

Research article

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New fossil records of Xyelidae (Hymenoptera) from the Middle Jurassic of Inner Mongolia, China

Yan ZHENG^{1,*}, Haiyan HU², Dong CHEN³, Jun CHEN⁴,
Haichun ZHANG⁵ & Alexandr P. RASNITSYN^{6,*}^{1,4}Institute of Geology and Paleontology, Linyi University, Shuangling Rd., Linyi 276000, China.^{1,4,5}State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, East Beijing Road, Nanjing 210008, China.²School of Agronomy and Environment, Weifang University of Science and Technology, Jinguang Road, Shouguang, 262700, China.³School of Environmental and Municipal Engineering, Qingdao University of Technology, Qingdao 266033, China.⁶Palaeontological Institute, Russian Academy of Sciences, Moscow, 117647, Russia.⁶Natural History Museum, London SW7 5BD, UK.

*Corresponding authors: zhengyan536@163.com, alex.rasnitsyn@gmail.com

²Email: huhaiyanzy@163.com³Email: chendong_cau@163.com⁴Email: rubiscada@sina.com⁵Email: hc Zhang@nigpas.ac.cn¹ urn:lsid:zoobank.org:author:28EB8D72-5909-4435-B0F2-0A48A5174CF9² urn:lsid:zoobank.org:author:91B2FB61-31A9-449B-A949-7AE9EFD69F56³ urn:lsid:zoobank.org:author:51D01636-EB69-4100-B5F6-329235EB5C52⁴ urn:lsid:zoobank.org:author:8BAB244F-8248-45C6-B31E-6B9F48962055⁵ urn:lsid:zoobank.org:author:18A0B9F9-537A-46EF-B745-3942F6A5AB58⁶ urn:lsid:zoobank.org:author:E7277CAB-3892-49D4-8A5D-647B4A342C13

Abstract. A new genus and two new species of Xyelidae Newman, 1834 (Hymenoptera Linnaeus, 1758), *Platyxyela tenuis* sp. nov. and *Scleroxyela daohugouensis* gen. et sp. nov. are described and illustrated from the Middle Jurassic Daohugou Beds of Ningcheng, Inner Mongolia, China. *Platyxyela tenuis* sp. nov. (Xyelinae Newman, 1834, Liadoxyelini Rasnitsyn, 1966) can be distinguished from its congeners by short forewing length and ovipositor sheath strongly narrowed toward acute apex. *Scleroxyela daohugouensis* gen. et sp. nov. is placed within Macroxyelinae Ashmead, 1898, Xyeleciini Benson, 1945 based on pterostigma completely sclerotised and costal space sclerotised before pterostigma, 1-Rs half as long as 1-M, and 1m-cu short. It is the first recorded species of Xyeleciini in Daohugou Beds. Furthermore, an updated key of identification of subfamilies and tribes of Xyelidae is provided. Our findings of new morphological data provide insights into the early evolution of Hymenoptera, as well as effectively enrich our understanding of the diversity of Xyelidae in the Mesozoic.

Keywords. Mesozoic, fossil insects, Daohugou, taxonomy, new taxon.

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Introduction

The small extant group of distinctive sawflies, Xyelidae Newman, 1834, has been considered to be the most primitive of Hymenoptera Linnaeus, 1758 (Rasnitsyn 1980; Zhang & Zhang 2000), and plays a vital role as an ancestral group in the early evolution of hymenopterans. This family has been reported as the earliest appearance on the hymenopteran cladogram from the Middle or Upper Triassic of Kyrgyzstan (Rasnitsyn 1964, 1969, 1980), and the Upper Triassic of Australia (Riek 1955; Engel 2005), South Africa (Schlüter 2000) and Argentina (Lara *et al.* 2014). The diversity of this family in the Mesozoic was much broader than today. Hitherto, more than 80 species within 47 genera attributed to Xyelidae have been reported from the Mesozoic (Rasnitsyn 1964, 1969, 1977, 1980; Zhang & Zhang 2000; Wang *et al.* 2012; Kopylov 2014; Zheng *et al.* 2019). In contrast, the incomparably better studied extant fauna of the family embraces 75 described species in 5 genera (Taeger *et al.* 2010; corrected for *Xyela* Dalman, 1819 according to Blank *et al.* 2013). Aguiar *et al.* (2013) provided still more impressive figures, 5 living genera and 63 species vs 47 extinct genera and 93 species. Yet, the past xyelid diversity is strongly underexplored as lots of undescribed fossils are known to be waiting for their explorer already stored in the collections with which the authors dealt now or dealt before. The present publication makes a small input to that end describing one new genus and two new species of Xyelidae from the famous mid-Jurassic Lagerstätte Daohugou in Northeastern China.

The Daohugou area is one of the most important insect fields containing abundant, diverse, and excellently preserved fossils (Rasnitsyn & Zhang 2004, 2010; Zhang 2012; Makarkin *et al.* 2013; Liu *et al.* 2014; Wang *et al.* 2016; Zheng *et al.* 2016; Zheng & Chen 2017). This holds true for the sawfly family Xyelidae, accounting for almost 15% of Hymenoptera in the Daohugou collection kept at the Nanjing Institute of Geology and Palaeontology, which early in the 21st century displayed at least two subfamilies and three tribes of Xyelidae (Rasnitsyn & Zhang 2004). We herein report the discovery of one new genus and two new species, *Platyxyela tenuis* sp. nov., and *Scleroxyela daohugouensis* gen. et sp. nov. based on two well-preserved xyelid specimens from the Middle Jurassic Daohugou Beds of

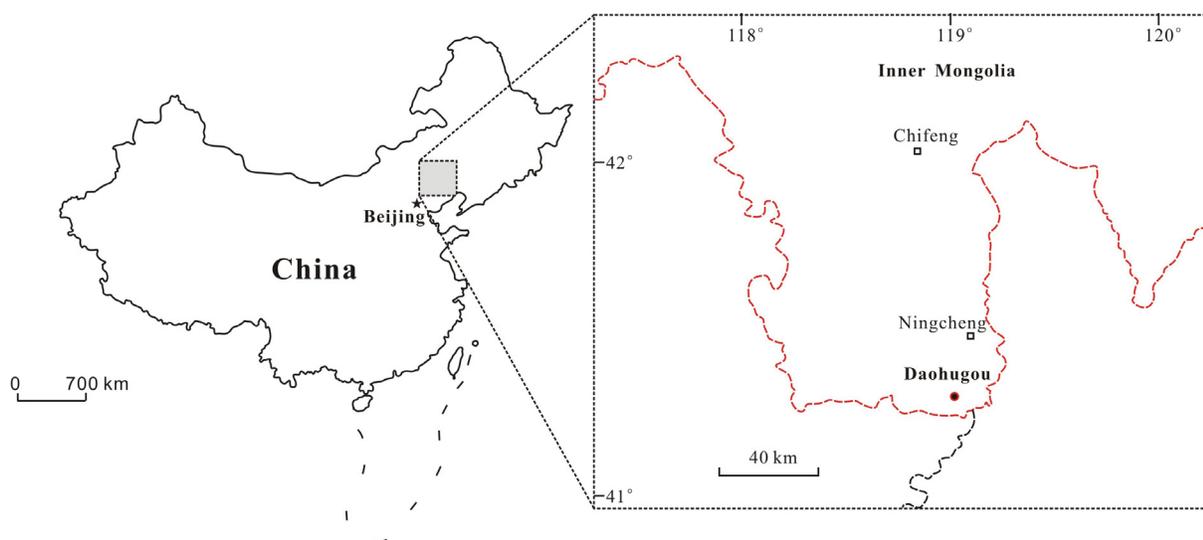


Fig. 1. Geographical sketch map showing the insect fossil locality in Daohugou area, Ningcheng City, Inner Mongolia, China.

Ningcheng, Inner Mongolia, China. The key to identification of subfamilies and tribes of Xyelidae is also updated and provided. Our findings present some new remarks on the early evolutionary history of the Xyelidae, and also expand the knowledge of the diversity of this family in the Mesozoic.

Material and methods

The fossil specimens studied were collected from Daohugou Village (41°8'38" N; 119°8'38" E), Shantou Township, Ningcheng City, Inner Mongolia, China (Fig. 1) and are deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGP, CAS). The locality is dated as the latest Middle Jurassic, Jiulongshan Formation (Chen *et al.* 2004).

The fossils were examined and photographed by standard paleontological methods, using the VHX 5000 digital microscope platform. Line drawings were done with CorelDRAW ver. 14.0 and Adobe Photoshop CS6. The measurements of specimens were made using NIH ImageJ software (<http://rsb.info.nih.gov/ij/>). The wing venation terminology used is basically adapted from Huber & Sharkey (1993).

Results

Order Hymenoptera Linnaeus, 1758
Suborder Symphyta Gerstaecker, 1867
Superfamily Xyeloidea Newman, 1834

Family **Xyelidae** Newman, 1834

Remarks

The system of Xyelidae considering its present and past diversity was developed a half century ago (Rasnitsyn 1966, 1969) and badly needs reconsideration now because the description of numerous new genera has made the diagnostic of tribes and subfamilies rather tricky and results in many mistakes. However this is a subject of a special work which is hardly possible to perform in the near future. In the meantime, to help current researches in the field of past diversity of the family, we have constructed an updated, although preliminary, key to the identification of the subfamilies and tribes of Xyelidae particularly addressed to fossil material.

Key to subfamilies and tribes of Xyelidae

1. Along R, cell 2r longer than, or as long as, or very rarely slightly shorter than, 1r. Triassic 2
– Along R, cell 2r shorter than or, very rarely, as long as 1r. J-R (Jurassic through Recent) 3
2. Rs two-branched (cell 4r present) Archxyelinae Rasnitsyn, 1964
– Rs simple (no 4r cell) Madygellinae Rasnitsyn, 1969
3. Costal space apical with no sclerotisation connecting C with R. Pterostigma not sclerotised (dark) except sometimes basally. Ovipositor long, extending behind abdomen, never very wide. Xyelinae 4
– Costal space apical with vertical sclerotisation between C with R delimited from pterostigma with costal break (membranose slit permitting pterostigma with distal wing to turn up and down at flight), or that area widely desclerotised, expanding to both end of costal space and base of pterostigma (as in Ceroxyelini). Pterostigma sclerotised (dark) basally or throughout, sometimes except centrally. Ovipositor not narrow, extending far behind abdomen only when very wide. Macroxyelinae 5

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- 4. 1-Rs longer than 1-M, 1m-cu longer than 0.6× 3-Cu. J-R..... Xyelini Newman, 1834
 – 1-Rs shorter than 1-M, 1m-cu at most 0.6× as long as 3-Cu. Jurassic and Early Cretaceous
 Liadoxyelini Rasnitsyn, 1966
 - 5. Sc hind branch entering R distal of Rs base 6
 – Sc hind branch entering R basal or at Rs base..... 7
 - 6. 1-Rs shorter than 1-M. Area around costal break widely desclerotised. 1st flagellomere much shorter
 than posterior flagellomeres together. Early Cretaceous Ceroxyelini Rasnitsyn, 1969
 – 1-Rs not distinctly shorter than 1-M. Area around costal break narrowly or not at all desclerotised.
 1st flagellomere not shorter than posterior flagellomeres together. J-R
 Macroxyelini Ashmead, 1898
 - 7. 1-Rs half as long as 1-M or shorter. Pterostigma sclerotised throughout or except centrally, usually
 with distinct desclerotisation around costal break. J-R Xyeleciini Benson, 1945
 – 1-Rs distinctly longer than half 1-M. Pterostigma rarely with distinct desclerotisation around costal
 break. Jurassic and Early Cretaceous..... 8
 - 8. Pterostigma sclerotised basally Angaridxyelini Rasnitsyn, 1966
 – Pterostigma sclerotised throughout (sometimes except centrally) Gigantoxyelini Rasnitsyn, 1969

Subfamily Xyelinae Newman, 1834

Tribe **Liadoxyelini** Rasnitsyn, 1966

Type genus

Liadoxyela Martynov, 1937.

Remarks

This tribe was proposed for four genera (*Liadoxyela* Martynov, 1937, *Kirghizoxyela* Rasnitsyn, 1966, *Anomoxyela* Rasnitsyn, 1966, and *Lydoxyela* Rasnitsyn, 1966) and five species from Jurassic and Early Cretaceous of Siberia and Central Asia, based on a set of diagnostic characters including short 1m-cu (about half as long as 3-Cu) as distinguishing it from Xyelini Newman, 1834, the only other tribe in subfamily Xyelinae (Rasnitsyn 1966). The next revision of Xyelidae and Symphyta in general (Rasnitsyn 1969) added another diagnostic feature, 1-Rs not longer than 1-M. One more genus (*Orthoxyela* Rasnitsyn, 1983) and two species from the Jurassic of Siberia have been added to the tribe since (Rasnitsyn 1983). Much later three further genera (*Platyxyela* Wang *et al.*, 2012, *Cathayxyela* Wang *et al.*, 2014, *Aequixyela* Wang *et al.*, 2014), each with one species from the Middle Jurassic of China, have been added to the tribe, even though not without confusion (Wang *et al.* 2012, 2014). The first genus was described in Macroxyelinae Ashmead, 1898 but later listed under Liadoxyelini Rasnitsyn, 1966 (Wang *et al.* 2014: table 1). Judging from their descriptions and the table 1, *Cathayxyela* and *Aequixyela* were equally described as members of Liadoxyelini, but this was under the title Xyelini which we consider a lapsus calami. We agree with the interpretation of *Platyxyela* and *Cathayxyela* as members of Liadoxyelini. However, *Aequixyela* differs from other Liadoxyelini considerably in having 1-Rs scarcely longer than 1-M, 1m-cu distinctly longer than half 3-Cu, pterostigma distinctly inflated (often in Xyelini but never in Liadoxyelini), and unlike all Xyelidae, ovipositor very short and narrow. Unusual is also the very short antennal flagellum, only comparable with that in living Macroxyelini Ashmead, 1898. The position of the latter genus needs special consideration: for the moment we consider it as Xyelinae incertae tribus.

Genus *Platyxyela* Wang *et al.*, 2012

Type species

Platyxyela unica Wang *et al.*, 2012.

Platyxyela tenuis sp. nov.

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Figs 2–3

Diagnosis

Forewing long (7.9 mm in length), ovipositor sheath as long as M+Cu and strongly narrowed toward acute apex.

Etymology

The specific name *tenuis*, thin, feminine gender of the Latin, referring to the thinness and delicateness of the body.

Type material

Holotype, female, NND0176 with well-preserved body, wings complete but legs incomplete; NIGP.

Locality and horizon

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

Comparison

Platyxyela tenuis sp. nov. is without pterostigma sclerotised completely, 1-Rs obviously shorter than 1-M and 1 m-cu half as long as 3-Cu, which indicate the position of the new species in Xyelinae, Liadoxyelini. This new species differs from *P. unica* in forewing length (7.9 mm vs 12.3–16.5 mm in *P. unica*), ovipositor sheath length and shape (ovipositor sheath relatively much longer and slowly narrowing to rounded apex in *P. unica*).

Description

Female sawfly in ventral view with approximately complete wings and full body. Head large and nearly round; eyes somewhat infuscated; antenna ca 2.7 times as long as width of head, scape about three times as long as pedicel, pedicel short, 0.11 times as long as 1st flagellomere, the latter thickened and elongated, but obviously shorter than flagellum; flagellum with at least eight segments, each longer than wide.

Thorax slightly wider than head. Propleura large, mesonotum with notauli distinct and complete, medial mesoscutal line long and thin, mesoscutellum strongly elevated. Mesopleuron smooth, without discernible wrinkles.

Forewing with pterostigma sclerotised basally only; pterostigma narrow and nearly half as wide as cell 2r; costal area obviously dilated proximad of base of Rs; Sc with two branches, Sc1 merging with C beyond origin of Rs, Sc2 short and almost vertical, meeting R before origin of Rs; Sc2 nearly equal to 1-Rs and the latter distinctly shorter than 1-M; 3-M about 3 times as long as 2-M; R strongly curved before origin of Rs and slightly thickened before pterostigma; cross vein 1r-rs subparallel to 2r-rs and 0.8 times as long as it; base of 2r-rs 0.7 times as distant from apex of pterostigma as from base of 1r-rs; Rs+M at least six times as long as 1-Rs; section of Rs between 1r-rs and 2r-rs arched toward lower

margin of forewing, end of Rs1 closer to pterostigma than to Rs2; M+Cu sinuate; 1m-cu 0.7 times as long as 2-Cu and half as long as 3-Cu; 2m-cu inclined towards wing base and half as long as 4-Cu; length proportions of cells 1r:2r:3R:4r:1m-cu:2m-cu = 1.8:0.9:1.2:1.9:1.7:2.1.

Hindwing with 1r-m long, meeting Rs it is very base; 1-M ca 0.3 times as long as 1r-m; m-cu not reaching 3r-m for about half of its (m-cu) length; cell 1cu long and widened at origin of M; cu-a arcuate basally; cell 1a slightly shorter than cell cua; M and Cu with free ends not reaching wing margin, 1A with no free end; 3A almost as long as M+Cu.

Foreleg thin and short. Midleg femur ca 4.8 times as long as wide, tibia slightly shorter than femur, tarsus with basitarsus as long as three following segments combined; first segment elongated and fourth segment shortest. Hindleg longer and wider than midleg, coxa long, femur ca 5.3 times as long as wide, tibia 1.25 times as long as femur and nearly $\frac{2}{3}$ as wide as femur, tarsus with four preserved segments, apparently similar to mid one in proportions.

Abdomen with nine visible segments; ovipositor sword-shaped, with sheath twice as long as valvifer II.



Fig. 2. Photograph of *Platyxyela tenuis* sp. nov. Holotype, NND0176. Ruler unit (top right): 1 mm.

Measurements

Body length (excluding ovipositor sheath) 7.8 mm long. Head width 1.2 mm, length 1.1 mm. Antennae not shorter than 3.2 mm, third antennal article ca 1.5 mm. Length of forewing ca 7.9 mm; maximum width of forewing ca 2.9 mm. Thorax 1.8 mm in length and abdomen 5.1 mm in length. Length of ovipositor 3.6 mm, with valvifer II 1.2 mm and ovipositor sheath 2.3 mm.

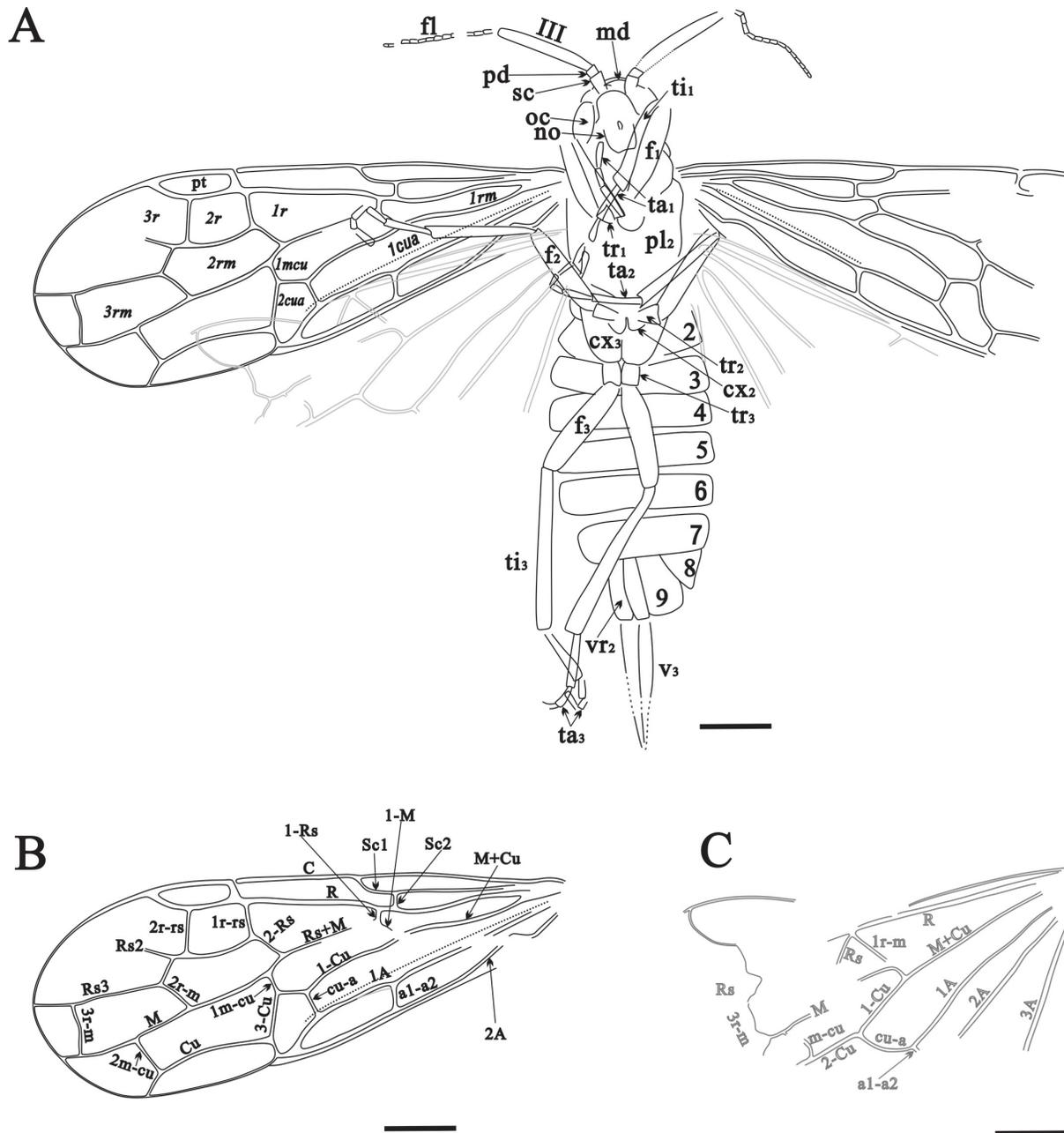


Fig. 3. Line drawings of *Platyxyela tenuis* sp. nov. **A.** Habitus, holotype. **B.** Left forewing. **C.** Left hindwing. Symbols: cx₂, cx₃ = mid and hind coxae; f₁, f₂, f₃ = fore, mid and hind femur; fl = flagellum; md = mandible; no = notaulus; oc = eye; pd = pedicel; pl₂ = mesopleuron; sc = scape; ta₁, ta₂, ta₃ = fore, mid and hind tarsus; ti₁, ti₃ = fore and hind tibia; tr₁, tr₂, tr₃ = fore, mid and hind trochanter; v₃ = ovipositor sheath; vr₂ = second valvifer; 1–9 = abdominal segments; III = enlarged third antennal segment; venational symbols standard, names of wing cells italicised. Scale bars: 1 mm.

Subfamily Macroxyelinae Ashmead, 1898

Tribe Xyeleciini Benson, 1945

Genus *Scleroxyela* gen. nov.

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Type species

Scleroxyela daohugouensis gen et sp. nov.

Etymology

The generic name is a combination of the Latin prefix *sclero*, referring to the forewing with pterostigma completely sclerotised, and *Xyela*, the type genus of Xyelidae. The gender is feminine.

Diagnosis

Forewing with pterostigma completely sclerotised; costal area sclerotised apically; Sc two-branched, with posterior branch short, vertical, joining R for short distance before origin of Rs, and anterior branch long, surpassing Rs base; 1-Rs distinct, obviously shorter than 1-M; crossvein 1r-rs subvertical, shorter than 2r-rs; 1m-cu short, ca 0.4 times as long as 3-Cu; cell 1m-cu long and narrow, 3.0 times as long as wide. Antenna with segment 3 distinctly longer than both head width and length of flagellum. Ovipositor sheaths longer than Rs+M.

Composition

Type species only.

Remarks

Scleroxyela gen. nov. is attributed to Macroxyelinae, based on the sclerotised pterostigma, and on the apex of the costal space before the pterostigma and the wide ovipositor sheaths, and to Xyeleciini Benson, 1945 based on the short 1-Rs and 1m-cu, and on the relatively long ovipositor sheaths (longer than in non-xyeleciine Macroxyelinae, even though shorter than in Xyelinae). It differs from the other xyeleciine genera by the absence of desclerotisation at the pterostigmal base, and also from *Xyelites* Rasnitsyn, 1966 and *Uroxyela* Rasnitsyn, 1966 in having a distinct 1-Rs and a long 3rd antennal segment, from *Microxyelecia* Rasnitsyn, 1969 in having a long 3rd antennal segment and a long fore Sc branch, and from *Xyelecia* Ross, 1932 in having a shorter flagellum, a longer ovipositor, and a long fore branch of Sc in the fore wing.

Scleroxyela daohugouensis gen. et sp. nov.

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Figs 4–5

Diagnosis

As for genus.

Etymology

The specific name is derived from Daohugou village, where the type specimen was found.

Type material

Holotype, female, NND0185; NIGP.

Locality and horizon

Daohugou Village, Wuhua Township, Ningcheng County, Chifeng City, Inner Mongolia, China: Jiulongshan Formation, Middle Jurassic (Callovian-Bathonian boundary).

Description

Female sawfly in ventral view with incomplete wings and body. Head large and subovate, with gena long and possibly postgenal bridge present, no eyes and ocelli visible in ventral view. Antenna ca 1.8 times as long as the width of head, scape with only apical part visible, obviously wider than pedicel, third segment approximately twice as thick as flagellum and distinctly longer than the latter.

Thorax obviously wider than head; propleurae smooth and relatively small, notauli well impressed, incompletely preserved, medial mesoscutal line long and deep; prosternum large, butterfly-like.

Forewing with pterostigma lanceolate and very narrow; costal area obviously widened proximad of base of Rs; Sc bifurcate, Sc1 connecting C beyond origin of Rs, Sc2 short and subvertical, meeting R before origin of Rs, Sc1 at least twice as long as Sc2; 1-Rs half as long as 1-M; crossvein 1r-rs subparallel to 2r-rs and 0.7 times as long as it; distance of 2r-rs to apex of pterostigma as long as distance from 2r-rs to 1r-rs; M+Cu almost straight; Rs+M approximately five times as long as 1-Rs; 3-Rs arching; 1m-cu not



Fig. 4. Photograph of *Scleroxyela daohugouensis* gen. et sp. nov. Holotype, NND0185. Ruler unit (top right): 1 mm.

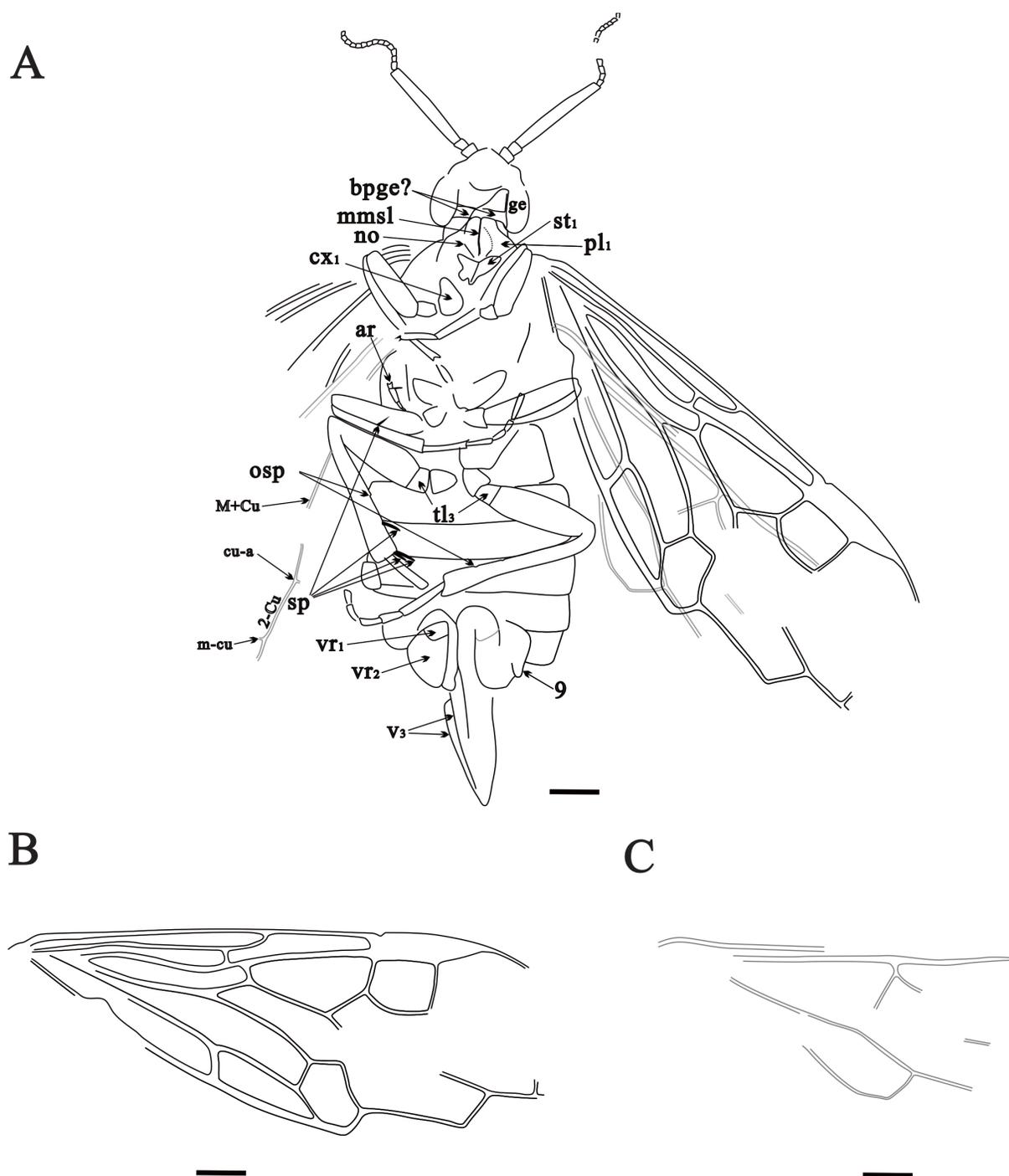


Fig. 5. Line drawings of *Scleroxyela daohugouensis* gen. et sp. nov. **A.** Habitus, holotype. **B.** Right forewing. **C.** Right hindwing. Symbols as in Fig. 3 except: ar = arolium; bpge? = possible postgenal bridge; ge = gena; mmsl = medial mesoscutal line; osp = attachment site of tibial spur; pl₁ = propleuron; sp = tibial spur; st₁ = prosternum; tl₃ = hind trochantellus. Scale bars: 1 mm.

preserved but as restored about as long as 2-Cu and half as long as 3-Cu; 2m-cu as long as M between it and 3r-m, inclined toward wing base; length proportion of cells 1r:2r:1mCu:2mCu=2.5:1.3:2.7:2.8.

Hindwing partly preserved, with 1-Rs short but distinct, 1-Cu as long as 1-M and 1r-m combined, cu-a about half as long as 1-Cu and 2-Cu.

Foreleg short with coxa, trochanters, femora, tibiae and incomplete tarsi seen. Forecoxae trapezoidal, ca 0.7 times as long as wide, trochanter ca 1.4 times as long as wide, foretibia with two spurs visible, one long and one short. Midleg with coxa large and trapezoidal, trochanter small and rectangular, femur slightly thicker than fore femur, tibia with one preapical spur visible, tarsus complete, with basitarsus shorter than three following segments combined, fifth segment about as long as third and fourth segments together, claw small, arolium distinct. Hindleg with coxa large and trapezoidal, trochanter small, wider than long, trochantellus not much smaller than trochanter, femur longer and wider than in midleg, tibia ca 0.7 times as long as femur and half as long as femur in width, with one preapical spur and socket of another more basal one visible and with two short apical spurs, tarsus longer and wider than in midleg, with fifth segment short or, rather, incompletely preserved, others similar to mid tarsus.

Abdomen with seven visible segments, ovipositor well developed, with wide sword-shaped sheath, gradually tapering toward narrowly rounded apex, length ratio of valvifer 1:valvifer 2:valvula 3 = 0.5:1.6:2.4.

Measurements

Body length excluding ovipositor sheath 11.5 mm. Head width 2.1 mm, length 1.5 mm. Antennae not shorter than 4.3 mm, third antennal article ca 2.1 mm. Incomplete forewing length as preserved ca 11.1 mm, maximum width ca 4.5 mm. Length of thorax 3.6 mm, abdomen 6.5 mm. Ovipositor sheath length 2.2 mm.

Discussion

Until now, five species of Xyelidae are described from the Middle Jurassic of Daohugou, including two of Macroxyelinae, Gigantoxyelini Rasnitsyn, 1969 (*Abrotoxyela lepida* Gao, Shih & Ren, 2009 and *A. multiciliata* Gao, Shih & Ren, 2009; Gao *et al.* 2009) and three in Xyelinae, Liadoxyelini (*Cathayxyela extensa* Wang, Rasnitsyn & Ren, 2014, *Platyxyela unica* Wang, Shih & Ren, 2012, and *Aequixyela immensa* Wang, Rasnitsyn & Ren, 2014; Wang *et al.* 2014; attribution of *Ae. immensa* to Liadoxyelini leaves certain doubts, see above). The present publication adds one new species to the genus *Platyxyela* already known there and one new genus and species representing a tribe, Xyeleciini, reported at Daohugou for the first time. As a result, the fauna of Xyelidae in Daohugou embraces now two subfamilies, four tribes (Liadoxyelini, Xyeleciini, Gigantoxyelini and Angaridyelini Rasnitsyn, 1966), five genera and seven species, of which one tribe (Xyeleciini), one genus and two species are recorded in Daohugou for the first time (Rasnitsyn & Zhang 2004; Gao *et al.* 2009; Wang *et al.* 2012, 2014; present paper). The record of Xyeleciini is the oldest one, since previously the earliest record of the tribe was in the Late Jurassic of Karatau in Kazakhstan (Rasnitsyn 1969). The new records help little in understanding general features of the biota and environments of Daohugou because Mesozoic Xyelidae show little distinct ecological diversity. As adults they were mostly palynophagous (Krassilov & Rasnitsyn 1982, 1999; Krassilov *et al.* 2003, 2007), and the same is known for larvae of most living Xyelinae (Blank *et al.* 2013, and references therein). Cretaceous and Cenozoic Xyelidae (living included) are known to be temperate insects avoiding hot climates (Rasnitsyn 1969; Rasnitsyn & Martínez-Delclòs 2000), but this does not necessarily hold true in the Jurassic (cf. Rasnitsyn 1980: 145–147). The only ecological inference possible to draw from the xyelid abundance in Daohugou is that the source territory was well forested, as the pollen found in the gut of Mesozoic Xyelidae is apparently characteristic mainly of trees (cf. above references). This inference is in accord with the presence of various xylophagous

Symphyla (Anaxyelidae, Siricidae) and parasites of xylophagous insects (Paroryssidae, Ephialtitidae, Praeaulacidae) in Daohugou (Rasnitsyn & Zhang 2004).

Conclusions

The description of *Platyxyela tenuis* sp. nov. and *Scleroxyela daohugouensis* gen. et sp. nov. enlarges considerably our knowledge of the composition of the xyelid fauna of Daohugou and supports the inference of forested shores of the Daohugou paleolake.

Acknowledgements

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