



New Archexyelinae (Hymenoptera: Xyelidae) from the Triassic Madygen Formation of Kyrgyzstan

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Abstract

One new genus and three new species of Archexyelinae (Xyelidae) are described from the Middle–Late Triassic Madygen Formation of Kyrgyzstan, including *Xyelinus scherbachov* sp. nov., *Triassoxyela sharovi* sp. nov., and *Microxyela minuta* gen. et sp. nov. Xyelidae is the most ancient hymenopteran family in fossil records and the only one known from the Triassic. Triassic xyelids are known from five localities throughout the whole Pangaea. The most diverse and abundant Triassic xyelid fauna comes from Madygen, with 16 genera and 34 species in the two subfamilies Archexyelinae and Madygellinae.

Keywords Insects · Sawflies · Mesozoic · Ladinian · Carnian · Dzhaylyaucho · Fossil · New taxa

Introduction

Xyelidae is the most plesiomorphic family in Hymenoptera (Ronquist et al. 1999, 2012). Today, it is a small relict family of sawflies comprising ca. 80 extant species in two subfamilies. The fossil records of Xyelidae are considerably more impressive, with ca. 160 extinct species in four subfamilies (Taeger et al. 2010). Xyelids played significant roles in hymenopteran assemblages throughout the whole Mesozoic, starting to lose their positions only in the Late Cretaceous. The oldest findings of Xyelidae come

from the Middle–Upper Triassic deposits of Middle Asia (Kyrgyzstan, Madygen Formation; Rasnitsyn 1964, 1969; Kopylov 2014) and from the Upper Triassic of Australia (Riek 1955; Engel 2005), South Africa (Great Karoo Basin, Molteno) (Schlueter 2000), Argentina (Potrerillos; Lara et al. 2014), and Southwest Japan (Mine Group; Oyama and Maeda 2020). These findings also represent the most ancient Hymenoptera fossils. Until now, Xyelidae remain the only hymenopteran family known from the Triassic.

The most diverse and abundant Triassic xyelid fauna comes from the Madygen Formation at the Dzhaylyaucho outcrop. The first hymenopteran fossils from Dzhaylyaucho were collected in the middle twentieth century during several expeditions of the Paleontological Institute, USSR Academy of Sciences. These expeditions brought about 25,000 insect fossils, including 37 specimens of Xyelidae described by Rasnitsyn (1964, 1969) in 13 genera and 24 species. In 2007 and 2009, after a long break, large-scale paleontological excavations were carried out at Dzhaylyaucho again. As a result, ca. 3000 fossil insect specimens were collected, including 16 specimens of Xyelidae. Seven specimens from the new collection belong to the subfamily Madygellinae and were described previously (Kopylov 2014). In this work, we present a description of the remainder of the collection belonging to the subfamily Archexyelinae.

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Materials and methods

All fossil material described herein comes from the Triassic Madygen Formation. The formation has been dated as Middle–Late Triassic (Ladinian–Carnian boundary, 237 ± 2 Ma) (Voigt et al. 2017; Moisan et al. 2021). It includes several insect-bearing outcrops. The most abundant insect fauna is known from Dzhaylyauchy outcrop located in Kyrgyzstan, Batken Region, 30 km west-north-west of the village of Samarkandyk (N $40^{\circ}3.2'$, E $70^{\circ}11.8'$; Kopylov 2014; Fig. 1). All hymenopteran fossils from the Madygen Formation were collected at Dzhaylyauchy.

Dzhaylyauchy outcrop with its enormous abundance of fossilized insects, plants and vertebrates is one of the most significant Triassic Lagerstätten. However, the state of preservation of Madygen specimens is often rather poor. The pigmentation of fossils is usually lacking, and the majority of the specimens are preserved as reliefs on shale surfaces. This kind of preservation demands using oblique lightening for imaging. SEM may also help to reveal some hidden structures. Another problem is stretching of embedding rocks that may lead to significant non-isometric deformations of samples. The amount and the direction of rock stretching are usually impossible to estimate precisely. Considering the high possibility of rock stretching, we bring all the examined wings to uniform proportions, with $2.8 \times$ ratio of wing length to width (Kopylov 2014). Nevertheless, it should be noted that this approach is rather rough and cannot reveal actual wing proportions and true direction of rock deformations. It also should be considered that comparison of not parallel segments, as well as angles as morphometric characters should be taken with caution.

The collection of Madygen hymenopterans includes 53 impressions in mudstones. Here, we examine nine specimens of Archexyelinae and Xyelidae subfam. indet. that were collected in 2007 and 2009 in the latest paleontological expeditions (Kopylov 2014). All examined materials including holotypes are deposited in the Paleontological Institute (PIN), Russian Academy of Sciences, Moscow.

The samples were collected, stored and prepared with standard paleontological methods (Kopylov 2019). The photos were acquired using Leica M205-C stereomicroscope with a Leica DFC495 camera at Cherepovets State University. SEM images were acquired with a Tescan Vega 3 SEM at PIN, Moscow; BSE and LVSTD detectors were used in low-vacuum mode without specimens sputter coating. Line drawings were prepared with Inkscape v.1.1, v.1.2.

Wing venation terminology follows Rasnitsyn (1969), with addition of vein abscissas numbers (Figs. 2, 3).

Systematic paleontology

Order **Hymenoptera** Linnaeus, 1758.

Superfamily **Xyeloidea** Newman, 1835.

Family **Xyelidae** Newman, 1835.

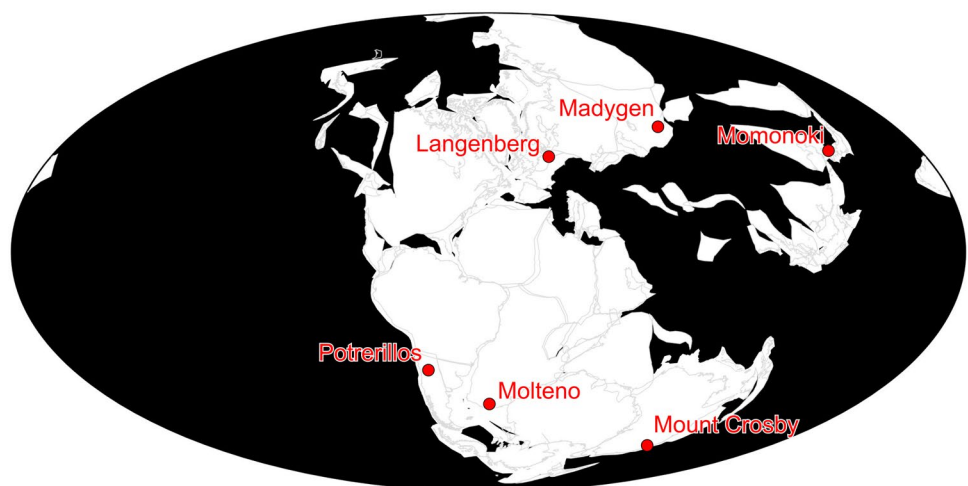
Subfamily **Archexyelinae** Rasnitsyn 1964.

Genus **Xyelinus** Rasnitsyn 1964.

Xyelinus scherbachov sp. nov.

Fig. 2.

Fig. 1 Paleogeographic map showing the hymenopteran localities in the Triassic (paleo-map and paleocoordinates are taken from PBDB 2022)



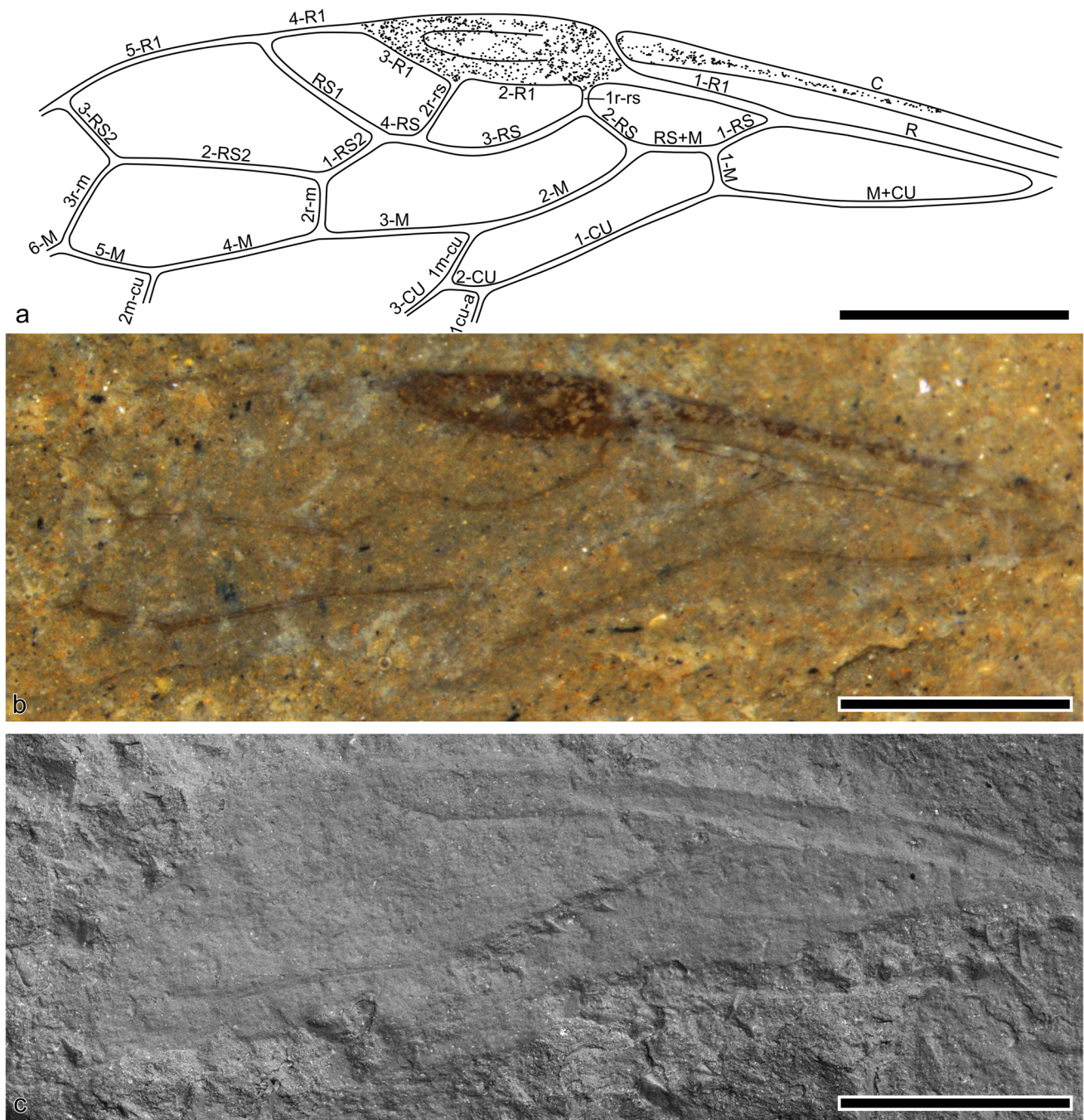


Fig. 2 *Xyelinus scherbachov* sp. nov., holotype PIN 5343/4: **a** reconstruction drawing with vein names; **b** photo; **c** SEM image. All scale bars 1 mm

LSID urn:lsid:zoobank.org:act:AC9085C7-B5B1-4EB4-AA11-6063477431E0

Etymology. In honor of Seryozha Shcherbachov, a hero from the novel “The Drummer’s Fate” by Arkady Gaidar.

Diagnosis. Fore wing with 1-RS longer than 1-M; 2r-rs longer than pterostigma width; RS + M occupies less than half of 1m-cu cell; 2-M is longer than 3-M; 3r-m inclined.

Type material. Holotype PIN 5343/4, part without counterpart impression in mudstone; imago, sex unknown; isolated fore wing with apex and anal part lost. Estimated

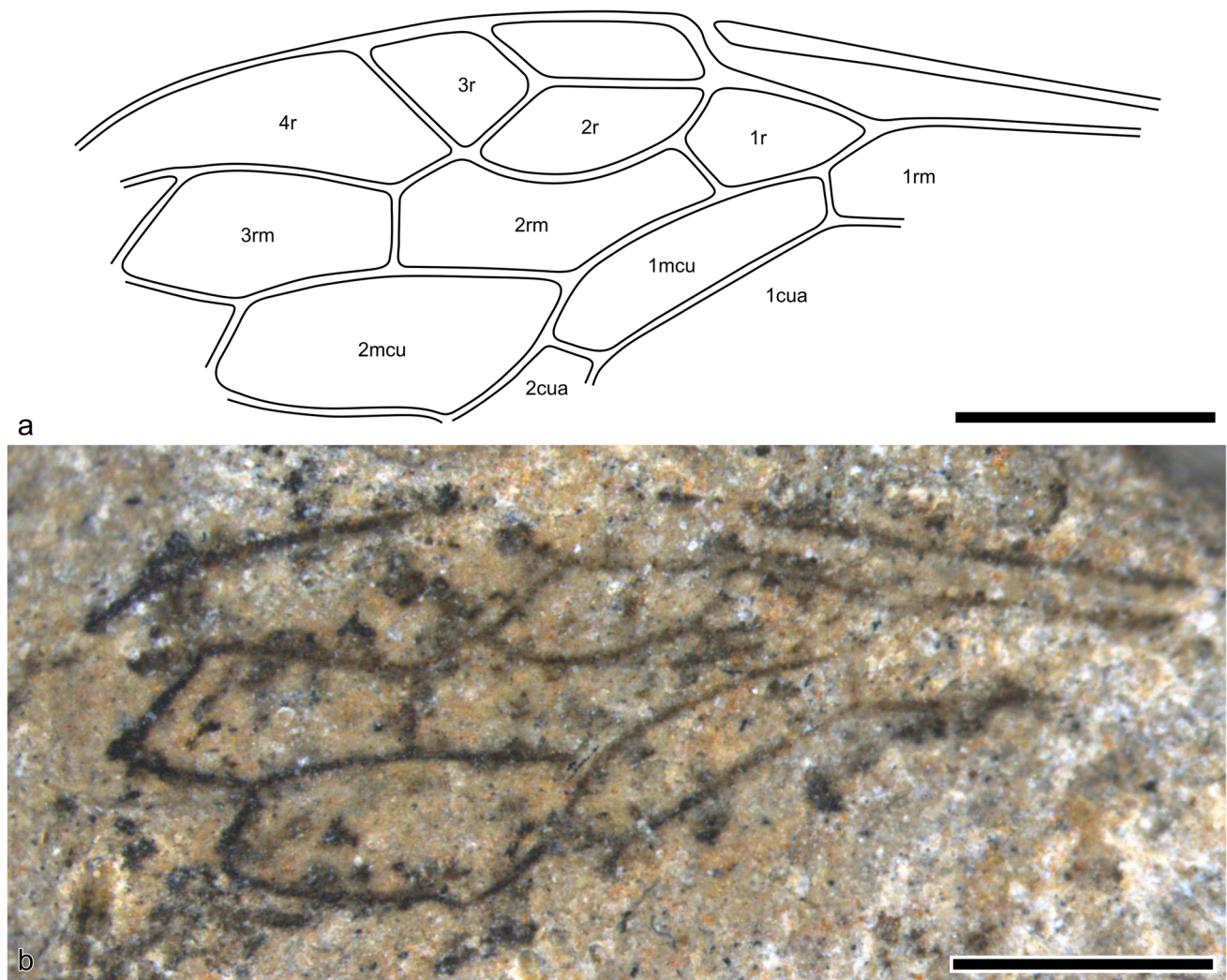


Fig. 3 *Triasoxyla sharovi* sp. nov., holotype PIN 5343/158: **a** reconstruction drawing with cell names; **b** photo. All scale bars 1 mm

longitudinal stretch is 1.05x, which may be considered insignificant. Deposited in PIN.

Locality and horizon. Madygen Formation (Dzhaylyauch area), Kyrgyzstan, Ladinian–Carnian.

Description. Fore wing 4.6 mmlong and 1.5 mmwide (as preserved), 4.7 mmlong and 1.6 mmwide (estimated size). Costal space 3.6× as wide as R vein. C thickened toward apex, separated from pterostigma. SC completely lost. Pterostigma sclerotized, 2r-rs joins near its 3/5. 2-R straight up to base of RS, with slight bend near point of divergence of 1-RS, the vein 1-R1 within the cell 1r arched forward. Cell 1r 1.2× as long as cell 2r. 2-R 1.5× as long as 1-R1. 1-R1 1.4× as long as 2-R1. 2-R1 1.3× as long as 3-R1, so the base of 2r-rs 1.3× as close to the apex of the pterostigma as to 1r-rs. The apex of 4-R1 2.2× as close to the apex of the pterostigma as to the apex of 2-RS3. 1-RS 1.7× as long as

1-M. 1-RS approximately equal to RS + M in length, 1-RS 1.1× as long as RS + M. 1-RS approximately equal to 2-RS, 1-RS 0.9× as long as 2-RS. 2r-rs inclinal. 1r-rs and 2r-rs located parallel to each other. 2r-rs flows proximal to the place of the branching of 4-RS. 1r-rs 0.4× as long as 2r-rs. 2r-rs 2.1× as long as 4-RS. 2-RS straight. 3-RS arched. 4-RS 0.2× as long as 1-RS1. 4-Rs 0.5× as long as 2-RS1. 1-RS1 0.7× as long as 2-RS2. 2-RS2 passing into 2-RS3 and creates a strong fracture 2r-m vertical; 2r-rs 1.5× as long as 2r-m; 3r-m inclined, at most 1.8× as long as 2r-m. M + Cu arcuate. 1mcu long and narrow, cell length 4.7× as long as cell width, parallel sided, not widened apically. 1 m-cu weakly dilating toward apex (maximum height of this cell 1.3× as great as length of 1-M). RS + M occupies less than a quarter of the side of cell 1mcu (RS + M 0.4× as long as 2-M). 2-M 1.7× as long as 3-M. 3-M 0.8× as long as 4-M. 4-M 1.9× as long as 5-M, so the base of 2 m-cu located distal to the middle of the 3rm cell.

Comparison. The new species is unique within the genus *Xyelinus* in: 1-RS longer than 1-M, 2r-rs longer than pterostigmal width, RS + M less than half of 1mcu cell, 2-M longer than 3-M, 3r-m inclined, 1mcu long and narrow, parallel sided. It also differs from *X. angustiradius* in the base of 2 m-cu located distal to the middle of the 3rm cell, and from *X. majus* in 2r-m vertical.

Remarks. The new species is assigned to *Xyelinus* based on RS bifurcating beyond 2r-rs, pterostigma sclerotized with 2r-rs joins near its basal 3/5th length, and absence of rs_1 – rs_2 crossvein.

Genus *Triasoxyla* Rasnitsyn 1964.

Triasoxyla sharovi sp. nov.

Fig. 3.

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Diagnosis. Fore wing with SC absent; 2r-rs joins RS next to RS1/RS2 bifurcation; RS2 straight near 3r-m junction; 5-R1 more than 2.5× as long as 4-R1.

Etymology. In memory of Soviet paleontologist Alexander G. Sharov, the discoverer of the Madygen fauna.

Type material. Holotype PIN 5343/158, part without counterpart impression in mudstone; imago, sex unknown; isolated fore wing with anal part lost. Estimated longitudinal stretch is 0.94x, which may be considered insignificant. Deposited in PIN.

Locality and horizon. Madygen Formation (Dzhaylyaucho area), Kyrgyzstan, Ladinian–Carnian.

Description. Wings—fore wing 4.3 mmlong and 1.5 mmwide (as preserved), 5.0 mmlong and 1.7 mmwide (estimated size). C and R only slightly thickened; costal space between them rather wide. C thickened toward apex. SC absent. Pterostigma not sclerotized, veins bordering it slightly thickened. R straight up to base of RS, with strong enough bend near point of divergence of RS. 1-R1 weakly arcuate. 1-R1 becomes thicker toward the base of the pterostigma, without gap at base of pterostigma. 1-R1 1.1× as long as 2-R1. 2-R1 1.6× as long as 3-R1, so the base of 2r-rs 1.6× closer to the apex of the pterostigma than to the base of 1r-rs. 5-R1 at least 2.5× as long as 4-R1 (5-R1 not completely preserved), so the apex of 1-RS1 closer to the apex of pterostigma than to the apex of 2-RS2. 1-RS 1.9× as long as 1-M. 1-RS as long as RS + M. 1-M forms an acute angle with Rs + M. RS + M 0.3× as long as 1mcu cell. 2-RS

straight. 3-RS arched backward. 2r-rs and 1r-rs parallel, inclined; 2r-rs 1.5× as long as 1r-rs. 2r-rs joins RS next to RS1/RS2 bifurcation. 1-RS1 1.3× as long as 2r-rs. 2-RS1 0.6× as long as 2-RS2. RS2 bent near 2r-m junction, and straight near 3r-m junction. 2r-m vertical; 2r-rs 1.4× as long as 2r-m; 3r-m strongly inclined, 1.7× as long as 2r-m. Cell 1mcu 3.9× as long as wide. 1 m-cu 0.7× as long as 3-Cu. 2-M as long as 3-M; 3-M 1.1× as long as 4-M; 4-M 1.2× as long as 5-M. M slightly bent next to 2 m-cu junction. 2 m-cu inclined.

Comparison. The new species is unique within *Triasoxyla* in having RS2 straight near 3r-m junction (in other species 3-RS2 bent forward); 5-R1 more than 2.5× as long as 4-R1 (in other species it is less than 2× so); 2-M as long as 3-M.

Remarks. The new species is assigned to *Triasoxyla* based on cell 3r very short, 1 m-cu shorter than 3-Cu, RS + M longer than 1-RS.

Genus *Microxyela* gen. nov.

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Type species. *Microxyela minuta* sp. nov.

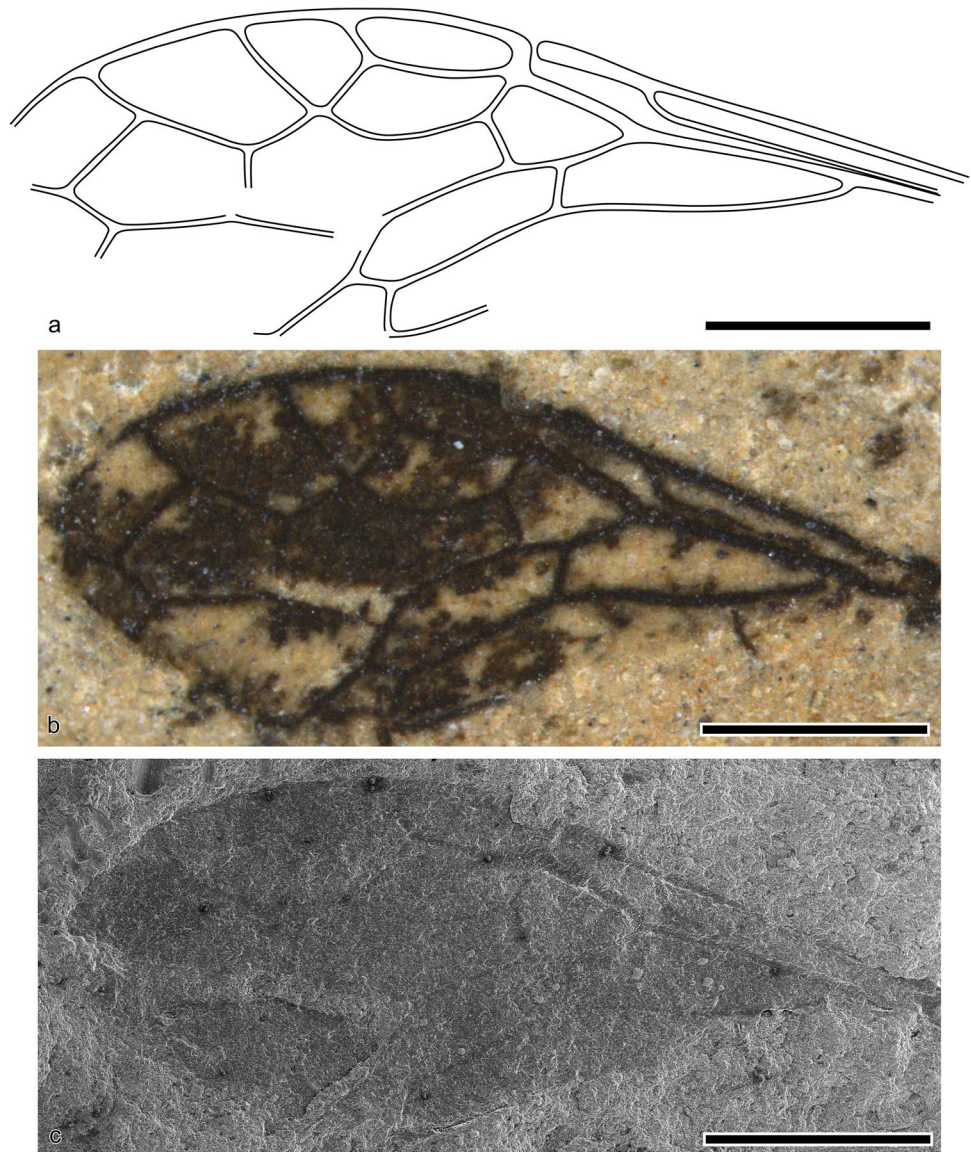
Etymology. From Greek ‘micros’—small, and genus *Xyela*. Gender feminine.

Diagnosis. Fore wing with SC present, joins C; pterostigma slightly sclerotized basally; 2r-rs joins RS slightly basad RS1/RS2 bifurcation; 1-RS longer than 1-M; 1-M forming obtuse angle with 1-Cu; 1 m-cu shorter than 3-Cu; cell 3rm short; M bent at 2 m-cu base.

Occurrence. Only Madygen Formation.

Comparison. The new genus is unique within Archexyelinae in having 2r-rs joining RS slightly basad of Rs bifurcation (excluding *Xyelinus* and *Euryxyela*), 1-M forming obtuse angle with 1-Cu (excluding *Lithoxyela* and *Asioxyela parvula*), cell 3rm short (excluding *Archexyela*, *Asioxyela* and *Leioxyela mitis*). With 1-RS longer than 1-M, pterostigma not sclerotized, 2r-rs joins near basal 3/4th pterostigmal length, longer than pterostigmal width, 2r-rs only 0.6× as long as RS1, cell 3r smaller than 2r, apex of 1-RS1 closer to apex of pterostigma than to apex of 2-RS3, RS + M shorter than 2-M, and 4-M longer than 5-M, the new genus is close to *Asioxyela*. It also differs from all other genera by its smaller size.

Fig. 4 *Microxyela minuta* sp. nov., holotype PIN 5343/5: **a** reconstruction drawing, proportions amended considering rock stretching; **b** photo; **c** SEM image. All scale bars 1 mm



Microxyela minuta sp. nov.
Fig. 4.

LSID urn:lsid:zoobank.org:act:85E6D1F1-7911-4F54-AEA0-B7285B6358F1

Diagnosis. As for genus, by monotypy.

Etymology. From Latin ‘minutus’—small, tiny.

Type material. Holotype PIN 5343/5, part and counterpart impression in mudstone; imago, sex unknown; isolated fore wing with anal part lost. The wing is compressed longitudinally due to rock deformation, estimated longitudinal stretch is 0.82x. Deposited in PIN.

Locality and horizon. Madygen Formation (Dzhaylyaucho area), Kyrgyzstan, Ladinian–Carnian.

Description. Fore wing 3.8 mm long and 1.6 mm wide (as preserved), 4.2 mm long and 1.5 mm wide (estimated size). C and R only slightly thicker than other veins; costal space 3.4× as wide as C vein. C thickened toward apex. SC joins C next to RS base. Pterostigma with veins bordering it slightly thickened. R before RS base straight, slightly bent at the point of RS divergence. 1-R1 weakly arcuate (the deviation from a straight line is not greater than the vein width). 1-R1 becomes thicker toward the base of the pterostigma, without gap at base of pterostigma. 2-R 1.8× as long as 1-R1. 1-R1 0.9× as long as 2-R1. 2-R1 2.8× as long as 3-R1, so the base of 2r-rs 2.8× closer to the apex of the pterostigma than to the base of 1r-rs. 4-R1 0.7× as long as 5-R1, so the apex of RS1

closer to the apex of pterostigma than to the apex of RS2. 1-RS $1.9\times$ as long as 1-M. 1-RS $1.6\times$ as long as RS + M. 1-M forms an acute angle with Rs + M. RS + M $0.3\times$ as long as 2-M. 2-RS straight, slightly longer than 1r-rs. 3-RS arched. 1-RS1 $1.8\times$ as long as 2r-rs. 2-RS2 $1.8\times$ as long as 3-RS2. M + Cu slightly S-shaped. Cell 1mcu long and narrow, $3.1\times$ as long as wide. 2r-rs inclined, parallel to 1r-rs. 2r-rs $1.5\times$ as long as 1r-rs. 4-RS very short, just as long as vein thickness. RS bent at 2r-m junction. 2r-m vertical; 2r-rs as long as 2r-m; 3r-m inclined, $1.5\times$ as long as 2r-m. 3-M as long as 4-M. 4-M $2.4\times$ as long as 5-M, so 2 m-cu joins M beyond 3rm cell midlength. 4-M and 5-M meet at obtuse angle.

The new collection also includes several specimens identified as previously described species or poorly preserved. Here, we give a brief discussion of these specimens.

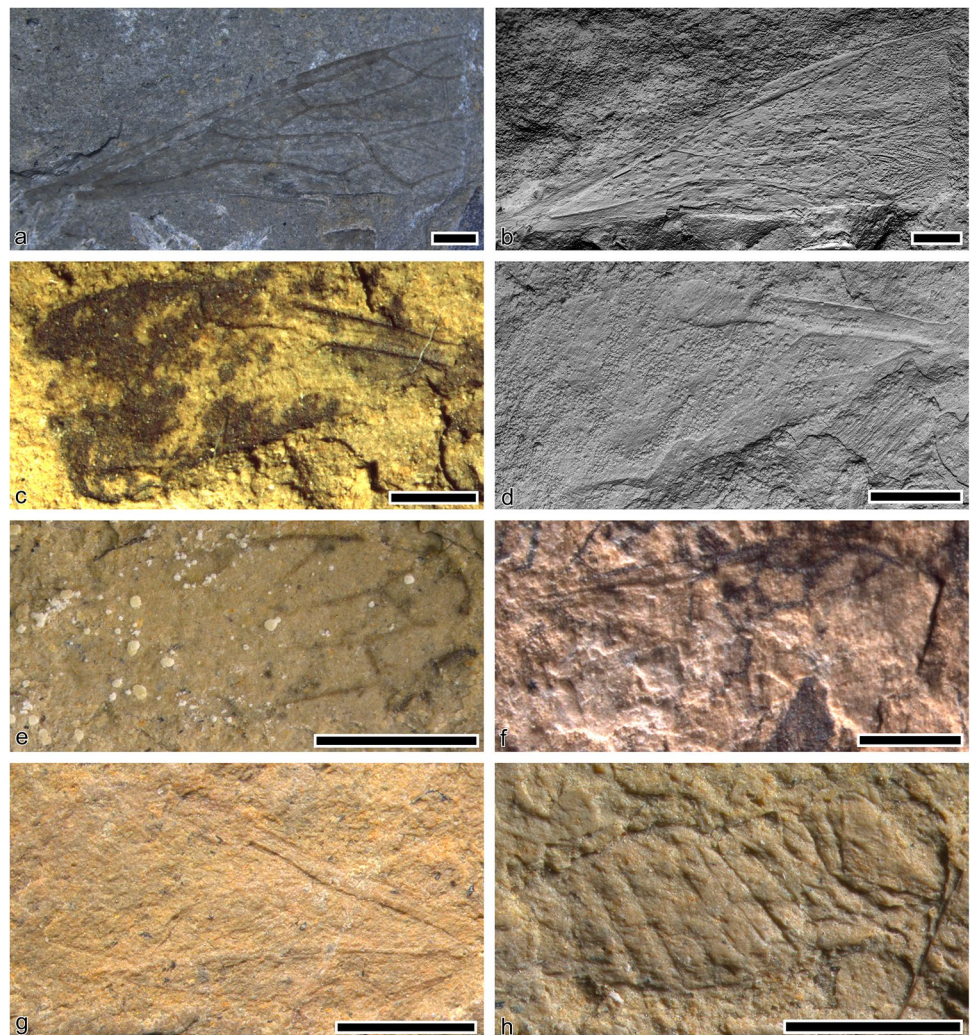
PIN 5343/1. Figure 5a, b. Fore wing with apex and anal part lost. Wing length is ca. 14 mm (estimation). By preserved venation and size, the specimen can be placed in

Ferganoxyela destructa Rasnitsyn 1969. The new specimen does not add any significant changes to the species diagnosis.

PIN 5343/2. Figure 5c, d. Fore wing with venation poorly preserved. Wing length is 5.2 mm (as preserved). The specimen is strongly stretched transversally (estimated longitudinal stretch is $0.75\times$). The remained traces of venation do not allow unambiguous identification. However, the shape of pterostigma (short and wide with 3-R1 long and subvertical) is unusual for Archexyelinae.

PIN 5343/3. Figure 5e. Fore wing with base and anal part lost. Wing length is ca. 4.5 mm (estimation). The preserved part of the wing with cell 2r long and narrow, 2r-rs meeting RS near RS1/RS2 bifurcation, apex of RS1 slightly closer to apex of pterostigma than to apex of RS2, 3r-m oblique, 4-M longer than 5-M suggests placing the specimen to *Ferganoxyela*. The sample is quite similar with *F. destructa* in venation, but much smaller.

Fig. 5 Undescribed hymenopteran specimens from Madygen Formation: **a, b** *Ferganoxyela destructa*, specimen PIN 5343/1; **c, d** Xyelidae subfam. indet., specimen PIN 5343/2; **e** *Ferganoxyela* sp., specimen PIN 5343/3; **f** Xyelidae subfam. indet., specimen PIN 5343/11; **g** Siricina fam. indet., specimen PIN 5343/13; **h** Siricina fam. indet., specimen PIN 5343/16. All scale bars 1 mm



PIN 5343/11. Figure 5f. Fore wing with venation poorly preserved. Wing length is ca. 3.7 mm (estimation). Pterostigma not sclerotized. 1-RS is much shorter than 1-M, which is very unusual for Archexyelinae, but characteristic of Madygellinae. Very small wing size also suggests placing the specimen into Madygellinae. On the other hand, cell 3r (3 + 4r?) is just 2 × as long as 2r (in Madygellinae 3 + 4r is much larger). With apical part of the wing not preserved, it cannot be confidently identified to subfamily level.

PIN 5343/13. Figure 5g. Fore wing with only costal and anal areas preserved. Wing length is ca. 4.3 mm (estimation). Can be undoubtedly identified as Hymenoptera: Siricina, but further identification is impossible.

PIN 5343/16. Figure 5h. Thorax and abdomen without head or wings. Probably belong to Hymenoptera: Siricina, but further identification is impossible.

Discussion

Xyelidae represent the most ancient hymenopterans in the whole fossil record and the only hymenopteran family known from the Triassic. They are known from only five localities and not earlier than the Middle–Late Triassic boundary (237 ± 2 Ma; Fig. 1). The xyelid fauna of the Madygen Formation remains the most diverse and abundant in the Triassic. It comprises 16 genera and 34 species within two subfamilies. It comprises 87% of the Triassic hymenopteran species diversity. Xyelids are also known from the Upper Triassic of Australia, Mount Crosby Formation (two species of Archexyelinae), Japan, Momonoki Formation (one species of Madygellinae), South Africa, Molteno Formation (one species not assigned to any subfamily) and South America, Potrerillos Formation (one species putatively assigned to Xyelinae). Barth et al. (2011) reported one fragmentary hymenopteran wing from the Upper Triassic of Langenberg near Seinstedt, Germany, and identified it as *Sepulenia* (Sepulcidae). They provided no illustrations for that specimen, so we can neither support nor falsify their interpretation, but we notice that isolated wings of Madygellinae may be easily confused with those of Sepulcidae, especially in case of incomplete preservations. Until this specimen is properly examined, we prefer to treat it as Hymenoptera fam. indet. Nevertheless, being the only Triassic hymenopteran finding in Europe, it is significant in terms of hymenopteran paleozoogeography. These findings show a wide distribution of Hymenoptera in both Gondwana and Laurasia in the Triassic.

The extreme rarity of Triassic hymenopteran finds, coupled with their near worldwide distribution, raises the question of how deep their hidden history extends.

Hymenopterans are not known from sediments below Middle–Upper Triassic boundary, including Anisian ‘Grès à Voltzia’ Formation (Vosges Mts., France, 242–247 Ma), the second richest fossil insect fauna of Triassic (Gall and Grauvogel-Stamm 2005). On the other hand, molecular dating suggests that Hymenoptera diversification began as early as the Late Paleozoic–Middle Triassic (329–239 Ma according to Peters et al. 2017). It can be assumed that the most ancient hymenopterans successfully avoided entering the fossil record for millions of years. We cannot give a reasonable explanation for this phenomenon, but we can assume that it is caused by the peculiarities of the ecology of these insects. Extant xyelid larvae are associated with trees, usually gymnosperms, and generally feed on the sporophylls and the pollen. We have no evidence that the trophic ecology of the Mesozoic xyelids differed significantly from modern ones. A number of finds of xyelids with pollen of gymnosperms in the intestines are known from the Cretaceous (Krassilov and Rasnitsyn 1982). Xyelids spend most of their lives in the larval stage. Their adults do not live long and are not prone to long-range flights, preferring to remain under the shelter of the forests. Thus, getting into the lakes where the burial takes place is extremely unlikely for them.

In the Triassic, Xyelidae were represented with three subfamilies (Table 1), with Archexyelinae the most diverse and abundant, and known from Madygen and Australia (Riek 1955; Rasnitsyn 1964, 1969; Engel 2005; Kopylov 2014). The next most diverse subfamily is Madygellinae, found in Madygen and Japan (Rasnitsyn 1969; Kopylov 2014; Oyama and Maeda 2020). In Potrerillos, Argentina, the only described xyelid is assigned to Xyelinae (Lara et al. 2014). And, finally, the only xyelid species from Molteno, South Africa, has been not assigned to any subfamily (Schlueter 2000).

Comparing the older and newer collections of Madygen xyelids gives us a remarkable example of the “collectors effect” in paleontology. In the older collections, acquired in the middle of the twentieth century, there is only 1 specimen of Madygellinae for 37 samples (<3%). In the new, twenty-first century collections, we have 16 specimens including 7 members of the Madygellinae (44%). During the large-scale Soviet excavations at Madygen, the main focus was not on searching tiny fossil insects, but rather in searching larger objects such as amazing Madygen vertebrates such as *Sharovipteryx* and *Longisquama* or giant orthopteroids like Titanoptera. It is natural that with this approach to field work, small samples more often were neglected by the field of view of the collectors. Contrary, the latest expeditions were focused on tiny insects. Madygellines are usually smaller than archexyelines. Furthermore, in older collections of Archexyelinae, we cannot find specimens with forewings smaller than 5 mm, while in modern collections such tiny specimens make up more than half of the sample. Most

Table 1 The list of described Xyelidae of the Triassic

Madygellinae		
<i>Chubakka madygensis</i>	Madygen (Kyrgyzstan)	Kopylov (2014)
<i>Madygella analoga</i>	Madygen (Kyrgyzstan)	Kopylov (2014), Rasnitsyn (1969)
<i>Madygella aristovi</i>	Madygen (Kyrgyzstan)	Kopylov (2014)
<i>Madygella bashkuevi</i>	Madygen (Kyrgyzstan)	Kopylov (2014)
<i>Madygella humioi</i>	Momonoki (Japan)	Oyama and Maeda (2020)
<i>Madygella kurochkini</i>	Madygen (Kyrgyzstan)	Kopylov (2014)
<i>Madygella levivenosa</i>	Madygen (Kyrgyzstan)	Kopylov (2014)
<i>Samarkandykia ryzhkovae</i>	Madygen (Kyrgyzstan)	Kopylov (2014)
<i>Samarkandykia shmakovi</i>	Madygen (Kyrgyzstan)	Kopylov (2014)
Archexyelinae		
<i>Archexyela crosbyi</i>	Mount Crosby (Australia)	Rasnitsyn (1964), Riek (1955)
<i>Archexyela ipswichensis</i>	Mount Crosby (Australia)	Engel (2005)
<i>Asioxyela parvula</i>	Madygen (Kyrgyzstan)	Rasnitsyn (1964, 1969)
<i>Asioxyela paurura</i>	Madygen (Kyrgyzstan)	Rasnitsyn (1969)
<i>Asioxyela smilodon</i>	Madygen (Kyrgyzstan)	Rasnitsyn (1964)
<i>Asioxyela grandipennis</i>	Madygen (Kyrgyzstan)	Rasnitsyn (1969)
<i>Dinoxyela armata</i>	Madygen (Kyrgyzstan)	Rasnitsyn (1969)
<i>Euryxyela euryptera</i>	Madygen (Kyrgyzstan)	Rasnitsyn (1964)
<i>Ferganoxyela destructa</i>	Madygen (Kyrgyzstan)	Rasnitsyn (1969)
<i>Ferganoxyela sogdiana</i>	Madygen (Kyrgyzstan)	Rasnitsyn (1969)
<i>Leioxyela antiqua</i>	Madygen (Kyrgyzstan)	Rasnitsyn (1964, 1969)
<i>Leioxyela grandis</i>	Madygen (Kyrgyzstan)	Rasnitsyn (1969)
<i>Leioxyela mitis</i>	Madygen (Kyrgyzstan)	Rasnitsyn (1969)
<i>Leioxyela mollis</i>	Madygen (Kyrgyzstan)	Rasnitsyn (1969)
<i>Lithoxyela fenestralis</i>	Madygen (Kyrgyzstan)	Rasnitsyn (1969)
<i>Madygenius extraradius</i>	Madygen (Kyrgyzstan)	Rasnitsyn (1969)
<i>Madygenius primitivus</i>	Madygen (Kyrgyzstan)	Rasnitsyn (1969)
<i>Microxyela minuta</i>	Madygen (Kyrgyzstan)	This paper
<i>Oryctoxyela anomala</i>	Madygen (Kyrgyzstan)	Rasnitsyn (1969)
<i>Oryctoxyela triassica</i>	Madygen (Kyrgyzstan)	Rasnitsyn (1969)
<i>Triassoxyela foveolata</i>	Madygen (Kyrgyzstan)	Rasnitsyn (1964, 1969)
<i>Triassoxyela sharovi</i>	Madygen (Kyrgyzstan)	This paper
<i>Triassoxyela orycta</i>	Madygen (Kyrgyzstan)	Rasnitsyn (1969)
<i>Xiphoxyela procrusta</i>	Madygen (Kyrgyzstan)	Rasnitsyn (1969)
<i>Xiphoxyela striata</i>	Madygen (Kyrgyzstan)	Rasnitsyn (1964, 1969)
<i>Xyelinus angustiradius</i>	Madygen (Kyrgyzstan)	Rasnitsyn (1964)
<i>Xyelinus major</i>	Madygen (Kyrgyzstan)	Rasnitsyn (1969)
<i>Xyelinus scherbachov</i>	Madygen (Kyrgyzstan)	This paper
Xyelinae		
<i>Potreriilloxyela menendezii</i>	Potreriillos (Argentina)	Lara et al. (2014)
Xyelidae inc. sed		
<i>Moltenia rieki</i>	Molteno (South Africa)	Schlueter (2000)

Madygen Formation (Dzhaylyaucho outcrop): Batken Region, Kyrgyzstan, N 40.0°, E 70.2°; Ladinian–Carnian boundary, 237 ± 2 Ma (Voigt et al. 2017; Moisan et al. 2021)

Momonoki Formation (Mine Group): Yamaguchi, Japan, N 34.2°, E 131.1°; Carnian, 237–228 Ma (Oyama and Maeda 2020)

Mount Crosby Insect Bed (Ipswich Series): Queensland, Australia, S 27.6°, E 152.8°; Norian 228–208 Ma (Raven et al. 2015)

Potreriillos Formation (Uspallata Group, Puesto Miguez): Mendoza Province, Argentina, S 33.1°, W 69.1°; Carnian, 237–227 Ma (Lara and Bashkuev 2020)

Molteno Formation (Great Karoo Basin, Birds River locality): Eastern Cape Province, South Africa, S 31.5°, E 26.8°; Carnian, 229–222 Ma (Schlueter 2000)

likely, the number of madygellines and tiny archexyelines in recent collections is greater because there was more attention to small objects.

With this work, we conclude the description of the Madygen hymenopterans. The collection of the Paleontological Institute is the world's only collection of Hymenoptera from this locality, obtained during numerous fieldworks since the 60s of the twentieth century. This work, together with previous studies (Rasnitsyn 1964, 1969; Kopylov 2014), provides an exhaustive description of the diversity of this, the most ancient of the hymenopteran faunas.

Supplementary file 1 (ZIP 744997 KB) **Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s12542-023-00666-6>.

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Data availability The fossil material described herein is housed in Paleontological Institute, Moscow, and available for public research. High-resolution images of fossil material described herein and in Kopylov (2014) are available in the online supplement to this paper.

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