



Paleontology

Evolutionary changes in the ovipositor shape of xyelid sawflies (Hymenoptera: Xyelidae) revealed by early fossils

Nozomu Oyama^{1,2,*}, Haruyoshi Maeda^{2,3}, Alexandr P. Rasnitsyn^{3,4}, Kenji Shinoda⁵,
Humio Takahashi⁵, Olivier Béthoux¹

¹CR2P (Centre de Recherche en Paléontologie–Paris)–Paris, Museum National d'Histoire Naturelle–Centre national de la recherche scientifique–Sorbonne Université, Paris, France, ²The Kyusyu University Museum, Fukuoka, Japan, ³Paleontological Institute, Russian Academy of Sciences, Moscow, Russia, ⁴Natural History Museum, London, UK, ⁵Mine City Office, Yamaguchi, Japan
*Corresponding author, email: nozomu.oyama@mnhn.fr

Disclaimer: Nagoya Protocol: The authors attest that all legal and regulatory requirements, including export and import collection permits, have been followed for the collection of specimens from source populations at any international, national, regional, or other geographic level for all relevant field specimens collected as part of this study.

Subject Editor: István Mikó

Received on 4 April 2024; revised on 7 October 2024; accepted on 4 November 2024

Considering taxonomic diversity, extant xyelid sawflies represent a very small subset of the past diversity of the group. A complementary approach to investigate evolutionary changes in this family is to consider ovipositor morphology, an ecologically important organ. New, well-preserved specimens from the Upper Triassic Ominé locality (Momonoki Formation, Mine Group; Carnian; Japan) and belonging to the †Madygellinae, one of the earliest Xyelidae subfamilies, are newly described and assigned to four new species, belonging to three genera (one being new). Two of the specimens expose body parts and wings, providing important information regarding ovipositor morphology. To further appreciate the evolution of this organ, we surveyed both fossil and extant Xyelidae. Extant forms display both extremes of the range of ovipositor types, namely the high aspect ratio “dagger-like” and “needle-like” types (in Xyelinae) and the low aspect ratio “short and wide” type (in Macroxyelinae). All known Triassic representatives display high aspect ratio ovipositor types. In contrast, Middle Jurassic to Lower Cretaceous sawflies show the highest diversity of ovipositor types for the family. Afterwards, the observed range declined and concentrated on the two, very distinct types known nowadays. Decline in ovipositor disparity was not contemporaneous in Xyelinae and Macroxyelinae: specialization occurred during the Jurassic-Cretaceous transition for the Xyelinae, while Macroxyelinae displayed their peak of diversity during the Lower Cretaceous, with a postponed decline. Ovipositor shape transition was probably accompanied with a larval diet change in Macroxyelinae. Ovipositor disparity therefore further contributes depicting extant Xyelidae as a subset on a once more diverse group.

Key words: Madygellinae, Japan, Triassic

Introduction

The order Hymenoptera (sawflies, wasps, ants, and bees) is one of the four hyperdiverse holometabolous insect lineages (Grimaldi and Engel 2005). These insects play important roles in terrestrial ecosystems as parasitoids, predators, herbivores, and pollinators (Grimaldi and Engel 2005). Uncertainties remain on the time of divergence of Hymenoptera from the remaining holometabolous insects, with which they are sister-group related. Time-calibrated molecular

phylogenies provide an age ranging from the early Carboniferous to the Devonian, whereas the age of the crown-group is more consistently retrieved around the Permian-Triassic boundary, or slightly earlier (Misof et al. 2014, Kjer et al. 2015, Tong et al. 2015, Peters et al. 2017, Blaimer et al. 2023). To some extent, this is consistent with the fossil record, with earliest members of the crown-group lineage Xyelidae occurring in several Triassic localities (whereas convincing earlier stem-group fossils remain to be discovered, or identified).

Unlike most other holometabolous lineages, which began to abound in fossil localities during the Triassic (Blagoderov et al. 2007, Beutel et al. 2024), the Hymenoptera became abundant and diverse in the Early Jurassic (Rasnitsyn 2002).

Extant Xyelidae, represented by five genera, are believed to represent a very small subset of the past diversity of the family (Jouault et al. 2021). The earliest known fossils are therefore likely to provide relevant information on the early ecological habits of the otherwise successful hymenopter lineage. Among the five sub-families composing the Xyelidae, the extinct †Archexyelinae, from the localities of Madygen (Kyrgyz Republic; Rasnitsyn 1964, 1969, Denisova et al. 2023) and Mt. Crosby (Australia; Riek 1955, Engel 2005), are mainly known from well-preserved wings but comparatively poorly preserved bodies; the †Madygellinae are known from isolated forewings only, from Madygen (Kyrgyz Republic; Rasnitsyn 1969, Kopylov 2014) and Ominé (Japan; Oyama and Maeda 2020); and fossils not placed in subfamily are known from Molteno (South Africa; Schlüter 2000) and Puesto Miguez (Argentina; Lara et al. 2014) (the Macroxyelinae and the †Daohugouinae (Rasnitsyn and Zhang 2004, Wang et al. 2019) have no Triassic record). The enigmatic mid-Cretaceous †Sypastoxyelidae must be mentioned for an exhaustive account on early Hymenoptera. They may compose the sister-group of the remaining Hymenoptera, as they display segmented cerci, a state assumed to represent a plesiomorphy within Hymenoptera (Zheng et al. 2021).

In summary, our knowledge of the overall morphology and ecology of early Xyelidae remains limited, for their fossils are rare

and often incomplete. Recently, well-preserved †Madygellinae fossils, including two specimens exposing body parts in addition to wings, were collected at the Triassic Ominé locality (Momonoki Formation; Fig. 1.1-4). It is the first discovery of such well-preserved remains for Triassic Hymenoptera. This new record allows a reconsideration of the subfamily diagnosis and systematics. In addition, the ovipositor is exposed in the two well-preserved specimens. This organ plays an important role in Hymenoptera ecology: the ovipositor of herbivorous sawflies is used to lay eggs into plant tissues (Naito et al. 2020), while those of various parasitic wasps allows them to reach insect larvae living within plant tissues and in other hidden or open places and to lay eggs inside them (Quicke 2014). Although numerous xyelid sawfly fossils preserving the ovipositor are known (Rasnitsyn 1969), the evolution in shape diversity of this important organ remains largely unexplored for Xyelidae. Based on the new material and a broad survey of more recent, well-preserved Xyelidae fossils, the significance and evolutionary trends of xyelid ovipositor shape is herein investigated.

Material and Methods

Geological Setting

The new specimens were collected from the Carnian (Upper Triassic) Momonoki Formation of the Mine Group, in the Ominé region (Mine, Yamaguchi Prefecture, Southwest Japan; Fig. 1; (Katayama 1939, Maeda and Oyama 2019). In this area the Mine Group is lithologically subdivided, in an ascending order, into the Hirabara,

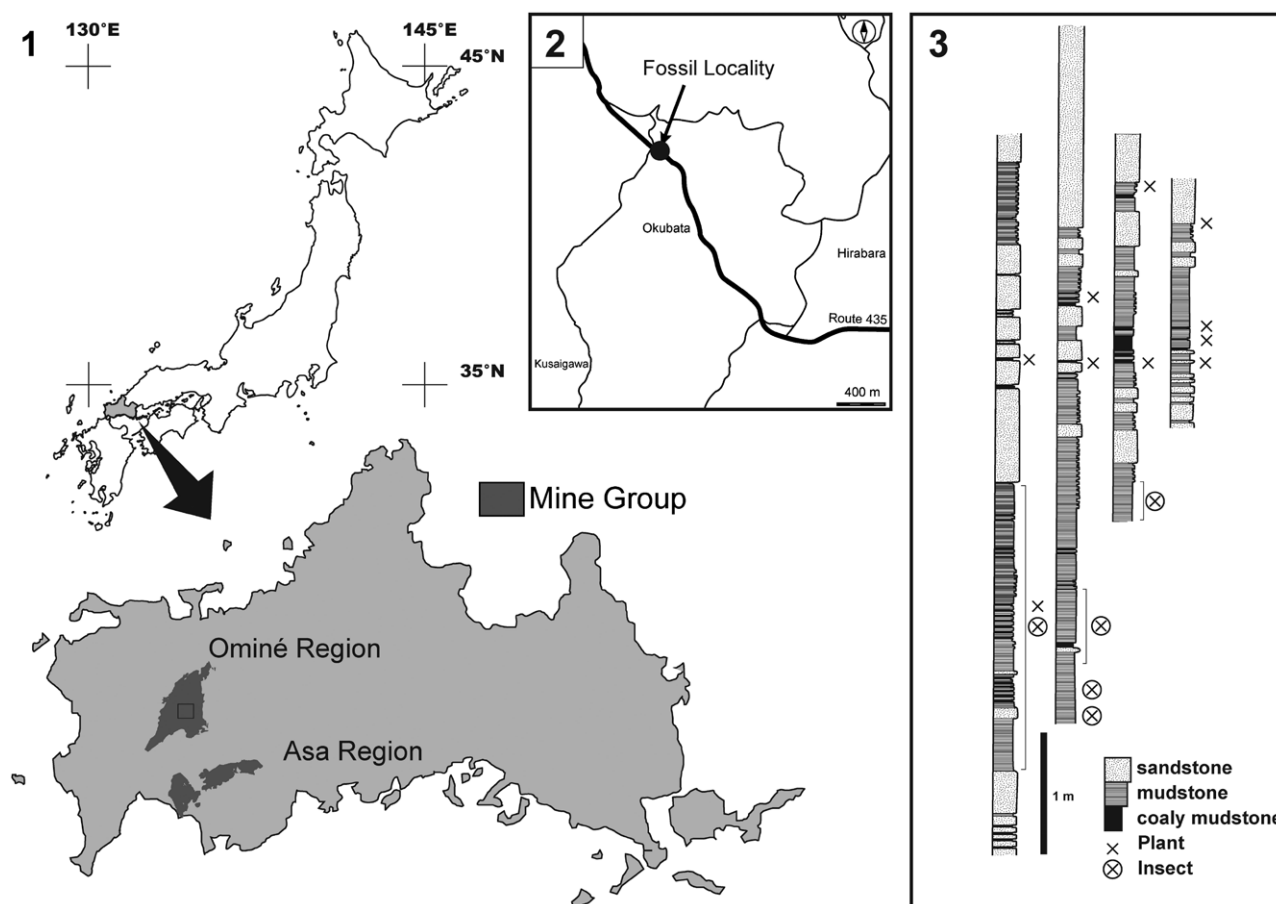


Fig. 1. Location and stratigraphy of the Ominé fossil locality (Upper Triassic Momonoki Formation: (1), study area in south-west Japan; (2), detailed map of study area; (3), columnar sections modified after Takahashi et al. (1997).

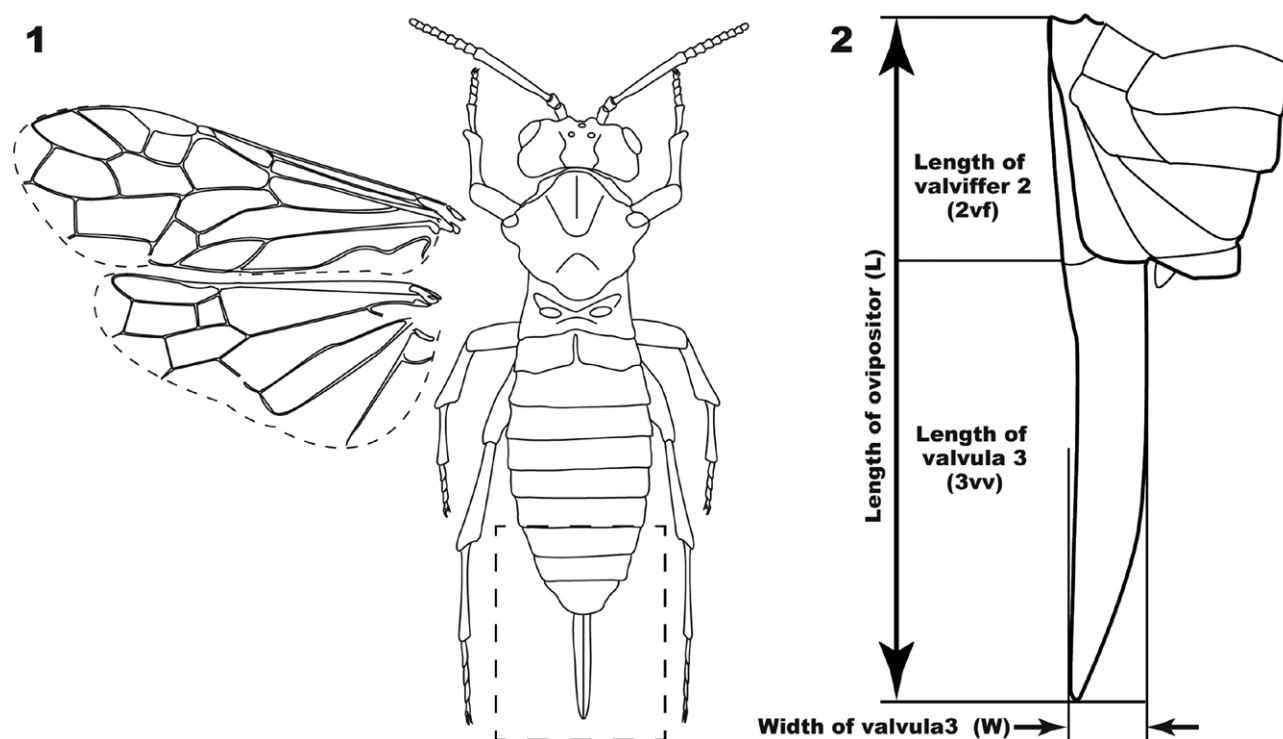


Fig. 2. Schematic morphology of Xyelidae based on a female of *Xyela*: (1), dorsal view; (2), terminology for ovipositor characteristics (lateral view).

Momonoki, and Aso Formations (Katayama 1939, Hase 1950, Tokuyama 1960, Kametaka 1999, Maeda and Oyama 2019). The Momonoki Formation represents nonmarine facies and is characterized by conglomerates, sandstones, and mudstones, with frequently intercalation of coal stems (Takahashi and Mikami 1975, Kametaka 1999). It yields abundant fossils of plants, insects, and fishes, and a dicynodont synapsid (Fujiyama 1973, Uyeno et al. 1996, Takahashi et al. 1997, Jinnouchi et al. 2018). The 1,000m-thick Momonoki Formation represents deltaic lacustrine environments including a delta plain, delta front or lagoon (Tokuyama 1958, Aizawa 1991, Kametaka 1999). The occurrence of *Paratrachyceras* cf. *hofmanni* and bivalves in the Hirabara Formation indicates a Carnian age (Hase 1951, Fujiyama 1973, Ishibashi et al. 1990).

Several thousand fossil insect remains, belonging to nine orders (including 24 species identified thus far), have been recovered from the Momonoki formation, mostly from a few outcrops along Road 435 in the Okubata area, from 1987 to 1990 (Fig. 1.2; Fujiyama 1973, 1991, Ueda 1991, Takahashi et al. 1997, Oyama and Maeda 2020, Oyama et al. 2020, 2023, Khramov et al. 2023). A 70-m thick nonmarine sequence, consisting of alternating beds of sandstone and mudstone, with coal seams, is exposed there, with insects most abundant in a ca. 20m-thick mudstone (Fig. 1.3; Aizawa 1991, Takahashi et al. 1992). The productive mudstone also contains plant fossils such as *Cladophlebis*, *Neocalamites*, *Podozamites*, *Baiera*, and *Taeniopteris* (Takahashi et al., 1992). Recently, the earliest unequivocal leaf-mines were reported from this site (Imada et al. 2022).

Material

Ominé

Thirty-three hymenopteran specimens were identified from specimens housed in the Mine City Museum of History and Folklore (MMHF), Kitakyushu Museum of Natural History and Human

History (KMNH), various private collections and among the sample collected by the senior author (altogether accounting for 3,900 fossil insects). Among them, six specimens, MMHF3-00096, 00097, 00098, 00099, 00100, and KMNH IP 000,101, are newly described here.

Comparative Analysis

Measurements of ovipositor shape were carried out on a number of Xyelidae specimens (summarized in Supplementary Table S1). In detail, we surveyed about 200 specimens of fossil Xyelidae housed in the Paleontological Institute (PIN; Moscow, Russia). Among them, 32 exposing a well-preserved ovipositor were selected (Supplementary Figs. S1–S9). Literature data on 24 well-preserved fossil Xyelidae species were also used (Supplementary Table S1). Moreover, three extant species of Xyelidae were also documented (Supplementary Fig. S10.1–3).

Documentation

The Ominé specimens and extant material of Hymenoptera were photographed using a Nikon D850 digital camera coupled with a Micro-Nikkor 55 mm F 2.8, or a Macro-Nikkor 65 mm F4.5 for close-up. Focus stacking was used. Specimens housed at the PIN were photographed using a Leica M165C stereomicroscope with the Leica DFC 420 camera. Resulting photographs were uniformly edited using Adobe Photoshop 2022 (Adobe Systems, San Jose, CA, USA). Drawings were made based on photographs and direct observation using Adobe Illustrator 2022 (Adobe Systems, San Jose, CA, USA). An attempt was made to manually reconstruct the specimen KMNH IP 000,101, composed of a partly disrupted forewing. Morphological terms and abbreviations are summarized in Supplementary Table S2, following previous accounts (Rasnitsyn 1969). By “arcuated,” we refer to a line forming an arc (as opposed to a straight line).

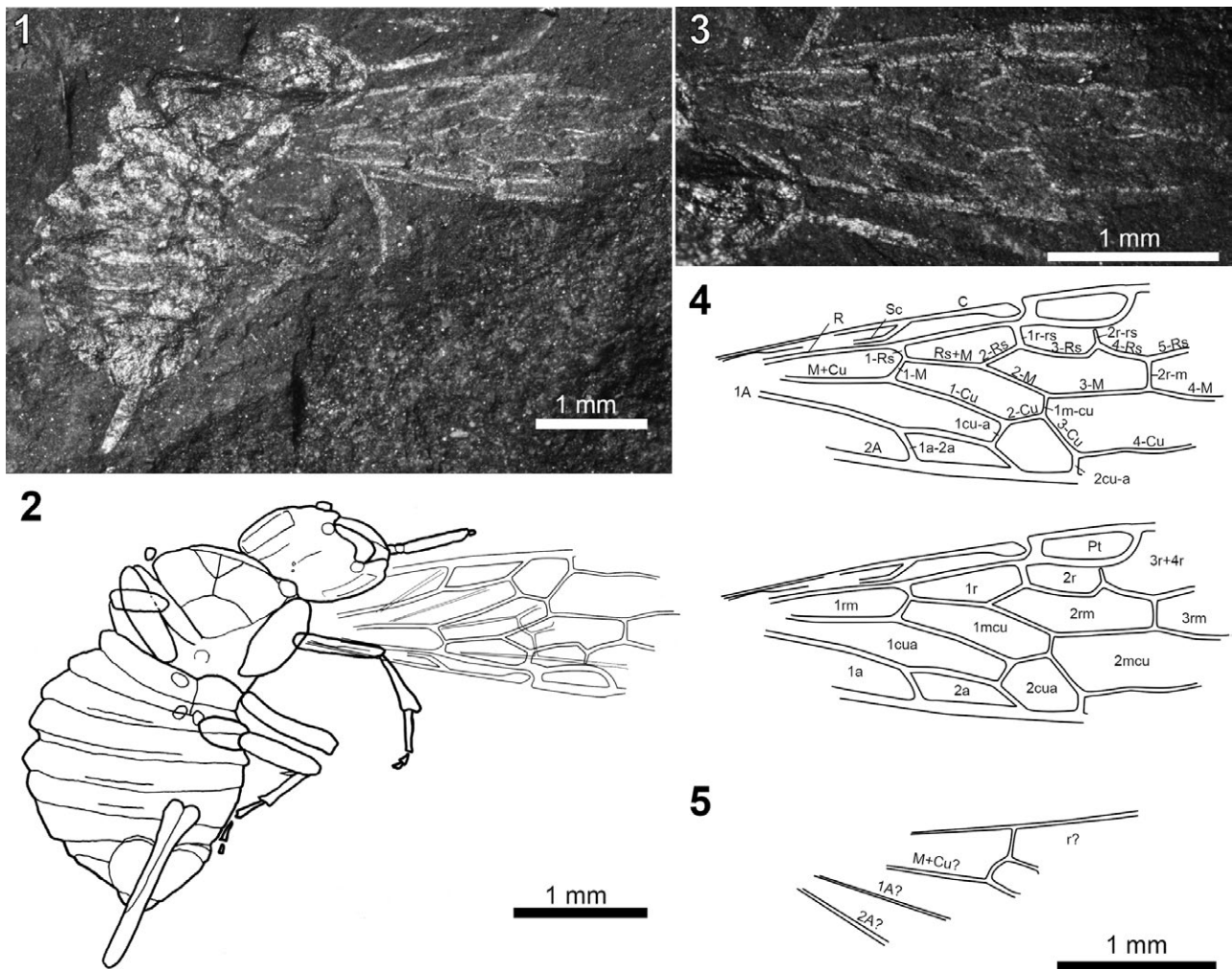


Fig. 3. †*Madygella fujiiyamai* sp. n. (Ominé; Upper Triassic; Japan), holotype specimen MMHF3-00096: (1 and 2), specimen overview, photograph (1) and line drawing (2); (3–5), details of wing venation, photographs (3) and line drawings of forewing (4) and hindwing (5). See [Supplementary Table 2](#) for abbreviations.

Measurements

Generally, ratios between particular elements of wing venation were obtained using projections perpendicular to the main wing axis. Ovipositor elements of Ominé specimens and extant Hymenoptera were measured using a Nikon Profile Projector V-12B. Other measurements were made based on new photographs or published data (see [Supplementary Table S1](#)). We followed a previously established framework ([Blank et al. 2013, 2017](#); and see [Fig. 2](#)), as follows: total length of ovipositor (L) as the combination of the lengths of valvifer 2 and valvula 3, both measured as straight lines along ventral edge of the sclerite; [Fig. 2.2](#)); and width of valvula 3 (W). Optimally, width should be measured from the ovipositor itself, i.e., the joined valvulae 1&2. At rest, these elements are ensheathed inside the pair of valvulae 3 (“saw sheaths”) in Xyelidae, making it impossible to measure their widths accurately. However, the widths of valvulae 3 and that of the joined valvulae 1&2 are correlated in Xyelidae (for Macroxyelinae, see [Blank et al. 2017](#), fig. 1E; for Xyelinae, see [Blank and Kramp 2017](#), figs. 2D,E), allowing the use of valvula 3 width as surrogate for that of the joined valvulae 1&2. We then calculated the W/L ratio, with low values indicating a slender ovipositor, and high values indicating a more “stout” ovipositor. Our dataset includes 56 fossil species and three individuals belonging to two of the extant species of Xyelidae ([Supplementary Table S1](#)).

Measuring a relative ovipositor length (i.e., body length excluding ovipositor vs. ovipositor length) may be seen as a more straightforward and biologically-relevant metric than the ovipositor W/L ratio. The latter was favored because it allowed compiling a larger dataset on fossil taxa, for body length cannot be accurately estimated for many incomplete and/or damaged fossils: we estimated that using the relative ovipositor length would entail the removal of 38% of the total dataset. Concurrently, we investigated whether ovipositor width composes, or not, a suitable surrogate for body length excluding ovipositor. Based on data on 6 species of *Megaxyela* from [Blank et al. \(2017\)](#), 3 species of *Pleroneura* from [Shinohara \(1995](#); for one species, with both maximum and minimum body length-excluding ovipositor), data on a specimen of *Xyelatana lugdunensis* (specimen MNHN-EY-EY6339; <http://coldb.mnhn.fr/catalognumber/mnhn/ey/ey6339>), and on 2 specimens of *Megaxyela* belonging two undetermined species and 1 specimen belonging to an undetermined *Xyela* species from our own data (so, $n = 14$), we recovered a strong correlation between ovipositor width and body length excluding ovipositor length ($R^2 = 0.8931$). Therefore, the terms “high aspect ratio” (e.g., W/L values ranging from 0.1 to 0.2) vs. “low aspect ratio” (e.g., W/L values ranging from 0.3 to 0.4) indeed are largely equivalent with “long relative to body” vs. “short relative to body”.

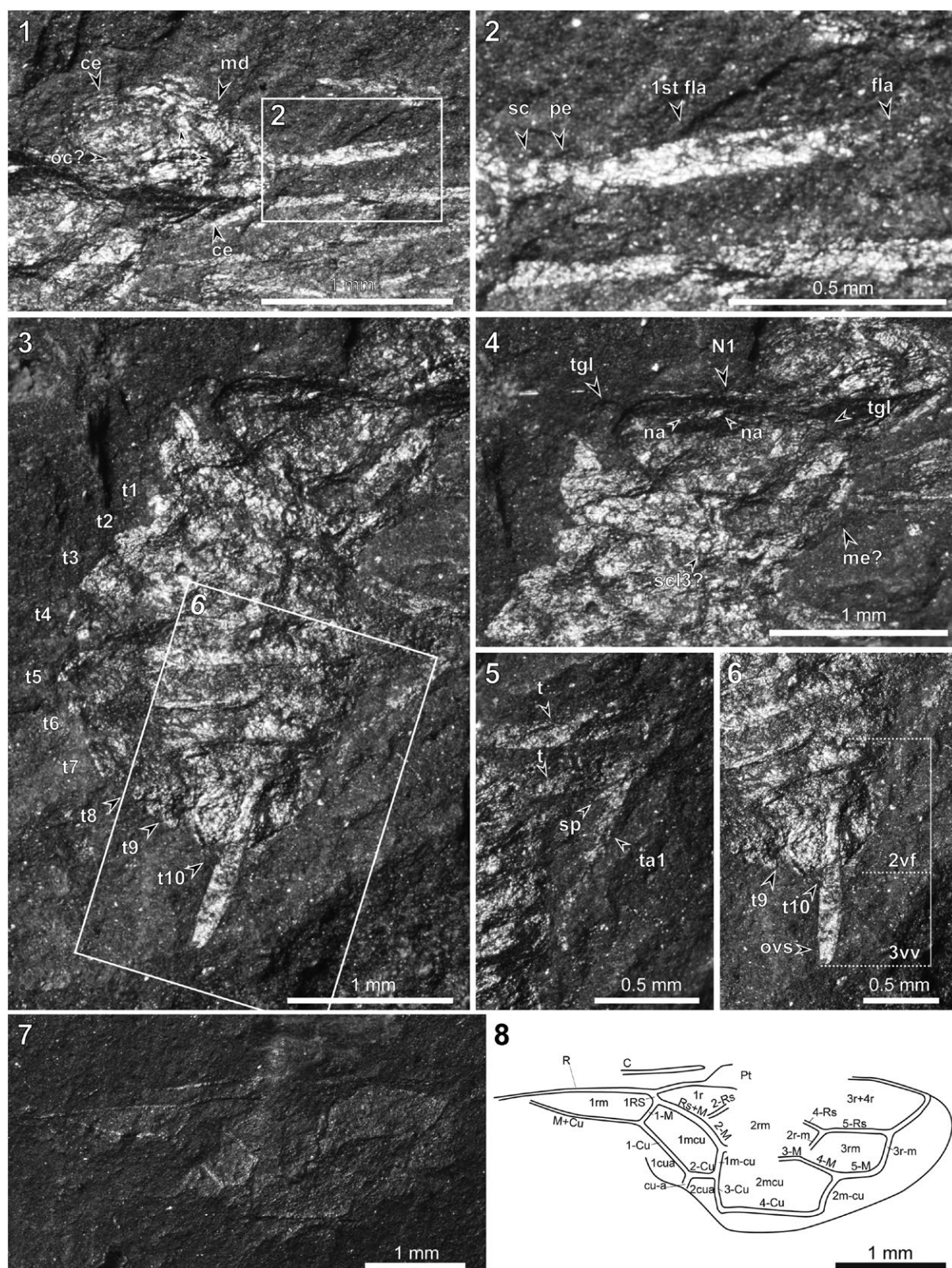


Fig. 4. Morphological details in †*Madygella* spp. from Ominé locality (Upper Triassic; Japan): (1–6), †*Madygella fujiiyamai* sp. n., holotype specimen MMHF3-00096; (1), head; (2), details of antenna (as located in 1); (3), thorax and abdomen; (4), details of thorax; (5), details of legs; (6), details of ovipositor (as located in 3); (7–8) †*Madygella* sp., specimen MMHF3-00099 (left forewing), photograph of positive adpression (7; flipped horizontally) and line drawing (8). See [Supplementary Table 2](#) for abbreviations.

Nomenclature

This paper and the nomenclatural acts it contains have been registered in Zoobank (www.zoobank.org), the official register of the International Commission on Zoological Nomenclature. The LSID (Life Science Identifier) number of the publication is: urn:lsid:zoobank.org:pub:EC640442-1112-467F-BCE5-44773D54E6E3

Results

Systematic Paleontology

Order Hymenoptera [Linnaeus 1758](#)

Suborder Symphyta [Gerstaecker 1867](#)

Family Xyelidae [Newman 1834](#)

Type genus. *Xyela* Dalman, 1819

Composition. Xyelinae [Newman 1834](#); Macroxyelinae [Ashmead 1898](#); †Archexyelinae [Rasnitsyn, 196](#); †Madygellinae [Rasnitsyn 1969](#); †Daohugoinae [Rasnitsyn and Zhang 2004](#).

Stratigraphic range. Middle/Late Triassic to Present.

Subfamily †Madygellinae [Rasnitsyn 1969](#)

Type genus. †*Madygella* [Rasnitsyn 1969](#)

Other genera. †*Chubakka* [Kopylov 2014](#) (Madygen locality); †*Samarkandykia* [Kopylov 2014](#) (Madygen and Ominé localities; for the latter, this study); †*Ominexyela* gen. sp. n. (Ominé locality; this study).

Stratigraphic range. Ladinian–Carnian (Triassic)

Occurrence. Madygen locality [Madygen Formation, Kyrgyz Republic; Ladinian–Carnian, Middle/Upper Triassic ([Shcherbakov 2008](#), [Voigt et al. 2017](#))]; Ominé locality [Momonoki Formation, Japan; Carnian, Upper Triassic ([Hase 1951](#), [Ishibashi et al. 1990](#))].

Revised diagnosis (modified from [Kopylov 2014](#)). Mandibles asymmetric, relatively large, bent and sickle-shaped; antenna with the first flagellomere enlarged, about five-six times as long as wide and apparently longer than following flagellomeres combined; ovipositor considerably long; forewing with narrow costal space; vein C thickened towards apex, sometimes almost reaching R while never contacting it and separated from Pt; vein Sc weak, joining only C, and sometimes preserved only at the wing base, transformed into fold or completely lost; pterostigma not sclerotized with its veins thickened; vein R straight up to the base of Rs with slight bend near the point of divergence of Rs; straight or arcuate antieriad within cell 1r without gap at base of pterostigma; vein Rs1 (anterior branch of Rs) lost without traces; vein M + Cu arcuate; cell 1mcu long and narrow, at least twice as long as wide; cell 1r along anterior margin subequal in length to 2r (except for *Ominexyela* gen. n.).

Comparison. The †Madygellinae differ from most other Xyelidae, except the extant *Xyela alberta* [Curran 1923](#) and the Upper Jurassic †*Lydoxyela excellens* [Rasnitsyn 1966](#), in the absence of 1-Rs. The †Madygellinae differ from all post-Triassic Xyelidae in the short cell 1r (subequal in length to cell 2r; with the exception of †*Ominexyela* gen. nov.). The subfamily differs from †Daohugoinae in the segmented distal flagellomeres, not completely sclerotized pterostigma, very

short Rs + M. Furthermore, it differs from Xyelinae, †Daohugoinae and Macroxyelinae in vein Sc without posterior branch, and in the narrow costal space (although a few exceptions exist in Xyelinae and Macroxyelinae). †Madygellinae also differs from Xyelinae in the apically thickened vein C; and from Macroxyelinae in the absence of characteristic sclerotization at the base of the pterostigma. Finally, it also differs from the Macroxyelinae in the long ovipositor.

Remarks. Relationships between subfamilies of Triassic Xyelidae are not fully elucidated ([Lara et al. 2014](#)). Based on wing venation characters, it has been argued that the †Madygellinae, previously known from wings only, derived from the †Archexyelinae ([Kopylov 2014](#)). One of the relevant character states regards the relative length of the 1r and 2r cells, subequal in length in both sub-families ([Lara et al. 2014](#)). The occurrence of this trait, unlikely to have been affected by post-depositional deformation, is confirmed in the new, well-preserved Ominé specimens ([Fig. 1](#)). To sum up, the †Madygellinae closely resembles the †Archexyelinae in morphological characters of forewing and body.

The material described below is informative on the range of body size and wing length in both subfamilies. Whereas the †Madygellinae have been previously regarded as generally small (ca. 3–6 mm in forewing length [Kopylov 2014](#)), the discovery of †*Ominexyela ishidai* gen. et sp. n., with its wing length of 9.6 mm and a body length of 17.2 mm, shows that the size range covered by the subfamily exceeds that of most other Xyelidae subfamilies [in †Archexyelinae, body length ranging from ca. 12.5 mm (†*Leioxyela mitis* [Rasnitsyn 1969](#)) to ca. 24.0 mm (†*Dinoxyela armata* [Rasnitsyn 1969](#)); in †Daohugoinae, from ca. 9.2 mm (†*Daohugoa longa* [Wang et al. 2019](#)) to ca. 17 mm (†*Daohugoa tobiassi* [Rasnitsyn and Zhang 2004](#)); in Xyelinae, from from ca. 4.2 mm (†*Xyela* (*Xyela*) *micrura* [Rasnitsyn 1995](#)) to ca. 13.0 mm (†*Xyelisca leptopoda* [Rasnitsyn 1969](#)); in Macroxyelinae, from ca. 5.0 mm (†*Microxyelecia brachycera* [Rasnitsyn 1969](#)) to ca. 19 mm (†*Ophthalmoxyela brachyura* [Rasnitsyn, 1966](#)); [Table 1](#)].

Genus †*Madygella* [Rasnitsyn, 1969](#)

Type species. †*Madygella analoga* [Rasnitsyn, 1969](#).

Other species. †*Madygella aristovi* [Kopylov 2014](#) (Madygen locality); †*Madygella bashkuevi* [Kopylov, 2014](#) (Madygen locality); †*Madygella kurochkini* [Kopylov, 2014](#) (Madygen locality); †*Madygella levivenosa* [Kopylov, 2014](#) (Madygen locality); †*Madygella humioi* [Oyama & Maeda, 2020](#) (Ominé locality); †*Madygella fujiiyamai* sp. n. (Ominé; this study)

Occurrence. Madygen locality [Madygen Formation, Kyrgyz Republic; Ladinian–Carnian, Middle/Upper Triassic ([Shcherbakov 2008](#), [Voigt et al. 2017](#))]; Ominé locality [Momonoki Formation, Japan; Carnian, Upper Triassic ([Hase 1951](#), [Ishibashi et al. 1990](#))].

Revised diagnosis. †*Madygella* can be distinguished from other madygellines by a smaller size (4.8 mm in total body length; 2.8–4.9 mm in forewing length); extremely short pronotum, with its anterior margins arcuated; mesonotum nearly triangle-shaped; forewing with vein 1-Rs shorter than Rs + M and rarely longer than 1-M; combined length of the cells 1r and 2r rarely shorter than that of 3r + 4r; height of the cell 3r + 4r nearly as high as that of 2r and pterostigma, sometimes height of cell 3r + 4r lower than that of 2r and pterostigma; vein Rs forming a clear angle at the point of connection with 2r-m.

Table 1. List of Triassic Xyelidae

Taxon	Deposit				Reference	Wing length (mm)	Body length (mm)
	Locality name	Age	Geological Formation	Country			
Madygellinae							
<i>Chubakca madygensis</i>	Madygen	Ladinian-Carnian	Madygen Formation	Kyrgyz Rep.	Kopylov 2014	2.3	–
<i>Madygella analoga</i>	Madygen	Ladinian-Carnian	Madygen Formation	Kyrgyz Rep.	Rasnitsyn 1969; Kopylov 2014	4.9	–
<i>M. aristovi</i>	Madygen	Ladinian-Carnian	Madygen Formation	Kyrgyz Rep.	Kopylov 2014	3.7	–
<i>M. bashkuevi</i>	Madygen	Ladinian-Carnian	Madygen Formation	Kyrgyz Rep.	Kopylov 2014	4.2	–
<i>M. kurochkini</i>	Madygen	Ladinian-Carnian	Madygen Formation	Kyrgyz Rep.	Kopylov 2014	3.2	–
<i>M. leviventosa</i>	Madygen	Ladinian-Carnian	Madygen Formation	Kyrgyz Rep.	Kopylov 2014	3.4	–
<i>M. humioi</i>	Ominé	Carnian	Momonoki Formation	Japan	Oyama and Maeda 2020	4.4	–
<i>M. fujiyama</i> sp. n.	Ominé	Carnian	Momonoki Formation	Japan	This study	2.8	4.8
<i>M. sp</i>	Ominé	Carnian	Momonoki Formation	Japan	This study	4.3	–
<i>Ominexyela ishidai</i> gen. sp. n.	Ominé	Carnian	Momonoki Formation	Japan	This study	9.6	17.2
<i>Samarkandykia ryzhkovae</i>	Madygen	Ladinian-Carnian	Madygen Formation	Kyrgyz Rep.	Kopylov 2014	4.7	–
<i>S. shmakovi</i>	Madygen	Ladinian-Carnian	Madygen Formation	Kyrgyz Rep.	Kopylov 2014	6.4	–
<i>S. baradai</i> sp. n.	Ominé	Carnian	Momonoki Formation	Japan	This study	5.6	–
<i>S. noharai</i> sp. n.	Ominé	Carnian	Momonoki Formation	Japan	This study	6.5	–
<i>S. sp.</i>	Ominé	Carnian	Momonoki Formation	Japan	This study	3.4	–
Archexyelinae							
<i>Archexyela crosbyi</i>	Mt. Crosby	Carnian	Mt. Crosby Formation	Australia	Riek 1955	9.0	–
<i>Archexyela ipswichensis</i>	Mt. Crosby	Carnian	Mt. Crosby Formation	Australia	Engel 2005	10.0	–
<i>Asioxyela parvula</i>	Madygen	Ladinian-Carnian	Madygen Formation	Kyrgyz Rep.	Rasnitsyn 1969	5.0	–
<i>Asioxyela paumra</i>	Madygen	Ladinian-Carnian	Madygen Formation	Kyrgyz Rep.	Rasnitsyn 1969	10.0–11.0	12.0–13.0
<i>Asioxyela smilodon</i>	Madygen	Ladinian-Carnian	Madygen Formation	Kyrgyz Rep.	Rasnitsyn 1964	7.0	over 11.2
<i>Asioxyela grandipennis</i>	Madygen	Ladinian-Carnian	Madygen Formation	Kyrgyz Rep.	Rasnitsyn 1964, 1969	14.0	–
<i>Dinoxyela armata</i>	Madygen	Ladinian-Carnian	Madygen Formation	Kyrgyz Rep.	Rasnitsyn 1969	–	24.0
<i>Euryxyela euryptera</i>	Madygen	Ladinian-Carnian	Madygen Formation	Kyrgyz Rep.	Rasnitsyn 1964	8.7	–
<i>Ferganoxyela destructa</i>	Madygen	Ladinian-Carnian	Madygen Formation	Kyrgyz Rep.	Rasnitsyn 1969	14.0	–
<i>Ferganoxyela sogdiana</i>	Madygen	Ladinian-Carnian	Madygen Formation	Kyrgyz Rep.	Rasnitsyn 1969	7.0	–
<i>Leioxyela antiqua</i>	Madygen	Ladinian-Carnian	Madygen Formation	Kyrgyz Rep.	Rasnitsyn 1964, 1969	9.5	–
<i>Leioxyela grandis</i>	Madygen	Ladinian-Carnian	Madygen Formation	Kyrgyz Rep.	Rasnitsyn 1969	15.0	–
<i>Leioxyela mitis</i>	Madygen	Ladinian-Carnian	Madygen Formation	Kyrgyz Rep.	Rasnitsyn 1969	11.5	15.5

Table 1. Continued

Taxon	Deposit			Reference	Wing length (mm)	Body length (mm)
	Locality name	Age	Geological Formation			
<i>Leioxyela mollis</i>	Madygen	Ladinian-Carnian	Madygen Formation	Rasnitsyn 1969	8.0–9.0	16.0
<i>Leioxyela lata</i>	Madygen	Ladinian-Carnian	Madygen Formation	Rasnitsyn 1964, 1969	6.2	–
<i>Lithoxyela fenestralis</i>	Madygen	Ladinian-Carnian	Madygen Formation	Rasnitsyn 1969	11.0	–
<i>Madygenius extraradius</i>	Madygen	Ladinian-Carnian	Madygen Formation	Rasnitsyn 1969	6.0–8.0	7.7
<i>Madygenius primitivus</i>	Madygen	Ladinian-Carnian	Madygen Formation	Rasnitsyn 1969	9.0	–
<i>Microxyela minuta</i>	Madygen	Ladinian-Carnian	Madygen Formation	Denisova et al. 2023	3.8	–
<i>Oryctoxyela anomala</i>	Madygen	Ladinian-Carnian	Madygen Formation	Rasnitsyn 1969	12.0	–
<i>Oryctoxyela triassica</i>	Madygen	Ladinian-Carnian	Madygen Formation	Rasnitsyn 1969	10.0	–
<i>Triassoxyela foveolata</i>	Madygen	Ladinian-Carnian	Madygen Formation	Rasnitsyn 1964	6.3	7.5
<i>Triassoxyela kirgizica</i>	Madygen	Ladinian-Carnian	Madygen Formation	Rasnitsyn 1964	11.5	–
<i>Triassoxyela orycta</i>	Madygen	Ladinian-Carnian	Madygen Formation	Rasnitsyn 1969	14.0	26.0
<i>Triassoxyela sharovi</i>	Madygen	Ladinian-Carnian	Madygen Formation	Denisova et al. 2023	4.3	–
<i>Xiphoxxyela procrusta</i>	Madygen	Ladinian-Carnian	Madygen Formation	Rasnitsyn 1969	14.0	19.0–22.0
<i>Xiphoxxyela? striata</i>	Madygen	Ladinian-Carnian	Madygen Formation	Rasnitsyn 1964	8.0	7.0
<i>Xyelinus angustiradius</i>	Madygen	Ladinian-Carnian	Madygen Formation	Rasnitsyn 1964	6.0	–
<i>Xyelinus major</i>	Madygen	Ladinian-Carnian	Madygen Formation	Rasnitsyn 1969	8.0	–
<i>Xyelinus scherbachovi</i>	Madygen	Ladinian-Carnian	Madygen Formation	Denisova et al. 2023	4.6	–
Xyelinae?						
<i>Poterilloxyela menendezi</i>	Puesto Miguez	Carnian	Poterillos Formation,	Lara et al. 2014	6.4	–
Subfamily incertae sedis						
<i>Moltenia rieki</i>	Molteno	Carnian	Molteno Formation	Schlüter 2000	8.0	–

Body (including ovipositor) and wing length data are used from original description. –, unpreserved.

†*Madygella fujiiyamae* sp. n.

urn:lsid:zoobank.org:act:0D8597AA-0C19-49E0-8E30-9266287639BC

Figs. 3 and 4.1–6

Etymology. The specific epithet honors Inenori Fujiyama, a Japanese paleontologist, for his valuable contribution to the knowledge of Japanese fossil insects.

Holotype. MMHF3-00096, a well-preserved female individual with most of the body preserved (Fig. 3).

Occurrence. Ominé locality [Momonoki Formation, Japan; Carnian, Upper Triassic (Hase 1951, Ishibashi et al. 1990)].

Diagnosis. Forewing characters: small (3 mm or less in length); section of vein R shortly after the origin of Rs straight; vein Rs + M about six times as long as 1-Rs; veins 2r-m and 2r-rs subequal in length; vein 3-Cu longer than the 1m-cu; pterostigma unsclerotized.

Description. Body length (excluding antenna but including ovipositor) 4.8 mm, width 1.8 mm; color pattern not preserved.

Head (Figs. 3.1,3 and 4.1–2) nearly circular and massive (Fig. 3.1), 0.7 mm in length with mandible, and 0.8 mm in width (as wide as thorax; Fig. 3.1 and 3); compound eyes (0.4 mm in length and 0.1 mm in width) relatively large, oval and located on lateral sides of head (Fig. 4.1), ocelli distinguishable; clypeus wavy and anteriorly slightly projecting at middle of head (Figs. 3.1,3 and 4.1); frons distinguishable; mandibles asymmetric, relatively large, bent and sickle-shaped (Fig. 4.1); scape, pedicel, and flagellum distinguishable (Fig. 4.1–2), antenna with first flagellomere enlarged, measuring 0.5 mm in length (nearly five times greater than width) and extremely longer than rest of the flagellomeres combined (Fig. 3.2), and antennal sockets located between compound eyes near mandible bases (Fig. 3.1).

Thorax (Figs. 3.1,3 and 4.4–5) almost as wide as head (Fig. 3.1,3), 1.1 mm in length and 1.4 mm in width for tegulae (Fig. 4.4); pronotum extremely short and its anterior margin arcuated (Fig. 4.4); mesonotum with medial line, tegulae, and notauli strongly impressed, without transscutal articulation (Fig. 4.4); mesonotum nearly triangle, anterior margin of mesonotum slightly arcuated and positor margin of mesonotum strongly arcuate (Figs. 3.3 and 4.4); median mesoscutal sulcus reaching to mesoscutellum (Figs. 3.3 and 4.4); notauli connected and forming “V” in anterior part of mesonotum (Figs. 3.3 and 4.4); the mesoscuto-scutellar sulcus forming a “V” that diverges posteriorly (Fig. 4.4); metanotum with small metascutellum, cenchri and metapostnotum unidentifiable (Fig. 4.4); some legs (coxa, femur, tibia, tarsus) observable, femur (of an undetermined leg) with one apical spur (Fig. 4.5).

Abdomen (Figs. 3.1–2 and 4.3,6), 2.4 mm in length without ovipositor sheath (with each tergum length being 0.3 mm, 0.3 mm, 0.3 mm, 0.2 mm, 0.2 mm, 0.2 mm, 0.2 mm, 0.3 mm, 0.2 mm, 0.1 mm from 1st to 10th, respectively), and 1.4 mm in width at the 1st tergum which splits medially (Figs. 3.1,3 and 4.3); ovipositor sheath long with constant width from the base to end of apical section (Fig. 4.6), 1.3 mm in length (0.7 mm for valvifer 2 and 0.6 mm for its valvula 3), 0.1 mm in width (length ratio of 0.08), and ovipositor unobservable.

Forewing: 2.8 mm long as preserved (to the end of the cell 2mcu), 1.2 mm wide (Fig. 3.2,4,5); C straight; costal space narrow and with nearly constant width from the base; Sc reaching C opposite base of Rs; R shortly after base of Rs straight and slightly dilating; Pt not

sclerotized with veins running along its periphery thick; 1r-rs weakly proclival; 2r-rs vertical, shorter than 4-Rs, and 1.6 times as long as 1r-rs; base of 2r-rs 3 times as close to apex of Pt as to 1r-rs; 1-Rs much shorter than 1-M; Rs + M about six times as long as 1-Rs; 2-Rs straight; 2r-m vertical, and as long as 2r-rs; 3-M straight.

Comparison. Despite the lack of most the apical part of the forewing in the holotype (and only known specimen), the small size, and (i) vein Rs curved at the point of 2r-m and (ii) vein 1-Rs shorter than 1-M and Rs + M support an assignment to the genus †*Madygella*. The species differs from †*M. aristovi*, †*M. bashkuevi*, and †*M. kurochkini* in Sc reaching C opposite the base of Rs, from †*M. levivenosa* and †*M. humioi* in the straighter section of R shortly after the origin of Rs. The species resembles *M. analoga* in the subequal lengths of the 2r-m and 2r-rs cells, and the 3-Cu longer than the 1m-cu cell, whereas it possesses an unsclerotized Pt in forewing unlike *M. analoga*. Therefore, the erection of a new species to accommodate the specimen MMHF3-00096 is justified.

†*Madygella* sp.

Fig. 4.7–8

Material. MMHF3-00099, a left forewing adpression with most of the median area of the wing, a section of C and the postero-basal area missing (Fig. 4.7–8).

Occurrence. Ominé locality [Momonoki Formation, Japan; Carnian, Upper Triassic (Hase 1951, Ishibashi et al. 1990)].

Description. Forewing 4.3 mm long, 1.5 mm wide (Fig. 4.7–8); costal space narrow; vein R basal to base of RS slightly arcuate, straight distal to base of RS and slightly dilating; vein 1-Rs much shorter than 1-M; vein Rs + M about four times longer than 1-Rs; vein 2-RS straight (2-RS joining RS + M); vein 1m-cu shorter than 3-Cu.

Comparison. The forewing of the specimen MMHF3-00099 has vein Rs forming a clear angle at the point of connection with 2r-m, and vein 1-Rs shorter than 1-M and Rs + M. These features are consistent with the diagnosis of †*Madygella*. The forewing length of MMHF3-00099 (4.5 mm) exceeds that of most other †*Madygella* species, with the exception of †*M. analoga* (4.9 mm). However, the lack of data on the pterostigma, and on veins 1r-rs, 2r-rs, 3-Rs and part of 3-M precludes any further comparison with this species. For these reasons the specimen MMHF3-00099 is best considered as †*Madygella* sp. Yet, further comparison with known †*Madygella* species is possible. The specimen MMHF3-00099 differs from †*M. bashkuevi*, †*M. kurochkini*, †*M. levivenosa* and †*M. humioi* in straight R at the base of Rs. MMHF3-00099 resembles †*M. fujiiyamae* sp. n. in straight R at the base of Rs, whereas MMHF3-00099 possesses slightly arcuated R within the cell 1r.

Genus †*Samarkandykia* Kopylov, 2014

Type species. †*Samarkandykia rzyzhkovae* Kopylov, 2014.

Other species. †*Samarkandykia shmakovi* Kopylov, 2014 (Madygen locality); †*Samarkandykia noharai* sp. n. (Ominé locality; this study); †*Samarkandykia baradai* sp. n. (Ominé locality; this study).

Occurrence. Madygen locality [Madygen Formation, Kyrgyz Republic; Ladinian–Carnian, Middle/Upper Triassic

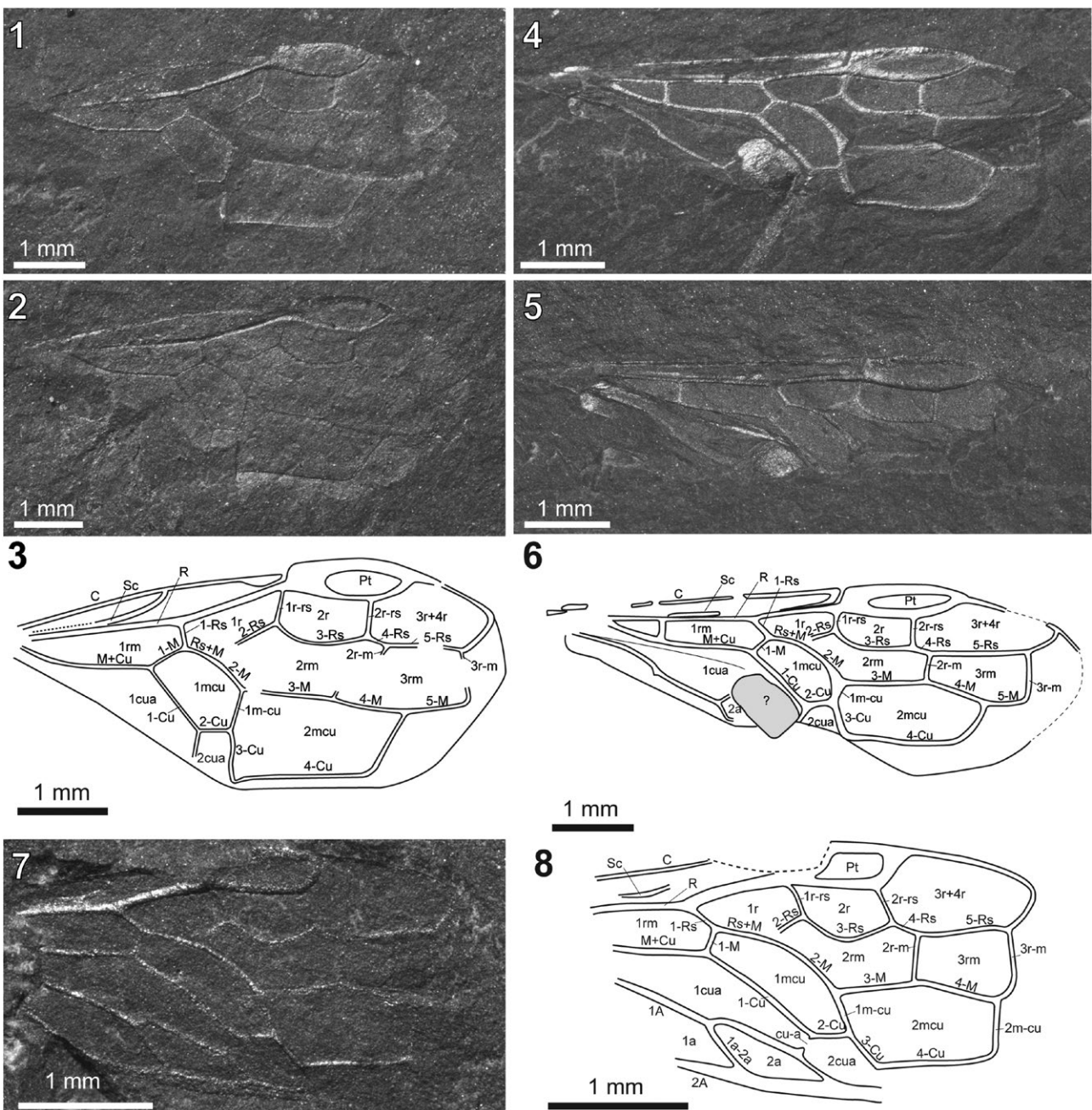


Fig. 5. Wing venation in †*Samarkandykia* spp. from Ominé locality (Upper Triassic; Japan): (1–3), †*Samarkandykia haradai* sp. n., holotype specimen KMNH IP 000,101 (right forewing), photographs of positive (1) and negative (2; flipped horizontally) adpressions, and line drawing (3; with the disrupted, posterior area tentatively relocated as if undamaged); (4–6), †*Samarkandykia noharai* sp. n., holotype specimen MMHF3-00097 (right forewing), photographs of positive (4) and negative (5; light-mirrored, flipped horizontally) adpressions, and line drawing (6); (7 and 8) †*Samarkandykia* sp., specimen MMHF3-00098 (right forewing), photograph of positive adpression (7) and line drawing (8). See [Supplementary Table 2](#) for abbreviations.

(Shcherbakov 2008, Voigt et al. 2017)]; Ominé locality [Momonoki Formation, Japan; Carnian, Upper Triassic (Hase 1951, Ishibashi et al. 1990)].

Revised diagnosis (modified from Kopylov 2014). Forewing medium-sized (4.5–6.5 mm); combined length of cells 1r and 2r longer than that of 3r + 4r; height of cells 3r + 4r lower than combined height of 2r and pterostigma; veins running along periphery of pterostigma sclerotized; veins Rs (4-Rs and 5-Rs) straight at the point of connection with 2r-m (2r-m lost in †*S. ryzhkovae*), vein 1-Rs subequal or longer than 1-M.

†*Samarkandykia haradai* sp. n.

urn:lsid:zoobank.org:act:69D2E5A6-D2AC-459F-AD6B-07F2E96B8DCB

Fig. 5.1–3

Etymology. The specific name honors Takayoshi Harada, who collected the holotype and donated it to KMNH.

Holotype. KMNH IP 000,101, well-preserved adpression of a right forewing in dorsal and ventral aspects, anal area missing, postero-distal area disrupted from the rest of the wing (Fig. 5.1–3).

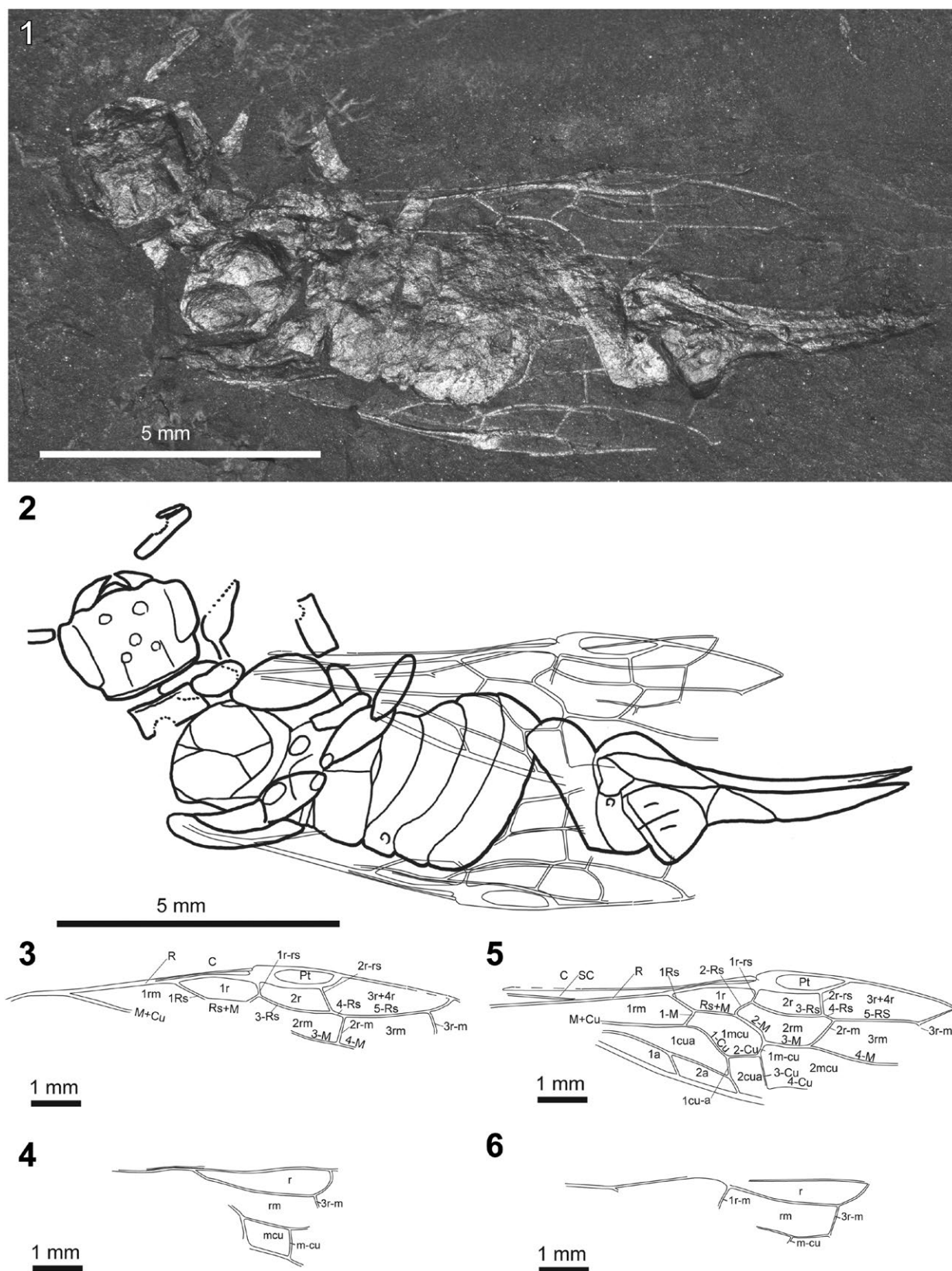


Fig. 6. †*Ominexyela ishidai* gen. et sp. n., (Ominé; Upper Triassic; Japan), holotype specimen MMHF3-00100, dorsal view: (1 and 2), specimen overview, photograph (1) and line drawing (2); (3–5), details of wing venation, line drawings; (3 and 4), left forewing (3) and hindwing (4) (flipped horizontally); (5 and 6) right forewing (5) and hindwing (6). See [Supplementary Table 2](#) for abbreviations.

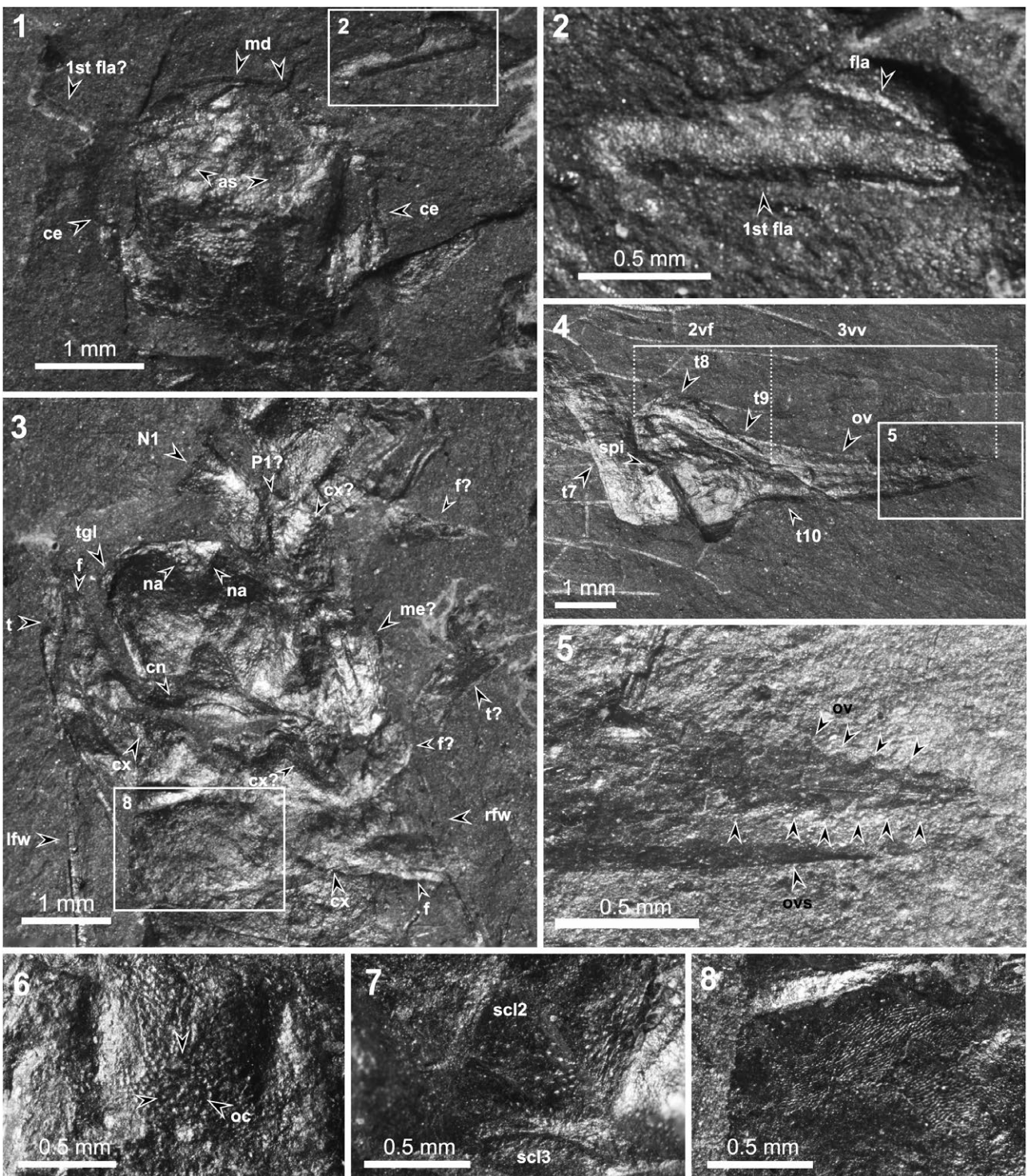


Fig. 7. Morphological details in †*Ominexyela ishida* gen. et sp. n. (Ominé, Upper Triassic, Japan): (1), head; (2), detail of antenna (as indicated in 1); (3) thorax and anterior part of abdomen; (4) ovipositor overview, with indications of ovipositor section; (5) detail of apical part of ovipositor (as indicated in 4; white arrows indicating teeth); (6) surface structure of head; (7) surface structure of thorax; (8) surface structure of abdomen (as indicated in 3). See [Supplementary Table 2](#) for abbreviations.

Occurrence. Ominé locality [Momonoki Formation, Japan; Carnian, Upper Triassic; (Hase 1951, Ishibashi et al. 1990)].

Diagnosis. Forewing characters: from wing base to the base of pterostigma, vein C distinctly arcuated (i.e., costal space wide, gradually broadening from base to its middle, then narrowing); vein Sc

developed over its entire length; vein R straight distal to origin of Rs; vein 3r-m shorter than 2r-m.

Description. Forewing 5.6 mm long, 2.7 mm wide (Fig. 5.1–3); vein C exhibiting an arcuate line from base to anterior margin; costal space wide, gradually widening from base to middle, then narrows



Fig. 8. Reconstruction of †*Ominexyela ishidaï* gen. et sp. n. (courtesy of Takumi).

to apex; vein Sc developed over entire length, joining C basal to base of Rs; vein R at base of Rs and within cell 1r straight; pterostigma not completely sclerotized, with its anterior edge particularly thick; combined length of cells 1r and 2r longer than that of 3r + 4r; height of cells 3r + 4r lower than combined height of 2r and pterostigma; vein 1r-rs weakly inclined; vein 2r-rs vertical, longer than 4-Rs, nearly as long as 1r-rs; base of vein 2r-rs three times as close to apex of pterostigma as to 1r-rs; vein 1-Rs slightly shorter than 1-M; vein Rs + M about 1.2 times as long as than 1-Rs; vein 2-Rs straight; vein 5-Rs five times longer than 4-Rs; cell 3r + 4r narrowing gradually from the base to the apex; vein 2r-rm greatly inclined, 2.3 times longer than 2r-rs; 3r-m shorter than 2r-m; vein 3-Cu 1.3 times as long as 1m-cu and forming a straight line with 1m-cu; free ends of veins M and Cu lost; vein 3r-m gradually passing into 5-M; vein 2m-cu gradually passing into 4-Cu; vein 3-M straight.

Comparison. Several diagnostic characters on KMNH IP 000,101 such as (i) pterostigma not completely sclerotized, with its anterior edge particularly thick, (ii) combined length of the cells 1r and 2r longer than that of 3r + 4r; height of the cells 3r + 4r lower than the combined height of 2r and pterostigma, (iii) vein 1-Rs slightly longer than 1-M and (iv) vein Rs (4-Rs and 5-Rs) straight at the point of connection with 2r-m, support an assignment to the genus †*Samarkandykia*. †*Samarkandykia haradai* sp. n. differs from †*S. ryzhkonae* and †*S. shmakovi* in the straighter vein R at the base of Rs, the vertical vein 2r-rs, and the free ends of veins M and Cu being lost. †*S. haradai* sp. n. resembles †*S. noharai* sp. n. (described below) in vein 2r-m being inclined, and the free end of veins M and Cu lost, but unlike it the present species possesses a straight vein 2-Rs,

and vein Sc developed over its entire length (i.e., until it reaches C), joining C basal to Rs base.

Remarks. Fig. 5.3 provides a tentative reconstruction of the complete forewing, with the posterior-distal area tentatively relocated as if undamaged.

†*Samarkandykia noharai* sp. n.

urn:lsid:zoobank.org:act:8A62080F-A548-46E0-81CD-737BB29D4E31

Fig. 5.4–6

Etymology. The specific name honors Masanori Nohara, who collected the holotype and donated it to MMHF.

Holotype. MMHF3-00097, well-preserved adpression of a right forewing in dorsal and ventral aspects, with base and apex missing (Fig. 5.4–6).

Occurrence. Ominé locality [Momonoki Formation, Japan; Carnian, Upper Triassic; (Hase 1951, Ishibashi et al. 1990)].

Diagnosis. Forewing characters: vein Sc developed over its entire length, joining C opposite 1r-rs; base of vein 2r-rs about 2.4 times as close to apex of pterostigma as to 1r-rs; vein 2r-m slightly inclined, 1.3 times shorter than 2r-rs; vein 3r-m 1.9 times as long as 2r-rs; vein Rs + M about 1.7 times as long as 1-Rs.

Description. Forewing 6.5 mm long, 2 mm wide (Fig. 5.4–6); vein C straight; costal space moderately wide, and nearly constant in width

from the base; vein Sc developed over entire length, joining C at the point of 1r-rs and sclerotized; vein R at base of Rs straight and within cell 1r weakly arcuate; pterostigma not completely sclerotized, with enclosing veins particularly thick at base; combined length of cells 1r and 2r longer than that of 3r + 4r; height of cell 3r + 4r lower than combined height of 2r and pterostigma; veins 1r-rs and 2r-rs vertical vein 2r-rs longer than 4-Rs, two times as long as 1r-rs; base of vein 2r-rs two times closer to apex of pterostigma than to 1r-rs; vein 1-Rs subequal in length to 1-M; vein Rs + M about five times as long as 1-Rs; vein 2-Rs weakly arcuate; vein 5-Rs five times as long as 4-Rs; cells 3r + 4r gradually narrowing from base to apex; vein 2r-m slightly inclined, 1.3 times shorter than 2r-rs; vein 3r-m 1.9 times as long as 2r-m; vein 3-Cu 1.8 times as long as 1m-cu, forming weakly arcuate line with 1m-cu; free ends of veins M and Cu lost; vein 3r-m gradually passing into 5-M; vein 2m-cu gradually passing into 4-Cu; vein 3-M straight.

Comparison. Several diagnostic characters on MMHF3-00097 such as (i) pterostigma not completely sclerotized, while its vein is particularly thick at the base, (ii) combined length of the cells 1r and 2r longer than that of 3r + 4r; height of the cells 3r + 4r lower than the combined height of 2r and pterostigma, (iii) vein 1-Rs subequal in length to 1-M and (iv) vein Rs (4-Rs and 5-Rs) straight at the point of connection with 2r-m support an assignment to the genus †*Samarkandykia*. Like †*S. haradai* sp. n., †*S. noharai* sp. n. differs from †*S. ryzhkovae* and †*S. shmakovi* in the straight vein R at the base of Rs, the vertical vein 2r-rs, and the free ends of veins M and Cu being lost. Also, vein 3-Cu is much longer than 1m-cu. The present species differs from †*S. haradai* sp. n. in vein 2-Rs weakly arcuate, and vein R within the cell 1r weakly arcuate. Vein Sc running when visible close to R until forming a bridge to C apex next to pterostigma base is possibly a unique character state of all Hymenoptera.

Remarks. †*Samarkandykia noharai* sp. n. bears a vein connecting R and M-Cu near base of 1rm cell. It probably represents an individual aberration because this morphological feature was found in no other species of Hymenoptera, extinct or extant.

†*Samarkandykia* sp.

Fig. 5.7–8

Specimen. MMHF3-00098, a right forewing adpression with most of basal part missing and a small portion of the apex (Fig. 5.7–8).

Occurrence. Ominé locality [Momonoki Formation, Japan; Carnian, Upper Triassic (Hase 1951, Ishibashi et al. 1990)].

Description. Forewing 3.4 mm long, 1.8 mm wide (Fig. 5.7–8); costal space moderately wide; vein Sc fragmentary, distant from R as preserved, possibly reaching C near level of Rs base; vein R at base of Rs curving slightly; vein R weakly arcuate within cell 1r; pterostigma not sclerotized, and its vein thickened; veins 1r-rs and 2r-rs proclival vein 2r-rs almost as long as 1r-rs; base of vein 2r-rs four times closer to apex of pterostigma than to 1r-rs; vein 1-Rs longer than 1-M; vein Rs + M longer than 1-Rs; vein 2-Rs straight; vein 5-Rs about three times as long as 4-Rs; cell 3r + 4r gradually narrowing from the base to the apex; vein 2r-m vertical, and longer than 2r-rs; vein 3r-m 1.5 times as long as 2r-m; vein 3-Cu approximately as long as 1m-cu, and forming a weak arcuate line with 1m-cu; free ends of veins M and Cu lost; vein 2m-cu gradually passing into 4-Cu; vein 3-M straight.

Comparison. The specimen MMHF3-00098 is small, and displays a strong sclerotization of the pterostigma edges, a combined length of the cells 1r and 2r longer than that of 3r + 4r, the height of the cell 3r + 4r lower than the combined height of 2r and pterostigma, 4-Rs and 5-Rs straight at the joint for 2r-m, and vein 1-Rs longer than 1-M. These features allow an assignment to the genus †*Samarkandykia*.

Compared with other species in this genus, the specimen MMHF3-00098 is most similar to other Ominé species in the lack of the distal ends of M and Cu and a wide costal space. More particularly, it is most similar to †*S. haradai* sp. n. owing to vein 3r-m being 1.5 times as long as 2r-m. However, the specimen MMHF3-00098 lacks several critical areas, including the end of vein Sc and part of the pterostigma base, making it impossible to assess its actual specific identity.

The specimen MMHF3-00098 can also be compared with †*S. shmakovi*, with which it shares a vein 3-Cu approximately as long as 1m-cu (but differs from it due to a wider costal space and Rs + M longer than 1-Rs). Finally, the specimen MMHF3-00098 differs from †*S. ryzhkovae* in vein 3-Cu approximately as long as 1m-cu, and the absence of the free ends of veins M and Cu.

Genus †*Ominexyela* gen. n.

urn:lsid:zoobank.org:act:24447BBB-5ADC-4EB2-878F-75D9FF650FE5

Etymology. The genus name combines the name of the type locality, Ominé, with the suffix “xyela,” traditionally used from Xyelidae.

Type species. †*Ominexyela ishidai* sp. n.

Species composition. Only †*Ominexyela ishidai* sp. n. (Carnian, Japan)

Occurrence. Ominé locality [Momonoki Formation, Japan; Carnian, Upper Triassic (Hase 1951, Ishibashi et al. 1990)].

Diagnosis. Body large (13.7 mm, excluding antenna and ovipositor); clypeus wavy and strongly projecting anteriorly at middle of head; pronotum rectangular with edged anterior margin; abdominal tergum 10 exceptionally long and cone-shaped; ovipositor extremely long and gradually narrowing to apex, apical section with teeth; forewing over 9 mm long, vein C having an arcuate line from base to the apex; costal space extremely narrow, especially opposite cell 1r; veins 4-Rs and 5-Rs almost aligned; vein 1-Rs longer than half of Rs + M; cell 3r + 4r narrow; vein 3-Cu clearly longer than 1m-cu.

Comparison. The genus shares diagnostic features of †Madygellinae, as follows: narrow costal space; vein Sc weakly developed; pterostigma not sclerotized, with its edges thickened; vein Rs simple (i.e., without anterior branch).

Compared with known †Madygellinae genera, the new genus is morphologically similar to †*Samarkandykia* in veins 4-Rs and 5-Rs being sub-aligned at the joint with 2r-m, and vein 1-Rs longer than 1-M. It differs from †*Samarkandykia* by the following traits: larger size (best appreciated using forewing length, with 9.6 mm in the type species, but 4.5–6.5 mm in †*Samarkandykia* spp., known from isolated wings); vein Sc vanishing before reaching C; costal space extremely narrow (particularly opposite the 1r cell). From other madygelline genera it differs as follows: from †*Madygella*, in having a larger body size (4.8 mm in †*Madygella fujiyamai* sp. n.), strongly

projected clypeus, nearly circular mesonotum, small mesoscutellum, and straight veins 4-Rs and 5-Rs at the joint with 2r-m; and from †*Chubakka* in bearing narrow cell 3r + 4r, straight veins 4-Rs and 5-Rs at the joint with 2r-m, and vein 5-Rs longer than 4-Rs. This justifies erection of the new genus.

†*Ominexyela ishidai* sp. n.

urn:lsid:zoobank.org:act:A3CB2E2B-6135-428C-B1B7-BED4B7A58321

Figs. 6–8

Etymology. The specific name honors Hideo Ishida, a fossil collector who collected the holotype and donated it to MMHF.

Holotype. MMHF3-00100, a well-preserved female individual with most of the body preserved (Figs. 6 and 7). The specimen was previously illustrated on plate 7.4 in Takahashi et al. (1997).

Diagnosis. As for the genus.

Description. Body (excluding antenna and ovipositor) 13.7 mm in length, and 3.3 mm in width at the widest part; color pattern not preserved (Fig. 6).

Head (Figs. 6.1,2 and 7.1–2,6) nearly circular and massive (Fig. 7.1), 2.3 mm in length with mandible, 2.6 mm in width (as wide as thorax; Fig. 7.1,2), and with densely distributed pits (Fig. 7.6); compound eyes (1.2 mm in length and 0.5 mm in width) relatively large, oval, and located laterally on the head (Fig. 7.1); ocelli in low triangle (Fig. 7.6); clypeus wavy and strongly projecting anteriorly at the middle of the head (Fig. 7.1); two parallel lines present on the occiput (Fig. 7.1); mandibles asymmetrical in size, relatively large, bent and sickle-shaped (Fig. 7.1); antennal sockets located between compound eyes distant from mandible bases; scape and pedicel indistinguishable; first flagellomere of antenna nearly six times longer than wide (1.2 mm in length and 0.2 mm in width) and longer than the rest of the flagellomeres combined (Fig. 7.1,2).

Thorax (Figs. 6.1,2, and 7.3,7) 2.6 mm long (0.3 mm for pronotum and 2.3 mm for mesonotum and metanotum) and 2.3 mm wide at tegulae (Fig. 7.3), i.e., nearly as wide as head (Figs. 6.1,2), with sparse pits present on its surface (Fig. 7.7); pronotum rectangular, with ridge on part of anterior margin (Fig. 7.3); mesonotum nearly circular, anterior and posterior margins of mesonotum slightly arcuated (Fig. 7.3), with medial mesoscutal sulcus, tegulae, and notauli strongly impressed, with no transscutal articulation (Fig. 7.3); medial mesoscutal sulcus reaching to mesoscutellum (Figs. 6.2 and 7.3); notaulus forming a “V” at anterior part of mesonotum (Fig. 7.3); mesoscuto-scutellar sulcus forming “V” pointing anteriorly (Fig. 7.3); metascutum with small metascutellum and cenchri, and metapostnotum unidentifiable (Fig. 7.3); coxa, femur, and tibia preserved (Figs. 6.1,2 and 7.3).

Abdomen (Figs. 6.1,2 and 7.3–5,8) 8.3 mm long (excluding ovipositor sheath) and 2.9 mm wide at the 1st tergum (Figs. 7.1–2), with a total of 10 terga (from the 1st to 10th tergum, length of 0.6 mm, 1.5 mm, 0.5 mm, 0.7 mm, 0.7 mm, 0.6 mm, 0.8 mm, 1.0 mm, 0.9 mm, and 1.0 mm, respectively); 1st tergum split medially (Figs. 6.1–2 and 7.3); dense network of ridges, somewhat fingerprint-like, present on surface of the 2nd tergum (Fig. 7.8); 10th tergum elongate and cone-shaped (Fig. 7.4); spiracles visible on the 4th and 8th terga (Fig. 6.1–2); ovipositor elongate, gradually narrowing from the base to the apex (Fig. 7.4), 5.65 mm long (2.2 mm for its valvifer 2,

3.45 mm for its valvula 3), and 0.51 mm wide (length ratio of 0.09), with serrate margins of apical section (Fig. 7.5); ovipositor sheath similar with ovipositor in outline except wider basally (Fig. 7.5).

Forewings well preserved (Fig. 6.3,5), in particular right forewing (Fig. 6.5), 9.6 mm long as preserved, and 2.7 mm wide; vein Sc developed only near the base of R; vein C somewhat arcuate posteriorly (possibly due to deformation); costal space extremely narrow, especially opposite cell 1r; portion of vein R basal to origin of Rs straight, slightly dilated, and then arcuate at cell 1r; pterostigma not sclerotized, with its basal edge thick; vein 2r-rs inclined, longer than 4-Rs, 1.8 times as long as 1r-rs; base of vein 2r-rs 2.4 times closer to apex of pterostigma than to 1r-rs; vein 1-Rs longer than 1-M; vein Rs + M about 1.6 times as long as 1-Rs; vein 2-Rs straight; vein 5-Rs five times as long as 4-Rs; cell 3r + 4r gradually narrowing from base to apex; vein Rs (4-Rs and 5-Rs) straight at 2r-m; combined length of cells 1r and 2r longer than that of 3r + 4r; height of cell 3r + 4r less than combined height of cell 2r and pterostigma, vein 2r-rm inclined, and 1.6 times as long as 2r-rs; vein 3-Cu three times longer than 1m-cu, and forming an arcuate line with it; vein 3-M weakly arcuate; hindwing partially preserved and at least 6.2 mm long (Fig. 6.4–5); veins C and Sc indistinguishable; vein R arcuate at base of Rs; cell r closed; vein 3r-m slightly shorter than adjacent sections of Rs and M.

Comparison. See generic comparison.

Discussion

Ovipositor Shape Among Xyelidae Fossils

Measurements of ovipositors of the Ominé material and of other fossil and extant Xyelidae are plotted in Fig. 9 (see also Supplementary Table S1). Two ovipositor shape categories can be roughly delimited, with high (W/L = 0.04–0.23) and a low aspect ratio (W/L > 0.26). The ovipositor of the selected extant species cover extreme positions of a wide range of aspect ratios: *Xyela* sp. is located in the high aspect ratio area (W/L = 0.11; and see Supplementary Fig. 10.3), while *Megaxyela* sp. belongs to the low aspect ratio area (W/L = 0.30–0.31; and see Supplementary Figs. 10.1–2). In contrast, the earliest members of Xyelidae, from the Triassic, are restricted to the high aspect ratio area (W/L = 0.04–0.11) with, for example, the ovipositors of †*Ominexyela ishidai* gen. et sp. n. and of †*Madygella fujiiyamae* sp. n. (W/L = 0.09, 0.08, respectively). In comparison with Triassic Xyelidae, their Jurassic counterparts occupy a broader range of ovipositor aspect ratios (W/L = 0.10–0.28), and document the earliest occurrence of the “low aspect ratio” shape category, with †*Abrotoxyela multiciliata* Gao et al., 2009. Upper Jurassic Xyelidae exhibit an even wider range of ovipositor aspect ratios, with extreme positions occupied by †*Enneoxyela karatavica* Rasnitsyn, 1965 (W/L = 0.04) and †*Nigrimonticola longicornis* Rasnitsyn, 1966 (W/L = 0.38; Supplementary Figs. 7.1–3). A similar, broad range characterizes Lower Cretaceous Xyelidae (W/L = 0.06–0.41), with †*Anthoxyela turgensis* Rasnitsyn, 1990 displaying the lowest ratio for all Xyelidae (W/L = 0.40; Supplementary Figs. 7.9–11). The Xyelidae are documented by a very scarce sample for the Late Cretaceous, with a single occurrence, †*Chionoxyela nivea* Rasnitsyn, 1993 (Supplementary Figs. 8.9–10), displaying a very low aspect ratio ovipositor (W/L = 0.36). The distribution of ovipositor aspect ratios for Cenozoic (Eocene) Xyelidae is overall similar to that observed for extant forms, with two clusters occupying the high aspect ratio area (W/L = 0.09–0.18), with, for example †*Megaxyela petrefacta* Rasnitsyn, 1969 (W/L = 0.15; Supplementary Fig. 9);

and a single occurrence for the low aspect ratio, with †*Proxylia pankowskii* Jouault et al., 2021 (W/L = 0.34).

Geographic Distribution of Early Xyelidae

The earliest fossil record of Xyelidae is from the Triassic, with most of the know species assigned to the subfamilies †Archexyelinae and †Madygellinae. Triassic Xyelidae have been found from five localities distributed in Southern Pangea [Mt. Crosby, Australia (Riek 1955, Engel 2005); Molteno, South Africa (Schlüter 2000); Potrerillos, Argentina (Lara et al. 2014)] and Northern Pangea [Madygen, Kyrgyz Republic (Rasnitsyn 1964, 1969, Kopylov 2014, Denisova et al. 2023); Ominé, Japan; (Oyama and Maeda 2020; and herein)] (Table 1; Fig. 10). Among them, the †Archexyelinae, consisting of 12 genera and 27 species, shows

the widest distribution, with occurrences in both hemispheres (Mt. Crosby and Madygen; Ominé material remaining to be described); while the †Madygellinae are restricted to Northern Pangea, with a similar taxonomic diversity in both Madygen and Ominé localities (Fig. 10). These data suggest that Xyelidae were already widespread by the Triassic. However, this view must be balanced in the light of abundance data: the entire fossil record of Xyelidae for Southern Pangea is composed of four wings; at Madygen, Xyelidae account for less than 1% of all insect occurrences (Denisova et al. 2023); and at Ominé, the entire Xyelidae (described †Madygellinae and yet undescribed †Archexyelinae) account for about 1% of all insect occurrences (N.O., pers. obs. 2024). In summary, early Xyelidae displayed a widespread distribution but a moderate taxonomic diversity and very low abundance.

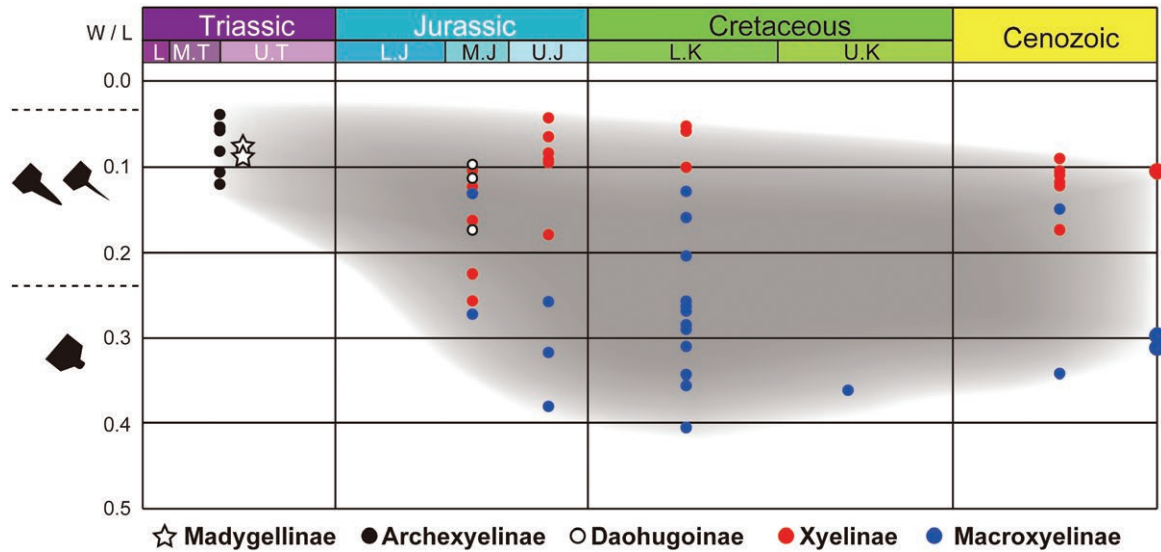


Fig. 9. Distribution of ovipositor shapes (W/L) of 56 fossil species and 2 extant species of Xyelidae during Triassic to Recent and major evolutionary trends. To make the distribution easier to read, aspect ratios are expressed as inverted numbers (W/L) on the vertical axis.

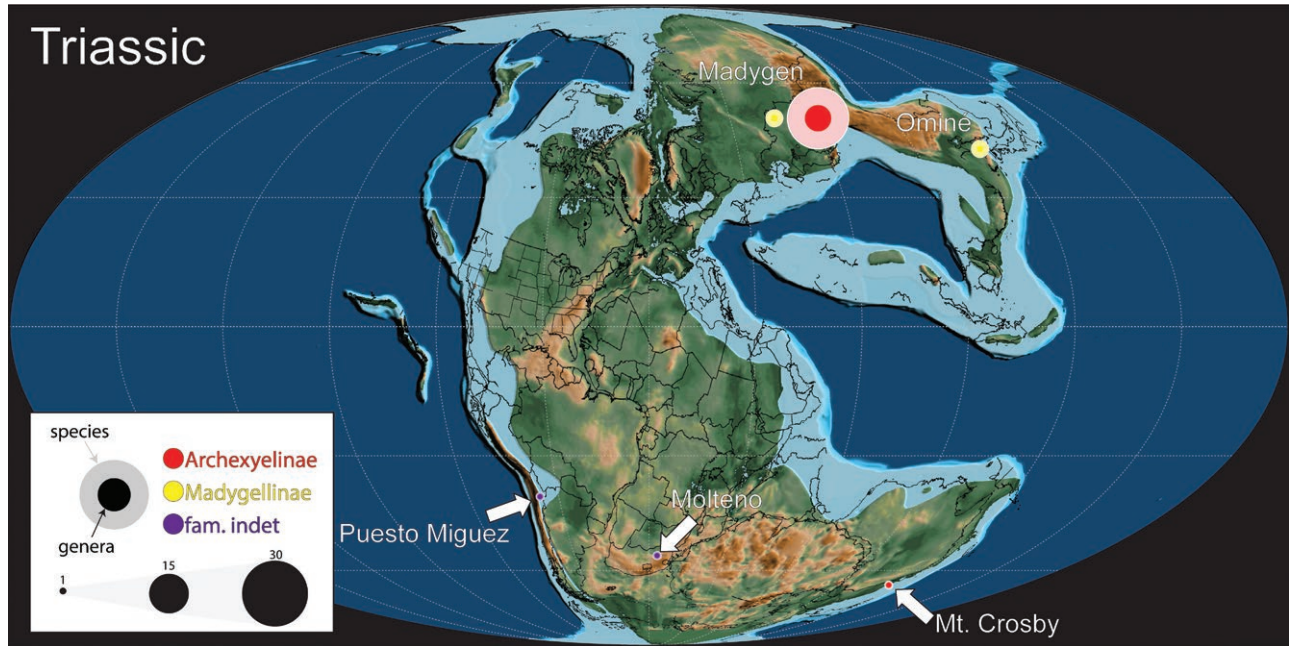


Fig. 10. Palaeomap with known occurrences of Triassic Xyelidae subfamilies. Location of fossil sites indicated by colored circles which size indicates local richness at the genus and species levels (†Archexyelinae not represented for Ominé). Paleomap modified from (Scotese 2021).

Past Disparity of Xyelidae

Considering taxonomic diversity, extant Xyelidae represent a very small subset of the past diversity of the family (Jouault et al. 2021). This evolutionary pattern can also be appreciated based on phenetic diversity, also called disparity. The diversity of ovipositor shapes in this group allows such investigation. In extant Hymenoptera in general, the ovipositor is used in diverse ways in the process of oviposition, e.g., to cut plant tissue, to drill into wood or to deliver eggs to a hidden or open host; or, in some groups, only to inject venom. The morphology and anatomy of ovipositor closely corresponds to these functions (Rasnitsyn 1969, Quicke et al. 1994, Vincent and King 1995, Vilhelmsen 2000, 2003, Weltz and Vilhelmsen 2014, Kumpanenko et al. 2019, Csader et al. 2021).

In extant Xyelidae, females are characterized by a well-developed ovipositor, falling into two narrow-range types. In Xyelinae it is characterized by a high aspect ratio, with a shape ranging from “long and wide” (i.e., “dagger-like”) to “long and narrow” (i.e., “needle-like”), with intermediate forms; while, in Macroxyelinae, it has a low aspect ratio (“short and wide” type) (Fig. 9). Despite a limited record, a wider variety of ovipositor types are known from fossil representatives. The material from Ominé, described herein, provides a useful documentation of ovipositor shapes in the earliest Xyelidae. There is a slight difference in the ovipositor morphology between the two newly documented species: in †*Madygella fujiyamai* sp. n. it is thin and not tapering, with a somewhat rounded apex; while in †*Ominexyela ishidai* gen. et sp. n. it is basally wider and is tapering (“wedge-shaped” outline), and has a sharper apex (i.e., needle-like apically). The former is best considered as “needle-like” ovipositor; while the latter is best considered as “dagger-like” ovipositor. In spite of such interspecific difference, these represent the earliest ovipositor styles in the evolutionary history of Hymenoptera, with high aspect ratio ($W/L = 0.04\text{--}0.11$; Fig. 9). These types are also present in Triassic †Archxyelinae (Rasnitsyn, 1964, 1969). We suppose that such ovipositor types were fit to lay eggs deep into plant tissues and particularly into the gymnosperm staminate cones (possibly, secondarily also into plant shoots as well) to secure the endophytic development of the larva, as it occurs in the living Xyelinae with a similar ovipositor shape (Smith 1967). Such high aspect ratio, “needle-” and “dagger-like” ovipositor types are known to occur, mainly in Xyelinae, in the Jurassic (†*Platyxyela tenuis* (Zheng, Hu, Chen, et al. 2021); $W/L = 0.11$), the Cretaceous (†*Xyela* (*Mesoxyela*) *mesozoica* Rasnitsyn, 1965; $W/L = 0.11$), and until present time (living *Xyela* spp.; $W/L = 0.11$) (Fig. 9; Supplementary Table S1).

Modifications from this ground plan took place during the Jurassic, in relation with the appearance of new taxa. Within Xyelinae, a “long and wide” ovipositor type ($W/L = 0.12\text{--}0.18$) is known in Middle Jurassic sawflies of the tribe Xyelini, such as †*Eoxyela tugnuica* Rasnitsyn, 1983. This type of ovipositor remained common in the Jurassic, Cretaceous and Cenozoic Xyelini. Moreover, in the Jurassic the Xyelinae are also represented by the Liadoxyelini, which displayed a broader range of ovipositor shapes ($W/L = 0.11\text{--}0.26$). Their extinction, at the Jurassic-Cretaceous transition, led to a loss in disparity for the subfamily. The “long and wide” ovipositor type was also typical for the short-lived Jurassic †Daohugoinae.

A “short and wide,” low aspect ratio ovipositor type ($W/L = 0.26\text{--}0.41$) appeared also in the Middle Jurassic, with the early Macroxyelinae †*Abrotoxyela multiciliata* Gao et al., 2009 ($W/L = 0.28$). The group diversified and flourished in the Upper Jurassic and more prominently in the Early Cretaceous (e.g., †*Anthoxyela turgensis* Rasnitsyn, 1990; $W/L = 0.41$), and declined

later on, nowadays composing a small relict group with a narrow range of ovipositor aspect ratio ($W/L = 0.30\text{--}0.31$). The appearance of this “short and wide” ovipositor indicates a transition from deep to subsurface insertion of the egg and, by implication, a departure from the endophytic development, within a male conifer cone (still preserved in extant *Xyela* species; Blank et al. 2013, Naito et al. 2020), in favor of the external development on leaves of stem-angiosperms (with further transformation into the feeding on leaves of elms and hickories by larvae of the extant *Macroxyela* and *Megaxyela*, respectively; Blank et al. 2017, Shinohara et al. 2017, Naito et al. 2020). It can then be assumed that ovipositor shape transition was accompanied with a larval diet change in Macroxyelinae (in contrast to Xyelinae). A similar switch to angiosperms is known to have occurred in tenthredinoid sawflies (Nyman et al. 2019), which also perform superficial insertions of eggs onto leaves using “short and wide” ovipositors (Vilhelmsen 2000, Weltz and Vilhelmsen 2014).

In summary, the fossil record of Middle Jurassic to Lower Cretaceous sawflies shows the highest diversity of ovipositor types for the family, with the high aspect ratio ones present in Xyelinae and †Daohugoinae and the “short and wide” type in Macroxyelinae. Afterwards, the range of ovipositor types slightly declined but, more importantly, concentrated on the two, very distinct types known nowadays. Also, specialization in ovipositor type diversity seemingly occurred during the Jurassic-Cretaceous transition for the Xyelinae, while Macroxyelinae displayed a peak of diversity during the Lower Cretaceous. In other words, decline in disparity was probably not contemporaneous in Xyelinae and Macroxyelinae.

Supplementary data

Supplementary data are available at *Insect Systematics and Diversity* online.

Specimen Collection Statement

The authors attest that all legal and regulatory requirements, including export and import collection permits, have been followed for the collection of specimens from source populations at any international, national, regional, or other geographic level for all relevant field specimens collected as part of this study.

Acknowledgments

We thank reviewers (Lars Vilhelmsen and an anonymous reviewer) and editors for their constructive suggestions and comments that helped us to improve this account. The authors thank staffs of the Mine City Museum of History and Folklore, Syougo Yoshinaga, Yukiko Arakawa, Fumiko Inakura, and Yuko Kazitani, for permitting access to the specimens. We are very grateful to Yasuhiro Ito, Yusuke Okazaki, Toshiharu Mita, Tetsuji Onoue, Munetoshi Maruyama, Koji Wakita, Hirokazu Yukawa, Takuya Imai, Rikio Matsumoto, Yoto Komeda, Akihiro Misaki, Yūsuke Minoshima, Hideo Ishida, Masahiro Nohara, Takayoshi Harada and all the members belonging to the Ammo. seminar and Entomological Laboratory for giving me many comments and suggestions.

Author contributions

Nozomu Oyama (Conceptualization [lead], Data curation [lead], Investigation [lead], Project administration [lead], Validation [lead], Visualization [lead], Writing—original draft [lead], Writing—review & editing [lead]), Haruyoshi Maeda (Data curation [supporting], Investigation [supporting], Methodology [supporting], Supervision [supporting], Writing—review & editing [supporting]),

Alexandr Rasnitsyn (Data curation [supporting], Investigation [equal], Validation [supporting], Writing—review & editing [equal]), Kenji Shinoda (Investigation [supporting], Resources [supporting], Supervision [supporting]), Humio Takahashi (Investigation [supporting], Resources [supporting], Supervision [lead]), and Olivier Béthoux (Conceptualization [supporting], Data curation [supporting], Formal analysis [equal], Writing—review & editing [equal])

Funding

This work was partly supported by JSPS KAKENHI Grant Number JP19J20625 and JSPS Postdoctoral Fellowship for Research Abroad (No.202360114) to N. O.

Data availability

All data generated or analysed during this study are included in this published article [and its [Supplementary information files](#)].

References

- Aizawa J. 1991. Fossil insect-bearing strata of the Triassic mine group, Yamaguchi prefecture. *Bull. Kitakyushu Mus. Nat. Hist.* 10:91–98.
- Ashmead WH. 1898. Part II. Descriptions of new parasitic Hymenoptera. *Proc. Entomol. Soc. Wash.* 4:155–171.
- Beutel RG, Xu C, Jarzembowski E, et al. 2024. The evolutionary history of Coleoptera (Insecta) in the late Palaeozoic and the Mesozoic. *Systematic Entomology*. 49(3):355–388. <https://doi.org/10.1111/syen.12623>.
- Blagoderov V, Grimaldi DA, Fraser NC. 2007. How time flies for flies: diverse Diptera from the triassic of Virginia and early radiation of the order. *Am. Mus. Novit.* 3572:1–39. [https://doi.org/10.1206/0003-0082\(2007\)509\[1:htfffd\]2.0.co;2](https://doi.org/10.1206/0003-0082(2007)509[1:htfffd]2.0.co;2)
- Blaimer BB, Santos BF, Cruaud A, et al. 2023. Key innovations and the diversification of Hymenoptera. *Nat. Commun.* 14:1212. <https://doi.org/10.1038/s41467-023-36868-4>
- Blank SM, Kramp K. 2017. *Xyela davidsmithi* (Hymenoptera, Xyelidae), a New Pine Catkin Sawfly with an Unusual Host Association from the Sierra Nevada. *Proc. Entomol. Soc. Wash.* 119:703–717. <https://doi.org/10.4289/0013-8797.119.specialissue.703>
- Blank SM, Shinohara A, Altenhofer E. 2013. The Eurasian species of *Xyela* (Hymenoptera, Xyelidae): taxonomy, host plants and distribution. *Zootaxa*. 3629:1–106. <https://doi.org/10.11646/zootaxa.3629.1.1>
- Blank SM, Kramp K, Smith DR, et al. 2017. Big and beautiful: the Megaxyela species (Hymenoptera, Xyelidae) of East Asia and North America. *Eur. J. Taxon.* 2017:1–46. <https://doi.org/10.5852/ejt.2017.348>
- Csader M, Mayer K, Betz O, et al. 2021. Ovipositor of the braconid wasp *Habrobracon hebetor*: structural and functional aspects. *J. Hymenopt. Res.* 83:73–99. <https://doi.org/10.3897/jhr.83.64018>
- Curran CH. 1923. A new genus and species of Xyelidae (Tenthredinoidea, Hymenoptera) from western Canada. *Can. Entomol.* 55:20–20. <https://doi.org/10.4039/ent5520-1>
- Denisova EA, Kopylov DS, Rasnitsyn AP. 2023. New Archexyelinae (Hymenoptera: Xyelidae) from the Triassic Madygen Formation of Kyrgyzstan. *PalZ.* 98:95–104. <https://doi.org/10.1007/s12542-023-00666-6>
- Engel MS. 2005. A new sawfly from the Triassic of Queensland (Hymenoptera: Xyelidae). *Mem. Queensl. Mus.* 51:558.
- Fujiyama I. 1973. Mesozoic insect fauna of East Asia Part 1. Introduction and upper triassic faunas. *Bull. Natl. Sci. Mus.* 16:331–386.
- Fujiyama I. 1991. Late Triassic insects from mine, Yamaguchi, Japan, Part 1. *Odonta. Bull. Natl. Sci. Mus.* 17:49–56.
- Gao T, Ren D, Shih C. 2009. The first Xyelotomidae (Hymenoptera) from the Middle Jurassic in China. *Ann. Entomol. Soc. Am.* 102:588–596. <https://doi.org/10.1603/008.102.0402>
- Gerstaecker A. 1867. Ueber die Gattung *Oxybelus* Latr. und die bei Berlin vorkommenden Arten derselben. In: *Zeitschrift für die gesammten Naturwissenschaft*. Vol. bd. 30 (1867). Berlin [etc.]: Wiegandt, Hempel & Parey. Available from <https://www.biodiversitylibrary.org/item/102864>
- Grimaldi D, Engel MS. 2005. Evolution of the Insects. Cambridge, England: Cambridge University Press. [https://doi.org/10.1653/0015-4040\(2007\)90\[588:eoti\]2.0.co;2](https://doi.org/10.1653/0015-4040(2007)90[588:eoti]2.0.co;2)
- Hase A. 1950. The stratigraphy of the Triassic system in the southwestern part of Yamaguchi Prefecture. *Mem. Fac. Sci. Kyushu Univ.* 2:101–128.
- Hase A. 1951. The triassic in yamaguchi prefecture. In: *Geological Survey of Japan, editor. Triassic stratigraphy of Japan*. Japan: Kogyo Gijyutsu Chishitsu Chosajo; p. 72–89.
- Imada Y, Oyama N, Shinoda K, et al. 2022. Oldest leaf mine trace fossil from East Asia provides insight into ancient nutritional flow in a plant–herbivore interaction. *Sci. Rep.* 12:1–21. <https://doi.org/10.1038/s41598-022-09262-1>
- Ishibashi T, Hashimoto K, Nohara M, et al. 1990. Triassic ammonites newly discovered in the western district of Yamaguchi Prefecture, Japan. *J. Geol. Soc. Jpn.* 96:771–774.
- Jinnouchi K, Kusuhashi N, Liu J, et al. 2018. Dicyodont fossils from the upper Triassic Momonoki formation, mine group, Yamaguchi, Japan. In: *The 167th Regular Meeting The Palaeontological Society of Japan*. p. 42.
- Jouault C, Aase A, Nel A. 2021. Past ecosystems drive the evolution of the early diverged Symphyta (Hymenoptera: Xyelidae) since the earliest Eocene. *Foss. Rec.* 24:379–393. <https://doi.org/10.5194/fr-24-379-2021>
- Kametaka M. 1999. Provenance of the upper triassic mine group, Southwest Japan. *J. Geol. Soc. Jpn.* 105:651–667. <https://doi.org/10.5575/geosoc.105.651>
- Katayama M. 1939. Stratigraphical study of the mine group. *Geol. Soc. Jpn.* 46:127–141.
- Khranov AV, Oyama N, Kenji S, et al. 2023. Late Triassic lacewings (Insecta: Neuroptera) from Japan. *Hist. Biol.* 36:2187–2195. <https://doi.org/10.1080/08912963.2023.2244519>
- Kjer KM, Ware JL, Rust J, et al. 2015. Response to Comment on ‘Phylogenomics resolves the timing and pattern of insect evolution’. *Science*. 349:487–448c. <https://doi.org/10.1126/science.aaa7136>
- Kopylov DS. 2014. New sawflies of the subfamily Madygellinae (Hymenoptera, Xyelidae) from the middle-upper Triassic of Kyrgyzstan. *Paleontolog. J.* 48:610–620. <https://doi.org/10.1134/s0031030114060070>
- Kumpanenko A, Gladun D, Vilhelmsen L. 2019. Functional morphology and evolution of the sting sheaths in Aculeata (Hymenoptera). *Arthropod Syst. Phylogeny*. 77:325–238. <https://doi.org/10.26049/ASP77-2-2019-08>
- Lara MB, Rasnitsyn AP, Zavattieri AM. 2014. *Potrerilloxyela menendezzi* gen. et sp. nov. from the Late Triassic of Argentina: the oldest representative of Xyelidae (Hymenoptera: Symphyta) for Americas. *Paleontolog. J.* 48:182–190. <https://doi.org/10.1134/s0031030114020075>
- Linnaeus C von. 1758. Hymenoptera. *Systema naturae, per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata*. T. I, pt. II. 553–583. <https://doi.org/10.5962/bhl.title.157601>
- Maeda H, Oyama N. 2019. Stratigraphy and fossil assemblages of the Triassic Mine Group and Jurassic Toyora Group in western Yamaguchi Prefecture. *J. Geol. Soc. Jpn.* 125:585–594. <https://doi.org/10.5575/geosoc.2019.0020>
- Misof B, Liu S, Meusemann K, et al. 2014. Phylogenomics resolves the timing and pattern of insect evolution. *Science*. 346:763–767. <https://doi.org/10.1126/science.1257570>
- Naito T, Shinohara A, Hara H, et al. 2020. Sawflies and woodwasps of Japan. Sapporo, Japan: Hokkaido University Press; p. 530
- Newman E. 1834. Attempted division of British insects into natural orders. *Entomol Magazine*. 11:379–430.
- Nyman T, Onstein RE, Silvestro D, et al. 2019. The early wasp plucks the flower: disparate extant diversity of sawfly superfamilies (Hymenoptera: ‘Symphyta’) may reflect asynchronous switching to angiosperm hosts. *Biol. J. Linn. Soc.* 128:1–19. <https://doi.org/10.1093/biolinnean/blz071>
- Oyama N, Maeda H. 2020. *Madygella humioi* sp. nov. from the Upper Triassic Mine Group, Southwest Japan: the oldest record of a sawfly (Hymenoptera: Symphyta) in East Asia. *Paleontol. Res.* 24:64–71. <https://doi.org/10.2517/2019pr005>
- Oyama N, Yukawa H, Maeda H. 2020. Mesozoic insect fossils of Japan: significance of the Upper Triassic insect fauna of the Mine Group, Yamaguchi Pref. *Bull. Mine City Mus. Yamag. Prefect. Jpn.* 33:1–13.

- Oyama N, Shinoda K, Takahashi H, et al. 2023. A new species of the Triassic genus *Ideliopsina* (Grylloblattida: Ideliidae) from the Ominé locality (Momonoki Formation, southwest Japan). *Palaeoentomology*. 6:205–213. <https://doi.org/10.11646/palaeoentomology.6.2.12>
- Peters RS, Krogmann L, Mayer C, et al. 2017. Evolutionary history of the hymenoptera. *Curr. Biol.* 27:1013–1018. <https://doi.org/10.1016/j.cub.2017.01.027>
- Quicke DLJ. 2014. The braconid and ichneumonid parasitoid wasps. Hoboken, New Jersey, USA: John Wiley & Sons; p. 704. <https://doi.org/10.1002/9781118907085>
- Quicke DLJ, Fitton MG, Tunstead JR, et al. 1994. Ovipositor structure and relationships within the Hymenoptera, with special reference to the ichneumonoidea. *J. Nat. Hist.* 28:635–682. <https://doi.org/10.1080/00222939400770301>
- Rasnitsyn AP. 1964. Novye triasovye preponchatokrylye Sredney Asii [New Triassic Hymenoptera of Central Asia]. *Paleontologicheskij Zhurnal*. 1:88–96.
- Rasnitsyn AP. 1965. Materialy do poznania biologii, systematyki i filogenezy rosliniarek z prodrodziny Xyelinae (Hymenoptera, Xyelidae). *Pol. Pismo Entomol.* 35:483–519.
- Rasnitsyn AP. 1966. Novye Xyelidae (Hymenoptera) iz Mezozoya Azii. *Paleontol. Zh.* 4:69–85.
- Rasnitsyn AP. 1969. Proiskhozhdenie i evolutsiya nizshikh pereponchatokrylykh [Origin and evolution of lower hymenoptera Hymenoptera.] *Trudy Paleontologicheskogo Instituta Akadmii Nauk SSSR*. 123:1–196.
- Rasnitsyn AP. 1983. Pereponchatokrylye nasekomye v Yure vostochnoy Sibiri. *Byull Moskovsk Obshch Isp Prir Ord Geologicheskij* 58:85–94.
- Rasnitsyn AP. 1990. Vespida. Hymenoptera. In: Rasnitsyn, A.P. editor. Late mesozoic insects of Eastern Transbaikalia. Moscow, Russia: Nauka; Moscow, Nauka. p. 177–205.
- Rasnitsyn AP. 1993. Melovye entomofauny basseyna r. Ul'i (zapadnoe Priokhot'e). In: Ponomarenko AG, editor. *Mezozoyskie Nasekomye i Ostrakody Azii*. Moscow, Russia: Nauka; p. 50–57.
- Rasnitsyn AP. 1995. Tertiary sawflies of the tribe Xyelini (Insecta: Vis). *Nat. Hist. Mus. Los Angel. County*. 450:1–14.
- Rasnitsyn AP, Zhang H. 2004. A new family, Daohugoidae fam. n., of siricomorph hymenopteran (Hymenoptera = Vespida) from the Middle Jurassic of Daohugou in Inner Mongolia (China). *Proc. R Entomol. Soc.* 75:12–16.
- Rasnitsyn AP. 2002. Superorder Vespidea Laicharting, 1781. Order Hymenoptera Linné, 1758 (=Vespida Laicharting, 1781). In: Rasnitsyn Alexandr P, Quicke DLJ, editors. *History of insect*. Dordrecht: Kluwer Academic Publishers; p. 242–255. <https://doi.org/10.1007/0-306-47577-4>
- Riek EF. 1955. Fossil insects from the Triassic beds at Mt. Crosby, Queensland. *Aust. J. Zool.* 3:654–691. <https://doi.org/10.1071/zo9550654>
- Schlüter TN. 2000. *Moltenia rieki* n. gen., n. sp. (Hymenoptera Xyelidae), a tentative sawfly from the Molteno Formation (Upper Triassic), South Africa. *Paläontologische Zeitschrift*. 74:75–78.
- Scotese CR. 2021. An atlas of phanerozoic paleogeographic maps: the seas come in and the seas go out. *Annu. Rev. Earth Planet. Sci.* 49:679–728. <https://doi.org/10.1146/annurev-earth-081320-064052>
- Shcherbakov DE. 2008. Madygen, Triassic lagerstätte number one, before and after Sharov. *Alavesia*. 2:113–124.
- Shinohara A. 1995. The sawfly genus *Pleroneura* (Hymenoptera, Xyelidae) in East Asia. *Jpn. J. Entomol.* 63:825–840.
- Shinohara A, Hara H, Kramp K, et al. 2017. Bird droppings on chestnut leaves or sawfly larvae: DNA barcodes verify the occurrence of the archaic *Megaxyela togashii* (Hymenoptera, Xyelidae) in Hokkaido, Japan. *Zootaxa*. 4221:zootaxa.4221.2.6. <https://doi.org/10.11646/zootaxa.4221.2.6>
- Smith DR. 1967. A review of the larvae of Xyelidae, with notes on the family classification (Hymenoptera). *Ann. Entomol. Soc. Am.* 60:376–384. <https://doi.org/10.1093/aesa/60.2.376>
- Takahashi E, Mikami T. 1975. Mesozoic: Triassic. In Yamaguchi PM, editor. *Geology of Yamaguchi Prefecture*. Yamaguchi, Japan: Yamaguchi Prefectural Museum; p. 93–109.
- Takahashi H, Naitou G, Ishibashi H, et al. 1992. National highway 435 road improvement study report, occurrence of plant fossils. *Bull. Mine City Mus. Yamag. Prefect. Jpn.* 8:1–23.
- Takahashi H, Ishida E, Nohara M, et al. 1997. Occurrence of insect fossils from the Late Triassic Mine Group. *Bull. Mine City Mus. Yamag. Prefect. Jpn.* 13:1–27.
- Tokuyama A. 1958. Late triassic palaeopharus in Japan. *Trans Proc. Palaeont. Soc. Jpn.* 32:291–296.
- Tokuyama A. 1960. On the pelecypod fauna of the late triassic hirabara formation in West Japan. *Jpn. J. Geol. Geogr* 31:201–217.
- Tong KJ, Duchêne S, Ho SYW, et al. 2015. Comment on 'Phylogenomics resolves the timing and pattern of insect evolution'. *Science*. 349:487–487. <https://doi.org/10.1126/science.aaa5460>
- Ueda K. 1991. A Triassic fossil of scorpion fly from Mine, Japan. *Bull. Kitakyushu Mus. Nat. Hist.* 10:99–103.
- Uyeno T, Takahashi F, Doi E, et al. 1996. Triassic fishes collected in Mine City and Sanyocho in Yamaguchi Prefecture. *Bull. Mine City Mus. Yamag. Prefect. Jpn.* 12:1–27.
- Vilhelmsen L. 2000. The ovipositor apparatus of basal Hymenoptera (Insecta): phylogenetic implications and functional morphology. *Zoologica Scripta*. 29:319–345. <https://doi.org/10.1046/j.1463-6409.2000.00046.x>
- Vilhelmsen L. 2003. Flexible ovipositor sheaths in parasitoid Hymenoptera (Insecta). *Arthropod. Struct. Dev.* 32:277–287. [https://doi.org/10.1016/S1467-8039\(03\)00045-8](https://doi.org/10.1016/S1467-8039(03)00045-8)
- Vincent JFV, King MJ. 1995. The mechanism of drilling by wood wasp ovipositors. *Biomimetics*. 3:187–201.
- Voigt S, Buchwitz M, Fischer J, et al. 2017. Triassic life in an inland lake basin of the warm-temperate biome - the Madygen Lagerstätte (southwest Kyrgyzstan, Central Asia). In: Fraser NC, Sues H-D, editors. *Terrestrial conservation Lagerstätten: windows into the evolution of life on land*. Edinburgh, Scotland: Dunedin; p. 65–104.
- Wang M, Rasnitsyn AP, Zhang H, et al. 2019. Revising the systematic position of the extinct family Daohugoidae (basal Hymenoptera). *J. Syst. Paleontol.* 17:1245–1255. <https://doi.org/10.1080/14772019.2018.1523238>
- Weltz CE, Vilhelmsen L. 2014. The saws of sawflies: exploring the morphology of the ovipositor in Tenthredinoidea (Insecta: Hymenoptera), with emphasis on Nematinae. *J. Nat. Hist.* 48:133–183. <https://doi.org/10.1080/00222933.2013.791941>
- Zheng Y, Hu H, Chen D, et al. 2021a. New fossil records of Xyelidae (Hymenoptera) from the middle Jurassic of inner Mongolia, China. *EJT*. 733:146–159. <https://doi.org/10.5852/ejt.2021.733.1229>
- Zheng Y, Hu H, Zhang H, et al. 2021b. New genus and species of syspastroxyelid sawflies (Insecta, Hymenoptera) from the mid-Cretaceous Kachin amber with a review of the family Syspastroxyelidae. *Cretac. Res.* 127:104940. <https://doi.org/10.1016/j.cretres.2021.104940>