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Madygella humioi sp. nov. from the Upper Triassic Mine Group, southwest Japan: the oldest record of a sawfly (Hymenoptera: Symphyta) in East Asia

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Abstract. A primitive sawfly, *Madygella humioi* sp. nov., belonging to the family Xyelidae (Hymenoptera: Symphyta), is newly described from the Upper Triassic Mine Group, Yamaguchi Prefecture, southwest Japan. The new species differs from the five previously known *Madygella* species in having a cell length of 1r plus 2r shorter than that of 3r+4r and a cell height of 3r+4r lower than 2r plus pterostigma in a forewing. To date, this is the oldest fossil record of sawflies in East Asia. Regarding genus *Madygella*, this is the first example found outside of the Kyrgyz Republic. This discovery provides an insight into the early evolution of the order Hymenoptera and suggests a widespread distribution of the pioneering genus *Madygella* during the Triassic period.

Key words: Hymenoptera, Japan, Mine Group, sawflies, Triassic, Xyelidae

Introduction

The oldest representatives of the order Hymenoptera are xyelid sawflies, belonging to the family Xyelidae. Their fossil records include specimens from Middle to Upper Triassic deposits in the Kyrgyz Republic (Rasnitsyn, 1964, 1969; Kopylov, 2014) and from Upper Triassic deposits in Australia (Riek, 1955; Grimaldi and Engel, 2005), Argentina (Lara *et al*., 2014), and South Africa (Schlüter, 2000). The Xyelidae family comprises four subfamilies: Xyelinae, Macroxyelinae, Archexyelinae, and Madygellinae. The extinct subfamily Madygellinae was a pioneering group of sawflies restricted to the Triassic period, comprising eight different species belonging to three genera occurring from the Middle to Upper Triassic in the Kyrgyz Republic (Rasnitsyn, 1969; Kopylov, 2014). Their existence in other areas is not known.

The Upper Triassic Mine Group, belonging to the Inner Belt of southwest Japan, yields abundant insect fossil assemblages (Fujiyama, 1973, 1991; Ueda, 1991; Figure 1). Fujiyama (1973) firstly described some parts of the orders Blattodea, Parapalecoptera, Hemiptera, and Coleoptera from this Group. Subsequently, examples of the orders Mecoptera (Ueda, 1991), Odonata (Fujiyama, 1991), Diptera, Ephemeroptera, Hymenoptera, Neroptera, Orthoptera, Plecoptera, and Trichioptera (Takahashi *et al*., 1997) were reported. More than half of specimens described consists of wings of individuals of Coleoptera and Blattodea (Fujiyama, 1991), while the occurrence of Diptera is rare and important for the Triassic (Kopylov, personal comm.).

The insect fauna of the Mine Group is closely related to those of the Mount Crosby Formation in Australia, the Madygen Formation in the Kyrgyz Republic, the Djam Djun Formation in Vietnam, and the Yan-chen Formation in Inner Mongolia (Fujiyama, 1973). Particularly, the Madygen Formation yields one of the richest Triassic insect fauna comprising 20 orders (Shcherbakov, 2008), and among them, 13 orders are common to the Mine Group.

From the Mine Group, more than 6,000 specimens have been collected since the initial discovery. Most specimens are stored at the Mine City Museum of History and Folklore, Mine City, Yamaguchi Prefecture, Japan. However, these samples remain largely to be exploited in details.

This paper focuses on the first discovery of sawflies in Triassic deposits of East Asia and sheds light on the early evolution of sawflies in this region. It provides the first example of sawflies from the pioneering genus *Madygella* found outside of the Kyrgyz Republic.

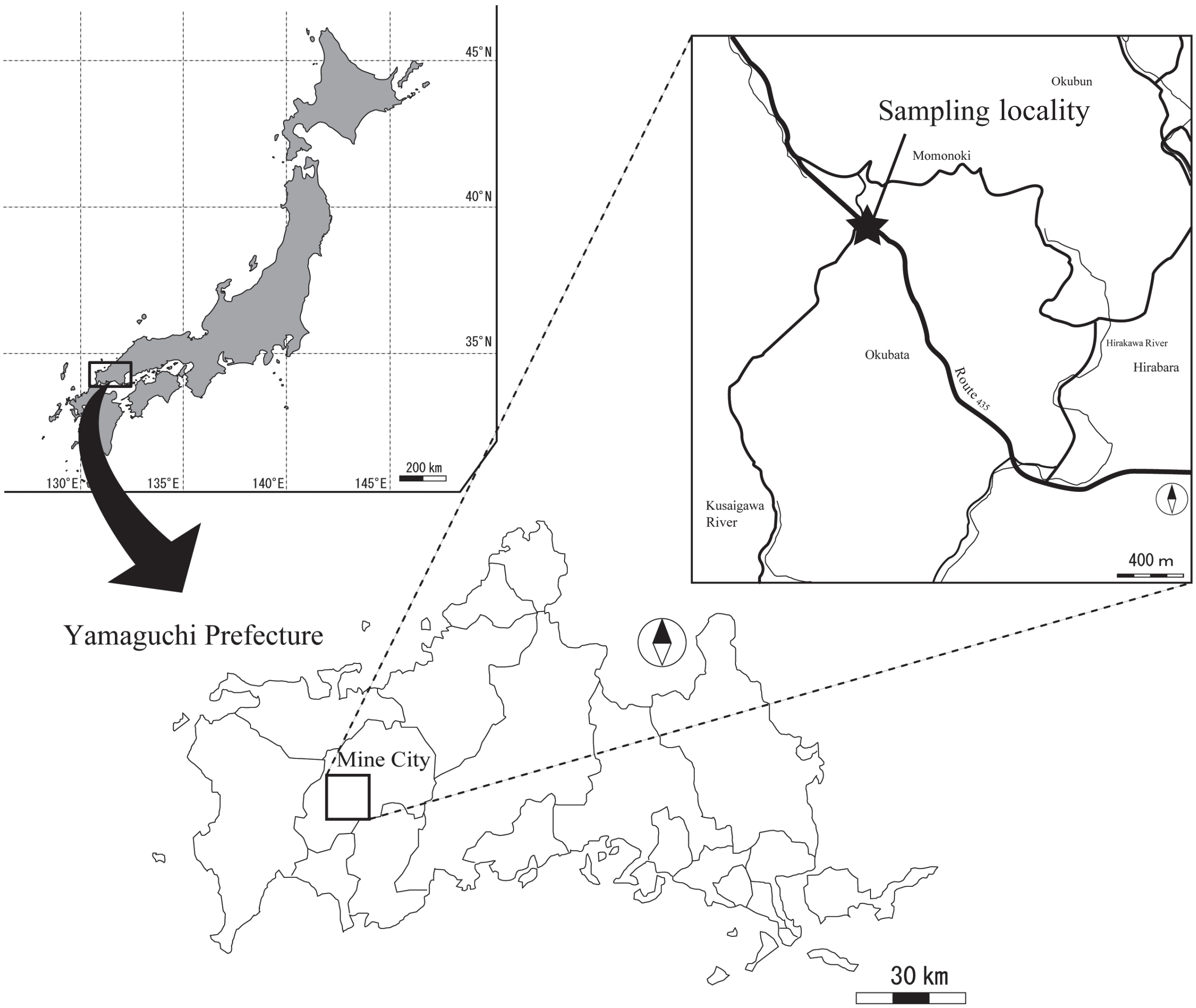


Figure 1. Locality of the *Madygella humioi* sp. nov. holotype (MMHF3-00091) in Mine City, Yamaguchi Prefecture, Japan.

Geological setting and fossil locality

The Triassic Mine Group, a thick clastic sequence, is lithologically divided into three units: the Hirabara, Momonoki, and Aso formations in ascending order in the Omine area, Mine City, Yamaguchi Prefecture, southwest Japan (Katayama, 1939; Kametaka, 1999; Figure 1). The lowermost Hirabara Formation is a marine deposit with a thickness of 250–1,000 m, which consists of conglomerate, sandstone, and mudstone intercalated with coal seams containing abundant marine bivalves (Hase, 1950; Tokuyama, 1960; Kametaka, 1999). The Momonoki Formation is a nonmarine deposit with a thickness of 800–1,200 m, which is composed of conglomerate, sandstone, and mudstone intercalated with coal seams (Takahashi and Mikami, 1975; Kametaka, 1999). The uppermost Aso Formation is a marine deposit with a thickness more than 1,500 m and is composed of sandstone and mudstone with marine bivalves (Hase, 1950; Tokuyama, 1958; Kametaka, 1999). Some bivalves (Tokuyama, 1960), ammonites (Ishibashi *et al*., 1990), plants (Katayama, 1939; Takahashi, 1973), and vertebrates (Hasegawa and Ota, 1975; Uyeno *et al*., 1996) have been reported from the Mine Group. The geological age of the Momonoki Formation is assigned to the Carnian stage of the Upper Triassic (Fujiyama, 1973; Kametaka, 1999).

The material reported in this paper was collected from the Momonoki Formation exposed along Route 435 at Okubata, Mine City, Yamaguchi Prefecture (Figure 1). From the same locality, Fujiyama (1991) and Ueda

(1991) previously reported some fossil insects. The specimen described in the present study (MMHF3-00091) is stored at the Mine City Museum of History and Folklore.

Abbreviations of morphological terms utilized in this paper are as follows (according to Rasnitsyn, 1969; Lara *et al*., 2014): C, costal vein; SC, subcostal vein; Pt, pterostigma; R, radial vein; RS (1-RS, 2-RS, 3-RS, 4-RS, 5-RS), radial sector and its sections; M (1-M, 2-M, 3-M, 4-M, 5-M), medial vein and its sections; Cu (1-Cu, 2-Cu, 3-Cu, 4-Cu), cubital vein and its sections; r (1r, 2r, 3r, 4r), radial cells; rm (1rm, 2rm, 3rm), radial-medal cells; mcu (1mcu, 2mcu, 3mcu), medio-cubital cells; cua (1cua, 2cua), cubito-anal cells; r-rs (1r-rs, 2r-rs), crossveins between R and RS; r-m (1r-m, 2r-m, 3r-m), radial-medal crossveins; m-cu (1m-cu, 2m-cu), medio-cubital crossveins; cu-a (1cu-a), cubito-anal crossveins.

Systematic description

Order Hymenoptera Linnaeus, 1758
Suborder Symphyta Linnaeus, 1758
Superfamily Xyeloidea Newman, 1834
Family Xyelidae Newman, 1834
Subfamily Madygellinae Rasnitsyn, 1969 emend. Kopylov, 2014

Type genus.—*Madygella* Rasnitsyn, 1969.

Diagnosis of subfamily.—Small sawfly. Forewings 2.8–5.8 mm long according to reconstructed proportions. Costal space narrow. C thickened toward apex, sometimes almost reaching R, but never touching it, separated from Pt. SC weak, joining only C, sometimes preserved only at wing base, transformed into fold, or completely lost. Pt usually not sclerotized, veins bordering it usually thickened. R straight up to base of RS, with slight bend near point of divergence of RS, usually straight within cell 1r, less often arcuate anteriad, without gap at base of Pt. RS1 (anterior branch of RS) lost without traces. 1r-rs not longer than 2r-rs. Cell 1r along anterior margin subequal in length to 2r. 1-RS either shorter or longer than 1-M. M+Cu arcuate (very rarely slightly S-shaped). Cell 1mcu long and narrow, at least twice as long as wide (Rasnitsyn, 1969, p. 50–51; Kopylov, 2014, p. 611).

Generic composition.—The subfamily consists of three genera: *Madygella* Rasnitsyn, 1969; *Samarkandykia* Kopylov, 2014; and *Chubakka* Kopylov, 2014 from the Middle-Upper Triassic of Kyrgyzstan.

Comparison.—The subfamily Madygellinae differs from other xyelid groups in the absence of RS1 (anterior branch) branches with rare exceptions: *Xyela alberta* (Curran, 1923) and *Lydoxyela excellens* (Rasnitsyn, 1966). The Madygellinae differs from subfamilies Xyelinae and Macroxyelinae in having the long cell 2r, and (for the majority of representatives of these two subfamilies) in the narrow costal space. It also differs from subfamily Xyelinae in having the apically thickened C and from subfamily Macroxyelinae in the absence of characteristic sclerotization at the base of the Pt.

Remarks.—The original diagnosis (Rasnitsyn, 1969) was considerably expanded by Kopylov (2014). We add this study as a new locality to the distribution.

Genus ***Madygella*** Rasnitsyn, 1969
Madygella Rasnitsyn, 1969, emend. Kopylov, 2014

Type species.—*Madygella analoga* Rasnitsyn, 1969.

Revised generic diagnosis.—1-RS shorter than RS+M and usually shorter than 1-M, rarely slightly longer. Length of cell 1r plus 2r longer than that of 3r+4r, sometimes length of cell 1r plus 2r shorter than that of 3r+4r; height of cell 3r+4r almost as high as that of 2r plus Pt, sometimes height of cell 3r+4r lower than that of 2r plus Pt. RS curved at point of 2r-m joining it.

Species composition.—*Madygella* genus consists of five species: *M. analoga* Rasnitsyn, 1969; *M. levivenosa* Kopylov, 2014; *M. kurochkini* Kopylov, 2014; *M. aristovi* Kopylov, 2014; *M. bashkuevi* Kopylov, 2014.

Comparison.—The present genus differs from *Samarkandykia* in 1-RS shorter than 1-M, RS curved at point of 2r-m joining it and 3r-m longer (up to 1.3 times) than 2r-m. The genus also differs from *Chubakka* in 2r-rs diverging in apical one-third of Pt, cell 1mcu weakly dilating toward apex.

Remarks.—Most characters of *Madygella humioi* sp. nov. match with the previous generic diagnosis. Unlike other *Madygella* species, however, *M. humioi* sp. nov. shows cell length of 1r plus 2r shorter than that of 3r+4r and cell height of 3r+4r lower than 2r plus Pt as described below. Taking these features into consideration, the generic diagnosis is slightly revised and updated here.

Madygella humioi Oyama and Maeda, sp. nov.

Figure 2

Etymology.—In honor of Humio Takahashi, director of the Mine City Museum of History and Folklore.

Holotype (MMHF3-00091).—A specimen of well preserved forewing without anal area from the Carnian deposits of the Momonoki Formation at Okubata, Omine area, Mine City, Yamaguchi Prefecture, southwest Japan (Figure 1). It is stored at the Mine City Museum of History and Folklore. Impression of other insects is overprinted on the surface.

Diagnosis.—*Madygella* species having a cell length of 1r plus 2r shorter than that of 3r+4r, and a cell height of 3r+4r lower than 2r plus Pt in a forewing.

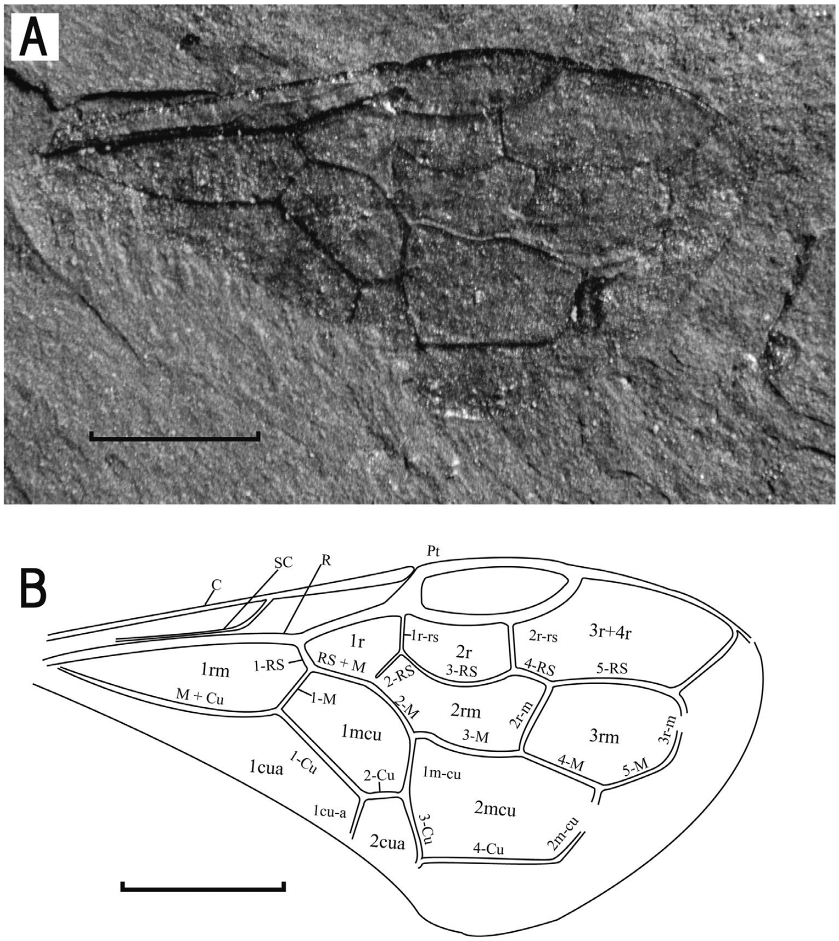


Figure 2. Forewing of *Madygella humioi* sp. nov., holotype MMHF3-00091 from the Upper Triassic Mine Group. **A**, photograph of the horizontal view; **B**, line drawing based on A with abbreviated terminology of vein and cell. Scale bars, 1 mm.

Description.—SC is developed over the entire length, joining C basal to RS base. Costal space is extremely wide. R at the base of RS has a weak curve, slightly dilates; within cell 1r, R is straight. The Pt is not sclerotized; the veins running along the periphery of the Pt are thickened. 2r-rs is inclival, shorter than 4-RS, 1.3 times longer than 1r-rs; the base of 2r-rs is 2.6 times closer to the apex of the Pt than to 1r-rs. 1-RS is much shorter than 1-M; RS+M is about 2 times longer than 1-RS. 2-RS is straight (2-RS joins RS+M). 5-RS is 3.1 times longer than 4-RS. 2r-rm is strongly inclined, 1.9 times longer than 2r-rs. 3r-m is probably longer than 2r-m. 1m-cu is subequal in length to 3-Cu. The free end of M and Cu are lost; 3r-m gradually passes into 5-M; 2m-cu gradually passes into 4-Cu. 3-M has a weak curve at the base of 3-M.

Measurements.—Forewings impression length, 4.5 mm; width, 2.3 mm.

Comparison.—The newly described species differs from subfamily Madygellinae in its extremely wide costal space.

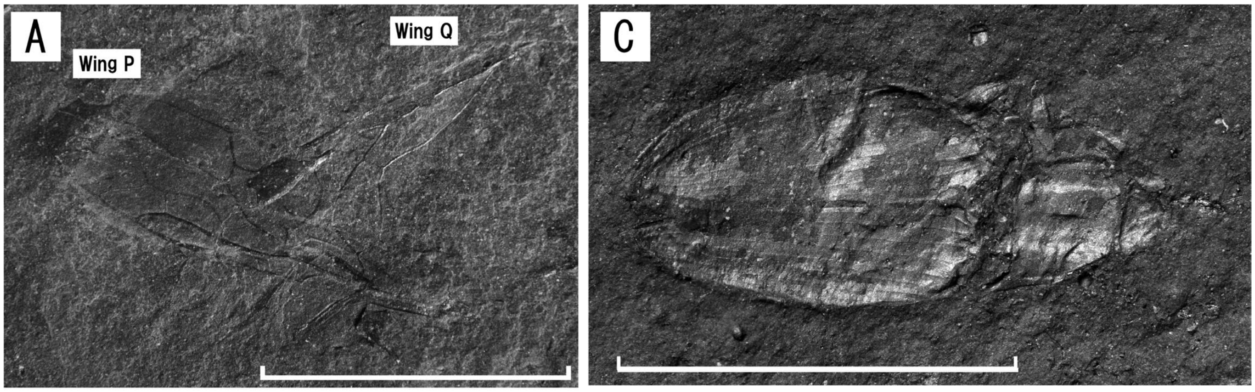
It is similar to the type species *Madygella analoga* and *M. levivenosa* in developing SC over the entire wing length. However, *M. humioi* sp. nov. differs from the type species in non-sclerotized Pt, strongly inclined 2r-m, same length of both 3-Cu and 1m-cu, absence of a free end of M with bend and slightly curved 3-M. *Madygella humioi* sp. nov. differs from *M. levivenosa* in inclival 2r-rs, strongly inclined 2r-m, same length of both 3-Cu and 1m-cu and distinctly curved basal 3-M.

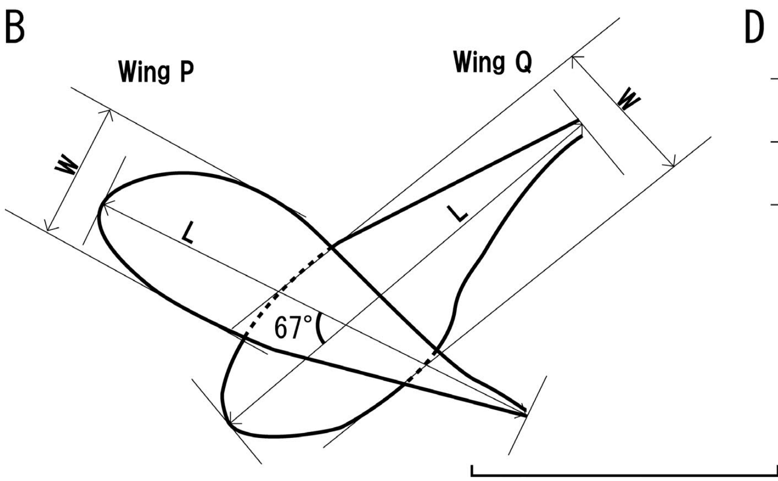
The newly described species is also similar to *Madygella bashkuevi* in strongly inclined 2r-m and curved 3-M. Strong 2r-m and curved 3-M are peculiar characteristic features to *M. bashkuevi* and *M. humioi* sp. nov. On the other hand, the new species is clearly distinct from *M. bashkuevi* in SC joining C basal to RS base and subequal 2r-rs and 1r-rs.

Table 1. Comparison of forewing characters in selected *Madygella* species. –, undescribed.

Characters/Taxa	***Madygella humioi*** **(this study)**	*M. analoga* (Rasnitsyn, 1969; Kopylov, 2014)	*M. aristovi* (Kopylov, 2014)
Length (mm)	**4.4**	4.9	3.7
Width (mm)	**2.3**	1.4	–
Length/Width	**1.9**	3.5	–
Sc	**joins C basal to RS base and is probably developed over the entire length**	deveolped over the entire length, joining C slightly distal to RS base	transformed into a fold
R (at base of RS)	**a weak curve slightly dilates**	a rather small cuve, slightly dilates	straight, slightly dilates
R (within 1r)	**weakly arcuate**	weakly arcuate	weakly arcuate
Pt	**not sclerotized the vien is thickened**	sclerotized	(sclerotized)
length of 1r plus 2r : 3r+4r	**1r plus 2r < 3r+4r**	1r plus 2r > 3r+4r	1r plus 2r > 3r+4r
height of 2r plus Pt : 3r+4r	**2r plus Pt > 3r+4r**	2r plus Pt < 3r+4r	(lost)
2r-rs	**inclival, 2r-rs > 4-RS, 2r-rs = 1r-rs (×1.3)**	inclival, 2r-rs > 4-RS, 2r-rs > 1r-rs (×1.8)	reclival, 2r-rs < 4-RS, (1r-rs lost)
2r-rs : 1r-rs (close to apex of Pt)	**2.6 times**	2.2 times	(1r-rs lost)
1-RS	**1RS < 1-M (remarkably)**	1-RS < 1-M (slightly)	1-RS < 1-M
RS+M	**RS+M > 1-RS (×about 2)**	RS+M > 1-RS (×2.5)	(RS+M lost)
2-RS	**straight (not joining)**	straight	(lost)
5-RS	**5RS > 4-RS (×3.1)**	5RS > 4-RS (×3.5)	5RS > 4-RS (×4.5)
2r-m	**incline (strongly), 2r-m>2r-rs (×1.9)**	(not incline), 2r-m = 2r-rs	(not incline), 2r-m > 2r-rs (×2.6)
3r-m	**3r-m > 2r-m**	3r-m > 2r-m (×1.2)	(lost)
3-Cu	**3-Cu = 1m-cu (subequal)**	3-Cu > 1m-cu (×1.5)	3-Cu (×1.6) < 1m-cu
M (free end)	**lost (3r-m passes into 5-M)**	present	(lost)
Cu (free end)	**lost (2m-cu passes into 4-Cu)**	lost (2m-cu passes into 4-Cu)	present
3-M	**slightly curved**	straight	straight

Characters/Taxa	*M. bashkuevi* (Kopylov, 2014)	*M. kurochkini* (Kopylov, 2014)	*M. levivenosa* (Kopylov, 2014)
Length (mm)	4.2	3.2	3.4
Width (mm)	–	–	2.3
Length/Width	–	–	1.5
Sc	only at wing base	at wing base (apex of Sc is effaced in the impression)	over the entire length (costal space is crumpled and SC is tucked under R in the impression)
R (at base of RS)	a weak curve, slightly dilates	a visible curve, slightly dilates	a rather small curve, dilates
R (within 1r)	straight	arcuate	weakly arcuate, then straight
Pt	not sclerotized, the vein is not thickened to a greater extent than C or R	sclerotized	not sclerotized, the vein is thickened
length of 1r plus 2r : 3r+4r	1r plus 2r > 3r+4r	(lost)	1r plus 2r > 3r+4r
height of 2r plus Pt : 3r+4r	2r plus Pt < 3r+4r	2r plus Pt < 3r+4r	2r plus Pt < 3r+4r
2r-rs	inclival, 2r-rs < 4-RS, 2r-rs > 1r-rs (×1.9)	inclival, 2r-rs > 4-R, 2r-rs > 1r-rs (×1.3)	vertical, 2r-rs > 4-R, 2r-rs > 1r-rs (×2.0)
2r-rs : 1r-rs (close to apex of Pt)	1.8 times	2.3 times	1.6 times
1-RS	1-RS < 1-M (remarkably)	1-RS > 1-M	1-RS < 1-M (slightly)
RS+M	RS+M > 1-RS (×3)	RS+M > 1-RS (×1.6)	RS+M > 1-RS (×1.4)
2-RS	straight	arcate	straight
5-RS	(5RS > 4-RS)	5RS > 4-RS (×3)	5RS > 4-RS (×3)
2r-m	incline (strongly), 2r-m > 2r-rs (distinctly)	(not incline), 2r-m > 2r-rs (×1.4)	(not incline), 2r-m > 2r-rs (×1.2)
3r-m	(lost)	(lost)	3r-m > 2r-m (×1.2)
3-Cu	(lost)	3-Cu = 1m-cu	3-Cu (×1.4) < 1m-cu
M (free end)	(lost)	present	lost (3r-m passes into 5-M)
Cu (free end)	(lost)	lost (2m-cu joins 4-Cu with sharp bend)	lost (2m-cu passes into 4-Cu)
3-M	curved (strongly)	straight	straight





D

	Wing P	Wing Q
Length	7.7	7.5
Width	2.3	2.5
Aspect Ratio	3.35	3.00

Figure 3. Insect fossils from the Mine Group not showing remarkable distortion. **A**, two partly overlapped wings of a sawfly (Wing P, Q, MMHF3-00095) from the same horizon of *Madygella humioi* sp. nov. **B**, outline of A with measurement axes and crossed-axes angle between the wings P and Q (67°). **C**, body parts of Coleoptera (MMHF3-00092) from the same horizon of *Madygella humioi* sp. nov. The body was vertically collapsed and flattened by compaction, but the planar geometry is not secondarily distorted and well preserved. **D**, measurements of B. Note aspect ratios of both wings are not disparate (3.00–3.35) even though orientations of the two wings are different. Scale bars, 5 mm.

Discussion

The fossil records of Triassic Hymenoptera were previously found from four regions: Kyrgyz Republic (Rasnitsyn, 1964, 1969; Kopylov, 2014), Queensland (Riek, 1955; Grimaldi and Engel, 2005), South Africa (Schlüter, 2000), and Argentina (Lara *et al*., 2014). Although East Asia has several contemporaneous fossil insect localities (Zheng *et al*., 2018), there was no previous record of individuals belonging to the order Hymenoptera in the region. *Madygella humioi* sp. nov. is the oldest record of sawflies in East Asia, including Japan. This discovery reveals that primitive Hymenoptera (xyelid sawflies) were already widespread in five isolated realms, and further expands our knowledge regarding the early evolution and diversity of sawflies during the Triassic period.

The taxonomic study of Triassic sawflies has been largely based on wing morphology as wings possess a higher potential for fossilization than other body parts (Grimaldi and Engel, 2005; Schlüter, 2000). However, the simple wing morphology is not always adequately diagnostic (Lara *et al*., 2014), in part due to the potential post-burial deformation of morphological characters (Kopylov, 2014). For example, *Madygella bashkuevi* from the Middle–Upper Triassic in the Kyrgyz Republic has inclined 2r-m and curved 3-M, but these could have resulted from secondary distortion by shear stress of tectonism (Kopylov, 2014). Thus, Kopylov (2014) adopted a standardizing proportion formula to reconstruct the original wing geometry.

Madygella humioi sp. nov. from the Mine Group also shows inclined 2r-m and curved 3-M (see Table 1). Taking Kopylov's results into consideration, we examined the mode of secondary distortion in our samples. Many insect wings from the Mine Group are variously scattered on a bedding plane without showing any preferred orientation. Therefore, the geometric disparity would be expected depending on their orientation if secondary distortion occurred. However, a close taphonomic observation reveals that most insect fossils in the Mine Group are not remarkably distorted, unlike Kyrgyz Republic samples. For example, two partly overlapped wings of a sawfly are preserved in a bedding plane of the shale (Figure 3A). Their crossed-axes angle is quite large, i.e., 67° (Figure 3B), while remarkable geometric disparity is not recognized between the two wings. Their aspect ratios are not disparate (3.00–3.35) even though orientations are different (Figure 3D). The minimum secondary distortion is also suggested by the preservational state of an intact fossil beetle (Coleoptera) found from the same horizon as *M. humioi* sp. nov. (Takahashi *et al*., 1997, pl. 8, fig. 3C). The body of the beetle was vertically collapsed and flattened by compaction, while the planar geometry was still intact and not remarkably distorted (Figure 3C). The line of evidence suggests that the inclined 2r-m and curved 3-M shown in *M. humioi* sp. nov. can be interpreted as an essential morphological character, rather than a secondary distortion.

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Authors contribution

Nozomu Oyama initiated the study and was primarily responsible for taxonomic aspects.

Haruyoshi Maeda revised the manuscript critically for important intellectual content. All authors contributed to the writing of the paper.