-cu. Cell 1mcu distinctly shorter than cell 2mcu 6
5. Pterostigma particularly wide (0.9 as wide as cell 1mcu). Vein 2r-m about as long as vein 2r-rs **Enspletoma gen. nov.**
- Pterostigma less wide (0.7 as wide as cell 1mcu). Vein 2r-m shorter than vein 2r-r *Blasticotoma* Klug, 1834
6. Cell 3r 1.3 times as long as cell 2r *Paremphytus* Brues, 1908
- Cell 3r scarcely longer than cell 2r *Runaria* Malaise, 1931
7. Pterostigma very wide ($\sim 2:1$). Sc lost *Leridotoma* Rasnitsyn & Ansoerge, 2000 (including '*Undatoma*' *rudgwickensis* Rasnitsyn & Jarzembowski, 1998)
- Pterostigma less wide ($> 2.5:1$). Sc usually present 8
8. Sc complete except hind branch, with stalk touching R *Abrotoma* Gao, Ren & Shih, 2009
- Sc in two parts (stalk disconnected with crossvein-like Sc_1) or stalk lost 9
9. Pterostigma wider ($\sim 3:1$), sclerotized. Cell 1mcu longer ($2.5:1$) *Xyelotoma* Rasnitsyn, 1968
- Pterostigma narrower ($4:1$), usually translucent centrally. Cell 1mcu shorter ($< 2:1$) *Xyelocerus* Rasnitsyn, 1968 (***Xyelocerus abruptus* Sun, Rasnitsyn, Zhuang & Shih sp. nov.**)
10. R+M long, Sc crossvein-like, pterostigma narrow ($3.5:1$) *Synaptotoma* Gao, Ren & Shih, 2009
- 1-Rs present even if short (no R+M), Sc not as crossvein only, pterostigma usually wider ($\leq 3:1$) 11
11. Sc lost *Undatoma* Rasnitsyn, 1977
- Sc with at least stalk distinct 12
12. Sc stalk ending on R (no distinct Sc_2) 13
- Sc forked apical into Sc_1 and Sc_2 14
13. Sc_1 lost. Cell 1mcu shorter, with its upper side two times as long as 1m-cu *Aethotoma* Gao, Shih, Engel & Ren, 2016
- Sc_1 present. Cell 1mcu longer, with its upper side three times as long as 1m-cu 15
14. Sc_1 started at end of Sc stalk ***Aduantoma* gen. nov.**
- Sc_1 and apex of Sc stalk far distant ***Apertoma* gen. nov.**
15. Sc with Sc_1 broken midway and with no adventitious basal hind branch *Paradoxotoma* Gao, Ren & Shih, 2009
- Sc complete and with adventitious basal hind branch ***Liberitoma* gen. nov.**
16. Cell 1mcu long ($2.5:1$), scarcely or not at all widened distally and oriented less oblique with wing axis; Sc with stalk and fore branch complete; 1-Rs distinct. (***Pseudoxylocerinae* subfam. nov.**) *Pseudoxylocerus* Nel, Petrulevicius & Henrotay, 2004
- Cell 1mcu short ($\leq 2:1$), scarcely or not at all widened distally and oriented strongly oblique with wing axis (***Dahurotomidae* subfam. nov.**) 17
17. 1-Rs distinct, Rs_2 present, Sc with stalk and both main branches complete *Pseudoxyela* Rasnitsyn, 1968
- 1-Rs and Rs_2 lost, Sc stalk, if present, disconnected from crossvein-like Sc_1 *Dahurotoma* Rasnitsyn, 1990

DISCUSSION

The present revision of the family Blasticotomidae *s.l.* reveals a complicated system composed of four subfamilies, 18 genera, and 37 species (25 fossil and 12 extant). The monotypic *Zippelia engeli* Rasnitsyn & Müller, 2023 is known solely from a larva and remains unplaced in a specific subfamily. The extant genera *Blasticotoma* and *Runaria* are intermixed with the extinct ones within the subfamily Blasticotominae.

The distribution of Blasticotomidae in space and time is uneven. The extant genera *Blasticotoma* and *Runaria* are distributed in the Palaearctic and Oriental realms, with most species centred in Eastern Asia, and only *B. filiceti* reaches Western Europe (Taeger et al. 2010, 2018). The extinct genera are known mainly from the Jurassic and Lower Cretaceous deposits. Exceptions are *Zippelia*, found in the mid-Cretaceous (lowermost Cenomanian) Kachin (Burmese) amber, and two Cenozoic records: *Paremphytus*

ostentus, discovered in the uppermost Eocene Florissant deposits in Colorado, USA, and *Enspletoma oligocaenica* from the upper Oligocene deposits in Enspele, Germany. Hence, the past Cenozoic distribution of Blasticotomidae was wider than in the present day (Holarctic rather than Palearctic and Oriental realms).

The distribution of Blasticotomidae was still broader in the Mesozoic. In the Early Jurassic, the only record referred to the end of the epoch (early Toarcian) and represents the

monotypical subfamily Pseudoxylocerinae in Western Europe. In contrast, the Middle and Late Jurassic Blasticotomidae (except for the end of the Late Jurassic) formed a rich and rather uniform assemblage of eight genera (*Abrotoma*, *Aduantoma*, *Aethotoma*, *Liberitoma*, *Paradoxotoma*, *Pseudoxyela*, *Xyelotoma*, and *Xyelocerus*) with 13 species, and all these genera were found only in Asia (China and Kazakhstan). The latest Jurassic and Early Cretaceous genera *Leridotoma*, *Synaptotoma*, and *Undatoma*, with nine species, made another assemblage

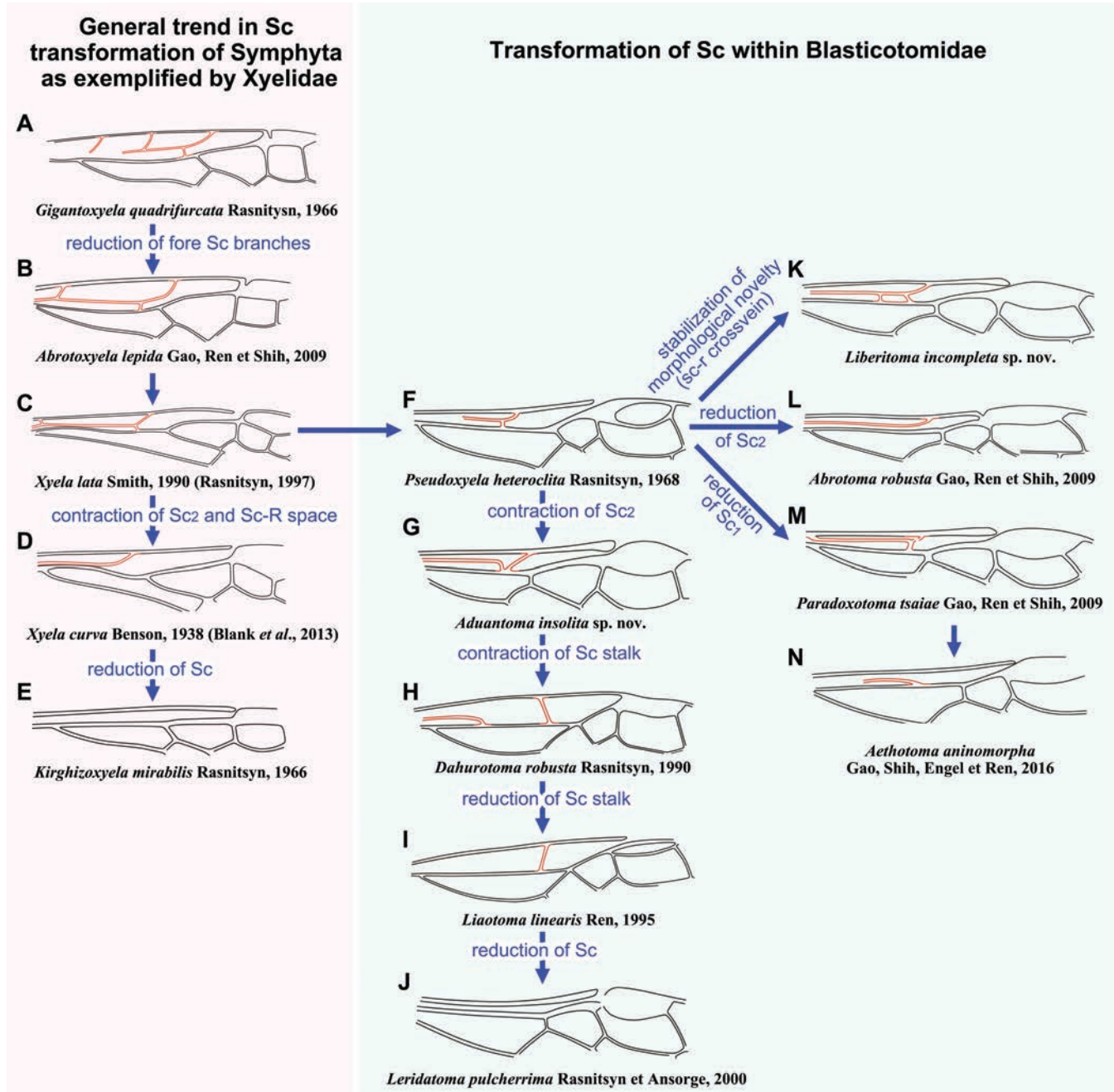


Figure 9. Vein Sc (shown in red) underwent a long transformation series embracing both states known in other Symphyta and some unique ones. A, *Gigantoxyla quadrifurcata* Rasnitsyn, 1966. B, *Abrotoxyla lepida* Gao, Ren & Shih, 2009. C, *Xyela lata* Smith, 1990. D, *Xyela curva* Benson, 1938. E, *Kirghizoxyla mirabilis* Rasnitsyn, 1966. F, *Pseudoxyela heteroclita* Rasnitsyn, 1968. G, *Aduantoma insolita*. H, *Dahurotoma robusta* Rasnitsyn, 1990. I, *Liaotoma linearis* Ren, 1995. J, *Leridotoma pulcherrima* Rasnitsyn & Ansorge, 2000. K, *Liberitoma incompleta*. L, *Abrotoma robusta* Gao, Ren & Shih, 2009. M, *Paradoxotoma tsaiae* Gao, Ren & Shih, 2009. N, *Aethotoma aninomorpha* Gao, Shih, Engel & Ren, 2016.

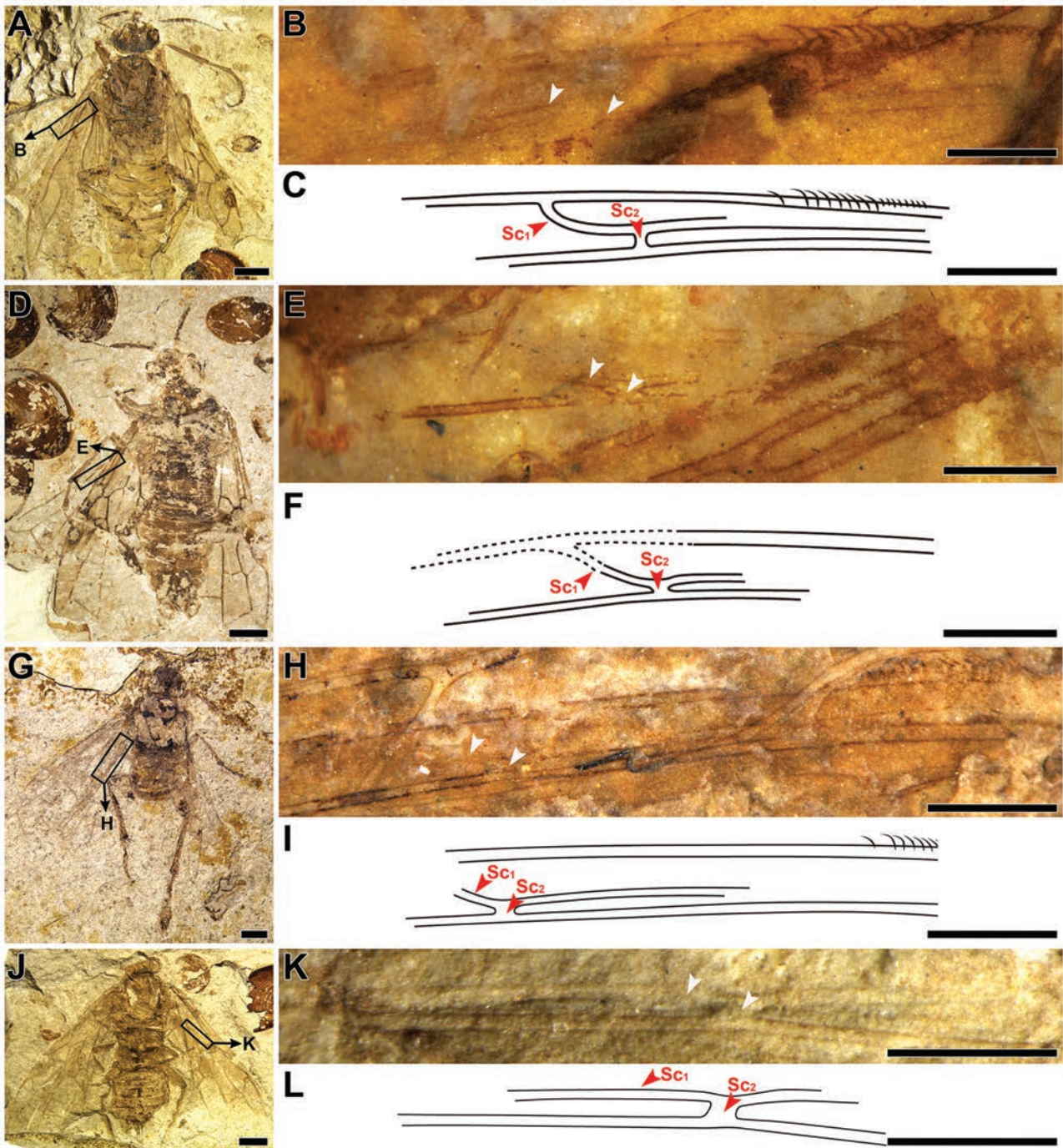


Figure 10. Vein Sc persisting in the hind wings of new fossil species of Blasticotomidae. A–C, habitus (A) and vein Sc (B, C) of the holotype of *Liberitoma tenella*, CNU-HYM-NN2022301. D–F, habitus (D) and vein Sc (E, F) of the holotype of *Liberitoma compta*, CNU-HYM-NN2022302. G–I, habitus (G) and vein Sc (H, I) of the paratype of *Liberitoma compta*, CNU-HYM-NN2022304. J–L, habitus (J) and vein Sc (K, L) of the paratype of *Liberitoma incompleta*, CNU-HYM-NN2022308. Scale bars: 2 mm in A, D, G, J; 0.5 mm in B, C, E, F, H, I, K, L.

recorded more widely in Eurasia (in China, East Siberia, England, and Spain). The sole mid-Cretaceous species of *Zippelia* in Myanmar represented an exotic biota, which existed at that time at an isolated West Burmese Terrain in the midst of the Tethys ocean (Zhang et al. 2018). No blasticotomids were found between the Mid-Cretaceous (earliest Cenomanian) and the latest Eocene. As a result, the limited and unevenly distributed fossil records of Blasticotomidae are insufficient

to construct a minimally comprehensive pattern of the diversification of the family, which specifically hinders a thorough assessment of events during the critical transition from the Cretaceous to the Palaeogene periods. Yet it is worth noting that the transformation between the ‘Jurassic’ and ‘Cretaceous’ generic assemblages of Blasticotomidae apparently occurred appreciably before the stratigraphic boundary between the Jurassic and Cretaceous.

Blasticotomidae *s.l.* demonstrated an unprecedented diversity of the subcosta veins in Hymenoptera. The most basal sawfly family, Xyelidae, also had substantial variability in the vein Sc, exhibiting a series of transformations that included the most basal character state known in Symphyta (Vilhelmsen 2001, Gao *et al.* 2009b, Ronquist *et al.* 2012). This most basal state was Sc giving a hind branch to R and several fore branchlets to C (Fig. 9A, B). The next was the state with only one fore branch of Sc connecting to C, and the basal crossvein visible as a humeral vein (Fig. 9C). The next major step was the Sc stalk approaching R as the hind Sc branch was lost (Fig. 9D; characteristic of *Xyela* Dalman except subgenus *Pinicolites* Meunier, cf. Rasnitsyn 1977). The last stage of this transformation series known in Xyelidae was the complete loss of Sc (diagnostic of several extinct genera, such as *Kirghizoxyela* Rasnitsyn 1966, cf. Rasnitsyn 1966, fig. 2) (Fig. 9E). This character state might have developed directly from the typical one, as depicted in Figure 9C, and not necessarily from that characteristic of *Xyela* (Blank *et al.* 2013).

The evolutionary transformation series within Blasticotomidae started from the typical (most common in Xyelidae and Pamphiliidae) character state of Sc with a simple apical fork as mentioned above, which is a rare one in that family (Fig. 9F). The series continued with character states, some of which were uncommon or even apparently unique within Hymenoptera. This character state was apparently a starting point for three different lines of modification: the loss of the fore branch (Sc₁; Fig. 9M, N) or the loss of the hind branch (Sc₂; Fig. 9L) or the contraction of Sc₂ such that the stalk Sc makes a bend towards R and sending Sc₁ to C immediately after touching R (Fig. 9G). Both character states shown in Figure 9D, I might have transformed further with a total loss of Sc (Fig. 9E, J). Besides these, the morphological diversity of Blasticotomidae demonstrated two more steps of Sc transformation before its complete loss: the free Sc stalk might shorten to leave Sc₁ far from the stalk as a lone crossvein (Fig. 9H), and then the stalk might be lost entirely to leave the crossvein-like Sc₁ to be the last remnant of Sc (Fig. 9I). Of the above broad diversity of character states found in Blasticotomidae, two (Fig. 9G, H) were apparently unique for the family and have not yet been recorded in any other hymenopterans.

One more putatively unique character state of Blasticotomidae, the supernumerary hind branch of Sc diagnostic for *Liberitoma*, is of a different nature (Fig. 9K). It is most probably a fixed (stabilized) venational novelty, because the additional hind veins of Sc in the forewing are apparently out of the ground plan of at least the entire clade Holomentabola + Paraneoptera. Venational malformations, although not uncommon in basal hymenopterans, including Blasticotomidae (Figs 1G, I and 6D), are typically individual variations and rarely become stabilized as taxonomically diagnostic characters. Indeed, the supernumerary vein characteristic of Pamphiliidae and *Sirex* L. in Siricidae, which is variably called ‘basal cu-a’, ‘1cu-a’, or ‘Cu1’, could be interpreted as a displaced free base of Cu rather than a stabilized malformation. Its form and position resemble the free Cu base in hind wings of Xyelidae and a similar, albeit rudimentary structure in the forewing of one of the ancient Xyelidae, *Potrerilloxyela*

menendezi Lara, Rasnitsyn & Zavattieri, 2014 (see fig. 4 of Lara *et al.* 2014). The case of *Liberitoma* having Sc with an adventitious basal hind branch needs special attention and seeking for more material to be established as possibly the first reliable example of this kind in basal hymenopterans.

The presence of Sc in the hind wing in extinct Blasticotomidae is notable (Fig. 10). Hind wing Sc persists in many Xyelidae and Pamphiliidae, and in some Siricidae and Anaxyelidae (Wang *et al.* 2016, 2017, Kopylov *et al.* 2020, Zheng *et al.* 2020, 2021, Zhuang *et al.* 2022), but is lost in the vast majority of Hymenoptera. It varies to form a simple vein ending on C (e.g. *Xyela lata* Smith, 1990; cf. Rasnitsyn 1997: fig. 3), or bearing an apical fork to meet both C and R (cf. *Cretosirex xiaoi* Wang, Rasnitsyn, Han & Ren, 2018; Wang *et al.* 2018: fig. 4C); rarely, it ends at the apex of the costal space, alone (in *Kulbastavia macrura* Rasnitsyn, 1963; cf. Rasnitsyn 1963: fig. 5b) or with a short branch entering either C (*Gigantoxyla quadrifurcata* Rasnitsyn, 1969; cf. Rasnitsyn 1969: fig. 1) or R (*Caenolyda reticulata* Linnaeus, 1758, Pamphiliidae). Tenthredinoidea generally lack Sc in their hind wings, with a striking exception of extinct Blasticotomidae where Sc persists as a stalk forked apically (Fig. 10A–C) or with the hind branch sometimes shortened up to zero (Fig. 10D–L).

In summary, the multi-branched Sc veins in forewings and hind wings in Blasticotomidae demonstrate the complexity and variability of wing venation patterns, which are different from other taxa within Hymenoptera. This unique evolution of the venation pattern even represents an unusual and different line of modification, which differs from the known evolutionary trend. This might suggest that Blasticotomidae have a special and important role in the evolution of wing venation of Hymenoptera.

CONCLUSION

The Blasticotomidae, a putatively basal group within the Tenthredinoidea superfamily, appears to be a diverse group of sawflies with a comparatively rich fossil record but limited extant diversity. There are four subfamilies and 15 genera in the late Early Jurassic to mid-Cretaceous of Eurasia, contrasting with only one subfamily and four genera in the Cenozoic, including only two extant genera mainly in East Asia. The morphological and taxonomical diversity of Blasticotomidae is very helpful in elucidating some general issues of morphological transformations of the wing venation of lower Hymenoptera.

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CONFLICT OF INTEREST

The authors declare no competing interests.

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