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Potrerilloxyela menendezi gen. et sp. nov. from the Late Triassic of Argentina: The Oldest Representative of Xyelidae (Hymenoptera: Symphyta) for Americas

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Abstract—*Potrerilloxyela menendezi* gen. et sp. nov. from the Potrerillos Formation, Cuyo Basin, early Upper Triassic, Mendoza Province, Argentina is described. It is included in the living family Xyelidae and tentatively placed in Liadoxyelini of Xyelinae, which is otherwise known only from the Jurassic of Asia. This record is the first for Hymenoptera in the Triassic of the New World and provides new evidence about the close faunal connections between Laurasia and Gondwana during Mesozoic times. The phylogenetic position of the new genus is discussed.

Keywords: Insecta, Hymenoptera, Xyelidae, Upper Triassic, Potrerillos Formation, Cuyo Basin, Argentina

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INTRODUCTION

The Hymenoptera is one of four "hyperdiverse" insect lineages along with Diptera, Lepidoptera, and Coleoptera (Grimaldi and Engel, 2005). It is one of the dominant life forms on Earth in terms of species number (above 153 000 named species; Aguiar et al, 2013) and highly diverse bionomically.

The oldest representatives of the Hymenoptera are known from the Middle to Late Triassic deposits in Kyrgyzstan in Central Asia and from the Upper Triassic of Australia and South Africa (Riek, 1955; Rasnitsyn, 1964, 1969, 1980; Schlüter, 2000; Engel, 2005). All Triassic Hymenoptera are similar in wing venation and antennal structure to Xyelidae, the only family of the Xyeloidea, which is generally accepted as either ancestral to the whole order (Rasnitsyn, 1969, 1988), or the most basal off-shoot of Hymenoptera (Sharkey et al., 2011). Since the mid-Jurassic, the Hymenoptera underwent continuous massive diversification.

There are few rich assemblages of insect fossils recorded in South America (Table 1). More than 80 species have been found in the Triassic strata of Argentina during the last decade (Brauckmann et al., 2010; Gallego et al., 2011; Martins-Neto et al., 2011; Lara et al., 2012). In the Los Rastros and Ischichuca formations of the Bermejo Basin, La Rioja Province, 510 specimens have been found. Additional material was collected in the Cerro de las Cabras, Potrerillos, and Cacheuta formations of the Cuyo Basin, Mendoza Province, and the Llantenes Formation of the Malargüe Basin, southern Mendoza Province. All these findings allow a better characterization of the real insect diversity and probable relationships to other Gondwanan Triassic insect faunas.

This article reports the first record of Hymenoptera in the Triassic of South America and the first record the subfamily Xyelinae in the Triassic deposits worldwide. The fossil under description sheds light on the early evolution of wing structures in Xyelidae.

GEOLOGICAL AND ENTOMOLOGICAL ASPECTS OF THE POTRERILLOS FORMATION

The Cuyo Basin is a Triassic rift basin located in western Argentina. It is mainly formed by Paleozoic rocks and Permian–Triassic volcanic–clastic complex

Table 1. The records of fossil Hymenoptera in South America (trace fossils excluded)

Region	Formation/ Basin/Epoch	Family	Taxon	References
Brazil	Crato Member, Santana Formation, Araripe Basin (Northeast), Lower Cretaceous	Tiphidae	Architiphia rasnitsyni Darling, 1990	Darling, Sharkey, 1990
		Formicidae or Ampulicidae	Cariridris bipetiolata Brandão et Martins-Neto, 1989	Brandão et al., 1989; Rasnitsyn in Dlussky, 1999
		Ephialtitidae	Cratephialtites kourios (Sharkey, 1990)	Rasnitsyn, 1999
		Scoliidae	Cretaproscolia josai Rasnitsyn et Delclos, 1999	Rasnitsyn, Delclos, 1999
		Sphecidae s.l.	Cretosphex magnus Darling, 1990	Darling, Sharkey, 1990
			Cretosphex parvus Darling, 1990	Darling, Sharkey, 1990
		Rhopalosomatidae	Mesorhopalosoma cearae Darling, 1990	Darling, Sharkey, 1990
		Sepulcidae	Prosyntexis gouleti Sharkey, 1990	Darling, Sharkey, 1990
			Prosyntexis legitima Martins-Neto et al., 2007	Martins-Neto et al., 2007b
		Proctotrupidae	Protopoctro asodes Sharkey, 1990	Darling, Sharkey, 1990
	Tremembé Formation, Taubaté Basin, Oligocene (São Paulo)	Ichneumonidae	Paratilgidopsis praecursora Martins-Neto, 1998	Martins-Neto, 1998
			Taubatehymen minuta Martins-Neto, 1998	Martins-Neto, 1998
	Fonseca Formation, Fonseca Basin, Oligocene (Minas Gerais)	Formicidae	Gen. et. sp. n. indet.	Martins-Neto, Mendes, 2002
			Fonsecahymen stigmata Martins-Neto et Mendes, 2002	Martins-Neto, Mendes, 2002
Argentina	Ventana Formation, Paleocene–Eocene (Río Negro)	Formicidae	Ameghinoia piatnitzkyi Viana et Haedo-Rossi, 1957	Viana, Haedo-Rossi, 1957
			Polanskiella smekali Rossi de Garcia, 1983	Rossi de Garcia, 1983
		Siricidae	Urocerus patagonicus Fidalgo et Smith, 1987	Fidalgo, Smith, 1987

of the Choiyoi Group (Fig. 1). The basin's fill is composed primarily of Triassic continental sediments, but also includes Jurassic/Cretaceous and Lower Tertiary nonmarine and volcanic rocks layers, which are in turn overlain by thick, upper continental Tertiary sediments.

In the Triassic succession of the basin, the terrigenous clastic record of the Uspallata Group reflects successive episodes of deposition. Two megasequences bounded by regional unconformities have been recognized (Kokogian and Mancilla, 1989; Kokogian et al., 1993). The first is composed of proximal fluvial deposits of the Rio Mendoza and Cerro de Las Cabras formations (late Middle Triassic). The upper megasequence is widely distributed and is characterized by fluvial, deltaic, and lacustrine depositional systems represented by the Potrerillos and Cacheuta formations (latest Middle to early Late Triassic) and overlain unconformably by fluvial sediments of the Rio Blanco Formation (late Late Triassic).

The fossil insect described herein was collected in yellowish mudstones of the uppermost section of the Potrerillos Formation (Fig. 1). Outcrops of this formation occur at the southern flank of Cerro Cacheuta, southernmost end of the Precordillera Mountain Range (Mendoza Province). The insect-bearing level is located about 200 m north of Puesto Miguez or Minas de Petroleo locality (cf. Jain, 1968; Stipanicic et al., 1996) (33°04′0.6″ S, S–69°06′33.6″ W, and at 1.386 m a.s.l.), and just a few centimeters above the

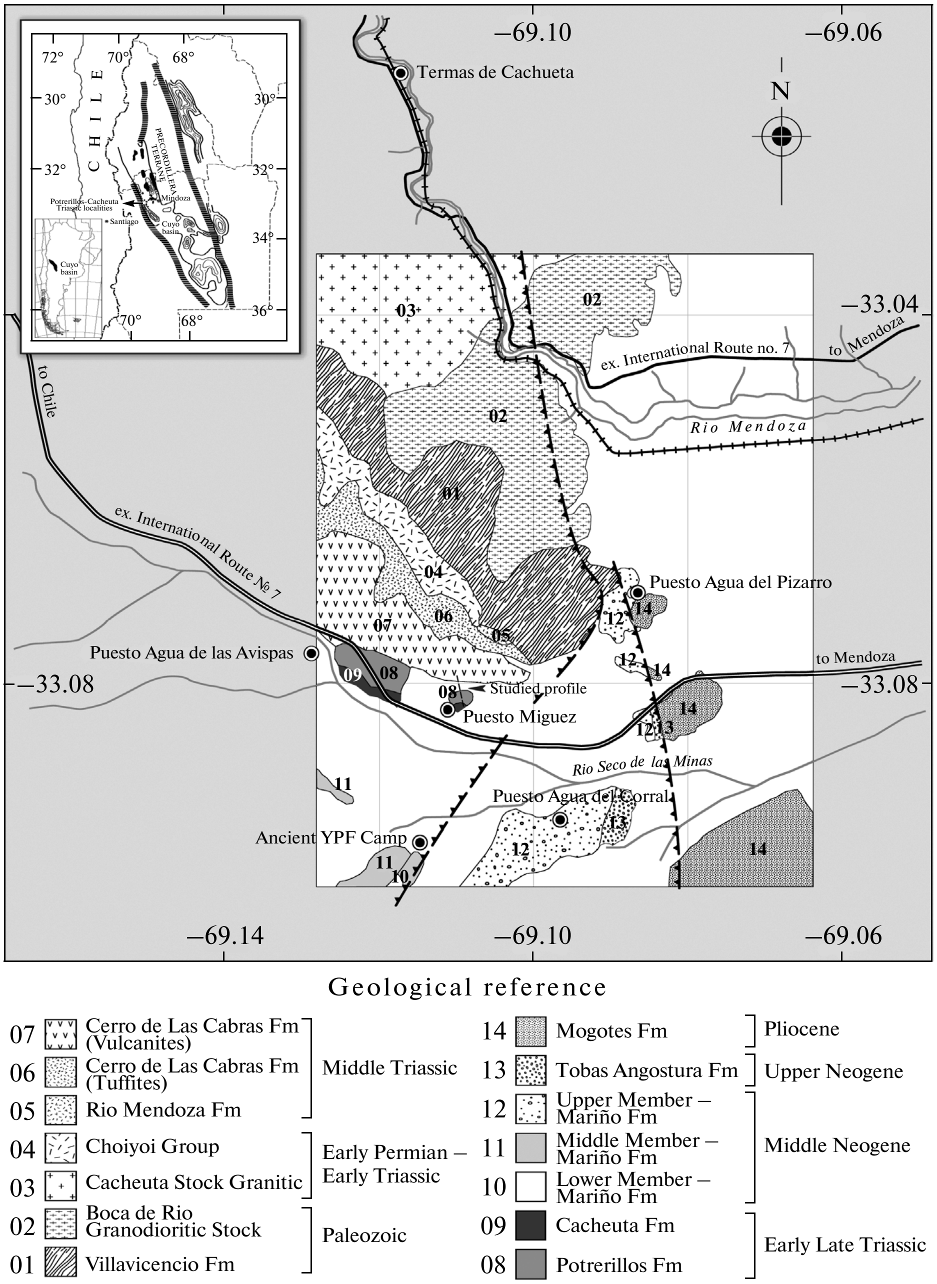

Fig. 1. Geologic map of the southeastern flank of the Cerro Cacheuta, south of the Precordillera of Mendoza Province. Note that the lower units of the Uspallata Group (Río Mendoza and Cerro de Las Cabras formations) crop out in this area, as was first described by Rébori (1979). Age known of the mapped units: (01) Devonian; (02) ?Early–?Late Carboniferous; (03) Middle to Late Permian; (04) Late Permian to Early Triassic; (05–07) late Middle Triassic; (08, 09) early Late Triassic; (10–12) Middle Miocene; (13) ?Middle Pliocene; (14) ?Late Pliocene (Series/Epoch according to *International...*, 2012).

level where Gallego et al. (2011) reported *Platyperla marquati* (Fig. 2). The total thickness of the outcrop in this section is 155 m and its sediments are transitionally overlain by black lacustrine shales of the Cacheuta Formation (Potrerillos/Cacheuta sedimentary succession) (for more details, see Gallego et al., 2011) (Fig. 3). The Potrerillos Formation represents braided streams, low sinuosity fluvial channels, and overbank deposits developed on a floodplain that passes upward into interdistributary bay-facies of lacustrine deltas and lacustrine basin deposits of the Cacheuta Formation (Zavattieri and Prámparo, 2006).

From a paleoentomological perspective, the contents of the Potrerillos Formation make it one of the most important Triassic units in Argentina, along with the Los Rastros Formation, in La Rioja Province. The Potrerillos Formation has yielded 229 specimens with 21 species now having been described and all of these

Fig. 2. Aerial view of the southern flank of the Cerro Cacheuta, southern Precordillera extremity, Mendoza Province, showing the Puesto Miguez (or Minas de Petróleo) locality. The *Potrerilloxyela menendezi*-bearing level is indicated. Image taken from *Google Earth* (2009).

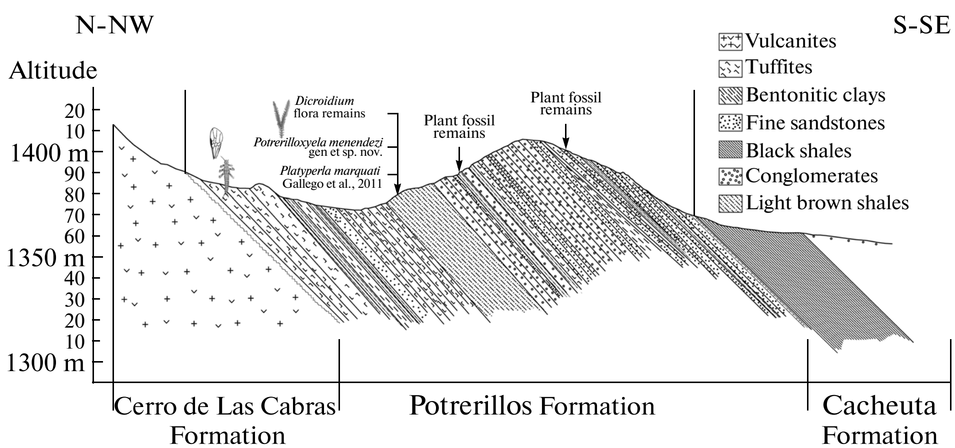

Fig.3. Detailed stratigraphic and sedimentological profile of the northern section of the Puesto Miguez locality; the *Potrerilloxyela menendezi*-bearing level in association with *Dicroidium* plant fossils is in the uppermost part of the Potrerillos Formation.

specimens coming from two specific areas in the southern extreme of the Precordillera range in Mendoza Province: (a) south of Cerro Cacheuta (at the Puesto Miguez, Quebrada del Durazno, and Agua de las Avispas localities) and (b) north of the Cerro Bayo (Quebrada del Puente locality), Potrerillos area. These records include a considerable amount of insect diversity, as collected and/or described by authors, including Wieland (1925, 1926), Tillyard (1926), Cabrera (1928), Pinto and Purper (1978), Marquat (1991), Storozhenko (1997), Martins-Neto and Gallego (1999), Martins-Neto et al. (2003, 2007a, 2008), Gallego et al. (2011), Lara et al. (2012). Beetles are quite common among these specimens (elytra and body fragments, rarely complete), although wing remains of blattids and hemipterans prevail. Other orders are also present, but remains occur only rarely (scorpionflies, miomopterons, orthopterons, dragonflies, stoneflies, and grylloblattids). The nearly complete absence of aquatic insects is characteristic, only represented by nymphs of Plecoptera and Grylloblattida (Gallego et al., 2011).

MATERIALS AND METHODS

The insect wing described in this paper was collected by Oscar F. Gallego during a field trip in 2010. It is housed in the Palaeoinvertebrate Collection of the Museo de Ciencias Naturales y Antropológicas "Juan Cornelio Moyano" (Mendoza city), under collection number MCNAM-PI 24604.

The photographs were taken using an Olympus SZ51 binocular microscope and an Olympus SP-350 digital camera (8.0 megapixels). The line drawing was made using Corel Draw 14. The venational symbols (Plate 1) are modified after Rasnitsyn (1969).

SYSTEMATIC PALEONTOLOGY

Order Hymenoptera

Suborder Symphyta

Superfamily Xyeloidea Newman, 1834

Family Xyelidae Newman, 1834

Subfamily ?Xyelinae Newman, 1834

Tribe ?Liadoxyelini Rasnitsyn, 1966

Genus *Potrerilloxyela* Lara, Rasnitsyn et Zavattieri, gen. nov.

Etymology. The genus name is derived from adding the name of the Potrerillos Formation to the generic name *Xyela*.

Type species. *P. menendezi* sp. nov.

Diagnosis. Pterostigma pale, only sclerotized at extreme base, otherwise membranous, with surrounding veins only slightly thicker than other wing veins. SC connected to C only very short distance beyond origin of RS, and probably meeting R basal or at most slightly distal of RS base. R almost straight (only slightly angled at RS base, resulting in costal space moderately narrow throughout). Basal section of RS much shorter than basal section of M. Cell 2r with its anterior margin slightly shorter than 1r. 1r-rs distinctly shorter than 2r-rs. 2r-m joining cell 3r just before RS fork. Cell 1mcu wide and low, 1m-cu subequal to 3Cu. Size moderate (type species forewing ca. 7 mm long).

Species composition. Type species.

Comparison. The new genus differs from all other Liadoxyelini in the basal position of 2r-m in respect to RS fork.

Remarks. The new genus is attributed to Xyelydae based on the branched RS combined with complete venation. Bifurcate RS is rare in Hymenoptera other than Xyelidae and always combined with the venation reduced or (in *Pseudoxyela* Rasnitsyn, 1968 in Xyelotomidae), otherwise modified (1RS very short, 2r-rs meeting pterostigma near its apex, etc.). The new genus differs from all other Xyelidae, except for some Cenozoic Xyelini, in the crossvein 2r-m meeting RS basal of the fork: all remaining Xyelidae have 2r-m meeting RS2 rather than the RS stalk. It differs from all Xyelini in having 1-RS shorter than 1-M. The reasons of subfamily and tribe attribution are presented in the *Discussion* below.

Potrerilloxyela menendezi **Lara, Rasnitsyn et Zavattieri, sp. nov.**

Etymology. In honor of Augusto Juan Menéndez, an attorney and amateur paleontologist in Mendoza Province.

Holotype. MCNAM-PI, no. 24604, part and counterpart; Puesto Miguez (or Minas de Petróleo), southern flank of Cerro Cacheuta, southern end of the Precordillera, Cuyo Basin, Mendoza Province, Argentina; uppermost Potrerillos Formation; early Late Triassic (equivalent to Carnian of marine sequences).

Description (Fig. 4). The fore wing pterostigma is large, lancet-like, almost symmetrical, not sclerotized, except for dark delimiting veins, with the crossvein 2r-rs at 0.7 of its length. C is not widened before the pterostigma. In SC, only the apex is preserved (apparently free from R) and it meets C only at a very short distance distal to the RS base. R is straight both before and after the RS base, where it is distinctly angular. The costal area is narrow, but widest near the origin of RS. 1R is oblique, about 0.6 as long as 1M. RS+M is about as long as 2RS and 0.8 times as long as 2M, terminating short of the midlength of cell 1mcu. 3RS is curved strongly basally. 4RS is slightly angular at junction with the crossvein 2r-m. Cell 2r is 0.9 times as long as 1r along its anterior margin. Cells 3r and 4r are approximately equal in length. 2r-rs is much longer than 1r-rs. The RS_1 apex is halfway between the pterostigma and RS_2 apex. 3M is straight. 2r-m is equidistant to the 2r-rs and RS fork, placed after the midlength of cell 2mcu, thin and flexible throughout most of its length. 3r-m is slightly distal to the midlength of cell 4r and inclined towards the posteroexternal wing margin. Crossvein 1m-cu is about as long as 3Cu and slightly longer than 2Cu. M+Cu is slightly angular at the midlength, with a vein rudiment there (possibly a rudiment of the base of free Cu; if this is the case, the vein lying basal to it is M and that distal to it is M+Cu). M and Cu have free apices distal to 3r-m and 2m-cu, respectively (unknown for R distal to RS_2). Cell 1mcu is long and narrow, slightly bent towards the posterior wing margin, and widened slightly apically. The crossvein 2m-cu is at the midlength of cell 3rm, bifurcating there (probably an individual aberration). The crossvein cu-a is near the end of cell 1mcu. The anal veins are standard in shape.

Measurements, mm. Preserved fore wing length, 6.0 (full length, ca. 6.4); fore wing width, 2.0.

Material. Holotype.

DISCUSSION

Accommodation of the new genus into the system of the family Xyelidae is problematic, primarily

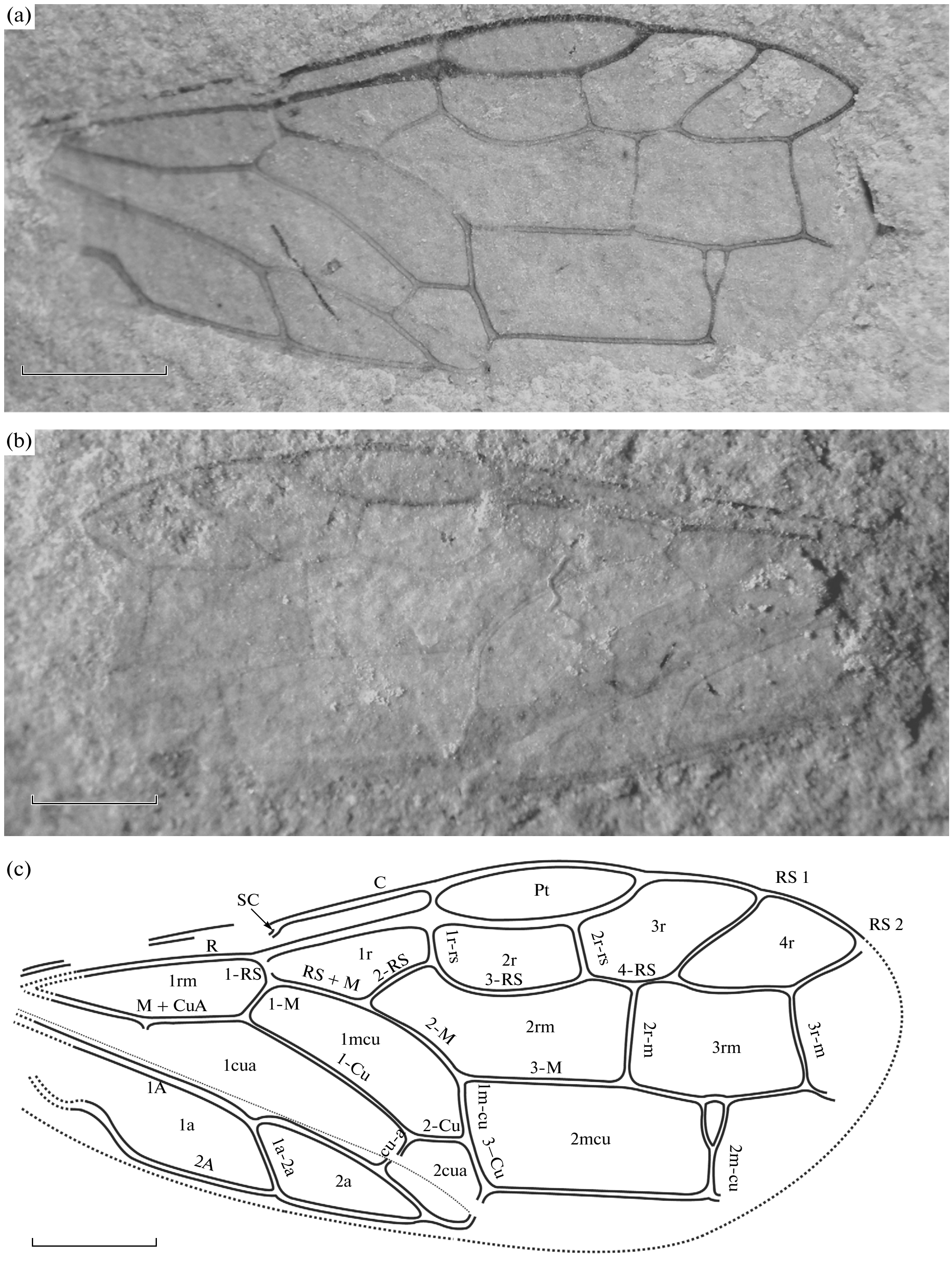

Fig. 4. *Potrerilloxyela menendezi* gen et. sp. nov., holotype MCNAM-PI, no. 24604: (a) photograph of part, (b) photograph of counterpart, (c) line drawing. Scale bars, 1 mm.

because the system itself is far from being clear. The vast majority of Xyelidae (47 out of 52 genera and 146 out of 211 species listed by Taeger et al., 2010) are extinct taxa often only known from wing morphology which is not always sufficiently diagnostic. As a result, the definition of the subfamilies and tribes is not at all straightforward and numerous exceptions should be considered.

Table 2. Diagnostic characteristics of the subfamilies in Xyelidae

Diagnostic characters	Archexyelinae	Xyelinae	Macroxyelinae
R	Straight, at most weakly angled at RS base, costal space narrow	Usually bent before or at RS base, with costal space well widened there, or sometimes straight	Usually bent before or at RS base, with costal space well widened there, or sometimes straight
Area at pterostigma base	When well preserved, C apex widened and often connected to R; desclerotization rare C	C apex very rarely widened to connect to R, no desclerotization	C apex widened and connected to R unless desclerotization present
Pterostigma	Sclerotized (darkened) at least in basal 0.3 or widely along borders	Only bordering veins can be sclerotized (sometimes considerably so basally)	Sclerotized (darkened) at least in basal 0.3 or widely along borders, sometimes also with basal desclerotization
Cell 1r vs. 2r along fore margin	Usually short, rarely more than 1.5 times as long as 2r	Long (usually more than 1.5 times as long as 2r)	Long (usually more than 1.5 times as long as 2r)
1r-rs	Shorter or longer 2r-rs	Shorter or longer 2r-rs	Short or subequal 2r-rs
1-RS	Longer, very rarely shorter 1-M	Longer 1-M (Xyelini) or shorter (Liadoxyelini)	Shorter or longer 1-M
Ovipositor	Long and not very wide	Long and not very wide	Short or, rarely, long and very wide

The subfamily Archexyelinae was initially diagnosed by the costal space not much widened near the midlength, the SC generally weak but when sufficiently preserved seen to reach the C apex before the pterostigma; absence of a crossvein connecting Sc with R; cells 1r subequal or slightly longer than cell 2r; cell 3r rarely longer than 2r; R between 1r-rs and 2r-rs only 0.3–0.4 times as long as between R+M and 1r-rs; and 1r-rs distinctly shorter than 2r-rs (Rasnitsyn, 1969). However, the type genus of the subfamily shows SC which both fails to reach the C apex (in *Archexyela crosbyi* Riek, 1955) and is connected to R with a crossvein (in *A. ipswichensis* Engel, 2005). An almost straight R and narrow costal space, not distinctly widened at the midlength are both found in a number of Xyelinae (*Eoxyela* Rasnitsyn, 1965, *Kirghizoxyela* Rasnitsyn, 1966 and others) and Macroxyelinae (*Nigrimonticola* Rasnitsyn, 1966, *Baissoxyela* Rasnitsyn, 1969).

Distinction of the Xyelinae and Macroxyelinae is also difficult, particularly when based on the wing alone. Rasnitsyn (1969) relied on morphology of the area near the pterostigmal base: in Macroxyelinae, the apex of C is widened posteriorly, with a sclerotization reaching R basal to the vertical slit before the pterostigma (unless the whole area is somewhat desclerotized leaving a considerable gap there). In contrast, Xyelinae were defined as having a C apex at most slightly widened and not connected to R and never with appreciable desclerotization there. However, such a desclerotization occurs rarely in Xyelinae as well (in *Orthoxyela* Rasnitsyn, 1983).

Taking into account available information about the hymenopteran wing and also the ovipositor shape, which is often known in fossils, it is possible to update somewhat the subfamily diagnostic features, even though it is left imperfect (Table 2). We do not consider the subfamily Madygellinae here, which is now reduced to its monotypic type genus. The taxonomic position of this taxon deserves reconsideration.

Thus, it is possible to conclude that *Potrerilloxyela* gen. nov. fits Xyelinae in two most reliable characters (pterostigma and area at pterostigmal base) and fits Archexyelinae in the remainder, which are considered as less reliable. Hence, we preliminary identify the new genus as a member of Xyelinae.

There are two tribes established in Xyelinae, Xyelini and Liadoxyelini (Rasnitsyn, 1966, 1969), which distinctions are not clearly determined yet. Rasnitsyn (1969) distinguished these as follows: 1-RS is longer than 1-M in Xyelini vs. shorter in Liadoxyelini, and 3-Cu is at most 1.5 times as long as 1m-cu in Xyelini vs. more than 1.5 times so in Liadoxyelini. However, *Kirghizoxyela* Rasnitsyn, 1966 and *Orthoxyela* Rasnitsyn, 1983, both classified in Liadoxyelini, have 1-RS slightly longer than 1-M, and *Xyela* (*Pinicolites*) spp. of Xyelini have 1m-cu short (cf. Rasnitsyn, 1995, 1997). A third character can be added there, the forewing size which is generally below 6 mm in Xyelini vs. above 6 mm in Liadoxyelini. There is an exception here as well, for *Xyelisca leptopoda* Rasnitsyn, 1969 has a forewing above 6 mm long as preserved and supposedly about 9 mm full length. Long 1-RS makes the position of *Xyelisca* well supported within Xyelini.

Based on the above observations, it is possible to note a contradictory character combinations in the new genus, with short 1-RS being indicative of Liadoxyelini and with long 1m-cu characteristic of Xyelini. The forewing size is slightly above the standard of Xyelini, but this character is not very reliable. Additional indication can be drawn from the Triassic age of the fossil under discussion. Liadoxyelini are known since the Early Jurassic (*Kirghizoxyela*, *Liadoxyela, Orthoxyela*), in contrast to Xyelini, which are only known since the Late Jurassic (with exception of *Xyelisca*, which is coeval with *Orthoxyela*). As a result, we tentatively attribute *Potrerilloxyela menendezi* gen. et sp. nov. to the tribe Liadoxyelini.

CONCLUSIONS

The family Xyelidae has had a great importance in the history of Hymenoptera. It was the only hymenopteran group in the Triassic and kept a considerable abundance during the Jurassic and Early Cretaceous. Currently, it includes 65 extant species of herbivorous wasps (Taeger et al., 2010), which feed on nectar and pollens, in shoots of fir or on leaves of deciduous trees. Xyelidae has a Holartic distribution now, being particularly abundant and diverse in North America. However, during the Mesozoic, they were more widely distributed and associated with warmer climates than presently preferred by species of the family (Grimaldi and Engel, 2005).

Potrerilloxyela menendezi gen. et sp. nov. is the oldest species of the order found in Argentina and in the whole of South America. Tentatively placed in Xyelinae, it represents the worldwide first record for subfamily in the Triassic Period and possibly an additional example of a limited effect of the Triassic–Jurassic extinction on insects.

This record also expands our knowledge of evolutionary history and diversity of basal Hymenoptera back in the Lower Mesozoic, suggesting that Xyelidae and, hence, the order Hymenoptera appears in the fossil record almost simultaneously in four regions of both supercontinents: Laurasia (Central Asia) and Gondwana (Australia, South Africa, and now South America).

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