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RESEARCH ARTICLE

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Potrerilloxyela menendezi Lara et al. 2014 (Hymenoptera: Xyelidae) from the Upper Triassic of Argentina revisited to explore transformation of the cubital vein in Hymenoptera

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ABSTRACT

Here, we report on our restudy of the holotype of *Potrerilloxyela menendezi* Lara, Rasnitsyn and Zavattieri 2014, focusing on the forewing. We found that the bases of cubitus and the anterior cubitus vein, normally lost in Hymenoptera, are present in *Potrerilloxyela menendezi* probably as a reversion (atavism). Other cases of reversions are rare in Hymenoptera: this being the oldest known, and the most similar to the groundplan of cubital system in Pterygota. Additionally, we discuss modifications of the cubital system observed in fossil and extant hymenopterans.

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Introduction

An atavism (or evolutionary throwback), as defined by Correns et al. (1912), is considered, as a sudden and uncommon reappearance (in one or more individuals of a derived taxon) of a character present in an ancestral taxon (either biological structure, e.g. teeth in birds, wings in wingless stick insects; or behavioural) that was lost during evolution in some members of a population (Cabej, 2012, 2018; Correns et al., 1912; Hall, 2007; Tomić & Meyer-Rochow, 2011; Zanni & Opitz, 2013). The reappearance of the lost ancestral character arises as a result of the activation of a suppressed ancestral developmental pathway under conditions of the changed developmental and genetic context (Cabej, 2012, 2018). However, the exact causes of what triggers and controls the reappearance are not known (Hall, 1984; Tomić & Meyer-Rochow, 2011).

Phenotypic reversals are in contradiction with Dollo's law (Dollo, 1893) which states: 'an organism is unable to return, even partially, to a previous stage already realized in the ranks of its ancestors'. Tomić and Meyer-Rochow (2011) mentioned that an atavism has to fulfil several criteria: a high degree of phenotypic resemblance to a character found in an ancestor (conserved character), occur as a fully developed character in adult stages, appear usually in one or a few individuals of a population, and an organism cannot have an atavistic structure if it was not previously found in its ancestry (Hall, 1995, 2007). However, it is controversial whether the study of atavisms can ever provide any concrete clues to the origin of evolutionary a novelty (McCune, 1990).

Xyelidae Newman 1834 (Middle – Upper Triassic to Recent) is a small extant group of herbivorous sawflies and has been considered to be the most primitive members of Hymenoptera Linnaeus, 1758, playing a vital role as an ancestral group in the early evolution of the order (Lara et al., 2014; Rasnitsyn, 1980; Zhang & Zhang, 2000; Zheng et al., 2021). Lara et al. (2014) described *Potrerilloxyela menendezi* (Hymenoptera: Xyelidae) as the first record of Hymenoptera from the Triassic of South America, and the first record of Xyelinae in the Triassic deposits worldwide, further discussing the taxonomic position within the subfamily.

In this study, we examined a probable case of 'atavism' or 'reversion' in *Potrerilloxyela menendezi* Lara, Rasnitsyn and Zavattieri 2014 (Hymenoptera: Xyelidae), Upper Triassic of the Potrerillos Formation, Cuyana Basin, in Mendoza Province, Argentina. *Potrerilloxyela menendezi* exhibits bases of forewing veins Cu and CuA that are otherwise lost in Hymenoptera and restored here as a reversion (atavism). Additionally, we discuss other cases of the reversion in the Order Hymenoptera, however this is the oldest known reversion within Hymenoptera and the most similar to the groundplan of the cubital system in Pterygota.

Material and methods

Some time ago (March – April 2023) one of the authors (AR) visited the Centro de Ecología Aplicada del Litoral (CECOAL-CONICET-Nordeste-UNNE), in Corrientes Province, Argentina, to explore the Triassic hymenopteran specimen and other Triassic insects kept there (e.g. beetles, grylloblattids, mecopterans, orthopterans).

In particular, the holotype of *Potrerilloxyela menendezi* Lara, Rasnitsyn and Zavattieri 2014 (MCNAM-PI Nº 24604) was restudied, and additionally treated to remove residues of the matrix left over some important parts of the fossil wing. The specimen was described based on a unique detached forewing collected in yellowish mudstones of the uppermost section of the Upper Triassic (Carnian) Potrerillos Formation, at the Puesto Miguez locality, south of Cerro Cacheuta, Cuyana Basin, in Mendoza Province, Argentina (Lara et al., 2014, figs. 1–2). *Potrerilloxyela menendezi* was referred to Xyelidae and, questionably, to Xyelinae, which made it the oldest representative of the latter subfamily. For more information on taxonomic, sedimentological and geological setting see Lara et al. (2014).

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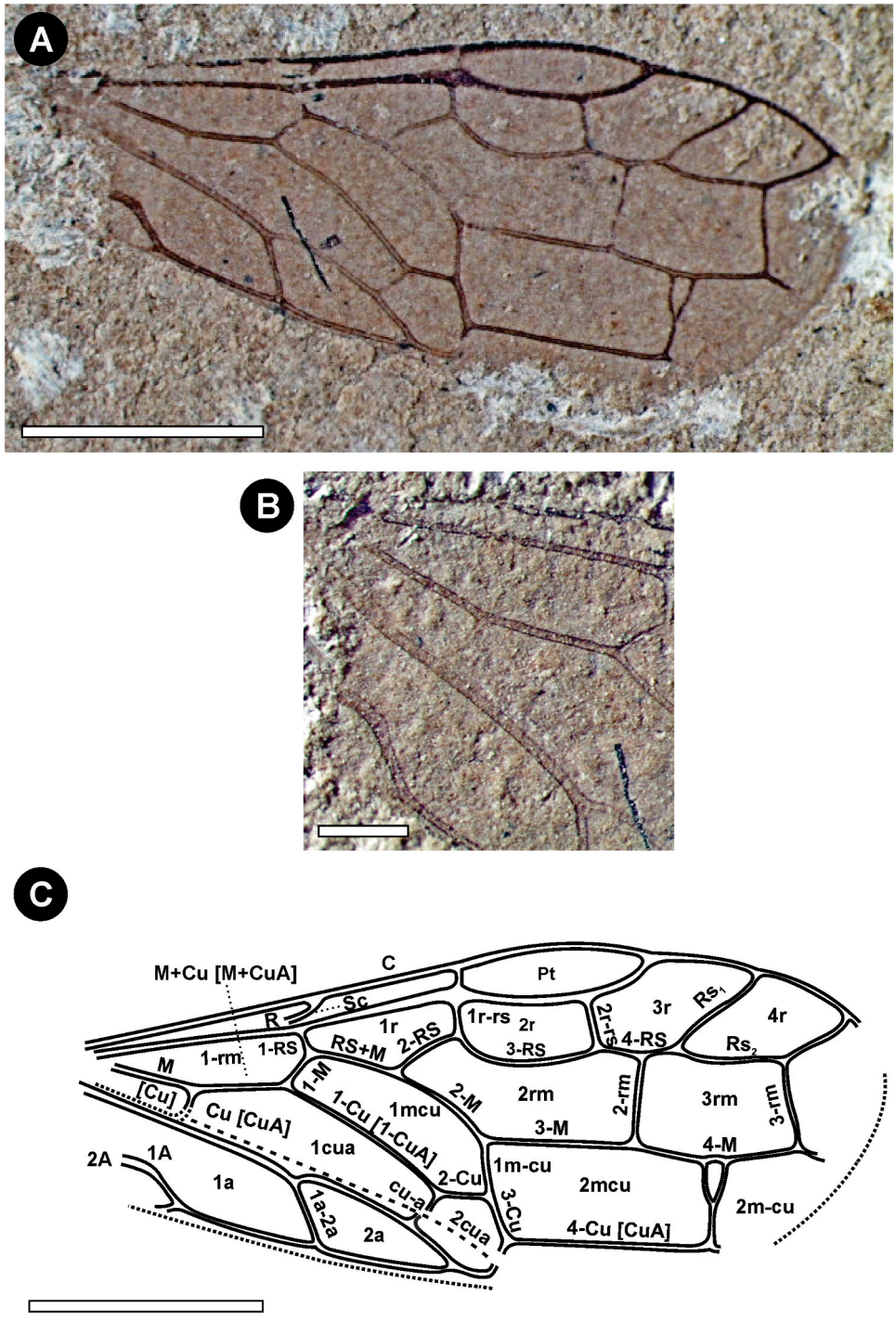


Figure 1. *Potrerilloxyela menendezi* Lara et al., 2014, Xyelidae, Late Triassic of Argentina, Holotype MCNAM-PI Nº 24604, forewing. (A) Wetted with alcohol to show vein pigmentation. (B) Basal wing fragment under oblique illumination to show spectral veins only expressed in relief. (C) Interpretation of wing venation with veins labelled. Explanation for all figures: dot lines denote spectral veins, dash lines – folds, other veinal symbols are standard except that symbols in square brackets added to regular ones are those used in insects other than Hymenoptera (CuA instead of just Cu). Scale bars = 2 mm (A, C), 0.5 mm (B).

To facilitate observation, all wings are arranged in the standard orientation (apical area to the right), and photographs of left-forewing specimens have been mirrored (indicated in the figure captions).

Institutional abbreviations

MCNAM-PI, Palaeoinvertebrate Collection of the Museo de Ciencias Naturales y Antropológicas 'Juan Cornelio Moyano', Mendoza Province, Argentina; GD NRW, Geologischer Dienst NRW, Krefeld, Germany; PIN, Paleontological Institute of the Russian Academy of Science, Moscow, Russia.

Other abbreviations

Forewing venation abbreviations: C, costa; Sc, subcosta; R, radius; RS, radius sector; Pt, pterostigma; M, median vein; CuA/CuP,

anterior/posterior cubitus; A_1 (=postcubitus, pCu)/A_2/A_3, first/second anal vein; cf, claval fold.

Results

The mentioned additional preparation of the holotype concerns particularly areas of C, Sc and Cu (Figure 1). As a result, C is now visible for its entire length, and Sc appears as an appreciable part of the vein rather than only its very apex (cf. Lara et al., 2014, fig. 4). However, the main result is the discovery of the free basal part of the cubital system. Now, we can see a section of Cu forming a distinct, even though mainly colourless (spectral) vein looking like a vertical crossvein and interpretable as a free base of CuA, joined basally with a long longitudinal stalk, a putative Cu base aligned anteriorly to the claval fold. As a result, the cubital system of *Potrerilloxyela menendezi* Lara, Rasnitsyn and Zavattieri 2014 appears as the least advanced within Hymenoptera and essentially agreeing with what is characteristic of the insect groundplan (see below), except that the common base of Cu is long here, so as CuA base is shifted unusually distal, and that CuP is lost as a distinct vein.

The insect groundplan structure of the cubital vein persists since the oldest insect fossils (e.g. *Herbstiala herbsti* Schmidt, 1953, Paoliidae, early Pennsylvanian of Germany) (Figure 2(A)) until many living forms. It starts as a more or less short stalk running between bases of the medial (M) vein and first anal vein (1A, also named postcubitus, pCu). The stem Cu further dichotomises into the anterior cubitus (CuA) and posterior cubitus (CuP) (Figure 2(A)). Normally and putatively in the insect groundplan, CuA is a convex vein (elevated over neighbour wing membrane) in the forewing and concave (impressed) vein in the hind one, and CuP is a concave vein in both wings. Typically, CuA bends forward at the fork until it receives a short and usually thickened hind branch of M (often named M_5) and then changes its direction again to be more parallel to M, whilst Cu stems and CuP runs adjacent to the claval fold from before.

Further modifications of the groundplan Cu are common, but we concentrate on those characteristics of the Order Hymenoptera. All known hymenopterans, both fossil and extant forms, have the cubital system modified, particularly in the forewings where both the Cu base and CuP are lost and CuA is fused with M to form a composite vein M+Cu (e.g. *Triassoxyela foveolata* Rasnitsyn, 1964, Xyelidae, Middle or Late Triassic of Madygen Formation, Kyrgyzstan) (Figure 2(B)). The vein M+Cu diverges into free M and CuA within the middle third of the wing. Unlike this, hindwings in Xyelidae (*Pleroneura coniferarum* Hartig, 1837, living) (Figure 3(A); also cf. Rasnitsyn, 1968, fig. 6a) and, rarely, in other basal Hymenoptera (e.g. *Gigasirex longipes* Rasnitsyn, 1968, Siricidae, Late Jurassic of Kulbastau Formation, Kazakhstan) retain CuA base near wing base (Figure 4(A)). At the same time, forewings of some disparate hymenopterans, both fossil and extant, reveal a vein comparable to an extent with the free CuA base as well. The

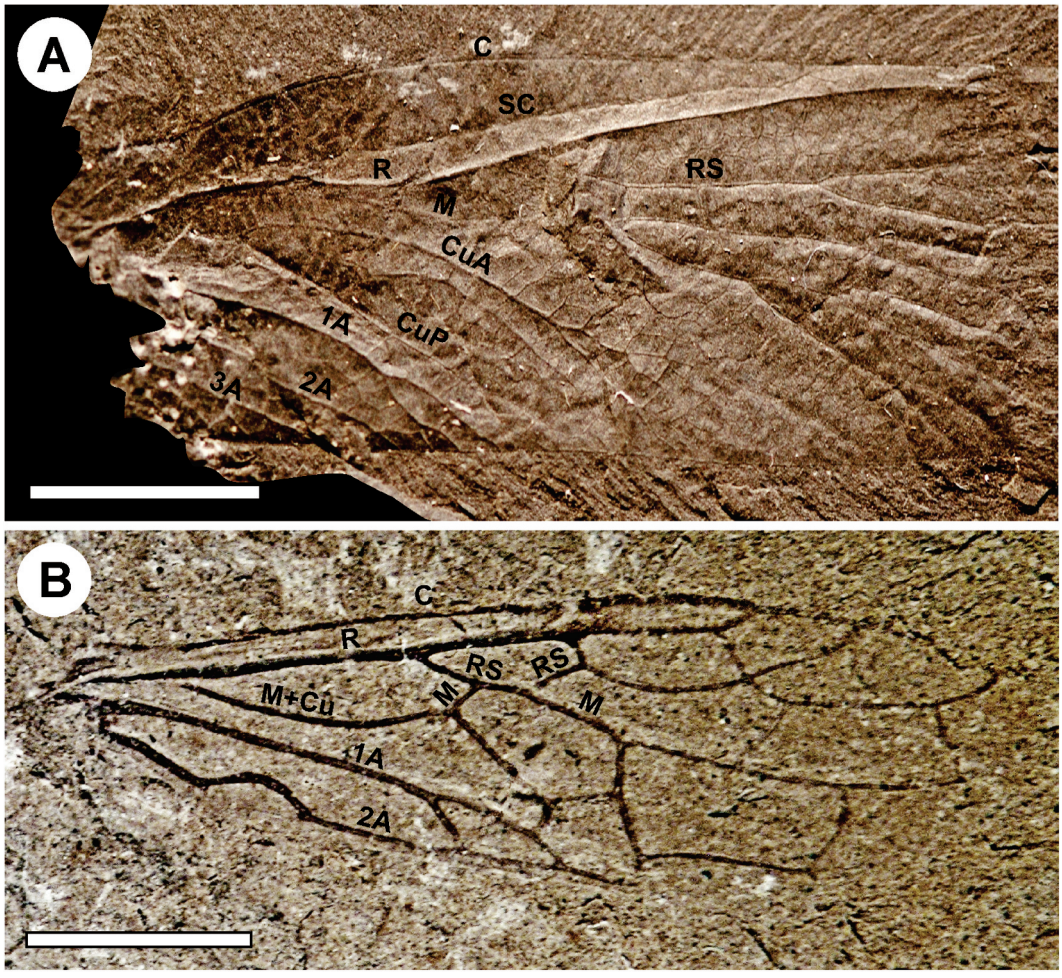


Figure 2. (A) *Herbstiala herbsti* Schmidt, 1953, Paoliidae, early Pennsylvanian (Westphalian A) of Germany, photo courtesy Jakub Prokop (Prokop et al., 2013, fig. 4F), Holotype GD NRW No. Kar 46, forewing (mirrored). (B) *Triassoxyela foveolata* Rasnitsyn, 1964, Xyelidae, Middle or Late Triassic of Madygen Formation, Kyrgyzstan, Holotype PIN 2070/1, forewing. Scale bars = 10 mm (A), 2 mm (B).

living examples are apparently only some Pamphilidae (e.g. *Caenolyda reticulata* Linnaeus, 1758, forewing) (Figure 3(B)) and Siricidae (e.g. *Sirex noctilio* Fabricius, 1793, forewing) (Figure 3(C)) displaying an extra 'cu-a crossvein' shortly before the fork of M+Cu. However, unlike the real crossvein, this one does not reach the claval fold. Taken alone, this version of the Cu system is not very convincing as evidence of a homology between the 'supernumerary cu-a' and the free base of CuA.

In other Hymenoptera, and particularly those attributed to the extinct family Sepulcidae (Cephoidea), there are other modifications of the Cu system (e.g. Cu stem lost). For example, in the Late Jurassic *Parapamphilius confusus Rasnitsyn* Rasnitsyn, 1968 from the famous Karatau locality in Kazakhstan (Figure 4(B)) and *Parabakharius parvus* Rasnitsyn, 1993 from the Middle Jurassic Bahar in Mongolia, but in the latter, this loss is less convincing because the fossil has a poorer state of preservation (Rasnitsyn, 1993, fig. 2). In *Dalduba faticana* Storozhenko, 1996 (Daldubidae) of the Late Carboniferous of Siberia, the stem CuP is lost in the forewings (Figure 4(C)).

However, the most relevant specimen in respect to the putative homology of the hymenopteran Cu system is *Potrerilloxyela menendezi* Lara, Rasnitsyn and Zavattieri 2014 (Xyelidae), Late Triassic of

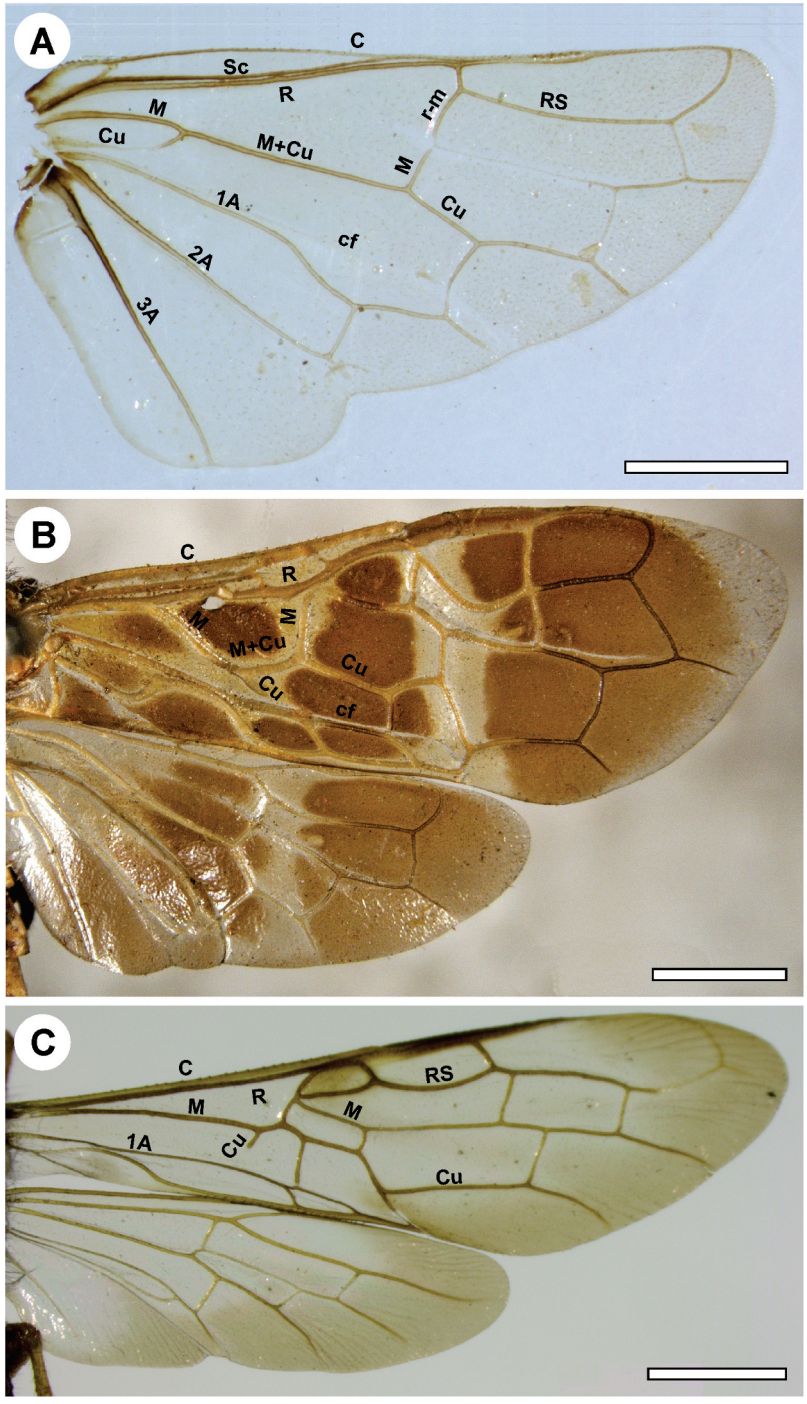


Figure 3. (A) *Pleroneura coniferarum* Hartig, 1837, Xyelidae, living, hindwing. (B) *Caenolyda reticulata* Linnaeus, 1758, Pamphiliidae, living, forewing. (C) *Sirex noctilio* Fabricius, 1793, Siricidae, living, forewing. Scale bars = 1 mm (A), 2 mm (B, C).

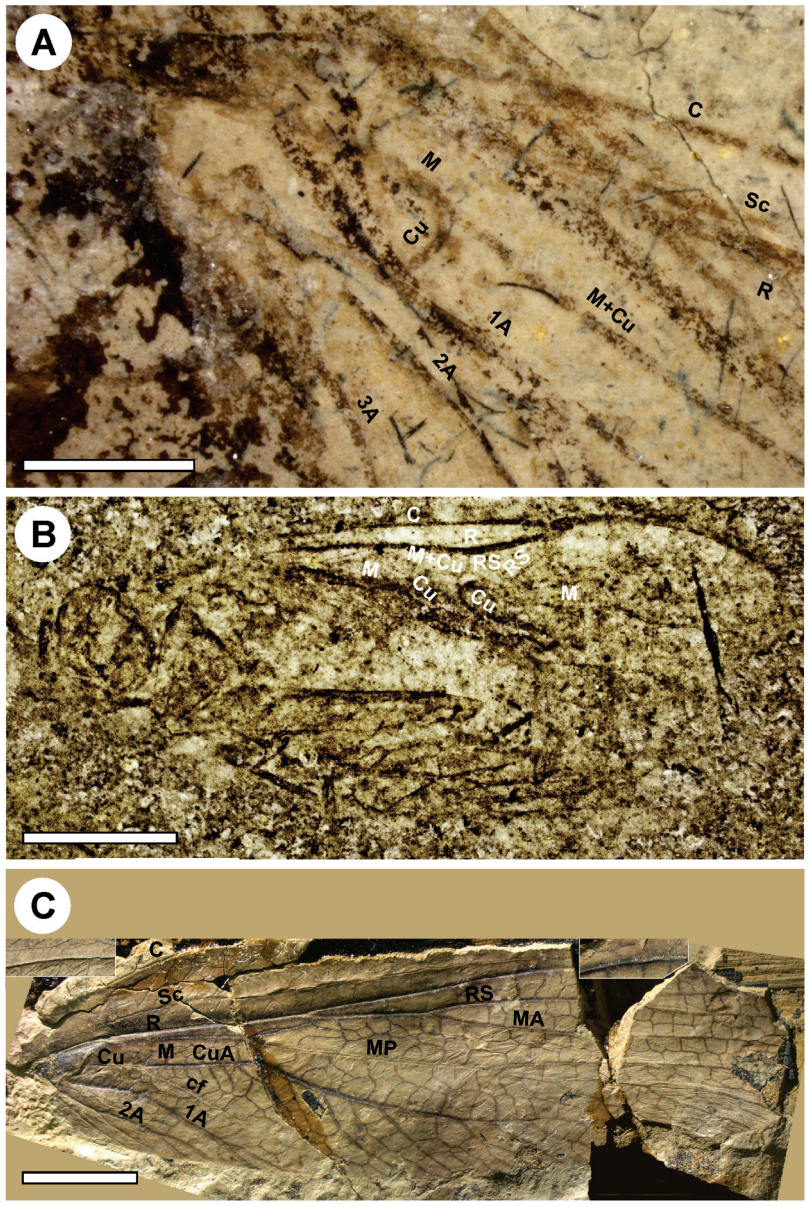


Figure 4. (A) *Gigasirex longipes* Rasnitsyn, 1968, Late Jurassic of Kulbastau Formation, Kazakhstan, Holotype counterpart, Holotype PIN 2066/3338, hindwing. (B) *Parapamphilius confusus* Rasnitsyn, 1968, Sepulcidae, Late Jurassic of Kazakhstan, Holotype PIN 2554/1303, forewing (mirrored). (C) *Dalduba faticana* Storozhenko, 1996, Daldubidae, Late Carboniferous of Siberia, Holotype PIN 3115/77, forewing. Photo courtesy D.E. Shcherbakov. Scale bars = 2 mm (A, B), 5 mm (C).

Argentina (Figure 1). First, because it reveals a generally less advanced wing morphology among Hymenoptera; second, because it belongs to the most basal hymenopteran family Xyelidae; and third, because it represents one of the oldest records for the order Hymenoptera from the Americas (being collected in the Upper Triassic deposits of the Potrerillos Formation in Argentina). In the Madygen Formation (Ladinian – Carnian), Central Asia, various Xyelidae were collected, and they are possibly older in age (e.g. *Triassoxyela foveolata* Rasnitsyn, 1964) (Figure 2(B)) (Voigt et al., 2017).

The distinctive cubital system in the forewing of *Potrerilloxyela menendezi* Lara, Rasnitsyn and Zavattieri 2014 (Figure 1) comprises of a long common base of Cu that uninterruptedly continues into the vertical basal section of CuA, that is equally a mainly spectral vein. In this section, the stem CuP is not visible as a real vein adjacent to the claval fold, but this is not surprising. The CuP generally tends to reduce much more often than CuA: in many insects, it is lost partially or completely (e.g. *Dalduba faticana* Storozhenko, 1996, Daldubidae, Late Carboniferous of Siberia) (Figure 4(C)). Also, in the hymenopteran hindwings, CuP is always lost even if CuA base is retained (Figure 3(A)).

Finally, as a result, in Figure 5 we can visualise the possible transformation series of the Cu vein in Hymenoptera. The starting point comprises the Pterygota groundplan cubital system observed in *Herbstiala herbsti* Schmidt, 1953 (early Pennsylvanian of Germany) (Figure 2(A)), with the Cu base diverging shortly into the anterior and convex CuA that turns forward for a while and then bowing more apical accordingly with other main vein systems, and the concave CuP that continues more or less closely the direction of Cu base to run closely anterior the claval fold (Figure 5(A)). A common next step (Figure 5(B)) in the transformation of the insect cubital system

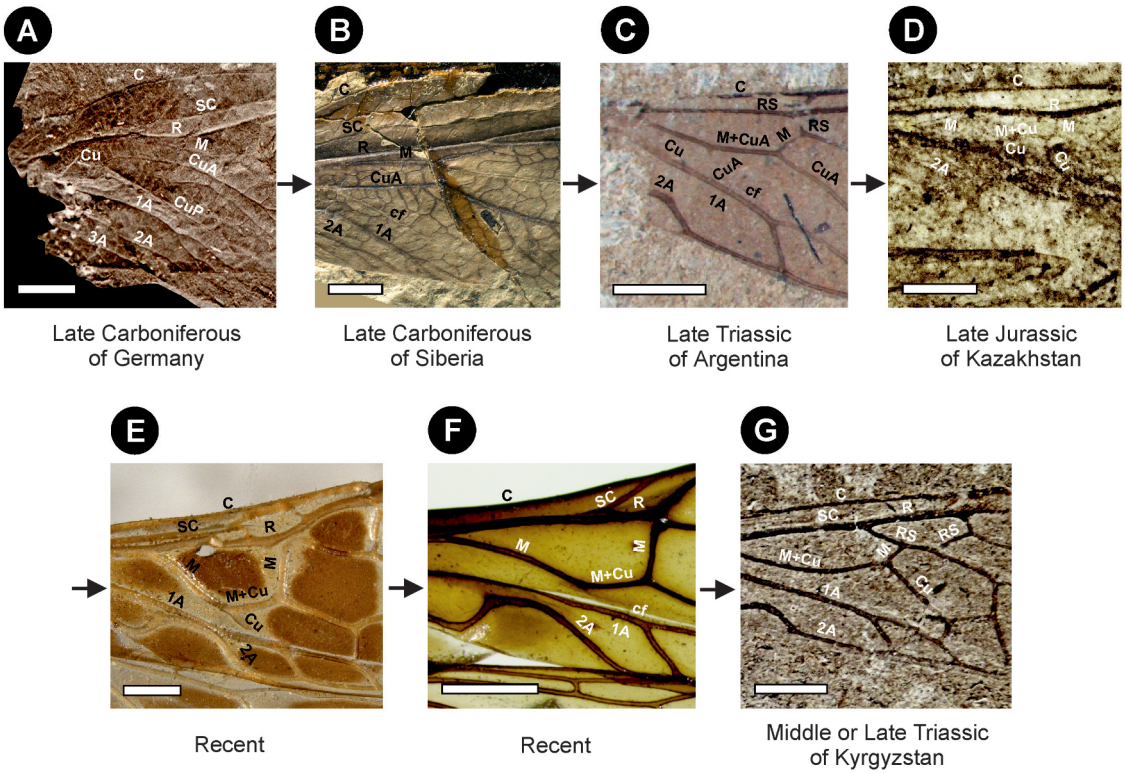


Figure 5. Transformation series of Cu in Hymenoptera. (A) Groundplan (*Herbstiala herbsti*, Paoliidae). (B) CuP lost (*Dalduba faticana*, Daldubidae). (C) CuA base shifted distal (*Potrerilloxyela menendezi*, Xyelidae). (D) Cu stem lost (*Parapamphilius confusus*, Sepulcidae). (E) CuA base shifted distal (*Caenolyda reticulata* L., Pamphiliidae, living). (F) CuA stem reduced to a stub (*Acantholyda erythrocephala* L., pamphiliidae, living). (G) CuA base lost (*Triassoxyela faveolata*, Xyelidae). Scale bars = 5 mm (A), 1 mm (B – G).

is the reduction of CuP vein in forewings (*Dalduba faticana* Storozhenko, 1996, Late Carboniferous of Siberia) (Figure 4 (C)). A characteristic of Hymenoptera, even though not unique to them, is the following fusion of CuA with M (M+CuA) at a distance in the middle part of the forewing and CuA base distally shifted (*Potrerilloxyela menendezi* Lara, Rasnitsyn and Zavattieri 2014, Late Triassic of Argentina) (Figures 1 and 5 (C)). The subsequent step includes the loss of Cu base from the forewing (*Parapamphilius confusus* Rasnitsyn, 1968, Late Jurassic of Kazakhstan) (Figures 4(B) and 5(D)). Then, the lone CuA base loses its connection with the claval fold, often with its basal end inclines distal (*Caenolyda reticulata* L., living) (Figures 3(B) and 5(E)). The next modification observed in cubital system comprise the reduction of CuA stem to a stub and additionally is observed to be a bend of the compound vein M & M+Cu (*Acantholyda erythrocephala* L., living) (Figure 5 (F)). The last state of the transformation series includes the total loss of the CuA stub, and is replaced by a gently arched compound vein M & M+Cu with no distinct bend (*Triassoxyela faveolata* Rasnitsyn, 1964, Middle or Late Triassic of Madygen Formation, Kyrgyzstan) (Figures 2(B) and 5(G)). However, the scheme presented in Figure 5 does not mean that Cu characteristic of *Potrerilloxyela menendezi* (i.e. with bases of Cu and CuA preserved, even though spectral) is plesiomorphic, in other words, that it was inherited directly from stem hymenopterans. The examples of Pamphiliidae, *Parapamphilius, Sirex*, etc., suggest that at least the free base of CuA could easily appear as a reversion, an atavism. This well might hold true for *Potrerilloxyela* as well, unless future fossils render evidence in favour to the hypothesis that *Potrerilloxyela* retains the groundplan Cu whilst all other Xyelidae have lost this character state.

Concluding remarks

We posit that the cubital vein morphology (retaining the bases of Cu and of CuA normally lost in Hymenoptera) of *Potrerilloxyela menendezi* Lara, Rasnitsyn and Zavattieri 2014 is example of an atavism (or reversion) case. This situation fulfils several of the criteria required to be evidence of an atavism mentioned by Tomić and Meyer-Rochow (2011), such as is not found in parents or immediate ancestors, appearing in adult stages and in a few individuals, and this atavistic structure was previously found in its evolutionary ancestry.

To conclude, unique and even incomplete fossils can reveal important features of deep time evolution, and the Triassic deposits of Argentina are a treasure of knowledge of the past life on the Earth.

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