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Two new fossil xyelids (Hymenoptera, Xyelidae) from the Middle Jurassic of Inner Mongolia, China

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ABSTRACT

One new genus *Evacuxyela* gen. nov., with two new species, *Evacuxyela conflata* sp. nov. and *Evacuxyela hsiaoae* sp. nov., is described and illustrated on the basis of two fossils from the Middle Jurassic Jiulongshan Formation of northeastern China. The new genus *Evacuxyela* gen. nov. is placed in the subfamily Macroxyelinae Ashmead, 1898, tribe Angaridyellini of Xyelidae, mainly based on veins C and R connected by a bridge next to pterostigma. The two new fossil species are similar, but differentiated by degree of expansion for hind femur, sclerotisation of pterostigma and venational details. In addition, the well-preserved spurs and expanded femora of hind legs provide important morphological characters to enhance our understanding of Xyelidae.

ZooBank ID (LSID): *Evacuxyela*: urn:lsid:zoobank.org:act:28654048-3C2C-434F-9800-BF70BD85C65A
Evacuxyela conflata: urn:lsid:zoobank.org:act:2F1CBEA3-B537-4286-9B79-6D5DFD469A8A
Evacuxyela hsiaoae: urn:lsid:zoobank.org:act:683F1C5E-5219-48C4-8011-CEBA5A08E255

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Macroxyelinae; fossil insects; morphological characters; spurs

Introduction

The earliest reported symphytans (Hymenoptera) of Xyelidae Newman, 1834, generally accepted as the most basal diverging clade of Hymenoptera Linnaeus, 1758, currently determine the timing of the appearance of Hymenoptera, and, thus, have a special significance in the evolutionary history of the Hymenoptera (Vilhelmsen 2001; Schulmeister et al. 2002; Schulmeister 2003; Ronquist et al. 2012; Wang et al. 2014b). The diversity of this family reached its apex from the Middle Jurassic to the Early Cretaceous, and was comparatively much higher than today (Gao et al. 2011). Hitherto, more and more genera belonging to four subfamilies of Xyelidae in the Mesozoic and Cenozoic have been reported (Riek 1955; Rasnitsyn 1977). These four subfamilies are Archexyelinae Rasnitsyn 1964; Macroxyelinae Ashmead, 1898; Madygellinae Rasnitsyn 1969; and Xyelinae Newman, 1834 (Rasnitsyn 1964; Abe and Smith 1991).

Archexyelinae and Madygellinae are distinguishable by long cell 2r, and Madygellinae differ from Archexyelinae by unbranched Rs (Schlüter 2000; Kopylov 2014; Zheng et al. 2021). Xyelinae and Macroxyelinae are the two common and the only two extant subfamilies of Xyelidae in the Mesozoic. Xyelinae, with two tribes of Liadoxyelini Rasnitsyn 1966 and Xyelini Newman 1934, have a long and narrow ovipositor, extending behind abdomen, and the costal space lacking apical sclerotisation connecting C with R_1 (Rasnitsyn 1966). Macroxyelinae are significantly differentiated from Xyelinae by possessing these diagnostic features: sclerotised apical bridge between C and R_1 next to pterostigma, short and wide ovipositor and at least partially sclerotised pterostigma (Dai et al. 2022). Macroxyelinae encompass five tribes: Xyeleciini Benson, 1954; Angaridyelini Rasnitsyn, 1967; Ceroxyelini Rasnitsyn 1969; Gigantoxyelini Rasnitsyn 1969; and Macroxyelini Ashmead, 1898 (Rasnitsyn 1969; Wang et al. 2014a).

The extinct tribe Angaridyelini of Macroxyelinae have been documented from Kazakhstan, Russia and China, including eight genera: *Angaridyela* Rasnitsyn, 1967; *Nigrimonticola* Rasnitsyn, 1967; *Ophthalmoxyela* Rasnitsyn, 1967; *Baissoxyela* Rasnitsyn, 1969; *Lethoxyela* Zhang and Zhang, 2000; *Ceratoxyela* Zhang and Zhang, 2000; *Liaoxyela* Zhang and Zhang, 2000; and *Leptoxyela* Dai, Rasnitsyn and Wang, 2022. Only one species within one genus (*Ceroxyela* Rasnitsyn, 1966) reported from Russia belongs to Ceroxyelini. Macroxyelini include two extant genera (*Macroxyela* Kirby, 1882 and *Megaxyela* Ashmead, 1898) and four extinct genera (*Chionoxyela* Rasnitsyn, 1993; *Anthoxyela* Rasnitsyn, 1977; *Brachyoxyela* Gao, Zhao and Ren, 2011; and *Paleoxyela*; Jouault, Aase and Nel, 2021) from Russia, China and USA. Gigantoxyelini include eight genera and have the same locality distribution as Angaridyelini (*Chaetoxyela* Rasnitsyn, 1966; *Gigantoxyela* Rasnitsyn, 1967; *Heteroxyela* Zhang and Zhang, 2000; *Isoxyela*, 2000; *Sinoxyela*, 2000; *Shartexyela* Rasnitsyn, 2008; *Abrotoxyela* Gao, Ren and Shih, 2009; and *Magnaxyela* Zheng, Chen, Zhang, and Zhang, 2020). Xyeleciini, another tribe of Macroxyelinae besides Macroxyelini that contain extant taxa, include the extant genus *Xyelecia* Ross, 1932 and six extinct genera (*Uroxyela* Rasnitsyn, 1966; *Xyelites* Rasnitsyn, 1967; *Microxyelecia*, 1969; *Bolboxyella* Rasnitsyn, 1990; *Scleroxyela* Zheng, Hu, D. Chen, J. Chen, Zhang and Rasnitsyn, 2021 and *Proxyelia;* Jouault, Aase and Nel, 2021) from Kazakhstan, Russia, USA and China. (Rasnitsyn 1980; Zhang and Zhang 2000; Gao et al. 2009; Zheng et al. 2019; Jouault et al. 2021).

Herein, we report two new fossil species of *Evacuxyela* gen. nov., belonging to Angaridyelini in Macroxyelinae, from Daohugou Village of northeastern China. The age of the fossil-bearing beds in the Daohugou Village area is considered as the Middle Jurassic, Jiulongshan Formation (Gao et al. 2021; Yang et al. 2022). The new genus offers more evidence of basal morphological characters of

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Macroxyelinae, and provides new insights into the early evolution and diversity of Xyelidae.

Material and methods

The holotype specimens of *Evacuxyela conflata* gen. et sp. nov. and *Evacuxyela hsiaoae* sp. nov. were collected from the latest Middle Jurassic, Jiulongshan Formation; Daohugou Village, Shantou Township, Ningcheng County, Chifeng City, Inner Mongolia, China. All specimens are housed at the fossil collection of the Key Lab of Insect Evolution and Environmental Changes, at the College of Life Sciences, Capital Normal University (CNUB; Dong Ren, curator), in Beijing, China.

The specimens were examined and photographed under a Nikon SMZ25 with an attached Nikon DS-Ri 2 digital camera system. Line drawings were prepared using Adobe Illustrator CC and Adobe Photoshop CC. The wing venation nomenclature used in this paper follows Huber and Sharkey (1993). Antennal thread means flagellar segments after the enlarged first flagellar segment. For wing venation, 1-Rs and 2-Rs refer to the first and second segments of Rs. 1-M means the first segment of M, and 1-Cu, 2-Cu and 3-Cu mean the first, second and third segments of Cu. Additionally, p/c means part and counterpart fossil.

Systematic Palaeontology

Order **Hymenoptera** Linnaeus, 1758
Suborder **Symphyta** Gerstaecker, 1867
Superfamily **Xyeloidea** Newman, 1834
Family **Xyelidae** Newman, 1834
Subfamily **Macroxyelinae** Ashmead, 1898
Tribe **Angaridyellini** Rasnitsyn, 1966
Genus ***Evacuxyela*** Dai, Shih and Rasnitsyn gen. nov.

Type species

Evacuxyela conflata Dai, Shih and Rasnitsyn sp. nov.

Etymology

The generic name is a combination of Greek '*Evacu-*', meaning empty and referring to the desclerotized pterostigma, and the genus name *Xyela*.

Diagnosis

Male (female unknown). Pterostigma not sclerotised; forewing with Sc triple-branched and the first branch intersecting with C nearly one-fourth of the length; Sc terminating at C distal to the origin of Rs; Sc_2 short, inclining towards basal of wings, intersecting R before the origin of Rs. Femur of hind leg expanded.

Species included

Type and *Evacuxyela hsiaoae* sp. nov.

Remarks

Evacuxyela gen. nov. is attributed Macroxyelinae based on the sclerotisation connecting C and R before pterostigma, and further to Angaridyellini based on a trace of basal infuscation of the pterostigma visible in the type species. It differs from all other genera of Angaridyelini by the Sc with three branches, by the pterostigma with a weak basal sclerotisation and by the hind femora being distinctly inflated at least in males.

Evacuxyela conflata Dai, Shih and Rasnitsyn sp. nov. (Figure 1).

Type material

Holotype: No. CNU-HYM-LB-2021022.

Etymology

The species name is from Latin '*conflatus*', meaning expanded and referring to the expanded femur of the hind leg.

Locality and horizon

Latest Middle Jurassic (late Callovian), Jiulongshan Formation; Daohugou Village, Shantou Township, Ningcheng County, Chifeng City, Inner Mongolia, China.

Diagnosis

This species is placed in *Evacuxyela* based on the pterostigma not being sclerotised, the costal area broad and Sc triple-branched. This species is characterised by a skinny and slim body, longer 1-Rs, Sc_1 bending sharply anteriorly after its mid-point and with stub at elbow, and a particularly expanded hind femur.

Description

Male sawfly in ventral view with incomplete wings (Figure 1A, B). Body length 10.3 mm (excluding antennae), forewing length (as preserved) 8.9 mm. Head and body brown, legs with some darker spots.

Head (width 1.9 mm) large and subovate, mandible slightly elongated at apex. Hypostomal bridge present, with distinct medial line of fusion. Antenna not preserved.

Thorax wider than head, medial mesoscutal line long and deep, joining with notauli, far from small triangular mesoscutellum, anepisternum large, preepisternum large, triangular, anteriorly ending in rather long suture joining anepisterna medially; other important characters not available.

Forewing (Figure 1A, B, G) with pterostigma not sclerotised except for weak basal infuscation (apparently a rudiment of basal sclerotisation usual in Angaridyelini); costal area broad and vein Sc closer to R than to C, Sc sub-parallel to R and with three branches; basal branch intersecting with C nearly one-fourth of the length and nearly as long as Sc_2; Sc_1 bending sharply anteriorly after its mid-point, with stub at elbow (Figure 1C); Sc_2 vertical, meeting R before origin of Rs; R gently curved before and after origin of Rs and thickened before pterostigma; 1-Rs roughly as long as 1-M; 1r-rs shorter than 2r-rs, inclined basal; 3-Rs arched posteriorly; 1m-cu about 0.5 time as long as 2-Cu; M+ Cu curved at middle; 1 m-cu shorter than half 3-Cu. Cell 1rm long and narrow, significantly longer than 1r; cell 1r about 1.8 times as long as wide and longer than cell 2r; cell 2r roughly rectangular, slightly longer than wide; cell 1cua narrow and long, distinctly broad at the point of the origin of vein M; cell 1 mcu nearly as long as cell 1r; cell 1a 2 times as long as 2a; cells 2mcu and 3rm incomplete.

Hind wing with 1-Rs very short (1r-m meeting Rs close to Rs base), m-cu and cu-a distant far more than length of m-cu, remaining parts not discernible.

Foreleg and middle leg partly preserved, both with small coxae, short trochanters and thin femora (as preserved), femur with many setae (Figure 1E, F). Hind leg with coxa large, about 1.6 times as long

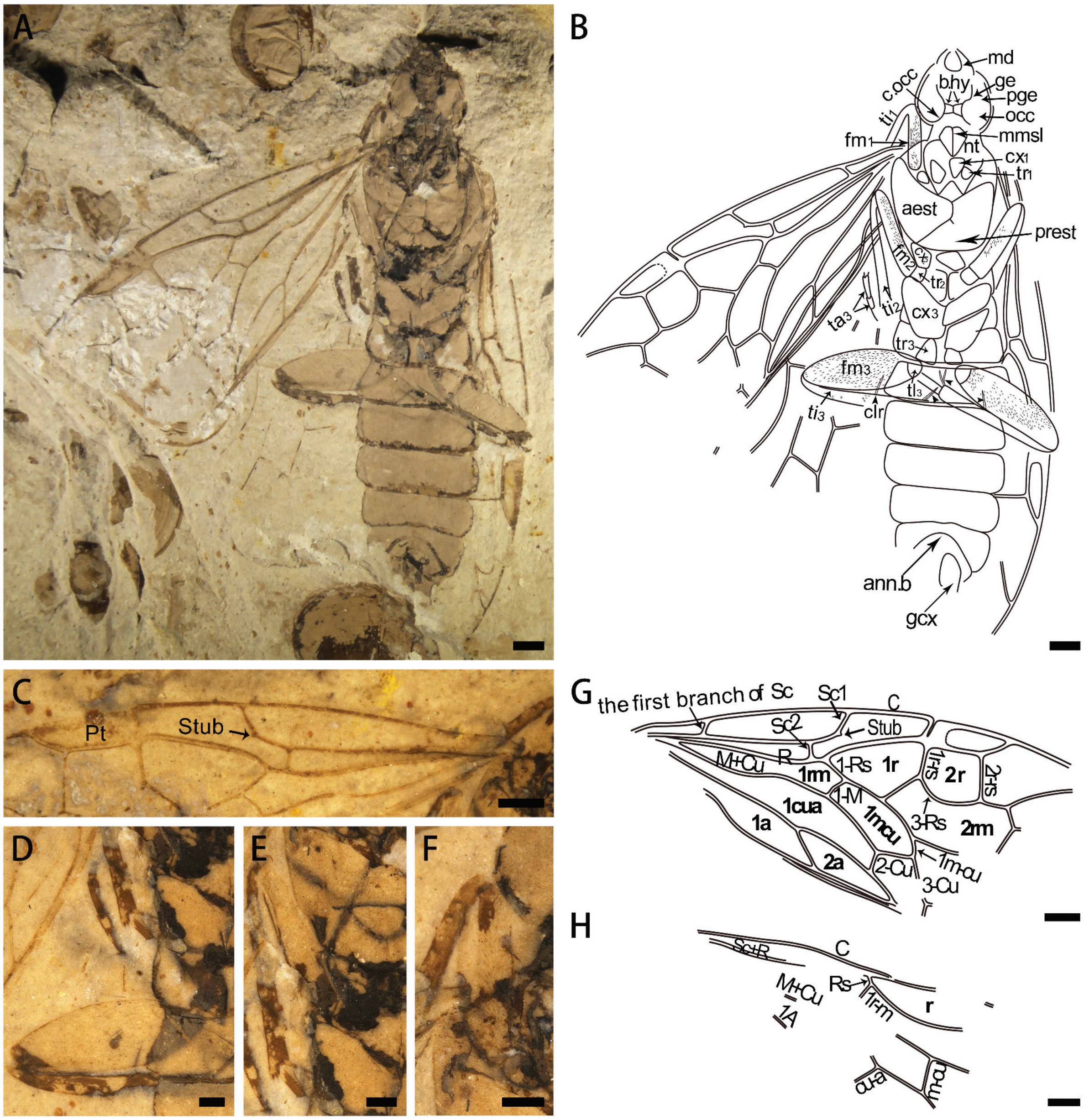

Figure 1. *Evacuxyela conflata* gen. et sp. nov., holotype, CNU-HYM-LB-2021022, male. A, ventral view as preserved. B, line drawing of ventral view. C, pterostigma and stub under alcohol. D, femur of hind leg under alcohol. E, femur of middle leg under alcohol. F, femur of foreleg under alcohol. G, line drawing of forewing. H, line drawing of hind wing. Scale bars: 1 mm in A–C, G–H; 0.5 mm in D–F. Abbreviations: aest, anepisternum; ann.b, basal ring; b.hy, hypostomal bridge; sr, spur; c.occ, occipital carina; cx_{1-3}, coxa of fore, mid, hind leg; fm_{1-3}, femur of fore, mid, hind leg; md, mandible; ge, gena; gcx, gonocoxa; mmsl, medial mesoscutal line; nt, notaulus; occ, occiput; pge, postgena; pt, pterostigma; prest, preepisternum; ta_3, tarsus of hind leg; ti_{1-3}, tibia of fore, mid, hind leg; tl_{1-3}, trochantellus of fore, mid, hind leg; tr_{1-3}, trochanter of fore, mid, hind leg.

as wide; trochanter small and trapezoid; trochantellus distinguishable; hind femur obviously expanded, densely setose (Figure 1D); hind tibia long, almost as long as femur, with long and sharp spurs (two apical and one preapical visible), with many setae and some spines; hind tarsus long, incomplete, other tarsi not preserved.

Abdomen with eight segments visible, genitalia poorly preserved, basal ring widely rounded basally.

Evacuxyela hsiaoae Dai, Shih and Rasnitsyn sp. nov. (Figure 2).

Type material

Holotype: No. CNU-HYM-LB-2021033 p/c, donated by Dr. Chungkun Shih.

Etymology

The specific epithet is dedicated to Ms. Shu-Chen Hsiao, for her dedication and contribution in setting up and managing the Children Are Us Foundation to educate, train and provide assistance and job opportunities for physically or mentally disadvantaged kids and adults.

Locality and horizon

Latest Middle Jurassic (late Callovian), Jiulongshan Formation; Daohugou Village, Shantou Township, Ningcheng County, Chifeng City, Inner Mongolia, China.

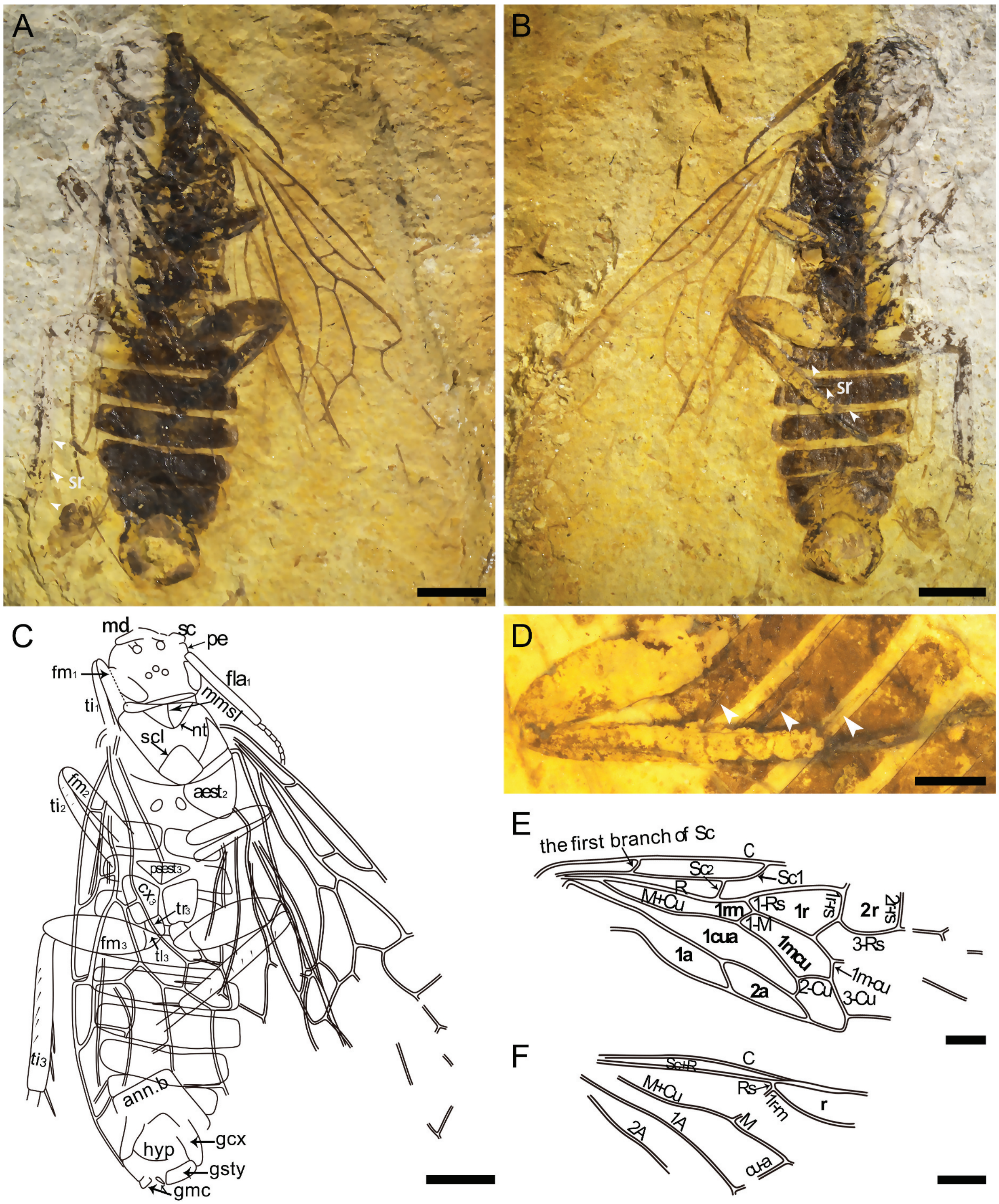

Figure 2. *Evacuxyela hsiaoae* sp. nov., holotype, CNU-HYM-LB-2021033 p/c, male. A, dorsal view as preserved. B, ventral view as preserved. C, line drawing of dorsal view. D, spur of tibia of hind leg under alcohol. E, line drawing of forewing. F, line drawing of hind wing. Scale bars: 2 mm in A–C; 1 mm in D–F. Abbreviations: aest$_2$, anepisternum; ann.b, basal ring; clr, spur; cx$_3$, coxa of hind leg; fm$_{1-3}$, femur of fore, middle, hind leg; fla$_1$, the first flagellomere; gcx, gonocoxa; gmc, gonomacula; gsty, gonostylus; hyp, hypopygium; md, mandible; mmsl, medial mesoscutal line; nt, notaulus; pe, pedicel; psest$_3$, postepisternum; sc, scape; scl, mesoscutellum; tl$_3$, trochantellus; ti$_{1-3}$, tibia of fore, middle, hind leg; tr$_3$, trochanter.

Diagnosis

The species can be differentiated from *Evacuxyela conflata* sp. nov. by head wider, 1-Rs shorter, basal Sc branch placed more distal, hind femur less thick and basal ring almost angular anteriorly. This species is placed in *Evacuxyela* gen. nov. based on pterostigma not sclerotised, costal area broad, Sc triple branched and body large.

Description

Male sawfly with full body but incomplete wings (Figure 2A, B, C). Body length 14.5 mm (excluding antennae). Body and antenna dark, legs with some darker spots.

Head (width 2.6 mm) wider than long, about as wide as mesonotum, apparently flat, eye (length 1.45 mm) in hind part of head, distant from mandible base for about half its length, ocelli in low triangle. Antenna long, scape and pedicel incomplete, first flagellomere 1.2 times as long as head wide, thread shorter than first flagellomere, with 10 segments visible, each twice as long as wide.

Thorax dark, notauli join medial mesoscutal line far from mesoscutellum, mesoscutellum large; cenchri short, oval, remaining parts of thorax not distinct.

Forewing (Figure 2A, C, E) with pterostigma not sclerotised; costal area broad, about 2 times as wide as cell 1rm; vein Sc triple-branched, with basal branch about as distant from wing base as from Sc_1 and nearly as long as Sc_2; Sc_2 reclival, meeting R before origin of Rs base; R weakly curved before and after origin of Rs and thickened before pterostigma; 1-Rs longer than half of 1-M, at most half as long as 2-Rs; 1r-rs shorter than 2r-rs, inclined basally; 3-Rs arched posteriorly; 1m-cu about 0.5 time as long as 2-Cu, and 0.4 time as long as 3-Cu; 1-Cu curved at middle. Cell 1rm long and narrow, significantly longer than 1r; cell 1r about 2.1 times as long as wide and longer than cell 2r; cell 2r roughly rectangular, length ratio of cells 1r:2r = 3:2; cell 1cua narrow and long, distinctly broad at the point of origin of vein M; cell 1mcu nearly as long as cell 1r; cell 1a 2 times as long as 2a; cells 2mcu, 2rm and 3rm incomplete.

Hind wing (Figure 2A, C, F) with 1-Rs short but distinct; boundary between 1-M and 1r-m obscure, M+Cu slightly curved; 1A and 2A also slightly curved.

Foreleg and middle leg partly preserved (for femora and tibiae only), hind leg with only tarsus lost, with coxa of medium size, about 1.3 times as long as wide; trochanter small, subquadrate; trochantellus delimited; femur thick and expanded medially, about 3.3 times as long as wide; tibia about 1.3 times as long as femur, with two succeeding (not paired) preapical and one apical spurs, all long, sharp and of equal length (Figure 2D); hind tibia with numerous setae.

Abdomen with eight segments and genitalia visible, basal ring almost angular anteriorly, hypopygium incomplete; gonocoxa wide, occupying a large part of hypopygium; gonostylus and gonostylus long, comparatively narrow, of subequal length, gonomacula preserved.

Discussion

Macroxyelinae and Xyelinae are two extant subfamilies in Xyelidae, and the morphological differences between these are distinct (Grimaldi and Engel 2005). Among them, the sclerotised pterostigma is an important diagnostic feature. So far, all of the reported species of Macroxyelinae possess a sclerotised pterostigmata, mainly of four types: completely sclerotised, sometimes with limited basal sclerotisation (Macroxyelini, Gigantoxyelini, some Xyeleciini), base widely desclerotized with C-R bridge lost (Ceroxyelini); medially desclerotized (some Xyeleciini); descleroticed except basally (Angaridyellini). In this study, we documented two new species with pterostigma non-sclerotised, which suggests that they are belong Xyelinae. At the same time, the head with a distinct hypostomal bridge (visible in *E. conflate* gen. et sp. nov.) is known within Xyelidae only in Xyelinae of the tribe Liadoxyelini (*Anomoxyela* Rasnitsyn, 1963), which might support a possible affinity of *Evacuxyela* to Xyelinae. However, a distinct trace of the basal sclerotisation of the pterostigma similar to that of Angaridyellini implies that *Evacuxyela* represents an aberrant member of the latter tribe having secondarily lost the pterostigmal sclerotisation and acquired the hypostomal bridge independently of *Anomoxyela*. This inference is strongly supported by the pre-pterostigmal C-R bridge being distinct in both species of *Evacuxyela* and found in no Xyelinae. For the present, that bridge is a reliable character distinguishing Macroxyelinae from Xyelinae.

An unusual feature of the fossils under description is their inflated hind femora, particularly thick in *E. conflata*: otherwise, an incrassate hind femur is not characteristic of Xyelidae. Hind legs are much enlarged in both sexes of *Megaxyela* (Macroxyelini), but their hind femora remain thin (Blank et al. 2017). Inflated hind femora are common in insects and usually use for jumping which could be the case in *Evacuxyela*. However, that genus is currently represented only by males, and discovery of respective females is necessary to reject a hypothesis that the modified hind femur is sex dependent and involved in mating or courtship.

Leg armament is rarely known in fossil Xyelidae, mainly because they are unknown from amber famous for good preservation of its inclusions whilst rock compression fossils uncommonly make it possible to see leg spurs, spines and setae. Fortunately, *Evacyxyela* fossils demonstrate jointly five hind tibial spurs: two apical, two lower subapical and one medial one which is similar with those of *Megaxyela* except that the latter has additionally one upper subapical spur. All spurs are of similar length which is unusual: normally in Hymenoptera (*Megaxyela* included), the posterior apical metatibial spur is distinctly longer than the anterior one. This might imply a somewhat aberrant preening behaviour of *Evacuxyela*, for the posterior apical metatibial spur plays a special role in cleaning (probably hind leg–hind leg rubbing: Behaviour 30 by Basibuyuk and Quicke 1999), as development of a special brush or comb in various groups, particularly among aculeate wasps suggests (Brothers 1975, character 68).

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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