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Diversity and new fossils of Xyelinae (Hymenoptera: Xyelidae) in the Middle Jurassic, Inner Mongolia, China

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ABSTRACT

Although the study of extinct species is crucial for diversification and evolutionary history of Hymenoptera, the past diversity of Liadoxyelini (Xyelidae, Xyelinae) is relatively poorly documented. Herein, one new fossil genus with one species, *Novoxyela bella* gen. et sp. nov., and one species, *Platyxyela elegans* sp. nov., are described and figured from the Middle Jurassic Daohugou Beds of Inner Mongolia, China. *N. bella* gen. et sp. nov. differs from other Liadoxyelini by combination of traits including unusual large head, pterostigma only sclerotised basally, 1-Rs almost as long as 1-M and 1 m-cu slightly shorter than 2-Cu. *P. elegans* sp. nov. exhibits unique features hitherto unknown among species of the *Platyxyela*, viz., pterostigma of medium width, completely sclerotised and ovipositor sheaths widest subapically. The diversity of known fossil species of Liadoxyelini and new forewing characters, as well as a new key to species of *Platyxyela*, are presented.

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Introduction

The Xyelidae Newman, 1834 is a well-known representative symphytan wasp lineage considered to be the earliest appearance of the basal Hymenoptera with the special evolutionary significance (Rasnitsyn 1980; Zhang and Zhang 2000; Grimaldi and Engel 2005). Currently, Xyelidae comprise five subfamilies: Archexyelinae, Rasnitsyn 1964, Macroxyelinae, Ashmead, 1898, Madygellinae, Rasnitsyn 1969, Xyelinae, Newman, 1834 (Rasnitsyn 1969, 1980; Rasnitsyn and Zhang 2004; Wang et al. 2019). However, the phylogenetic relationships among xyelid subfamilies remain under discussion (Lara et al. 2014; Wang et al. 2019). Xyelid fossil taxa are dated from the Middle or Upper Triassic of Kyrgyzstan (Rasnitsyn 1964, 1969, 1980; Kopylov 2014), and the Upper Triassic of Australia (Riek 1955; Engel 2005), South Africa (Schlüter 2000), Argentina (Lara et al. 2014) and Japan (Oyama and Maeda 2020). Specifically, the diversity of this family, as far as we know, was greatly diverse during Mesozoic than previously thought and much broader than today (Schlüter 2000; Gao and Ren 2008; Zheng et al. 2021), with more than 80 described Mesozoic species within 48 genera (Rasnitsyn 1966; Zhang and Zhang 2000; Zheng et al. 2021; Dai et al. 2022).

Xyelinae are a not uncommon subfamily of Xyelidae in the Mesozoic and are composed of two tribes: Xyelini, Newman, 1834 and Liadoxyelini, Rasnitsyn 1966. The latter clearly differs from Xyelini in forewing venation 1-RS shorter than 1-M and 1 m-cu (Rasnitsyn 1966; Zhang and Zhang 2000; Zheng et al. 2021). The tribe Liadoxyelini currently includes eight genera and eleven species (Rasnitsyn 1966, 1983; Wang et al. 2012, 2014; Zheng et al. 2021). The four genera and five species have primarily been assigned: *Liadoxyela praecox* Martynov, 1937 from the Lower Jurassic of Kirgizia and Cisbaykalia, *L. excellens* Rasnitsyn, 1966 from the Upper Jurassic of South Kazakhstan, *Kirghizoxyla mirabilis* Rasnitsyn, 1966 from the Early Jurassic of Kirgizia, *Anomoxyla*

incerta Rasnitsyn, 1966 from the Upper Jurassic of South Kazakhstan and *Lydoxyela excellens* Rasnitsyn, 1966 from the Upper Jurassic of South Kazakhstan. *Orthoxyela rectiradiata* Rasnitsyn, 1983 from the later Early Jurassic of Siberia has been assigned to this tribe based on 1-Rs not longer than 1-M. *Platyxyela unica* Wang et al., 2012 was initially erected and assigned to the Macroxyelinae Ashmead, 1898 based on two well-preserved fossils from the Middle Jurassic of China and was later transferred to Liadoxyelini (in table 1 of Wang et al. 2014). Subsequently, two genera with two species from Middle Jurassic Jiulongshan Formation, China, *Cathayxyela extensa* Wang et al., 2014 and *Aequixyela immense* Wang et al., 2014, were established in Liadoxyelini as well. Same year, the oldest xyelids, *Potrerilloxyela menendezii* Lara, Rasnitsyn & Zavattieri, 2014, were described from early Upper Triassic, Argentina and tentatively placed in Liadoxyelini. As of now, *Aequixyela* is morphologically very different from other Liadoxyelini, and its tribe position remains uncertain (Zheng et al. 2021). Recently *Platyxyela tenuis* Zheng et al., 2021 has been added to the tribe by Zheng et al. (2021).

In order to discuss the presently known diversity of Liadoxyelini and to gain a comprehensive understanding of the early natural history of Xyelidae, we integrate statistic data with morphological study of the Jurassic Xyelinae characters. In this paper, we re-evaluate taxonomic classifications and diversity of Liadoxyelini and herein report the discovery of one new genus and species *Novoxyela bella* gen. et sp. nov. and one species *Platyxyela elegans* sp. nov. from Middle Jurassic strata in the Daohugou, Inner Mongolia, China.

Material and methods

The fossil specimens collected from the Daohugou Bed were reported herein, located in Daohugou Village (N: 41° 8'38", E: 119° 8'38"), Shantou Township, Ningcheng City, Inner Mongolia,

China (see figure 1 in Zheng et al. 2021). The locality is dated as the latest Middle Jurassic, Jiulongshan Formation, which dated at 164 ~ 165 Ma, near Bathonian-Callovian boundary, based on $^{40}\text{Ar}/^{39}\text{Ar}$ and U-Pb radiometric techniques (Chen et al. 2004). All the specimens are deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGP, CAS).

Fossil materials described herein were examined and photographed by standard palaeoentomological methods, using VHX 5000 digital microscope platform. Illustrations and line drawings were prepared with software programmes CorelDraw 20.0 and Adobe Photoshop CS6. The quantitative measure of specimen was done using NIH ImageJ 1.42q software (<http://rsb.info.nih.gov/ij/>). Wing venation terminology used is herein basically adapted from Rasnitsyn (1969) and Rasnitsyn and Zhang (2010). Venation nomenclature: Rs, radial sector; M, media; Cu, cubitus; 1 r-rs, first radial crossvein; 2 r-rs, second radial crossvein; cu-a, first anal crossvein; 2cu-a, second anal crossvein; 1 m-cu, first mediocubital crossvein; 2 m-cu, second mediocubital crossvein. Cell: 1 r, 2 r, 3 r, 4 r, 1 m, 2 m, 2 mcu.

Systematic palaeontology

Order Hymenoptera Linnaeus, 1758
Suborder Symphyta Gerstaecker, 1867
Superfamily Xyeloidea Newman, 1834
Subfamily Xyelinae Newman, 1834
Tribe Liaoxyelini Rasnitsyn, 1966
Genus *Novoxyela* gen. nov.

Type species

Novoxyela bella gen. et sp. nov.

Diagnosis

Head unusual large with big eyes; antennomere 3 much longer than other flagellomeres combined; forewing with costal area narrow, pterostigma membranous, only sclerotised (darkened) at extreme base; vein Sc two-branched, Sc1 terminating at C beyond level of Rs base, Sc2 short, subvertical or weakly oblique, joining R before origin of Rs for a distance; R almost straight; 1-Rs apparently equal to half of 1-M; 1 m-cu slightly shorter than 2-Cu but much shorter than half of 3-Cu; 2 m-cu meeting M distinctly before midlength of cell 3 rm.

Etymology

The generic name is a combination of the Latin prefix *nov-* (new), referring to the head large and unusual, and *Xyela*, the type genus of Xyelidae. The gender is feminine.

Composition

Type species only.

Remarks

Novoxyela gen. nov. is attributed to Liadoxyelini based on the costal space apical and pterostigma without sclerotisation, 1-Rs shorter than 1-M and 1 m-cu much shorter than 3-Cu. *Novoxyela* gen. nov. differs from *Liadoxyela* Rasnitsyn, 1966 in vein R only sclerotised at extreme base of pterostigma (vs. vein R much thickened at base of pterostigma), costal area narrow (vs. costal area wide), 1-Rs apparently equal half of 1-M (vs. 1-Rs slightly shorter than 1-M); differs from *Kirghizoxyela*

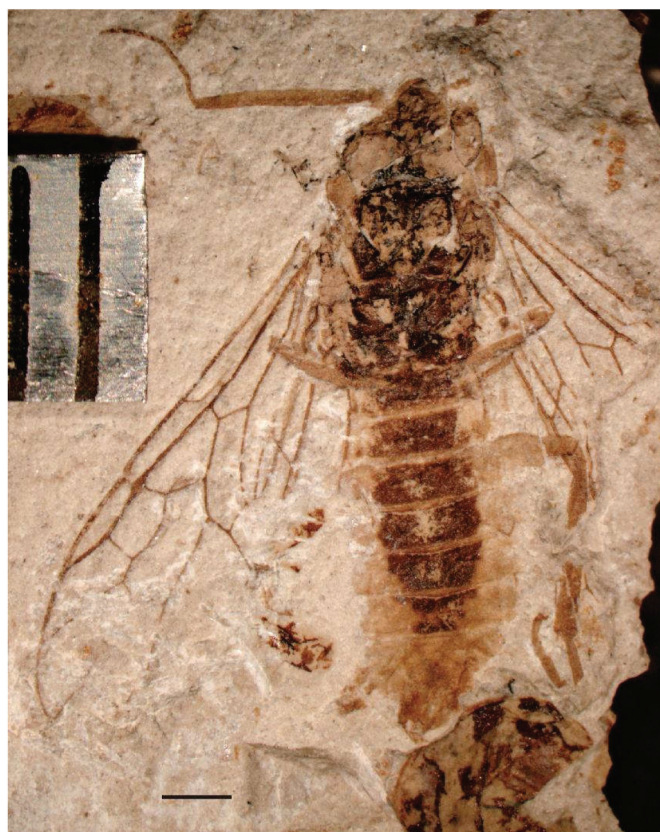


Figure 1. Photograph of *Novoxyela bella* gen. et sp. nov., holotype, NIGP200742, dorsal view. Scale bar = 1 mm.

Rasnitsyn, 1966 in Sc developed and bifurcate (vs. Sc not developed), 1-Rs shorter than the half of 1-M (vs. 1-Rs and 1-M almost equal length); differs from *Anomoxyla* Rasnitsyn, 1966 in head and eyes large (vs. head short and eyes small) and venationally in 2 m-cu meeting M behind midlength of cell 3 rm (vs. before midlength of cell 3 rm) (Rasnitsyn 1966), and from *Lydoxyela* Rasnitsyn, 1966 in two-branched Rs. *Novoxyela* gen. nov. resembles *Orthoxyela* Rasnitsyn, 1983 in Sc2 extremely short, but can be distinguished from the latter by 1-Rs much shorter than 1-M (vs. 1-Rs longer than 1-M) (Rasnitsyn 1983). *Novoxyela* gen. nov. can be differentiated from *Platyxyela* Wang et al., 2012 by Sc2 half as long as 1-Rs (vs. Sc2 nearly equal to 1-Rs), antennomere 3 longer than the other flagellomeres combined (vs. antennomere 3 shorter than the other flagellomeres combined) (Wang et al. 2012). The new genus is similar to *Cathaxyela* Wang et al., 2014 in having pterostigma unsclerotized, R almost straight, 1-Rs much shorter than 1-M and 1 r-rs shorter than 2 r-rs, but differs from the latter in Sc two-branched, Sc1 meeting C well behind Rs base (vs. Sc1 not distinct, Sc2 scarcely behind Rs base) (Wang et al. 2014). The new genus shares with *Potrerilloxyela* Lara, Rasnitsyn & Zavattieri, 2014 in pterostigma membranous except sclerotised at extreme base and R almost straight, but can be distinguished from it by Sc connected to C far behind origin of Rs (vs. Sc connected to C only very short distance behind origin of Rs), 2 m-cu joining cell 4 r (vs. 3 r), 1 m-cu shorter than half of 3-Cu (vs. 1 m-cu subequal to 3-Cu) (Lara et al. 2014).

Novoxyela bella gen. et sp. nov. (Figures 1, 2)

Diagnosis

As for genus because of monotype.

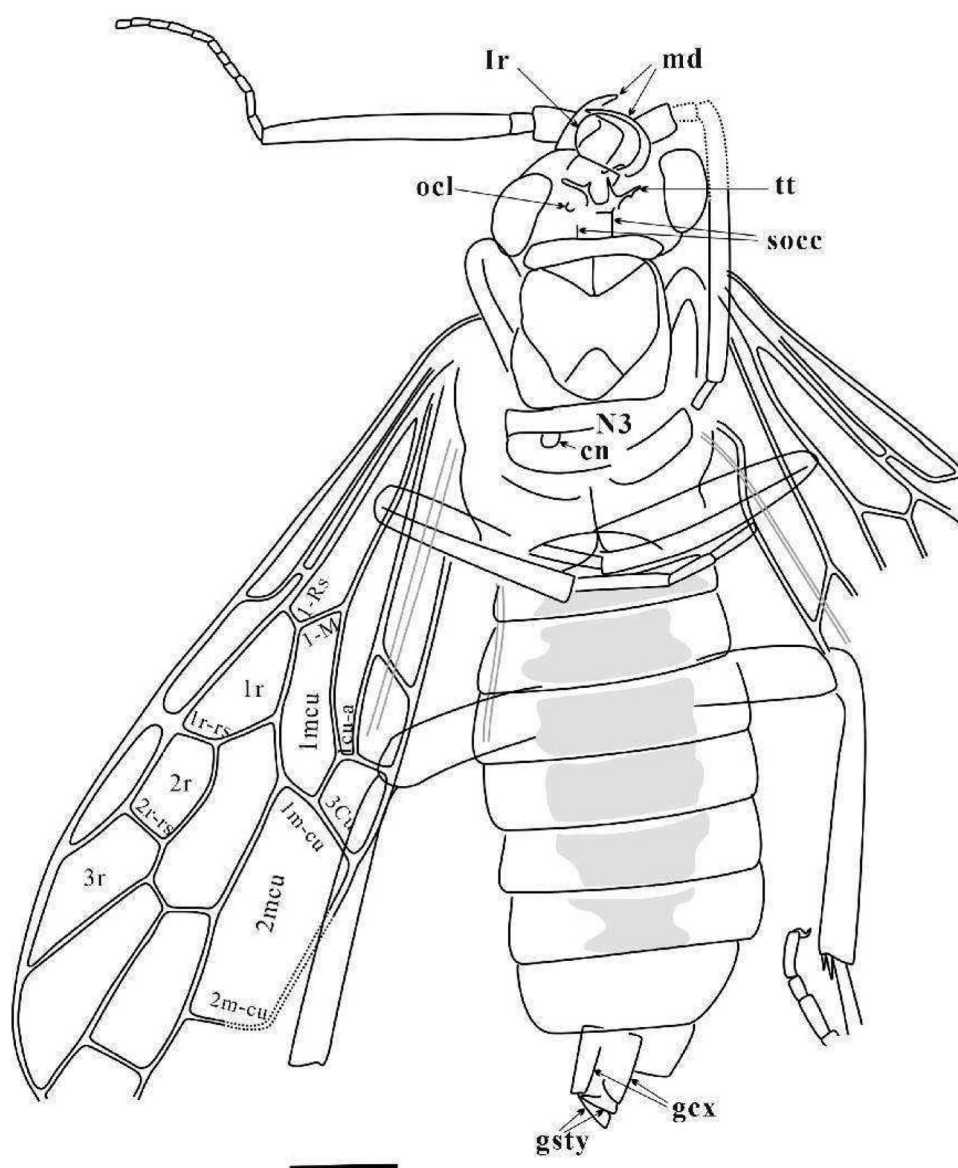


Figure 2. Line drawing of *Novoxyela bella* gen. et sp. nov. Scale bar = 1 mm. Symbols: lr = labrum, md = mandible, ocl = ocellus, tt = tentorium, socc = occipital suture, N₃ = metanotum, cn = cenchri, gsty = gonostylus, gcx = gonocoxa.

Etymology

The species name is from the Latin '*bella*' meaning pretty, referring to the well-preserved and delicateness of the forewing and body.

Holotype

Male, No. NIGP200742; well-preserved with almost complete body, antennae, forewings, but hindwings and legs incomplete; kept at NIGP.

Locality and horizon

The holotype was collected from Daohugou Village, Wuhua Township, Ningcheng County, Chifeng City, Inner Mongolia, China, Jiulongshan Formation, Middle Jurassic (Callovian-Bathonian boundary).

Description

Male sawfly preserved in dorsal view, with left antenna and forewing, mid legs nearly complete; head, thorax, abdomen and genitalia well preserved; right antenna preserved basally; right forewing preserved partly, and left and right hind wings hardly visible. Colour generally pale brown with thorax, most of veins and abdominal terga 1–7 much darker (terga 2–7 except laterally).

Head unusual massive, much wider than high (ca. 2.07 mm wide and 0.84 mm high), eyes extraordinarily large (ca. 0.39 mm wide and 0.87 mm long), kidney-shaped, occupying most of head sides; ocellus small; tentorium visible with thin anterior and dorsal arms; mandible large and sharp, sickle-shaped (ca. 0.24 mm in width and 0.86 mm in length), with dentition not clearly visible. Antenna with 14 segments preserved, and at least 2.11 times as long as width of head; scape ca. 0.30 mm wide and 0.37 mm long, about 1.58 times as long as pedicel; pedicel short, wider than that of length; third

segment ca. 2.37 mm in width and 0.26 mm in length, about 1.19 times as long and 2.37 times as wide as remaining flagellomeres.

Thorax narrower than head, pronotum short and trapezoid; mesonotum with notauli distinct and complete, distant from scutellum for about scutellum length; cenchri small, slightly wider than long. Forewing as preserved, ca. 2.47 mm at maximum width, 8.46 mm length; costal area narrow but slightly widened before base of Rs; pterostigma long and narrow, lancet-like, not sclerotised, except for dark delimiting veins, half as wide as cell 2 r and twice as long as cell 2 r; Sc with two branches, Sc1 merging with C well behind origin of Rs, Sc2 short and subvertical, almost half as long as 1-Rs, and connected to R for 3 times as long as Sc2 distance before origin of Rs; 1-Rs 0.47 times as long as 1-M; M+ Cu bent; length proportions of vein 1-M: Rs+M: 2-M: 1-Cu = 0.51: 0.86: 0.59: 0.18; 3-M about 2.5 times as long as 2-M; R distinctly thickened, almost straight both before and after Rs base; 1 r-rs strongly inclined towards base of wing and 2 r-rs slightly inclined towards apex of wing, 1 r-rs 0.78 times as long as 2 r-rs; 3-Rs arched posteriorly; end of Rs1 closer to pterostigma than to Rs2; M+ Cu slightly curved in its basal half; 1 m-cu 0.68 times as long as 2-Cu and 0.49 times as long as 3-Cu; cell 1 r large, elongate and triangular; cell 2 r small and trapezoidal; cell 3 r and cell 4 r narrow and elongate; length proportions of cells 1 r: 2 r: 3r: 4 r = 1.43: 0.96: 1.60: 1.89, respective maximum width ratio = 0.63: 0.56: 0.64: 0.84; cell 2 rm ca. 0.72 mm wide and 2.00 mm long, longer than cell 3rm (ca. 0.63 mm wide and 1.54 mm long); cell 2 m-cu broader, about 2.39 times as long as wide, and at least 1.5 times as long and wide as cell 1 m-cu; cell 1cu narrow and elongate, distinctly broader at M base, about 10.43 times as long as wide. Hind wing incompletely preserved. Fore leg with femora and tibiae partly visible; mid leg with femur and tibia thin as preserved, tarsus with three segments preserved, ca. 0.95 mm, 0.46 mm and 0.48 mm long, respectively; hind leg with femur with thick and remarkably wider (ca. 0.51 mm wide) than tibia (ca. 0.32 mm wide); tibia long, about 1.47 times as long as mid tibia and about 1.06 times as wide as mid tibia, and with two short, sharp pre-apical spurs; tarsus middle part vaguely visible, shorter than in midleg, with third to fifth segment ca. 0.45 mm, 0.21 mm and 0.41 mm; claw lacking inner tooth.

Abdomen with eight visible segments, slightly wider than mesonotum. Genitalia small, with gonocoxa narrow, rectangular, apparently at least twice as wide as gonostylus; gonostylus small, narrow.

Measurements

Body length 9.37 mm (except antenna and mandible). Head 2.07 mm wide, antenna not shorter than 4.87 mm (scape incompletely preserved) long, with first flagellomere 2.37 mm long. Forewing length 8.46 mm and maximum width 2.47 mm. Length of thorax 2.76 mm, abdomen 5.18 mm. Mid leg with femur 2.01 mm long, tibia 3.18 mm long and 0.32 mm wide; hind leg with tibia 2.17 mm long and 0.31 mm wide; genitalia 0.54 mm long.

Genus *Platxyela* Wang et al., 2012

Type species

Platxyela unica, 2012

Other included species

P. tenuis Zheng et al., 2021 and *P. elegans* sp. nov.

Platxyela elegans sp. nov. (Figures 3–4)

Diagnosis

Differs from *P. unica* Wang et al., 2012 and *P. tenuis* Zheng et al., 2021 in ovipositor widening towards apex (vs. narrowed apically).

Etymology

The species name is after the Latin '*elegans*' meaning elegant, referring to the entire morphologies of fossil preserved.

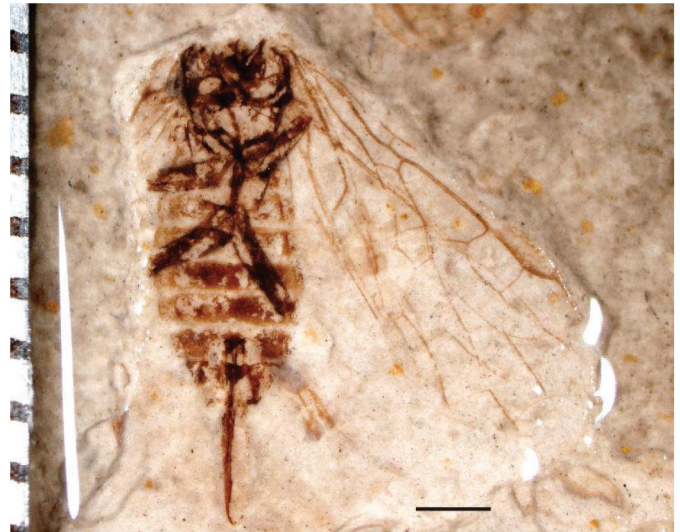


Figure 3. Photograph of *Platxyela elegans* sp. nov., holotype, NIGP200743, ventral view. Scale bar = 1 mm.

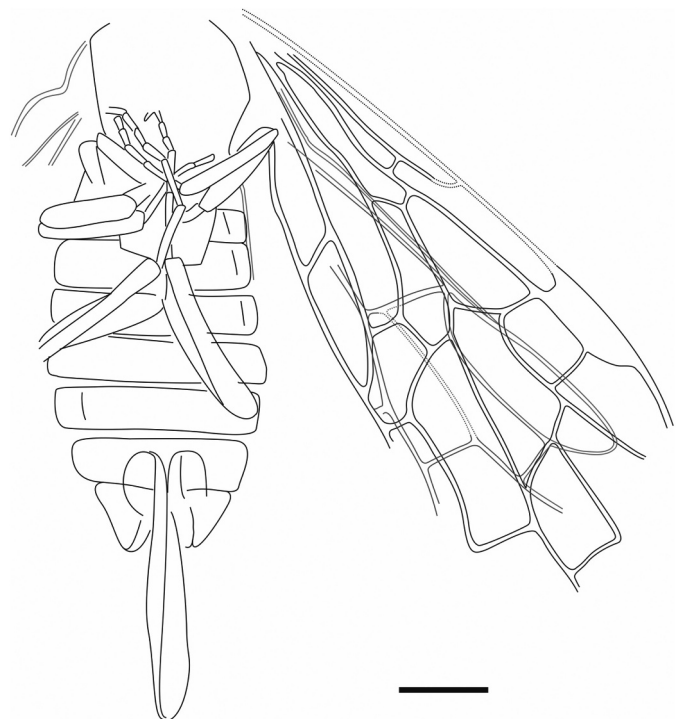


Figure 4. Line drawing of *Platxyela elegans* sp. nov. Scale bar = 1 mm.

Holotype

Female, No. NIGP200743. Well preserved with forewing, hindwing, mid- and hindlegs, ovipositor, but head absent; kept at NIGP.

Description

Female sawfly preserved in ventral view, body incomplete with head and left forewing and hind wing entirely absent, right forewing and hind wing slightly damaged distally, legs partly missing, thoracic structure obscure. Colour pattern apparently mostly dark.

Forewing costal space obviously widened before the origin of Rs, pterostigma sclerotised fully, broaden and at least 0.60 times as wide as cell 2 r; vein R significantly curved at base of Rs and thickened before pterostigma; Sc two-branched, Sc1 connecting with C just beyond origin of Rs, Sc2 nearly as long as 1-Rs, subvertical, meeting R before origin of Rs; 1-Rs much shorter than 1-M; M+ Cu slightly arcuate anteriorly; crossvein 1 r-rs subparallel to 2 r-rs and 0.80 times as long as latter; base of 2 r-rs 0.7 times as distant from apex of pterostigma as from base of 1 r-rs; 3-Rs slightly arched towards hind margin of forewing in its basal half; Rs+M about 3.67 times as long as 2-M and 2.28 times as long as 2-Rs; 2-M 0.19 times as long as 3-M; 2 r-m inclined towards wing base, and 3r-m towards apex of wing; 1 m-cu 0.60 times as long as 2-Cu and 0.36 times as long as 3-Cu; 2m-cu inclined towards base of wing and 0.43 times as long as 4-Cu; cell 1 r large, triangular, about twice as long as cell 2 r; cell 2 rm large, about twice as long as cell 2 r; cell 1 m-cu elongate and narrow; cell 2cu quadrangular and large; the length proportions of cells 1 r: 2 r: 2 rm: 3 rm: 1 m-cu: 2 m-cu: 1 cua: 2 cua = 1.76: 0.92: 2.13: 1.33: 1.81: 2.28: 2.18: 0.63. Hindwing partly preserved, 1-Rs not developed (1 r-m connected to R just at Rs base), long; 1-M approximately one-third as long as 1 r-m; m-cu meeting cell 2 rm+3 rm 1.25 times of its length before 3 r-m; Cell r rounded, cell m-cu long and widened distally.

Abdomen with eight visible segments, widest near mid-length, length of segments 2–7 measured medially (mm): 0.40, 0.53, 0.43, 0.47, 0.51 and 0.74, respectively; ovipositor elongate, sword-shaped, widest before apex, almost as long as cells 2 rm and 3 rm combined, with sheath 3.25 times as long as valvifers.

Measurements

Body preserved length 6.09 mm (excluding ovipositor sheath and head); incomplete forewing length as preserved ca. 7.52 mm, full wing length probably 7.6 mm, maximum width ca. 2.92 mm, pterostigma 1.38 mm long and 0.46 mm wide; length of thorax 2.12 mm, abdomen 3.97 mm; fore leg with incomplete femur ca. 0.50 mm, tibia ca. 0.90 mm; middle leg with femur 1.08 mm long, tibia 1.21 mm long; hind leg with coxa 0.25 mm long and 0.31 mm wide, femur 1.49 mm long, tibia 1.85 mm long and tarsus 1.91 long; ovipositor sheath length 2.97 mm.

Remarks

New species differs from both congeners in ovipositor widest before apex (vs. narrowing apical), additionally differs from *P. unica* by smaller size (forewing length probably 7.6 mm, vs. more than 12 mm) and from *P. tenuis* by pterostigma completely sclerotised (vs. sclerotised basally).

Discussion

Daohugou Biota as one of the most famous insect deposits and has been documented with many important and well-preserved Middle Jurassic fossil, especially some hymenopteran fossils (Rasnitsyn and Zhang 2010; Wang et al. 2012; Zheng et al. 2019; Zheng et al. 2021). In this study, we describe one new genus within one species *Novoxyela bella* gen. et sp. nov. and one species *P. elegans* sp. nov. of Xyelidae from Daohugou stratum in China, which provide an added glimpse into the evolutionary history of early hymenopterans as well as diversified significantly by the Middle Jurassic.

Up to now, five genera and eight species are reported in fauna of Xyelidae from Daohugou attributed to two subfamilies, Xyelinae with the tribe Liadoxyelini, and Macroxyelinae Ashmead, 1989 with tribes Xyeleciini, Gigantoxyelini and Angaridylini Rasnitsyn 1966 (Rasnitsyn, 1969, 1983; Wang et al. 2012, 2014; Zheng et al. 2019). Based on the key to subfamilies and tribes of Xyelidae proposed by Zheng et al. (2021), tree genera and five species key out in the Liaoxyelini, *Cathayxyela extensa* Wang, Rasnitsyn & Ren, 2014, *Platyxyela unica* Wang, Shih & Ren, 2012, *P. tenuis* Zheng et al., 2021, *P. elegans* sp. nov. and *N. bella* gen. et sp. nov. have been reported from Daohugou biota (for *Aequixyela immensa* Wang et al., 2014, also described in Liadoxyelini, see Zheng et al. 2021). Comparison with 8 genera and 13 species of Liadoxyelini has been recorded up to now (Table 1); our findings improve our knowledge of variation on wing venation and body features of xyelid species from Daohugou Biota, which also highlight the underestimated diversity of Symphyta.

Interestingly, our findings further confirm hypothesis that the fossil assemblages of Liadoxyelini are predominantly Jurassic (Rasnitsyn 1980, 2002; Rasnitsyn and Zhang 2004). As a result, they are not uncommon in Daohugou, tend to be common in the early Middle Jurassic, but gradually decrease in taxa number in the Late Jurassic, and even almost completely disappear in the Cretaceous in the fossil record.

Novoxyela bella gen. et sp. nov. is undoubtedly a new record and the third described genus of Liadoxyelini in Daohugou hitherto supported by unusual large head, pterostigma sclerotised only basally; Sc two branches and 1-Rs shorter than 1-M, providing important characters which can enhance our knowledge on diverse morphological characters of Xyelidae in Mesozoic. Although only partially preserved, *P. elegans* sp. nov. possesses well diagnostic characters in forewing venation and ovipositor. In spite of considerable similarity among *Platyxyela* species (Table 2), *P. elegans* sp. nov. can be easily distinguished by unusual form of ovipositor widening towards apex. However, our understanding of the phylogenetic relationships among these groups remains fragmentarily.

Table 1. The diversity of known fossil species of Liadoxylini, Xyelinae. -, undescribed.

Taxon	Locality and Horizon	Sex	Pterostigma	Sc	Vein			Length (mm)				Reference
					1-Rs and 1-M	1 m-cu and 3-Cu	1 r-rs and 2-rs	R	Body	Forewing	Ovipositor/ Genitals	
<i>Anomoxyla incerta</i> Rasnitsyn, 1963	Kazakhstan, Upper Jurassic	-	without sclerotised	two branches, Sc2 shorter than 1-Rs	1-Rs much shorter than 1-M	1 m-cu half as long as 3-Cu	1 r-rs shorter than 2 r-rs	bent	9.60	7.80	-	Rasnitsyn 1966
<i>Cathoxyela extensa</i> Wang et al., 2014	China, Middle Jurassic	male	pale, narrow	appressed to R, with no Sc2	1-Rs 0.5–0.7 times as long as 1-M, 1-M bends towards wing base	3-Cu at least 1.5 times as long as 1 m-cu	1 r-rs shorter than 2 r-rs	straight	7.50	5.80	-	Wang et al. 2014
<i>Kirghizoxyla mirabilis</i> Rasnitsyn, 1966	Kirgizia, Lower Jurassic	-	unsclerotised, narrow (half as narrow as cell 2 r)	not developed	1-Rs almost equal to 1-M	3-Cu twice as long as 1 m-cu	1 r-rs shorter than 2 r-rs	Straight, thickened	-	6.00	-	Rasnitsyn 1966
<i>Liadoxyla buriatica</i> Rasnitsyn, 1983	Transbaikalia, Middle Jurassic	male	only sclerotised basally, narrow	two branches, meeting R before origin of Rs	1-Rs slightly longer than 1-M	1 m-cu less than half of 3-Cu	1 r-rs longer than 2 r-rs	slightly bent	8.50	7.50	1.60	Rasnitsyn 1983
<i>L. chengdeensis</i> Ren et al., 1995	China, Upper Jurassic	-	only sclerotised basally, narrow	Sc two-branched, Sc2 meeting R just at the origin of Rs and equal to it	1-Rs shorter than 1-M, and 1-M straight	1 m-cu about 0.35 times as long as 3-Cu	1 r-rs much shorter than 2 r-rs	nearly straight	-	8.00	-	Ren et al., 1995
<i>L. iensis</i> Rasnitsyn, 1969	Siberia, Lower or Middle Jurassic	-	sclerotised basally, broaden	two branches, meeting R just at origin of Rs, Sc2 slightly shorter than 1-M	1-Rs distinctly shorter than 1-M, and latter slightly curve	1 m-cu almost 0.3 times as long as 3-Cu	1 r-rs slightly shorter than 2 r-rs	bent and thickened	-	8.00	-	Rasnitsyn 1969
<i>Liadoxyla praecox</i> Martynov, 1937	Kirgizia, Lower Jurassic	-	sclerotised basally, broaden	two branches, Sc2 connecting to C just at origin of Rs	1-Rs slightly shorter than 1-M	1 m-cu shorter than half of 3-Cu	1 r-rs shorter than 2 r-rs	thickened, bent	-	10.00	-	Rasnitsyn 1966
<i>Lydoxyla excellens</i> Rasnitsyn, 1966	Kazakhstan, Upper Jurassic	female	unsclerotised, broaden and wider than cell 2 r	probably two branches, Sc1 not preserved, Sc2 far before R base	1-Rs half as long as 1-M	1 m-cu half as long as 3-Cu	1 r-rs longer than 2 r-rs	slightly bent	10.00	7.00	3.00	Rasnitsyn 1966
<i>Novoxyla bella</i> gen. et sp. nov.	China, Middle Jurassic	male	pale, only narrow sclerotised at extreme base	two branches, Sc2 as long as half of 1-Rs	1-Rs much shorter than 1-M	1 m-cu almost half as long as 3-Cu	1 r-rs shorter than 2 r-rs	almost straight	9.37	8.46	0.54	In this study
<i>Orthoxyla rectiradiata</i> Rasnitsyn, 1983	Transbaikalia; Early or Middle Jurassic	-	scarcely thickened even basally	two branches, Sc2 0.17 times as long as 1-Rs	1-Rs longer than 1-M, 1-M straight	1 m-cu less than half as long as 3-Cu	1 r-rs slightly shorter than, and parallel to 2 r-rs	straight, thickened	6.00	-	-	Rasnitsyn 1983
<i>Platxyela unica</i> Wang, Shih & Ren, 2012	China, Middle Jurassic	female	completely sclerotised	two branches, Sc2 longer than 1-Rs	1-Rs longer than half 1-M, 1-M straight	1 m-cu less than half of 3-Cu	1 r-rs shorter than 2 r-rs	curved, not thickened	16.50	12.30	6.30	Wang et al. 2012
<i>P. tenuis</i> Zheng et al., 2021	China, Middle Jurassic	female	sclerotised basally only	two branches, Sc2 nearly equal to 1-Rs	1-Rs distinctly shorter than 1-M,	1 m-cu half as long as 3-Cu	1 r-rs shorter than 2 r-rs	straight, thickened	10.10	7.90	2.30	Zheng et al. 2021
<i>P. elegans</i> sp. nov.	China, Middle Jurassic	female	completely sclerotised	two branches, Sc2 nearly equal to 1-Rs	1-Rs half as long as 1-M, 1-M slightly curved	1 m-cu less than half of 3-Cu	1 r-rs shorter than 2 r-rs	curved and strongly thickened	6.09	7.52	2.97	In this study
<i>Porterilloxyla menendezii</i> Lara, Rasnitsyn & Zavattieri, 2014	Argentina, Early-late Triassic	-	pale, only sclerotised at extreme base, wide	only apex of Sc1 preserved	1-Rs much shorter than 1-M, 1-M slightly curved	1 m-cu subequal to 3-Cu	1 r-rs distinctly shorter than 2 r-rs	almost straight	-	6.40	-	Lara et al. 2014

Table 2. Comparison of forewing morphological characters in *Platyxyela* species.

Taxa Characters	<i>P. elegans</i> (this study)	<i>P. unica</i> (Wang et al. 2012)	<i>P. tenuis</i> (Zheng et al. 2021)
Length (mm)	7.52	12.30	7.90
Width (mm)	2.92	2.91	2.90
Pterostigma	sclerotised fully	sclerotised fully	sclerotised basally only
Length of pterostigma	1.38	1.17	1.23
Width of pterostigma	0.46	0.38	0.35
Cell 2 r	1.48 times as wide as pterostigma	2.11 times as wide as pterostigma	1.68 times as wide as pterostigma
Sc2	as long as 1-Rs	slightly longer than 1-Rs	nearly as long as 1-Rs
Costal area	widened before the origin of Rs	widened before the origin of Rs	widened before the origin of Rs
2-Rs vs. 1 r-rs	2-Rs much longer than 1 r-rs	2-Rs as long as 1 r-rs	2-Rs nearly equal to 1 r-rs
1 r-rs vs. 2 r-rs	1 r-rs shorter than 2r-rs, about 0.9 times as long as it	1 r-rs subparallel to 2r-rs, about 0.6 times as long as it	1 r-rs subparallel to 2r-rs and 0.8 times as long as it
3-M vs. 4-M	3-M about twice as long as 4-M	3-M about 1.5 times as long as 4-M	3-M with 1.25 times as long as 4-M
1 m-cu vs. 3-Cu	1 m-cu 0.4 times as long as 3-Cu	1 m-cu 0.3 times as long as 3-Cu	1 m-cu 0.5 times as long as 3-Cu
Angle between 2r-m and 3-M	53.91°	96.79°	123.61°

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