

New fossil Xyelidae (Insecta, Hymenoptera) from the Lower Cretaceous Yixian Formation of northeast China

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ABSTRACT

Three new species, *Brachyoxyla conjunctiva* sp. nov., *Brachyoxyla leei* sp. nov. and *Brachyoxyla elliptica* sp. nov., in the tribe Macroxyelini, subfamily Macroxyelinae of the family Xyelidae, are described and illustrated. All type specimens were collected from the Lower Cretaceous (Barremian–Aptian) Yixian Formation. *Brachyoxyla conjunctiva* sp. nov. and *Brachyoxyla leei* sp. nov. were from Huangbanjigou, Beipiao City, Liaoning Province, China, and *Brachyoxyla elliptica* sp. nov. from Sandaogou, Duolun County, Inner Mongolia, China. These specimens are assigned to a previously erected genus *Brachyoxyla* Gao, Zhao and Ren, 2011 based on the characters: vein Sc joining R distad origin of Rs and antenna with thread (terminal part of flagellum distal to the enlarged first flagellomere) longer than the first flagellomere. A key to species of *Brachyoxyla* is provided.

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1. Introduction

Xyelidae are a small family of herbivorous sawflies comprising more than 85 species within 50 genera (Zhang and Zhang, 2000; Kopylov, 2014; Zheng et al., 2021). As the earliest reported symphytans (Hymenoptera) from Triassic species, Xyelidae have a special significance in the evolutionary history of the Hymenoptera (Wang et al., 2014a). Xyelidae are composed of four subfamilies: Archexyelinae Rasnitsyn, 1964; Macroxyelinae Ashmead, 1898; Madygellinae Rasnitsyn, 1969 and Xyelinae Newman, 1834 (Rasnitsyn, 1969; Abe and Smith, 1991).

Macroxyelinae, established by Ashmead (1898), are the common subfamily of Xyelidae in the Mesozoic. Diagnostic characters of Macroxyelinae are the sclerotized apical bridge between C and R₁ next to pterostigma, short and wide ovipositor, and at least partially sclerotized pterostigma (Rasnitsyn, 1966). Macroxyelinae encompass

five tribes: Angaridyelini Rasnitsyn, 1967; Ceroxyelini Rasnitsyn, 1969; Gigantoxyelini Rasnitsyn, 1969 Macroxyelini Ashmead, 1898 and Xyeleciini Benson, 1954 (Rasnitsyn, 1969). Currently, Macroxyelinae are distributed in 29 genera for 46 reported fossil species (Gao et al., 2009; Wang et al., 2012; Jouault et al., 2021; Dai et al., 2022).

The tribe Macroxyelini Ashmead, 1898 currently includes six genera: *Brachyoxyla* Gao, Zhao and Ren, 2011, *Anthoxyela* Rasnitsyn, 1977, *Chionoxyela* Rasnitsyn, 1993, *Macroxyela* Kirby, 1882, *Megaxyela* Ashmead, 1898 and *Paleoxyela* Jouault et al., 2021. The tribe differs from the other Macroxyelinae except Ceroxyelini in having Sc₂ ending to R₁ behind Rs base, and from Ceroxyelini in having a pterostigma not widely desclerotised basally and in having antennal thread subequal in length to the first flagellomere or, usually, much shorter than that.

Many important mid-Mesozoic fossil discoveries have been documented in the northeast of China, for example, salamanders (Gao and Shubin, 2003), pterosaurs (Wang et al., 2002), feathered dinosaurs (Xu and Zhang, 2005), birds (Hou et al., 1995) and wonderful insects, such as Mecoptera, Hemiptera, Hymenoptera (Ren et al., 2009; Wang and Ren, 2009; Wang et al., 2019). The Yixian Formation is found in six regions of the western Liaoning

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Province, eastern Inner Mongolia, and northern Hebei Province (Gao et al., 2021). However, the oldset studies were not consensual on the age of the Yixian Formation with ages ranging from the Upper Jurassic to the Lower Cretaceous (Zheng et al., 2003; Zhou et al., 2003; Chen et al., 2004). Recent studies, based on U–Pb dating suggest an age comprised between 120 and 130 Ma and consider the Yixian Formation as Lower Cretaceous, Barremian–Aptian age (Chen et al., 2015). The position of the biota of the Yixian Formation within the Jehol Biota, to which it belongs, is discussed by Rasnitsyn (2020).

Recently, we collected three well-preserved new fossil specimens of Xyelidae from the Yixian Formation. After detailed examinations, we consider these specimens as belonging to a previously erected genus *Brachyoxyla* Gao, Zhao and Ren, 2011.

2. Material and methods

The holotype specimens of *Brachyoxyla conjunctiva* sp. nov. and *Brachyoxyla leei* sp. nov. were collected from Huangbanjigou, Chaomidian Village, Shangyuan Township, Beipiao City, Liaoning Province, China. The holotype specimen of *Brachyoxyla elliptica* sp. nov. was collected from Sandaogou, Nanyingpan Village, Duolun County, Inner Mongolia, China (Fig. 1). All specimens are housed in the fossil collection of the Key Lab of Insect Evolution and Environmental Changes, at the College of Life Sciences and Academy for Multidisciplinary Studies, Capital Normal University (CNU; Dong Ren, curator), in Beijing, China.

The specimens were examined and photographed under a Nikon SMZ25 stereomicroscope and 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 1st and

2nd segments of Rs. 1-M means the 1st segment of M, and 1-Cu, 2-Cu and 3-Cu mean 1st, 2nd and 3rd segments of Cu.

This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The LSID for this publication: urn:lsid:zoobank.org:pub:BAAvv843F6-E7AC-4F46-BA75-B6EAF5863A33.

3. Systematic palaeontology

Order Hymenoptera Linnaeus, 1758

Superfamily Xyeloidea Newman, 1834

Family Xyelidae Newman, 1834

Subfamily Macroxyelinae Ashmead, 1898

Tribe Macroxyelini Ashmead, 1898

Genus *Brachyoxyla* Gao, Zhao and Ren, 2011

Type species: *Brachyoxyla brevinodia* Gao, Zhao and Ren, 2011

Emended diagnosis. Pterostigma sclerotised entirely or desclerotized only medially. Sc₁ conspicuously longer than Sc₂. Sc₂ joining R close from separation of Rs from R (distance between 1-Rs and Sc₂ equal 1-M). 1-Rs and 1-M subequal in length (one at most 1.5 times as long as another).

Remarks. Adding three new species to the two previously known species, allows us to emmed the genus diagnosis, as it is proposed above. When applied, the diagnosis makes possible to distinguish *Brachyoxyla* from *Anthoxyela* Rasnitsyn, 1977 by pterostigma strongly sclerotized (vs. only sclerotised basally in *Anthoxyela*) as well as from *Macroxyela* Kirby, 1882 (vs. nearly fully desclerotised except basally in *Macroxyela*), from *Megaxyela* Ashmead, 1898 by short 1-Rs (vs. some twice as long as 1-M in *Megaxyela*), from *Chionoxyela* Rasnitsyn, 1993 by long 1-Rs (vs. half as long as 1-M in *Chionoxyela*), from *Paleoxyela* Jouault, Aase, and Nel, 2021 by short distance between Sc₂ and R (vs. Sc₂ joining R far from 1-Rs originating point in *Paleoxyela*). Additionally *Brachyoxyla* differs from

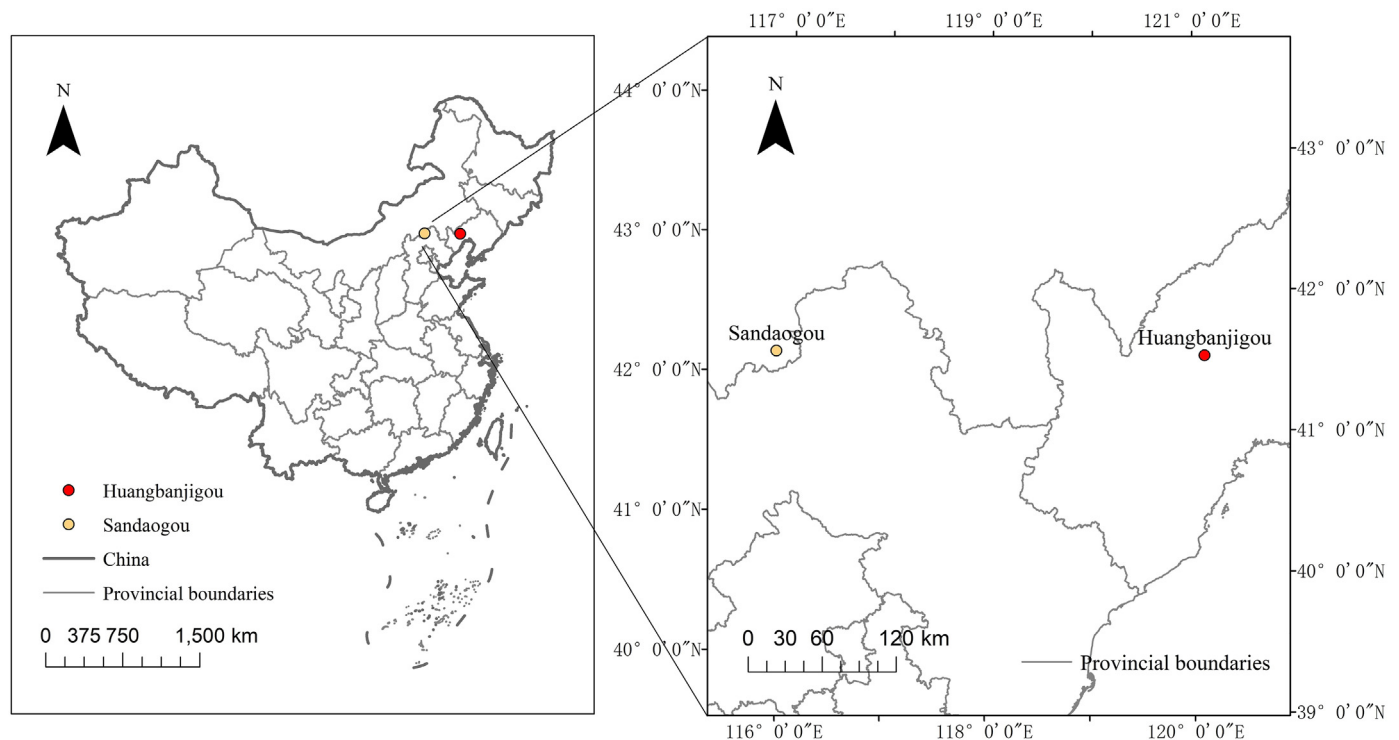


Fig. 1. Geographical sketch map showing the insect fossil locality Huangbanjigou, Chaomidian Village, Shangyuan Township, Beipiao City, Liaoning Province, China and Sandaogou, Nanyingpan Village, Duolun County, Inner Mongolia, China.

Macroxyela and *Megaxyela* by its longer antennal thread with up to 18 flagellomeres (vs. several times shorter than first flagellomeres in *Macroxyela* and *Megaxyela*).

Key to the species of *Brachyoxyela*

1. 1-Rs₂ forking at 2r-rs.....*Brachyoxyela conjunctiva* sp. nov.
1-Rs₂ forking far distad to 2r-rs.....2
2. Sc₂ joining R distad origin of Rs base at a distance distinctly longer than length of Sc₂.....*Brachyoxyela leei* sp. nov.
Sc₂ joining R extremely close to Rs base (shorter than the length of Sc₂).....3
3. 1-Rs as long as 1-M.....*Brachyoxyela gracilentia* Gao, Zhao and Ren, 2011
1-Rs shorter than 1-M.....4
4. First flagellomere nearly equal in length to thread; 1m-cu approximately equal to 2-Cu.....*Brachyoxyela brevinodia* Gao, Zhao and Ren, 2011
First flagellomere distinctly longer than thread; 1m-cu shorter than 2-Cu.....*Brachyoxyela elliptica* sp. nov.

Brachyoxyela conjunctiva Dai, Shih, and Rasnitsyn sp. nov.
(Figs. 2, 3)

Holotype. No. CNU-HYM-LB-2021016 p/c (part and counterpart), housed at the College of Life Sciences and Academy for Multidisciplinary Studies, Capital Normal University. LSID: urn:lsid:zoo-bank.org:act:F96EF723-9E76-4771-B99A-4D70A251F2EC.

Etymology. The species name is from the Latin “conjunctivus”, meaning connective and referring to 1-Rs₂ connected to 2r-rs directly.

Locality and horizon. Huangbanjigou, Chaomidian Village, Shangyuan Township, Beipiao City, Liaoning Province, China; Lower Cretaceous (Barremian–Aptian), Yixian Formation.

Diagnosis. Head long and narrow before eyes, clypeus elongate, labrum subquadrate. Antenna with thread at least as long as one-half of length of first flagellomere; pterostigma desclerotized medially; Sc₂ joining R distad origin of Rs at a distance longer than its own length; 1-Rs₂ aligned with 2r-rs; 1-Rs as long as 1-M; 2-Cu slightly shorter than 3-Cu. Ground color dark.

Description. A female sawfly in dorsal view with nearly complete body and wings. Color brown, particularly on head, mesoscutum and abdomen.

Head large, elongate before eyes. Eyes elongate-ovoid, ocelli small. Genae and clypeus unusually long. Antenna very long, scape ca. 4.5 times as long as wide, apparently thicker than pedicel and about 4 times as long as wide, apparently thicker than pedicel and about 4 times as long as wide; antennal thread about 0.6 time the length of first flagellomere, with 18 segments visible, each ca. 1.5 times as long as wide. Labrum subquadrate (slightly longer than wide).

Thorax slightly wider than head; pronotum short dorsomedially; mesoscutum with all usual sutures (medial, notauli and V-like ones); cenchri small, slightly wider than long.

Forewing with pterostigma desclerotized in middle, longer than cell 2r; costal area broad, Sc sub-parallel to C, with two branches, posterior branch (Sc₂) connected to R distad origin of Rs base,

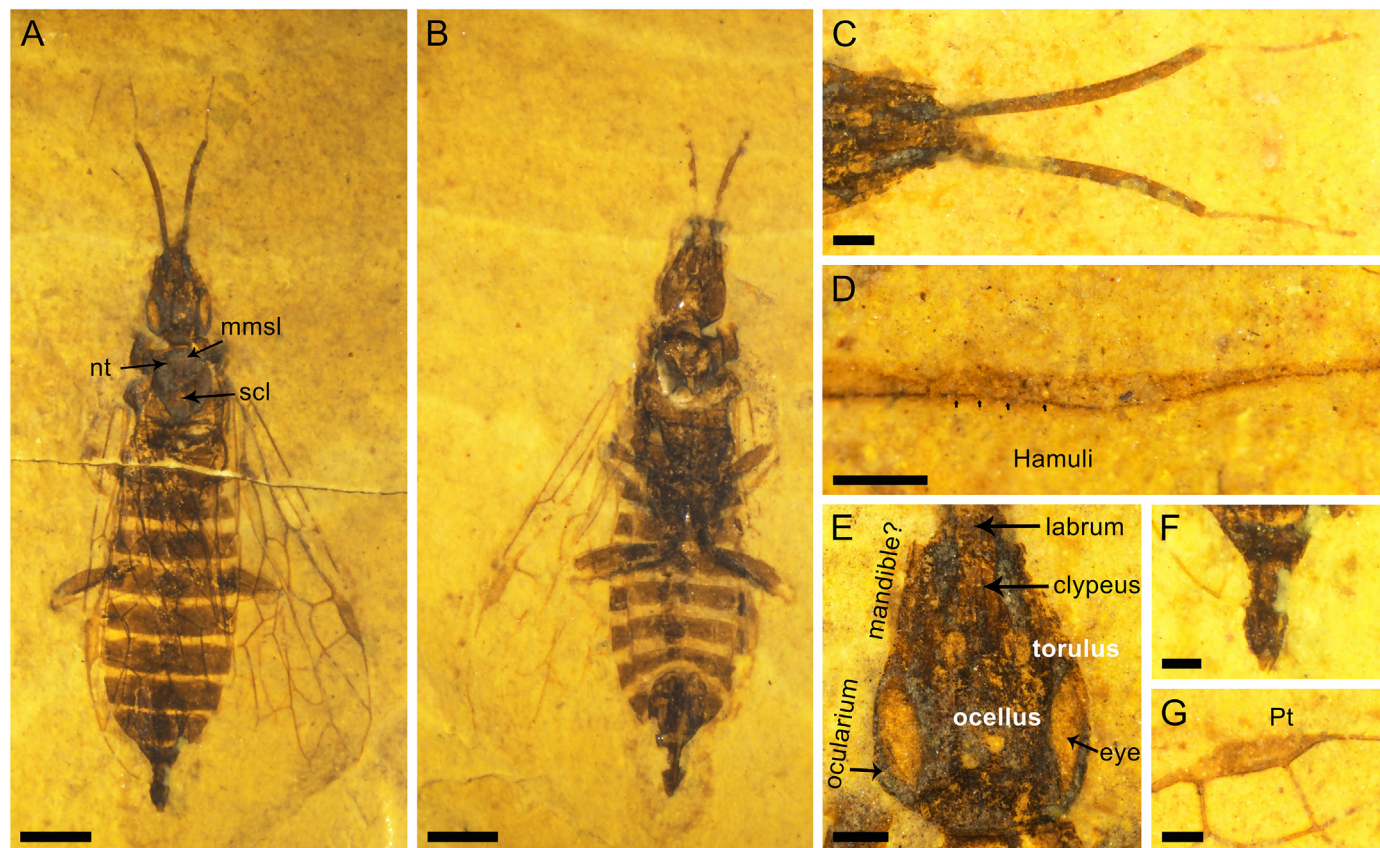


Fig. 2. *Brachyoxyela conjunctiva* sp. nov., holotype, CNU-HYM-LB-2021016, female. A, dorsal view under alcohol. B, ventral view under alcohol. C, antenna in dorsal view under alcohol. D, hamuli in dorsal view under alcohol. E, head in dorsal view under alcohol. F, ovipositor in dorsal view under alcohol. G, pterostigma in dorsal view under alcohol. Scale bars: 2 mm in A–B; 0.5 mm in C, E–G; 0.25 mm in D. Abbreviations: nt, notaulus; scl, mesoscutellum; mmsl, medial mesoscutal line; pt, pterostigma.

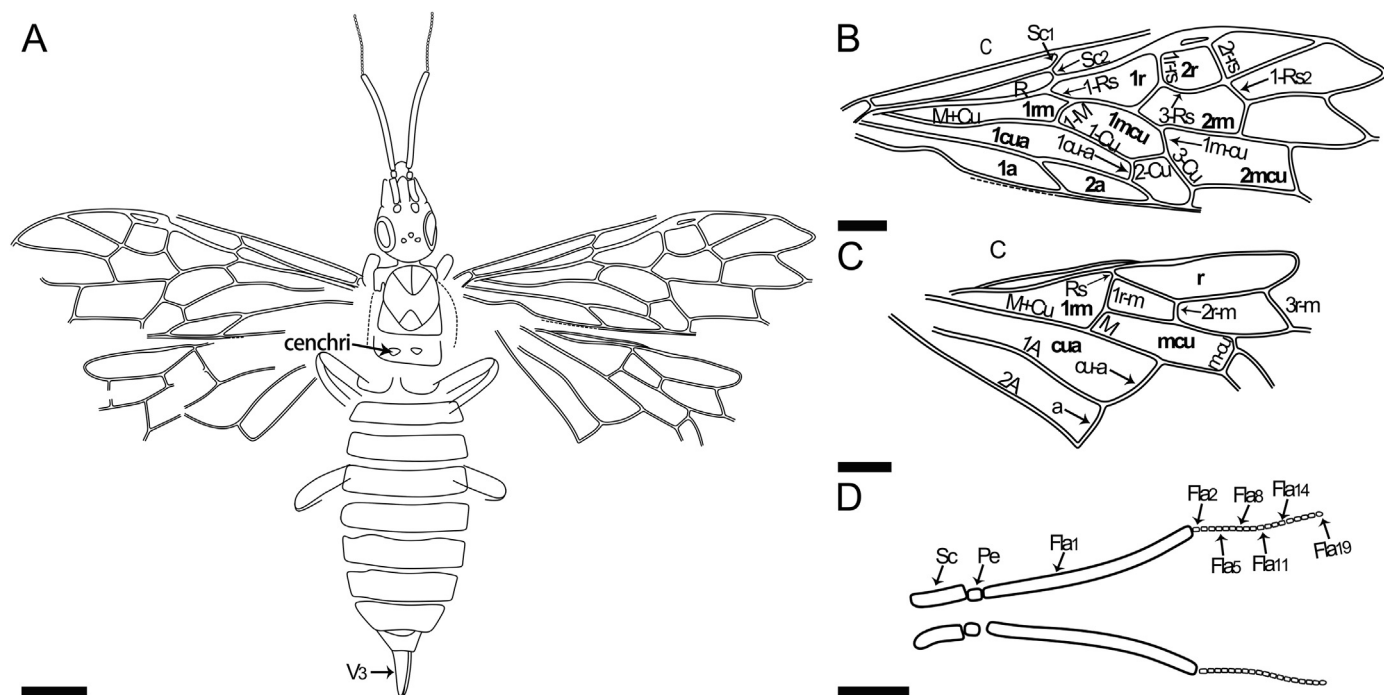


Fig. 3. *Brachyoxyela conjunctiva* sp. nov., A, line drawing of dorsal view with forewing and hind wing artificially extended from body. B, line drawing of forewing. C, line drawing of hind wing. D, line drawing of antenna. Scale bars: 2 mm in A; 1 mm in B–D. Abbreviations: Sc, scape; Pe, pedicel; Fla₁–Fla₁₉, flagellomeres I–XIX; V₃, ovipositor sheath.

anterior branch (Sc₁) connected to C at level of Rs + M base; R slightly curved before origin of Rs and thickened before pterostigma; 1-Rs nearly as long as 1-M; 1r-rs slightly shorter than 2r-rs, inclined basally, 3-Rs arched posteriorly; 1-Rs₂ aligned with 2r-rs; M + Cu slightly curved in its basal third; 1m-cu longer than half 3-Cu; 1-Cu nearly straight; 2-Cu slightly shorter than 3-Cu. Cell 1r long and triangular shaped, significantly longer than 2r; cell 2r trapezoidal; length ratio of cells 1r: 2r = 2 : 1; cell 1cua narrow and elongate, distinctly broad at the base of 1-M; cell 1mcu about 2.7 times as long as wide, nearly as long as 1r and 2rm; cell 1a ca. 2 times as long as 2a.

Hind wing with 1-Rs extremely short (1r-m meeting Rs close to Rs base); 1-M shorter than 1r-m; m-cu near middle of cell 3rm, right wing m-cu with adventitious vein, cu-a about 1.5 times as long as a; M + Cu and 2A nearly straight; 1A slightly curved at mid-length, 1A and 2A without free end. Cell 1rm elongate, triangular, as wide as cell cua; the latter broad and long, as long as cell a.

All legs partially preserved, tibiae and femora not clearly visible and tarsi not preserved, femora fusiform and tibiae slender, much longer than wide.

Abdomen with 9 segments visible, ovipositor with sheath sword-shaped, length ratio of ovipositor to vein C of forewing 0.21.

Measurements. Body length 15.4 mm (including ovipositor sheath), head about 1.9 mm wide, antenna at least 5.9 mm long, first flagellomere 3.1 mm long, forewing 11.3 mm long, ovipositor sheath 1.4 mm long.

Brachyoxyela leei Dai, Shih, and Rasnitsyn sp. nov.

(Fig. 4)

Holotype. No. CNU-HYM-LB-2021007, housed at the College of Life Sciences, Capital Normal University, donated by Dr. Chungkun Shih. LSID: urn:lsid:zoobank.org:act:543BFC75-0B6F-49CB-94DE-EF8D7EF805E5.

Etymology. The specific name is in honor of Feng Chuan (Austine) Lee for his support, counseling, and friendship to C. K. Shih, his

contributions to project developments and implementation of key projects, and his assistance for insect fossil research. The specific epithet is to be treated as a noun in genitive case.

Locality and horizon. Huangbanjigou, Chaomidian Village, Shangyuan Township, Beipiao City, Liaoning Province, China; Lower Cretaceous (Barremian–Aptian), Yixian Formation.

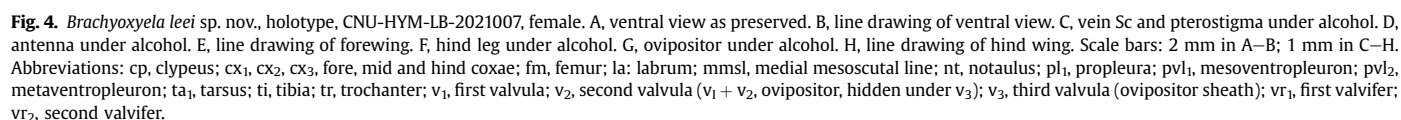
Diagnosis. Head narrow and short before eyes, clypeus and labrum transverse. Antenna with thread shorter than first flagellomere; pterostigma desclerotized medially; Sc₂ joining R distad origin of Rs at a distance longer than its length; 1-Rs longer than 1-M, 2-Cu nearly as long as 3-Cu. Ground color pale.

Description. Female sawfly in ventral view, antenna and forewing nearly complete, abdomen and ovipositor relatively well-preserved, apex of the legs and hind wings missing.

Head massive and nearly round, approximately 1/5 of the length of the body. Eyes wide, occupying lateral surface, a large part of head. Ocelli small. Clypeus transverse. Labrum wide, transverse. Antenna with first flagellomere very thin, as long as cell 2rm and longer than thread, thread segmentation indistinct.

Thorax slightly distorted and incompletely preserved.

Forewing with pterostigma desclerotized medially, longer than cell 2r; Sc closer to R than to C and with two branches, connected to R and C well distad origin of Rs, near level of base of Rs + M; R nearly straight except slightly angular at base of Rs and Sc₂, thickened before pterostigma; 1-Rs slightly longer than 1-M and slightly shorter than 2-Rs; M + Cu slightly curved in its basal third; 1r-rs nearly as long as 2r-rs; 3-Rs arched posteriorly; 1m-cu apparently longer than half 3-Cu; 2-Cu nearly as long as 3-Cu; cell 1r long and rather triangular, significantly longer and wider than 2r; cell 2r trapezoidal; length ratio of cells 1r: 2r = 2 : 1; cell 1cua narrow and long, distinctly broader at the point of the origin of vein M; cell 1mcu about 2.6 times as long as wide and nearly as long as cell 1r; cell 2mcu longer than cell 2rm; cell 2a nearly as long as cell 1mcu. Hind wings incomplete, 1r-m virtually meeting Rs close to Rs base; 1r-m longer than 1-M; crossvein 2r-m not preserved, cu-a



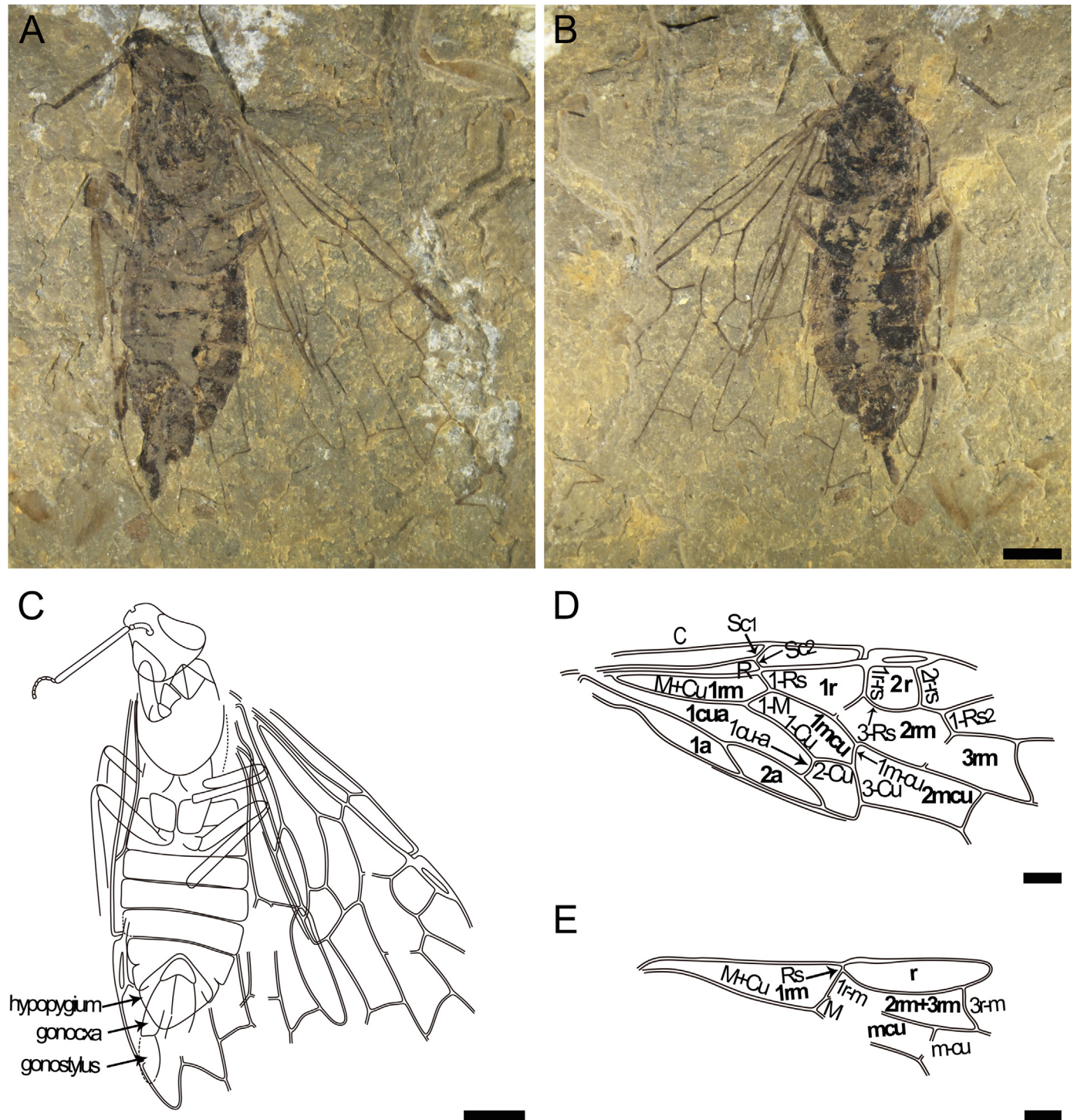


Fig. 5. *Brachyoxyla elliptica* sp. nov., holotype, CNU-HYM-LB-2021014, male. A, ventral view as preserved. B, dorsal view as preserved. C, line drawing of ventral view. D, line drawing of forewing. E, line drawing of hind wing. Scale bars: 2 mm in A–C; 1 mm in D–E.

originating near middle of cell mcu; M + Cu nearly straight. Cell 1rm elongate; cell cua broad and long.

Legs partly preserved, foreleg with thin femur; hind leg with coxa elongate, about 1.6 times as long as wide; femur thick and slightly wider medially, about 4 times as long as wide; hind tibia at least as long as femur; tarsi not preserved.

Abdomen with 8 segments visible, ovipositor with sheath sword-shaped, extending to the seventh abdominal segment, second valvifers incomplete, inner valvulae well-preserved.

Measurements. Body length 13.9 mm (including ovipositor sheath), head about 1.8 mm wide, antenna at least 4.8 mm (incompletely preserved) long, first flagellomere 2.5 mm long, forewing 11.2 mm

long, ovipositor sheath 1.3 mm long, hind leg with femur 2.9 mm long and 0.7 mm wide.

Brachyoxyela elliptica Dai, Shih, and Rasnitsyn sp. nov. (Fig. 5)

Holotype. No. CNU-HYM-ND-2021014 p/c (part and counterpart), housed at the College of Life Sciences, Capital Normal University. LSID: urn:lsid:zoobank.org:act:AA0DF07D-444A-4D81-93F9-87D8A9514BBD.

Etymology. The species name is from the Latin “ellipticus”, meaning oval and referring to the large and oval eyes.

Locality and horizon. Sandaogou, Nanyingpan Village, Duolun County, Inner Mongolia, China; Lower Cretaceous, Yixian Formation.

Diagnosis. Head narrow and short before eyes. Antenna with thread shorter than first flagellomere; pterostigma desclerotized medially; Sc₂ joining R immediately distad origin of Rs (distance between Sc₂ and 1-Rs base shorter than the length of Sc₂); 1-Rs shorter than 1-M, 2-Cu as long as 3-Cu. Ground color dark.

Description. An incomplete male sawfly in ventral view, with only right antenna, left forewing, part of hind wing, legs and body well-preserved.

Head subovate basally, narrowed but not much protruding before eyes. Eyes wide, kidney-shaped, nearly occupying one third of head lateral surface. Ocelli small. Antenna with first flagellomere narrow, about 3 times as wide as thread; thread may incomplete, of eight more or less elongated segments.

Thorax slightly distorted, not well-preserved.

Forewing with pterostigma desclerotized medially, 2/5 thinner than cell 2r; R slightly curved before origin of Rs base and thickened before pterostigma; 1-Rs shorter than 1-M, and about twice as short as 2-Rs; crossvein 2r-rs slightly curved and distinctly longer than 1r-rs, 3-Rs arched toward the lower margin of forewing; 1m-cu twice as short as 2-Cu; 2-Cu as long as 3-Cu; M + Cu almost straight. Cell 1r long and narrow, significantly longer than 2r; cell 2r trapezoidal; length ratio of cells 1r: 2r = 2 : 1; cell 1cu narrow and longer, distinctly broad at the base of 1-M; cell 1mcu about 2.6 times as long as wide and nearly as long as cell 1r; cell 2mcu ca. 2.7 times as long as wide; 2rm and 3rm partly preserved; cell 1a ca. 1.6 times as long as 2a.

Hind wings incomplete, 1-Rs short, crossvein 1r-m long, meeting Rs close to Rs base; 1-M straight, apparently shorter than 1r-m; crossvein cu-a and anal veins not preserved; M + Cu slightly curved in its basal third. Cell 1rm elongate, triangular; cell r rounded apically.

Legs incomplete, fore femur thin; hind leg with coxa elongate, about 1.3 times as long as wide; trochanter small; femur thick and slightly wider medially, about 5.6 times as long as wide; hind tibia longer than femur, tarsi not preserved.

Abdomen with 8 segments visible, genitalia protruding from abdomen, hypopygium large; gonocoxa wide, occupying a large part of hypopygium; gonostylus long, but partly preserved.

Measurements. Body length 13.5 mm (including genitalia), head about 1.6 mm wide, antenna at least 4.9 mm (incompletely preserved) long, first flagellomere 3 mm long, forewing 13.3 mm long (as preserved), hind leg with femur 2.7 mm long and 0.5 mm wide.

4. Discussion

Macroxyelini are another tribe of Macroxyelinae with Xyeleciini encompassing extant and extinct taxa. This tribe includes two extant and four extinct genera: *Macroxyela* Kirby, 1882 (living, in North America); *Megaxyela* Ashmead, 1898 (living, in North America and East Asia); *Anthoxyela* Rasnitsyn, 1977 (the Early Cretaceous of China and Siberia); *Brachyoxyela* Gao, Zhao and Ren, 2011 (the Early Cretaceous of China); *Chionoxyela* Rasnitsyn, 1993 (the Late

Cretaceous of the Russian Far East) and *Paleoxyela* Jouault, Aase and Nel, 2021 (the Eocene of western North America, Florissant). *Brachyoxyela* was erected to accommodate two species from Huangbanjigou, Beipiao City, Liaoning Province (Gao et al., 2011). The present publication adds three new species to the genus *Brachyoxyela*, among which two new species *B. conjunctiva* and *B. leei* are from Huangbanjigou and one new species *B. elliptica* is reported from Sandaogou, Nanyingpan Village, Duolun County, Inner Mongolia. The age of the fossil-bearing beds in the Nanyingpan Village area is considered as the Lower Cretaceous, Yixian Formation. Sandaogou is an important fossil insect locality, containing abundant and well-preserved insect fossils, same as Daohugou and Huangbanjigou (Swisher et al., 1999; Ren et al., 2019).

So far, three species of Symphyta have been reported from Duolun County, including two species of Siricoidea, *Sinanxyela dorunensis* Hong, 1982 (Hong, 1982) and *Hoplitolyda duolunica* Gao, Shih, Rasnitsyn and Ren, 2013 (Gao et al., 2013); and one species of Pamphilioidea, *Rectilyda stricta* Wang, Rasnitsyn, Shih and Ren, 2014 with nygmata, which are prominent glandular structures on the wings of insects (Wang et al., 2014b). But the superfamily Xyeloidea have not been recorded from this locality until the present study, and *B. elliptica* sp. nov. is the first fossil xyelid from this locality.

Although sclerotized pterostigma is a significant diagnostic character for the subfamily or tribe in the family Xyelidae, the pivotal role of sclerotized pterostigma becomes more limited, because the preservation may (sometimes) alter the preservation of pterostigma. In addition, more and more new specimens, which have different types of pterostigma, have been discovered and described. The degree of sclerotized pterostigma is still an important diagnostic feature at any time, other identified characters should also be considered in the meantime, such as the length of the first flagellomere and the length ratio of 1-Rs and 1-M of forewing. In this study, three specimens belonging to *Brachyoxyela* are described mainly based on many synapomorphies, for example, vein Sc meeting R distad origin of Rs and the longer first flagellomere.

5. Conclusions

Xyelidae are a small family of herbivorous sawflies comprising more than 85 species within 50 genera (Zheng et al., 2021). As the earliest reported symphytans (Hymenoptera) from the Triassic, Xyelidae have a special significance in the evolutionary history of the Hymenoptera (Wang et al., 2014a). Macroxyelinae are a common subfamily of Xyelidae in the Mesozoic (Dai et al., 2022).

We described three new species, *Brachyoxyela conjunctiva* sp. nov., *Brachyoxyela leei* sp. nov. and *Brachyoxyela elliptica* sp. nov., in the tribe Macroxyelini, Macroxyelinae of the Xyelidae. All type specimens were collected from the Lower Cretaceous (Barremian–Aptian) Yixian Formation: *B. conjunctiva* and *B. leei* from Huangbanjigou, Beipiao City, Liaoning Province, China, and *B. elliptica* from Sandaogou, Duolun County, Inner Mongolia, China.

The degree of sclerotized pterostigma is still an important diagnostic feature, but other identified characters, such as the length of the first flagellomere and the length ratio of 1-Rs and 1-M of forewing, should also be considered in the diagnosis. In this study, three new species of *Brachyoxyela* are described, mainly based on many synapomorphies, e.g., vein Sc meeting R distad origin of Rs and the longer first flagellomere, to further diversify Xyelidae in the Early Cretaceous.

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References

- Abe, M., Smith, D.R., 1991. The genus-group names of Symphyta (Hymenoptera) and their type species. *Esakia* 31, 1–115. <https://doi.org/10.5281/zenodo.2771>.
- Chen, P.J., Wang, Q.F., Zhang, H.C., Cao, M.Z., Li, W.B., Wu, S.Q., Shen, Y.B., 2004. Discussion on the stratotype of Jianshangou of Yixian Formation. *Science in China Series D* 34, 883–895.
- Chen, J.S., Li, W.W., Liu, M., Xing, D.H., Yang, J.L., 2015. U-pb isotopic age of the volcanic rocks of the Yixian formation in Jianping Machang of Western Liaoning and its geological significance. *Journal of Jilin University* 45 (2), 471–482. <https://doi.org/10.13278/j.cnki.jjuese.201502111>.
- Dai, L.Y., Rasnitsyn, A.P., Shih, C.K., Wang, M., Ren, D., 2022. New Fossil Xyelidae (Hymenoptera: Symphyta) from the Mesozoic of Northeastern China. *Insects* 13 (4), 383. <https://doi.org/10.3390/insects13040383>.
- Gao, K.Q., Shubin, N.H., 2003. Earliest known crown group salamanders. *Nature* 422 (6930), 424–428. <https://doi.org/10.1038/nature01491>.
- Gao, T.P., Ren, D., Shih, C.K., 2009. *Abrotaxyla* gen. nov. (Insecta, Hymenoptera, Xyelidae) from the Middle Jurassic of Inner Mongolia, China. *Zootaxa* 2094 (1), 52–59. <https://doi.org/10.11646/zootaxa.2094.1.6>.
- Gao, T.P., Zhao, Y.Y., Ren, D., 2011. New fossil Xyelidae (Insecta, Hymenoptera) from the Yixian Formation of western Liaoning, China. *Acta Geologica Sinica* 85 (3), 528–532. <https://doi.org/10.1111/j.1755-6724.2011.00447.x>.
- Gao, T.P., Shih, C.K., Rasnitsyn, A.P., Ren, D., 2013. *Hoplitolyda duolunica* gen. et sp. nov. (Insecta, Hymenoptera, Praesiricidae), the Hitherto Largest Sawfly from the Mesozoic of China. *PLoS One* 8 (5), e62420. <https://doi.org/10.1371/journal.pone.0062420>.
- Gao, T.P., Shih, C.K., Ren, D., 2021. Behaviors and interactions of insects in ecosystems of mid-mesozoic northeastern china. *Annual Review of Entomology* 66 (1), 337–354. <https://doi.org/10.1146/annurev-ento-072720-095043>.
- Hong, Y.C. (Ed.), 1982. *Mesozoic Fossil Insects of Jiuquan Basin in Gansu Province*, vol. 187. Geological Publishing House, Beijing. [https://doi.org/10.1206/0003-0082\(2002\)363<0001:tssrma>2.0.co;2](https://doi.org/10.1206/0003-0082(2002)363<0001:tssrma>2.0.co;2).
- Huber, T.H., Sharkey, M.J., 1993. Structure. In: Goulet, H., Huber, T.H. (Eds.), *Hymenoptera of the World: An Identification Guide to Families*. Centre for Land and Biological Resources Research, Ottawa, Ontario, pp. 13–59.
- Hou, L.H., Zhou, Z.H., Martin, L.D., Feduccia, A., 1995. A beaked bird from the Jurassic of China. *Nature* 377, 616–618. <https://doi.org/10.1038/377616a0>.
- Jouault, C., Aase, A., Nel, A., 2021. Past ecosystems drive the evolution of the early diverged Symphyta (Hymenoptera: Xyelidae) since the earliest Eocene. *Fossil Record* 24 (2), 379–393. <https://doi.org/10.5194/fr-24-379-2021>.
- Kopylov, D.S., 2014. New sawflies of the subfamily Madygellinae (Hymenoptera, Xyelidae) from the Middle-Upper Triassic of Kyrgyzstan. *Paleontological Journal* 48 (6), 610–620. <https://doi.org/10.1134/S0031030114060070>.
- Rasnitsyn, A.P., 1966. New Xyelidae (Hymenoptera) from the Mesozoic of Asia. *Paleontologicheskii Zhurnal* 1966 (4), 69–85.
- Rasnitsyn, A.P., 1969. Origin and evolution of Lower Hymenoptera. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR* 123, 1–196.
- Rasnitsyn, A.P., 2020. Entomofauna of Khasurty and Jehol Biota. In: Kopylov, D.S., Rasnitsyn, A.P., Aristov, D.S., et al. (Eds.), *The Khasurty Fossil Insect Lagerstätte*, *Paleontological Journal*, vol. 54 (11), pp. 1235–1238. <https://doi.org/10.1134/S0031030120110027>.
- Ren, D., Labandeira, C.C., Santiago-Blay, J.A., Rasnitsyn, A.P., Shih, C.K., Bashkuev, A., Logan, M.A.V., Hotton, C.L., Dilcher, D., 2009. A probable pollination mode before Angiosperms: Eurasian, long-proboscid scorpionflies. *Science* 326 (5954), 840–847. <https://doi.org/10.1126/science.1178338>.
- Ren, D., Shih, C.K., Gao, T.P., Wang, Y.J., Yao, Y.Z. (Eds.), 2019. *Rhythms of Insect Evolution – Evidence from the Jurassic and Cretaceous in Northern China*. John Wiley and Sons, Wiley Blackwell, p. 707.
- Swisher, C.C., Wang, Y.Q., Wang, X.L., Xu, X., Wang, Y., 1999. Cretaceous age for the feathered dinosaurs of Liaoning, China. *Nature* 400 (6739), 58–61. <https://doi.org/10.1038/21872>.
- Wang, Y., Ren, D., 2009. New fossil palaeontinids from the Middle Jurassic of Daohugou, Inner Mongolia, China (Insecta, Hemiptera). *Acta Geologica Sinica* 83 (1), 33–38. <https://doi.org/10.1111/j.1755-6724.2009.00004.x>.
- Wang, X.L., Zhou, Z.H., Zhang, F.C., Xu, X., 2002. A nearly completely articulated rhamphorhynchoid pterosaur with exceptionally well-preserved wing membranes and “hair” from Inner Mongolia, northeast China. *Chinese Science Bulletin* 47 (3), 226–232. <https://doi.org/10.1360/02tb9054>.
- Wang, M., Shih, C.K., Ren, D., 2012. *Platyxyela* gen. nov. (Hymenoptera, Xyelidae, Macroxyelinae) from the Middle Jurassic of China. *Zootaxa* 3456 (1), 82–588. <https://doi.org/10.11646/zootaxa.3456.1.4>.
- Wang, M., Rasnitsyn, A.P., Ren, D., 2014a. Two new fossil sawflies (Hymenoptera, Xyelidae, Xyelinae) from the Middle Jurassic of China. *Acta Geologica Sinica* 88 (4), 1027–1033. <https://doi.org/10.1111/1755-6724.12269>.
- Wang, M., Rasnitsyn, A.P., Shih, C.K., Ren, D., 2014b. A new Cretaceous genus of xyelydid sawfly illuminating nygmata evolution in Hymenoptera. *Evolutionary Biology* 14 (1), 1–11. <https://doi.org/10.1186/1471-2148-14-131>.
- Wang, Y.M., Wang, M., Shih, C.K., Rasnitsyn, A.P., Yao, J., Ren, D., Gao, T.P., 2019. A new sawfly of Megalodontesidae (Insecta, Hymenoptera, Pamphilioidea) with pectinate antennae from the Early Cretaceous of China. *ZooKeys* 893, 115–123. <https://doi.org/10.3897/zookeys.893.38512>.
- Xu, X., Zhang, F.C., 2005. A new maniraptoran dinosaur from China with long feathers on the metatarsus. *Naturwissenschaften* 92 (4), 173–177. <https://doi.org/10.1007/s00114-004-0604-y>.
- Zhang, H.C., Zhang, J.F., 2000. Xyelid Sawflies (Insecta, Hymenoptera) from the Upper Jurassic Yixian Formation of Western Liaoning, China. *Acta Palaeontologica Sinica* 39 (4), 476–492. <https://doi.org/10.1111/j.1755-6724.2011.00447.x>.
- Zheng, S.L., Zheng, Y.J., Xing, D.H., 2003. Characteristics, age and climate of Late Jurassic Yixian flora from western Liaoning. *Journal of Stratigraphy* 27 (3), 233–241. [https://doi.org/10.1016/S0955-2219\(02\)00073-0](https://doi.org/10.1016/S0955-2219(02)00073-0).
- Zhou, Z.H., Barrett, P.M., Hilton, J., 2003. An exceptionally preserved lower Cretaceous ecosystem. *Nature* 421, 807–814. <https://doi.org/10.1038/nature01420>.
- Zheng, Y., Hu, H., Chen, D., Chen, J., Zhang, H.C., Rasnitsyn, A.P., 2021. New fossil records of Xyelidae (Hymenoptera) from the Middle Jurassic of Inner Mongolia, China. *European Journal of Taxonomy* 733 (1), 146–159. <https://doi.org/10.5852/ejt.2021.733.1229>.