A cockroach wing from the Mangrullo Formation Lagerstätte (?Early Permian, Uruguay) with affinities to Carboniferous representatives of the Order Blattodea (#29942)

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A cockroach wing from the Mangrullo Formation Lagerstätte (?Early Permian, Uruguay) with affinities to Carboniferous representatives of the Order Blattodea

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A new species of a large cockroach is described, represented by a left forewing from the Early Permian Mangrullo Formation, an ancient *Konservat-Lagerstätte* of Uruguay. The specimen is exceptionally well preserved in both part and counterpart, possibly favoured by pyrite precipitation, a common mineral in the unit. The venation of the wings is clearly marked and it is possible to distinguish the morphology of the main veins, allowing relating the specimen to the oldest known Carboniferous (Westphalian) blattids. The Uruguayan specimen may be assigned to Phyloblattidae, although it possesses a connecting vein between M and CuA which is typically present in the members of Archimylacridae, a family not yet found in the Paraná Basin. Therefore, the familiar and generic affinities of the Uruguayan new specimen are yet in discussion but its unique morphology and its geographic and stratigraphic position, suggest that it belongs to a new species. When compared to other blattids from Carboniferous and Permian deposits of South America and elsewhere Pangea, our specimen shares characters with Late Carboniferous-Early Permian blattids from Brazil, particularly in its large size. However, intriguingly, the Uruguayan blattid also presents a strong similarity in the vein distribution to *Qilianiblatta namurensis* Zhang et al., 2012, clearly a smaller blattid species from the Westphalian of China. Sc, RA, RP, MA, MP, CuA, CuP, and CV veins display the same distribution in the Chinese and the Uruguayan taxa, as well as they share a lesser development of the primary vein dichotomy. The apparent close relationship of the Uruguayan new species to the oldest known blattids, would suggest an older age to the Mangrullo Formation ranging from the latest Carboniferous to the earliest Permian, an age that can be also supported by the macrofloral assemblage, and the affinities of the pygocephalomorph crustaceans from the same levels.

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ABSTRACT.– A new species of a large cockroach is described, represented by a left forewing from the Early Permian Mangrullo Formation, an ancient Konservat-Lagerstätte of Uruguay. The specimen is exceptionally well preserved in both part and counterpart, possibly favoured by pyrite precipitation, a common mineral in the unit. The venation of the wings is clearly marked and it is possible to distinguish the morphology of the main veins, allowing relating the specimen to the oldest known Carboniferous (Westphalian) blattids. The Uruguayan specimen may be assigned to Phyloblattidae, although it possesses a connecting vein between M and CuA which is typically present in the members of Archimylacridae, a family not yet found in the Paraná Basin. Therefore, the familiar and generic affinities of the Uruguayan new specimen are yet in discussion but its unique morphology and its geographic and stratigraphic position, suggest that it belongs to a new species. When compared to other blattids from Carboniferous and Permian deposits of South America and elsewhere Pangea, our specimen shares characters with Late Carboniferous-Early Permian blattids from Brazil, particularly in its large size. However, intriguingly, the Uruguayan blattid also presents a strong similarity in the vein distribution to *Qilianiblatta namurensis* Zhang et al., 2012, clearly a smaller blattid species from the

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Keywords: Insecta, Blattodea, Late Carboniferous- Early Permian, Uruguay.

INTRODUCTION

In Uruguay, Paleozoic fossil insects are only represented by isolated wings (Pinto et al., 2000) found in calcareous levels of the Early Permian Mangrullo Formation (Fig. 1), where pygocephalomoph crustaceans, permineralized fragmentary trunks and scattered mesosaur remains were the only fossils found (Piñeiro, 2002; 2006; Piñeiro et al., 2012a,b). From these coarse to fine limestone facies several well preserved positive and negative imprints of isolated wings were described as Hemiptera belonging to Cicadopsyllidae Martinov 1931, and to the new family Perlapsocidae. Two new species were erected, *Paracicadopsis mendezalzolai* and *Perlapsocus formosoi* (Pinto et al., 2000), a discovery that opened a new line of research for the Upper Palaeozoic deposits of Uruguay. At the time that Pinto et al. (2000) described those specimens representing the first Paleozoic record of insects for Uruguay, the age of the Mangrullo Formation was controversial. While a Late Permian age was proposed by the palynological associations found in Uruguay (Bossi and Navarro, 1981; Beri and Daners, 1985) following the same line of reasoning suggested for the Iratí Formation (e.g., Daemon and Quadros, 1970; Mezzalira, 1980), biostratigraphic studies based mainly on macrofloral correlation along to the presence of the mesosaurid and pygocephalomorph crustaceans association present in all these units, place the South American Iratí (Brazil) and Mangrullo (Uruguay) formations and the Whitehill Formation from South Africa into the Lower Permian (Huene, 1940; Oelofsen, 1981). Accordingly, the new hemipteran species described by Pinto et al. (2000) for the Mangrullo Formation are similar to components of the Lower Permian Russian entomofauna.

The Early Permian, or even a Permo-Carboniferous age (vide Huene, 1940) appears also supported by the presence of pygocephalid and tealliocaridid pygocephalomorph representatives (Piñeiro, 2002; 2006), taxa that are only found in Late Carboniferous sequences of Laurentia (Brooks, 1962; Schram, 1979). However, geochronological data from zircons of the Iratí bentonites gave an age of 278±2 Ma (Artinskian) for this unit (Santos et al., 2006), although other similar analyses suggested an older age, close to the Permo-Carboniferous boundary (Rocha-Campos, personal communication, 2014).

Several new specimens showing an outstanding preservation of wings and part of the body were recently collected from the same levels where the cicadopsyllids appeared. Although these new specimens are currently under study, it is possible to anticipate the presence of a moderately diverse insect fauna in the Mangrullo Formation limestone (Fig. 1).

Blattodea (cockroaches) is an ecologically important order of insects, being one of the phylogenetically basal most groups. They became dominant during the Carboniferous and along 320 millon years of evolution, a total of 27 families have been described (Zhang et al., 2012; Wei & Ren, 2013). The earliest fossil record of cockroaches dates back to Late Carboniferous, and show evidence that tegmines have been appeared early as an adaptation for protection (Zhang et al, 2012). In the Paleozoic, eight extinct insect families have been recorded, being Phyloblattidae the longest within Blattodea (Vrsansky et al, 2012). In South America, there are seven species of Phyloblattidae recorded from the Itararé Group of Brazil (Carboniferous-Permian) (see Rösler et al., 1981; Pinto, 1972a,b, Pinto and de Ornellas, 1978, 1980; Pinto, 1990) and from the Rio Genoa Formation (Early Permian) of Argentina (Ricetti et al., 2016), but no blattids have been found in the Early Permian Iratí Formation, despite insects have high preservational potential in this *konservatlagerstätte* (Silva et al., 2017). Here, we describe one well preserved left forewing part and counterpart which represents the first and only record of Blattodea for Uruguay, and could be one of the oldest records of the group worldwide. The reconstruction of the main venation of the wing will allow us to determine its taxonomical affinities by comparison to the earliest representatives of the clade. We will also propose some hypotheses to explain the repercussion of this finding in the currently accepted biogeographical context of Gondwanan Pangaea.

MATERIALS

The material described herein (FC-DPI 8710) is a well preserved left forewing (part and counterpart) collected by one of us (GP) in El Baron locality (Mangrullo Formation, Cerro Largo County) and it is housed in the Fossil Invertebrate Collection of the Department of Paleontology at Facultad de Ciencias-UdelaR, Montevideo, Uruguay (FC-DPI).

METHODS

The specimen FC-DPI 8710 was examined and it was dawn in dry state under a stereomicroscope with incorporated camera lucid (NIKON HFX-DX). Photographs were made directly using a digital camera NIKON under sided crossed light and others were taken using the camera integrated to the stereomicroscope and processed with the software Infinity Analize, for more detailed images. Drawings were calibrated to the photographs scales and improved using Photoshop CS 8.0 graphic software. We followed the wing venational groundplan of Lameere (1923).

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Barona: urn:lsid:zoobank.org:act:7CE17B81-0818-498C-87C1-937B75795F40

Barona arcuata: urn:lsid:zoobank.org:act:6A6269D2-A7EC-4EF2-B802-32AAFFBE69D4.

GEOLOGICAL SETTING

The Early Permian Mangrullo Formation crops up in north and northeast Uruguay (Fig. 1), extending to Brazil and thus forming part of the Paraná Basin as the correlative of the Iratí Formation (Daemond & Quadros, 1970). It was deposited in a restricted, moderately hypersaline lagoon (Piñeiro et al., 2012), mostly under low energy conditions thus favouring the development of the highly fossiliferous mudstone-dominated facies. However, limestone and breccias that could have been deposited by more energetic episodes are also represented, but showing the presence of asymmetric ripple marks in the uppermost levels, which can represent the returning to the original conditions of a marginal, and in some way, very quiet environment. These environmental conditions can be supported by the presence of very well-preserved insect wings associated to plant remains (well-preserved leaf cuticles and trunks) found in the limestone and also in the mudstone facies (Pinto et al., 2000). This assemblage represents a Konservat-Lagerstätte which is characterized by the exquisite preservation of the specimens, including very delicate soft tissues (Piñeiro et al., 2012a,b).

SYSTEMATIC PALAEONTOLOGY

Class Insecta Linnaeus, 1758

Superorder Dictyoptera Latreille, 1829

Order Blattodea Brunner von Wattenwyl, 1882

Family insertae sedis

Genus ***Barona*** gen.nov

Type species. ***Barona arcuata*** gen. et sp. nov.

Etymology. The generic name (feminine) refers to the El Baron Ranch, where the type specimen was found. The specific name is based on the arcuate feature of the CuP vein.

Holotype. FC-DPI 8710 (Fig. 3). A left forewing preserved as part and counterpart housed at the Facultad de Ciencias Collection of fossil invertebrates (acronym FC-DPI) of Montevideo, Uruguay.

Type Locality and Age. El Baron Ranch, Cerro Largo County, from non-bituminous shale of the Mangrullo Formation Konservat Lagerstätte, Early Permian (?Artinskian).

Diagnosis.

C completely marginal; elongate and coastal area which is wide at the base but narrows posteriorly; Sc pectinate with 6 branches in 45° angle; R sigmoid, ending at wing tip, with 7 bifurcated branches; M with 23 branches extending to wind margin; M forked into MA and MP, with multiple bifurcated branches; RA and MA weakly differentiated; Cu divided into CuA and CuP, near the wing base; CuA with branches; CuP very well-marked and sharply arcuated; connecting vein CV *arculus* (*sensu* Bethoux, 2005) present between M and CuA; R, M, and CuA strongly developed; AA and AP with numerous branches and cross venation in middle and basal area of wing.

Description

The specimen, FC-DPI 8710 (Fig. 3), consisting in part and counterpart of an elongate, ellipsoid left forewing, length/ width: 32mm x 12, 5 mm (length two times and a half longer than the width), is exceptionally well-preserved in both part and counterpart, possibly favoured by pyrite precipitation, a common preservation found in the Mangrullo Formation (see Piñeiro et al., 2012b). The venation of the wing is clearly marked and it is possible to distinguish the morphology of the main veins. The C vein is completely marginal; the coastal area is elongate and narrow but wider at the base; Sc pectinated with 6 branches in 45° angle; R sigmoid, ending at wing tip, with 7 bifurcated branches; M with 23 branches extending to wind margin; M forked into MA and MP, with multiple bifurcated branches; RA and MA weakly differentiated; Cu divided into CuA and CuP, near the wing base; CuA with branches; CuP vein is very well-marked and follows a sharply arcuate direction to the internal border of the tegmina; connecting vein CV *arculus* (*sensu* Bethoux, 2005) present between M and CuA; R, M, and CuA veins strongly developed; AA and AP with numerous branches and cross venation in middle and basal area of wing (Fig. 3).

Comparisons

The venation present in FC-DPI 8710 shares most of the characters with the family Phyloblattidae: an elongated and narrow costal area, Sc pectinate, RA and MA weakly differentiated, sigmoid CuA, a wide space between the CuP and AA veins, and a great distribution of the transverse venation, forming a scalariform cross venation and some reticulate areas. The subcostal vein is very separated from the radial vein, which allows us to place the specimen among the oldest known, Carboniferous blattids.

The new Uruguayan blattid *Barona arcuata* was compared to other Gondwanan representatives of the group (Fig. 4) such as the Brazilian phyloblattid *Anthracoblattina mendezi* Pinto and Sedor (2000), from the Permo-Carboniferous Itararé Group (Ricetti et al. 2016), and also to several Carboniferous and Early Permian phyloblattids from the Laurasian region of

Pangaea, especially the Chinese taxon *Qilianiblatta namurensis* (Stephanian) (Zhang et al., 2013; Guo et al., 2013), which features the major anatomical similitude (particularly in vein distribution). Although *Barona*, as well as *Qilianiblatta* and *Anthracoblattina*, are all large forewings, the latter is substantially larger (42 mm against 32 of *Barona* and 18 to 25 of *Qilianiblatta*). *Barona* and *Qilianiblatta* differ from *Anthracoblattina* in the following characters:

a) Costal area is wide at the base, while it is narrow in *Anthracoblattina*.
b) RA and RP are weakly differentiated but yet conserve the plesiomorphic arrangement, lacking translocations (Guo et al., 2013). These veins appear as no clearly differentiated in *Anthracoblattina*.
c) Anal field is well delimitated by first AA and the deeply incised and arquate CuP, while it is discrete in *Anthracoblattina*.
d) CuA seems to be slightly curved and smoothly sigmoid in *Barona*, and it is almost straight in *Anthracoblattina*.
e) *Barona* and *Qilianiblatta* possess a small cross veinlet (Cv) uniting CuA to M, which is absent in *Anthracoblattina*.

Nevertheless, *Barona arcuata* displays some characters that fit the archimylacrid venational groundplan, such as the connection vein (Cv) between CuA and M and a characteristic scalariform cross venation present in Westphalian archimylacrids (Zhang et al., 2012). This groundplan has been considered the most plesiomorphic one within Blattodea (Schneider 1983) from which could have evolved all the known more derived phyloblattids (Zhang, 2012).

DISCUSSION

Blattids integrate the Early Permian (~280 Ma, cf. Santos et al., 2006) entomofauna found in the Mangrullo Formation of Uruguay, confirming the wide distribution of this group in South America and elsewhere. The Mangrullo Formation represents an ancient Konservat-Lagerstätte preserved in a moderately hypersaline lagoon, under poorly oxygenated bottom conditions, an environment with a high potential of soft tissues preservation (Piñeiro et al., 2012). Most of the insect wings collected until now could be referred to groups known to have aquatic or semiaquatic adaptations, such us hemipterans and coleopterans. There is evidence that in the Upper Permian, some schizophoroid beetles went adapted to the aquatic habitat, and Mesozoic beetles lived on the surface of the water but did not swim (Ponomarenko, 2003).

Barona arcuata constitutes the first and oldest record of Blattodea for Uruguay (Fig. 3), it shows several plesiomorphic characters that are typical of Carboniferous cockroaches, such as a thick and arched anal margin, with well defined anal area, four main venation arising from the anterior end of the wing; the front veins, particularly the subcostal extends beyond the middle length of the wing, where possibly meets the costa vein; the radial and the median veins extend to the apex and cover the anterior and posterior area respectively; the cubital veins are simple and reach the posterior (medial) margin at the middle length of the wing. All the cubital veins are arcuate and bifurcated once before to reach the posterior (medial) margin.

Permian cockroaches are distinguished by the fusion of R and M, in a way that only three principal veins reach together from the anterior end of the wing (Sellards, 1904; 1906).

FC-DPI 8710 appears to be similar to species of *Anthracoblattina*, specially to *A. mendesi* (Ricetti et al., 2016) from the purposed earliest Permian (or Permo-Carboniferous) Campáleo area, State of Santa Catarina, Brazil, and also to *Anthracoblattina archangelsky* from the

Carboniferous Rio Guenoa Formation of the Chubut Province, Argentina (Pinto and Mendez, 2002) mainly sharing the large anal field, the absence of R and M fusion and its large size. However, the distribution of some of the main venations is different (i.e. those branches of the Anal area of *Barona* are not regularly spaced, not appearing to reach the posterior (medial) margin; the slightly concave, instead straight CuA; the number of MA and MP branches not equivalent; first fork for R near the basal end and the presence of the connecting vein CV, which is absent in the *Anthracoblattina* species. Comparisons to the other Carboniferous and Permo-Carboniferous taxa from Brazil are difficult because of the fragmentary nature of the specimens, and much of them would require a detailed previous revision and redescription (cf. Ricetti et al., 2016).

On the other hand, the Uruguayan blattid seems to be related to *Qilianiblatta namurensis* from the Namurian-Westphalian (Carboniferous) of China, which is the oldest Blattodea recorded at this moment (Zhang et al, 2012; Guo et al., 2013). The diagnosis of this new species includes too many similarities with China blattids, as for instance the C, Sc, RA, RP, MA, MP, CuA, CuP, and CV veins having the same distribution, even though they varied in the number of vein branches and cross venation density, the latter being probably originally more widely distributed, but masked by weathering or incorrect use of the light during examination. Like the Chinese blattids, this new Uruguayan species has the CuP arcuate and the base of the wing much sclerotized and well-marked, along to displays primary dichotomy of veins, which is less developed. The main differences are the size (length 32 mm in *Barona arcuata* against 25 mm as maximum known in *Qilianiblatta*), and the number of branches present in the main veins, a character that could be intraspecifically variable (Bethoux et al., 2011). Size variation can be within the range of one species, or may be related to sexual differentiation, as may be in the case of *Qilianiblatta namurensis*, where apart from the holotypic specimen, other smaller and even more complete individuals are known (see Guo et al., 2013). Indeed, intraspecific body size variation in cockroaches can be very high (Roth, 1990). Nevertheless, taking into account the geographic and stratigraphic distance between the Uruguayan cockroaches and those from China, along to their unique morphology (Fig. 3), we consider that the large cockroach from the Mangrullo Formation supports the erection of a new taxon.

We could suggest that FC-DPI 8710 is a Phyloblattidae because of the general venation distribution, but the cross vein uniting M to CuA (Cv, Fig. 3B) characterizes only the Archimylacridae (Ross, 2010). The Phyloblattidae groundplan and its possible diphyletic origin, is still in doubt (Zhang et al, 2012) and thus, the familiar affinities of the new Uruguayan blattid are yet in discussion.

The age of the Mangrullo Formation revised in the light of the new fossils. –The age of the Mangrullo Formation has remained controversial for several decades, when geologists and even palaeontologists thought it as has been deposited in the Middle of the Permian or even later (Beri and Daners, 1995). Later, when fossils started to appear, they revealed an older age to these strata, and new studies placed Mangrullo and its correlative Iratí Formation into the Early Permian (Artinskian). However, particular fossils belonging to this ancient Konservat-Lagerstatte, suggest affinities to Carboniferous, rather than to Permian assemblages. The pygocephalomorph crustaceans are related to families mainly represented in sequences of Late Carboniferous age from North America (Brooks, 1962) and Europe (Schram, 1979) (Piñeiro et al., 2012). While rare Pygocephalidae findings have been also described for the Petrolia Formation, a unit thought to be Leonardian in age (Hotton et al., 2002), Pygocephalidae and Tealliocarididae are essentially Late Carboniferous families. Plant associations are also good evidence for establish chronostratigraphical correlations among strata. Low altitude geological sequences are favourable to plant preservation, even more when preserved under reducing conditions (Wagner, 2003). Compressed cuticles and permineralized trunks, which are more common in the mudstone levels, show more affinities to species that are components of the *Phyllotheca- Gangamopteris* flora (Piñeiro, 2006; Cristiano-De Souza et al., 2014); some taxa representing this flora are *Calamites*, *Paracalamites*, *Schizoneura*, *Annularia*, *Cordaites*, *Sphenophyllum*, along to occasional permineralized trunks preliminarily assigned to Equisetales and Lepidondendrales (e.g. *Stigmaria*, *Lepidodendron*, and *Walkia*) (Fig. 5), These plants are associated to insects, partial mesosaur skeletons and almost complete pygocephalomorph remains. This 'Carboniferous-like' scenario could be explained by the conservative behaviour of the Gondwana floras since the late Carboniferous to the Early Permian, but there is new lines of evidence, that suggest other hypotheses. Three geographically well delimited floral provinces can be recognized in the Carboniferous and Early Permian, the tropical Euramerican, the temperated Angara (North Africa) and the also temperated Gondwanan (DiMichele et al., 2001). Within each province, plants and insects should be adapted to the prevalent conditions, particularly the changing climate. There were similar climatic conditions in the north provinces than in Gondwana during the Carboniferous and also, the Late Carboniferous climatic conditions prevailed into the Early Permian (DiMichele et al., 2001) and this can explain the presence of taxonomically equivalent floral assemblages in both the Euramerican and the Gondwana realms (see below). Both the macro and micro-plant assemblage from the Mangrullo Formation suggest a temperate climate, although under moderately xeric conditions (Piñeiro et al., 2012b) during the Late Carboniferous and probably the earliest Permian.

The apparent older, maybe Permo-Carboniferous age of the Mangrullo Formation is now reinforced by the presence of *Barona arcuata*, and many no yet described insect wings that advisor the presence of a moderately diverse entomofauna, as is typical of temperate rather than a postglacial cold climate, that may include the oldest representatives of several successful insect families.

Thus, was the Mangrullo Formation a refuge where Carboniferous communities survived into the Permian? Or it represents an older assemblage than previously thought? Perhaps new geochronological studies involving zircon dating from the several bentonitic levels intercalated between the fossiliferous levels will allow for a better constraint of the age of the Mangrullo Formation Konservat-Lagerstatte, but this will be the subject of a forthcoming paper.

Paleobiogeographic considerations. –It is interesting to remark that the most common Late Paleozoic insects around the world are cockroaches, meaning that as most insects, they have a high dispersion rate and also high resistance to transport. They were adapted to several environments, including the marginal lagoonal settings (Schneider and Werneburg, 2003). In particular the Phyloblattidae are an ancient group represented mostly in the Carboniferous and Early Permian of Euramerian (Schneider, 1983; Broutin et al., 1990; Schneider and Werneburg, 1993; Hmicht et al., 2003, 2005) as well as in the Carboniferous and Permo-Carboniferous of the Gondwanan South American realm (see Pinto et al., 1992; Pinto and Mendez, 2002; Ricetti et al., 201 Recent discoveries of blattids in the Souss Basin of northern Africa (Morocco sequences) suggested a comparatively older age for these deposits, within the Westphalian (Hmicht et al., 2003, 2005). Thus, there are closely related blattids in the Permo-Carboniferous of Euramerian as well as in Gondwana, which are associated to a mixed flora containing typical Carboniferous assemblages that include some Permian species. As the Westphalian plants and insects found in

Morocco are closely related to those present in Carboniferous series of Europe, but the Early Carboniferous flora (Visean-Namurian) of western Africa (Niger) contains only Gondwanan representatives, while during the Middle Permian (Kungurian to Wordian) these last floras are mixed by inclusion of earliest Permian Euramerian taxa, Broutin et al. (1990, 1995) suggested that there could have been a first invasion of Euramerian elements into Gondwana during the Early Permian. It is clear also that some migration of Gondwana representatives to Euramerian has occurred via Morocco, as there is evidence of mixed floras in the Permian of southern Spain (Hmicht et al., 2003). Consequently with the flora migration, similar insect dispersion is expected, given the long intimate interaction shown by these groups since their earliest evolution. However, the original dispersal center is not easy to determine, but it is evident that these evolutionary biogeographic patterns were climatically constrained. The presence of blattids in the Late Carboniferous or Permo-Carboniferous strata from Brazil and Uruguay support the hypothesis that the Gondwanan glaciations occurred in the Earliest (Late Visian) rather than the Late Carboniferous as has been demonstrated by geochemical and paleomagnetic previous studies (see Caputo et al., 2008; Barham et al., 2012). This is thus congruent with the xeric conditions suggested by the macro and microfloral components found in the Mangrullo Formation (Piñeiro, 2006) and the established seasonally arid climate propicied by the paleogeographic position of Pangaea during the earliest Permian or Permo-Carboniferous times.

CONCLUSIONS

The new species is the first record of Blattodea for Uruguay and it is one of the oldest of Gondwana. Like Carboniferous blattid species from China, this new Uruguayan specimen has a conservative venational groundplan respect to Permian blattids, but the familiar affinities of the new taxon are yet in discussion because it shares several features with basal phyloblattids but possesses the Cv, a unique vein and a characteristic scalariform cross venation present in Westphalian archimylacrids. The closely similar morphology of the Uruguayan specimen to *Qilianiblatta namurensis* could suggest an older age for the insect bearing levels of the Mangrullo Formation close to the Carboniferous-Permian limit, or the Late Carboniferous fossil record of Chinese-like blattids would extended into the Lower Permian. However, an older age than the Early Permian that has been suggested is also funded by the floral association and the affinities of the pygocephalomorph crustaceans to typically Carboniferous families. The Permo-Carboniferous age for the Mangrullo Konservat-Lagerstätte is supported by recent studies that place the southern glaciations into the Early (Visiano), rather the Late Carboniferous, which is coincident with the temperate, although xeric conditions suggested by the plant associations.

Author contribution. All authors listed have made a substantial, direct and intellectual contributions to the work, and approved it for publication.

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FIGURE CAPTIONS

Figure 1- Geographic location of the insect bearing Mangrullo Formation. A, Map of Uruguay showing the location of Cerro Largo county (in yellow) at north eastern Uruguay; B, Photograph showing the black shales of the Mangrullo Formation at the El Baron locality. White arrow points to equivalent levels to those where the holotype of the Uruguayan cockroach was found; C, Detailed map of the area of outcrops of the Mangrullo Formation. Pink asterisk points the location of the El Barón locality at the Cerro Largo County.

Figure 2- Stratigraphic section of the locality where the new Uruguayan blattid was found. A, Photographs of the deposits of the Mangrullo Formation that have yielded the fossil insects; the white arrow indicates the levels of the Mangrullo Formation, where the new blattid was found and red arrow point to the levels that have yielded other insect groups; B, stratigraphic profile of the Mangrullo Formation showing the position of other recovered insect wings, currently under study; C, References.

Figure 3- FC-DPI 8710, left forewing, preserved as part and counterpart. A, Photographs of the wing as preserved. Scale bar: 10 mm; B, Distribution and terminology of veins: C, costa; Sc, Subcosta; RA, Anterior Radius; RP, Posterior Radius; MA, Anterior Media; MP, Posterior Media; CuA, Anterior Cubitus; CuP, Posterior Cubitus; AA, Anterior Anal; AP, Posterior Anal; CV, Connecting vein. Scale bar: 5mm.

Figure 4. Comparative venation distribution between the Uruguayan new blattid. (A) *Barona arcuata*, (B) the Chinese *Qilianiblatta namurensis* and (C) the Brazilian *Anthracoblattina mendezi*.

Figure 1

Description of a new blattid from the Early Permian of Uruguay

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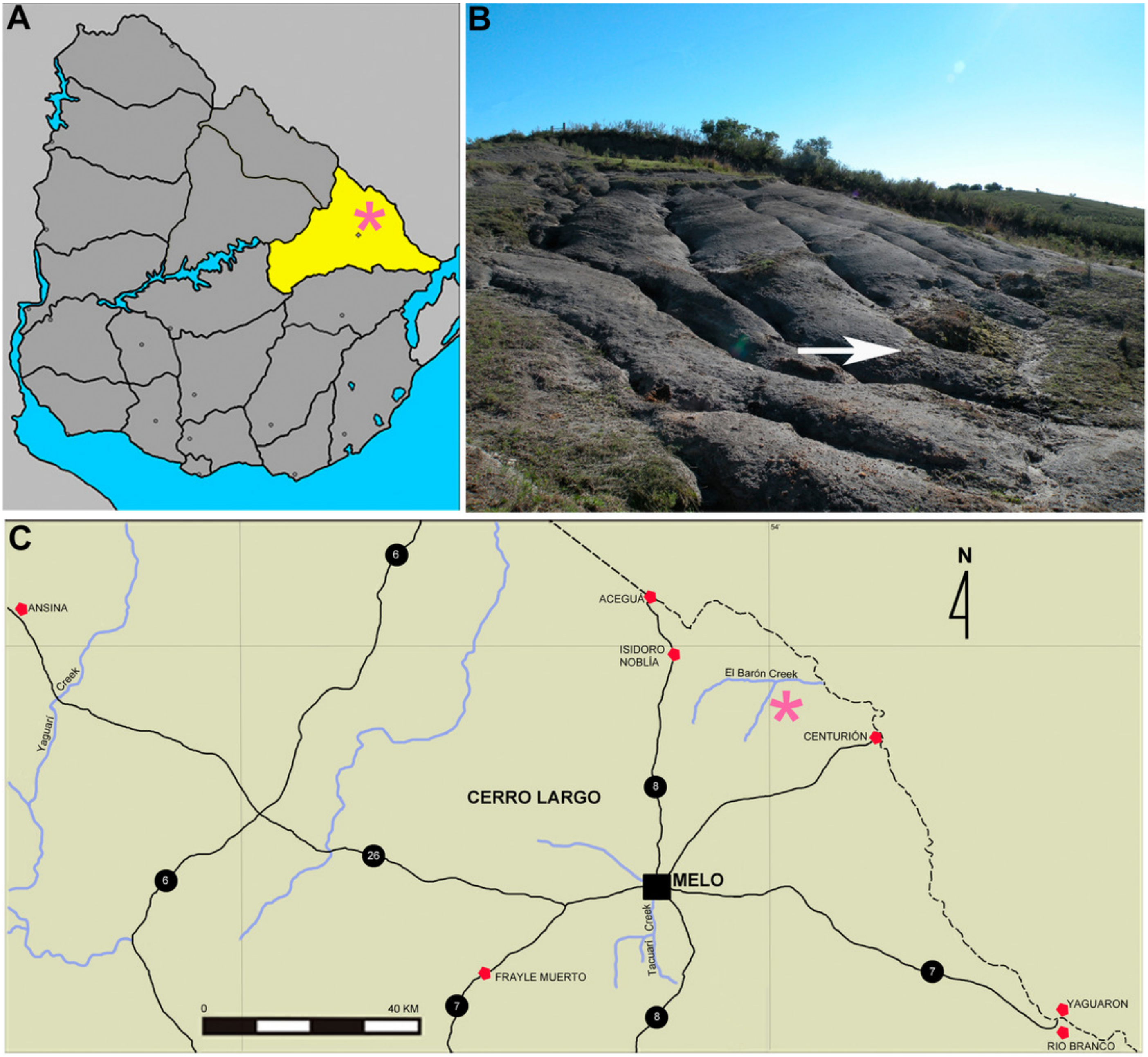
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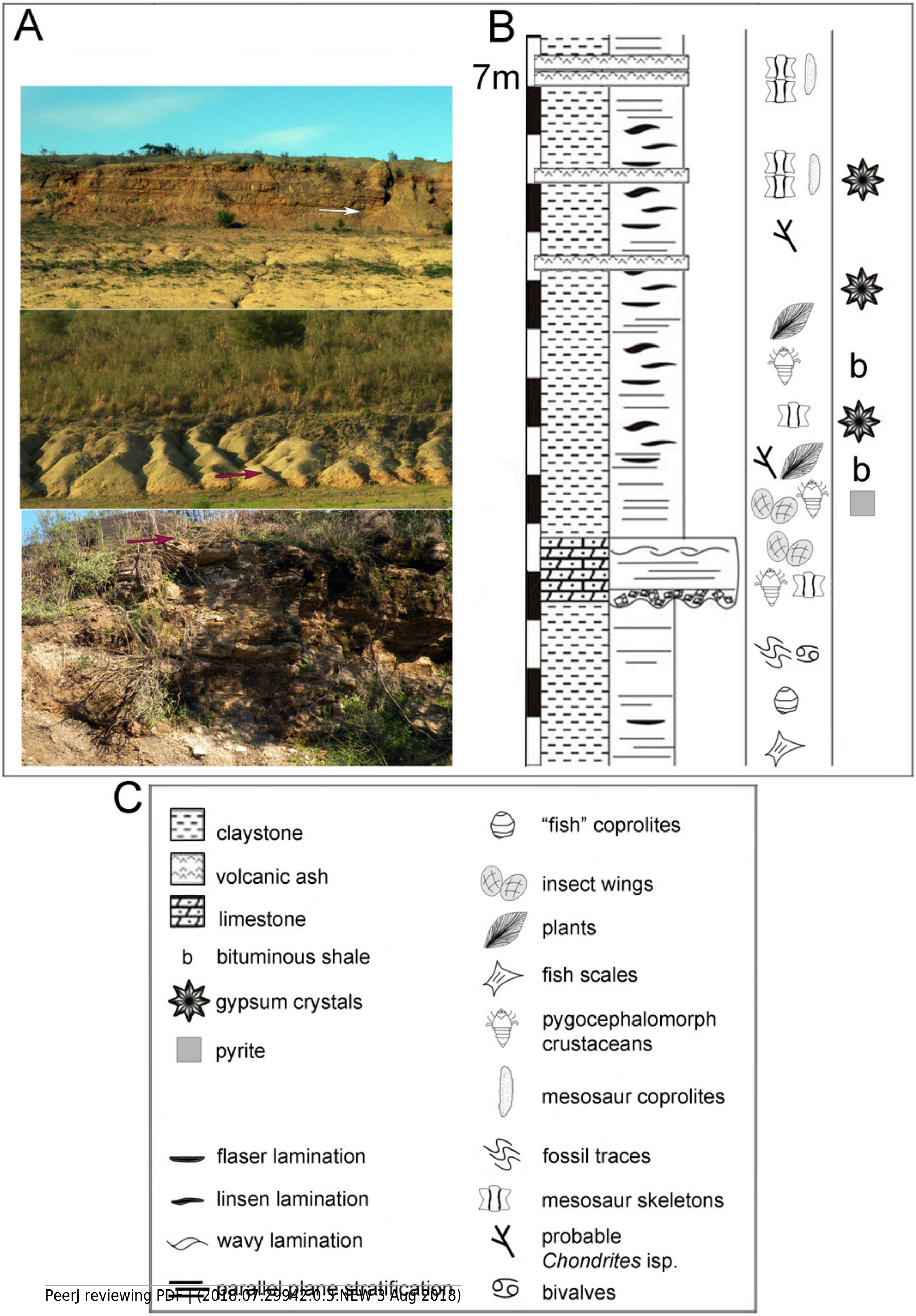
B
C
ANSINA
Yaguarí Creek
6
ACEGUÁ
ISIDORO NOBLÍA
El Barón Creek
CENTURIÓN
N
8
CERRO LARGO
26
6
MELO
Tacuarí Creek
FRAYLE MUERTO
7
0
40 KM
8
7
YAGUARON
RIO BRANCO

Figure 2

Description of a new blattid from Uruguay

Stratigraphic section of the locality where the new Uruguayan blattid was found. (A) Photographs of the deposits of the Mangrullo Formation that have yielded the fossil insects; the white arrow indicates the levels of the Mangrullo Formation, where the new blattid was found and red arrow point to the levels that have yielded other insect groups; (B) stratigraphic profile of the Mangrullo Formation showing the position of other recovered insect wings, currently under study; (C) References.


A
B
7m
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b
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claystone
volcanic ash
limestone
b bituminous shale
gypsum crystals
pyrite
flaser lamination
linsen lamination
wavy lamination
parallel plane stratification
"fish" coprolites
insect wings
plants
fish scales
pygocephalomorph crustaceans
mesosaur coprolites
fossil traces
mesosaur skeletons
probable *Chondrites* isp.
bivalves

Figure 3

Description of a new blattid from the Early Permian of Uruguay

FC-DPI 8710, left forewing, preserved as part and counterpart. (A) Photographs of the wing as preserved. Scale bar: 10 mm; (B) Distribution and terminology of veins: C, costa; Sc, Subcosta; RA, Anterior Radius; RP, Posterior Radius; MA, Anterior Media; MP, Posterior Media; CuA, Anterior Cubitus; CuP, Posterior Cubitus; AA, Anterior Anal; AP, Posterior Anal; CV, Connecting vein. Scale bar: 5mm.

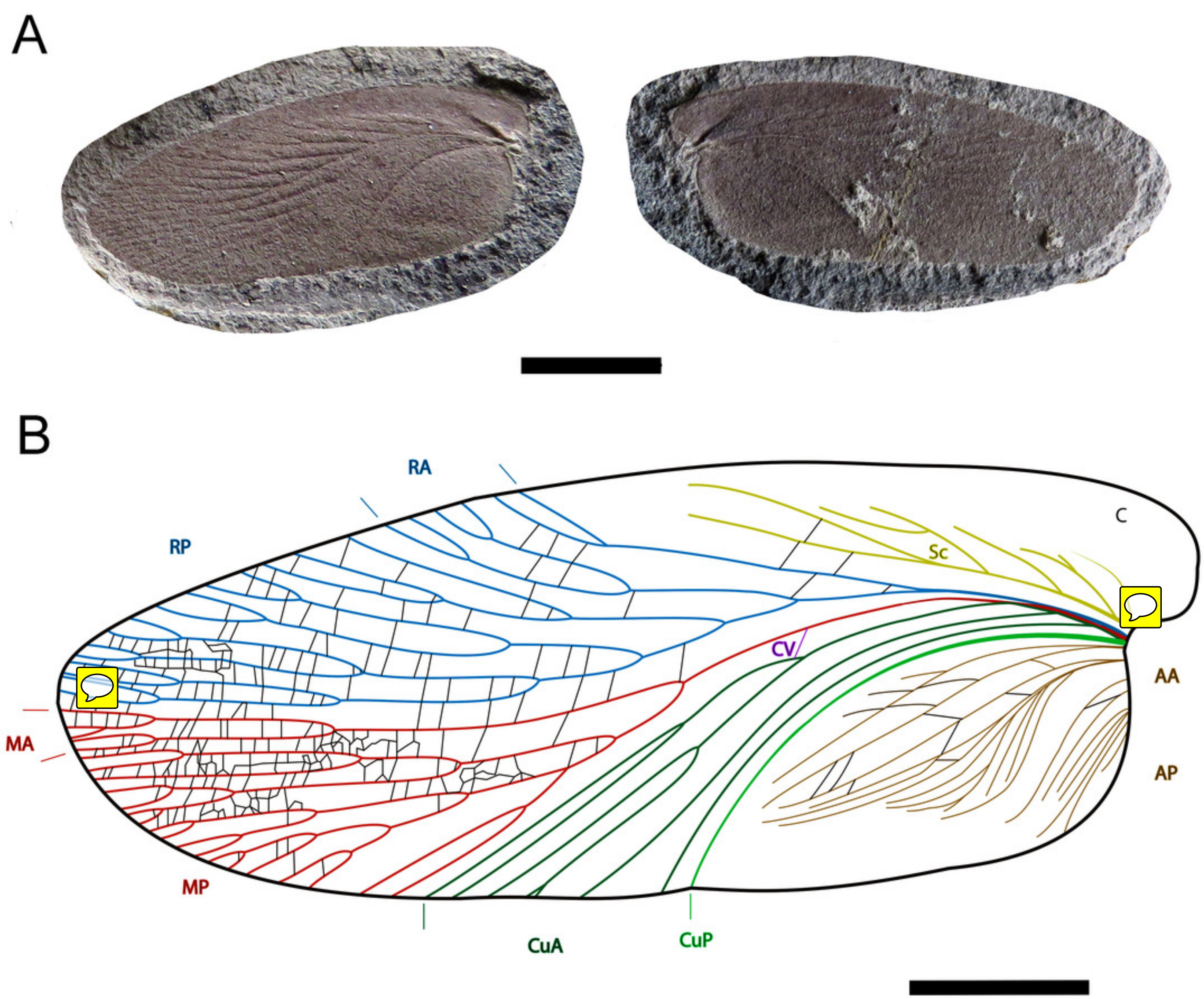

Figure 4

Description of a new blattid from the Early Permian of Uruguay

Comparative venation distribution between the Uruguayan new blattid. (A) *Barona arcuata*, (B) the Chinese *Qilianiblatta namurensis* and (C) the Brazilian *Anthracoblattina mendezi* .