

A new phylloblattid dictyopteran—first fossil insect from the Arroyo Totoral Formation (Cisuralian, Permian) of La Rioja Province, Argentina

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The first fossil insect from the Cisuralian (Lower Permian) Arroyo Totoral Formation, south of Sierra de los Llanos, Paganzo Basin, southeastern La Rioja Province, Argentina is reported. A new species of Phylloblattidae (Dictyoptera), *Anthracoblattina macucaí* sp. nov., is described from an almost complete forewing and based on its general venation scheme (e.g., distinct narrowing of the strip-like costal field near wing base, widened areas between the main veins, Sc pectinated, R and M slightly sigmoidal, twigs provide fan-like covering of the wing apex, the first forks of both R and M located between the first third and the half of the wing length, CuA straight, ends at the transition of the wing tip into the posterior wing border, CuP fluently curved, broad interspace between CuP and AA, cross-venation anastomosing-striate to reticulate). Additionally, we discuss the taxonomic position of *A. macucaí* sp. nov. in relation to other phylloblattid species described from Carboniferous–Permian South American outcrops. Finally, we analyze this new fossil “cockroachoids” within its paleofloristic context and depositional environment. *A. macucaí* sp. nov. represents the first known Permian insect found for both the La Rioja Province and the Arroyo Totoral Formation, pointing the unit as promising for the search of fossil insects in Argentina.

Key words: Dictyoptera, Phylloblattidae, Arroyo Totoral Formation, Cisuralian, Permian, Argentina.

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Introduction

Even though the Permian (~299–252 Ma) paleontological assemblages were characterized by many relictual Carboniferous groups, they were also marked by the emergence of new insect orders (i.e., basal relatives of plecopterans, mecopterans, psocopterans, and beetles) (Grimaldi 2009). The Permian insect record derives mainly from Euramerican biotic province such as Wettin (Germany), Souss (Morocco) (upper Pennsylvanian), Obora (Czech Republic), and Elmo (Kansas, USA); Angara biotic province including Tsherkarda (Urals, Russia) (lower Permian); Kaltan and Suriekovo (Kuznetsk Basin, West Siberia, Russia), and Soyana (Arkhangelsk Region, north-eastern European

Russia) (upper Permian) (Schneider 1978; Rasnitsyn et al. 2015; Belahmira et al. 2019; Garrouste et al. 2025); and Gondwanan province such as Australia (Sydney Basin) (Jell 2004) and South Africa (Karoo Basin) (e.g., Pretorius et al. 2021; Prevec et al. 2022; Nel et al. 2023), followed by South America and India (Zherikhin 2002; Schlüter 2003; Ricetti et al. 2016; Nel et al. 2018).

The South American Paleozoic entomofauna is extremely diverse, comprising a total of 37 fossil insect species belonging to various groups, including palaeodictyopteroids, protodonatans, “protorthopterans”, “cockroachoids”, grylloblattids, ephemeropterans, hemipterans, miomopterans, perlapsocidans, beetles, glosselytrodeans, and permopsocidans (Lara et al. 2023). Fossil insects, represented by forewing impressions, have been collected and described from Permian

outcrops in Brazil, Uruguay, and Argentina. However, compared to the Northern Hemisphere and/or its Triassic counterpart, the quantitative data available for the Permian assemblages are sparse (Lara 2016; Lara et al. 2023).

In Argentina, Permian insect records are known from the Bajo de Véliz (Paganzo Basin, San Luis Province) and Río Genoa (Tepuel Genoa Basin, Chubut Province) formations (Martins-Neto et al. 2007; Lara et al. 2023). In this article, we report and describe the first fossil insect from the lower Cisuralian (lower Permian) of the Arroyo Totoral Formation, La Rioja Province, Argentina. We erect a new species, *Anthracoblattina macucaei* sp. nov. (Dictyoptera: Phylloblattidae), based on the venation pattern of a single forewing. In addition, we discuss the taxonomic implications of this new taxon and compare with “cockroachoids” members described from various other upper Paleozoic South American outcrops. Finally, we re-evaluate the paleoenvironmental and taphonomic conditions of the unit, previously assessed primarily on its floristic content, in light of this insect fossil. Despite being well-known by its abundant fossil flora (e.g., Cúneo 1984; Cúneo and Archangelsky 1996; Archangelsky et al. 1996), this finding reveals the Arroyo Totoral Formation as a new locality for the search of

fossil insects in Argentina, adding to the paleoentomological assemblages worldwide.

Nomenclatural acts.—This published work and the nomenclatural acts it contains have been registered in ZooBank: urn:lsid:zoobank.org:pub:D02460B5-C1F9-4858-9ECB-C593373B0FD1.

Institutional abbreviations.—BAPb, Museo Argentino de Ciencias Naturales “B. Rivadavia” (MACN), Buenos Aires, Argentina; CRI-PI, “Colección de Paleoinvertebrados”, Centro Regional de Investigaciones Científicas y Transferencia Tecnológica de La Rioja (CRILAR-CONICET), Anillaco, Argentina; FC-DPI, Departamento de Paleontología de la Facultad de Ciencias, Universidad de la República del Uruguay (UdelaR), Montevideo, Uruguay; MCN.P, Museu de Ciências Naturais, Curitiba, Paraná, Brazil; UFRGS-P-I, Museu de Paleontologia do Departamento de Paleontologia e Estratigrafia da Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

Other abbreviations.—C, costa; CuA, anterior cubitus; CuP, posterior cubitus; l, wing length; M, media; MA, anterior media; MP, posterior media; R, radius; RA, anterior radius; RP, posterior radius; Sc, subcosta; w, wing width.

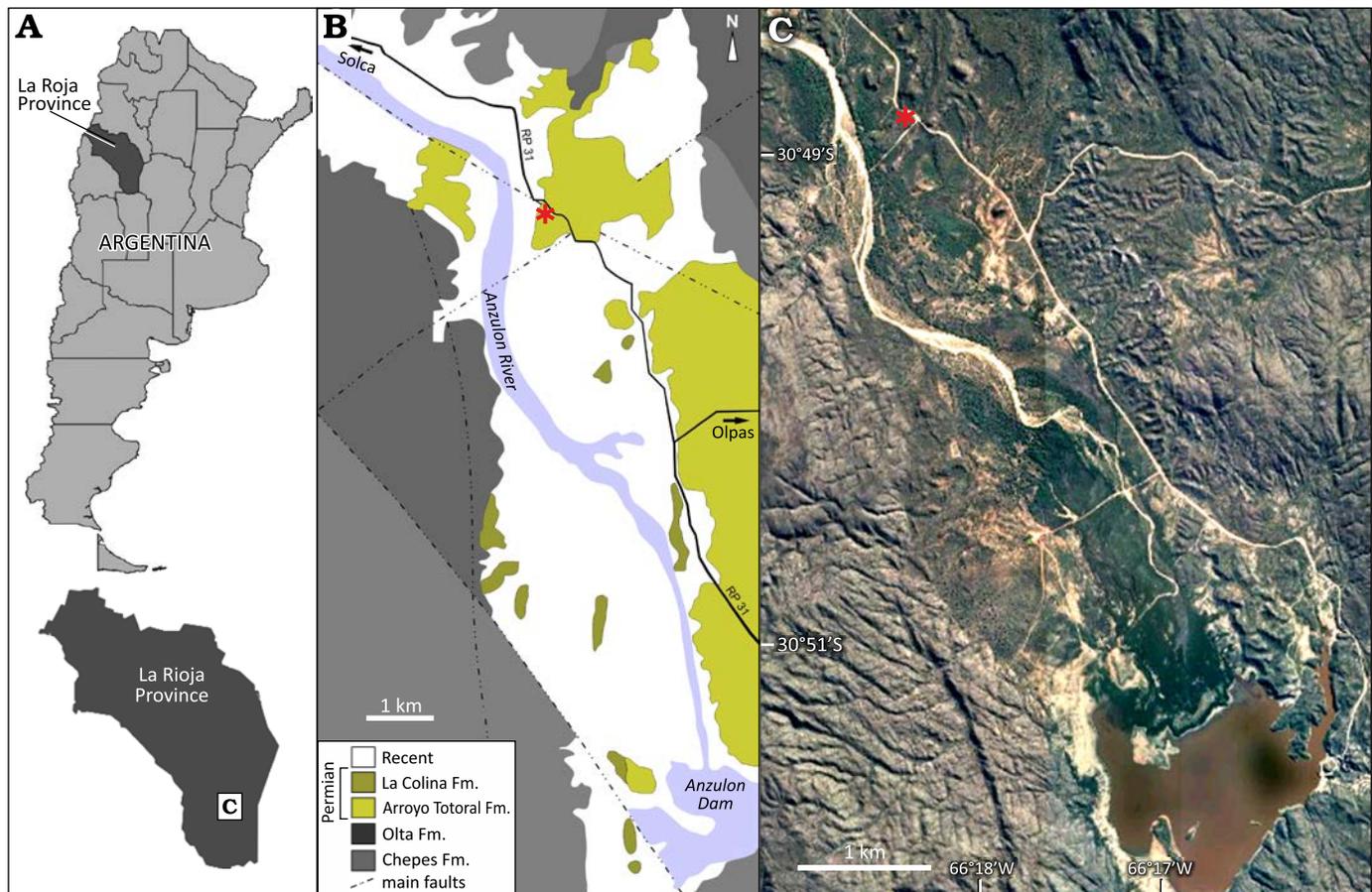


Fig. 1. **A.** A sketch map of Argentina and La Rioja Province. **B.** Generalized map of southeastern La Rioja Province showing the location of the Arroyo Totoral Formation (Asselian–Sakmarian, lower Cisuralian, Permian), south of Sierra de los Llanos, eastern sector of the Paganzo Basin. **C.** Aerial view of the southeastern La Rioja Province. The fossil insect site is indicated by red asterisk. Abbreviations: Fm., Formation.

Geological setting

The Arroyo Totoral Formation (Andreis et al. 1984) crops out in the eastern sector of the Paganzo Basin, southeastern La Rioja Province, where it lies unconformably on the crystalline basement and is overlain by the Permian La Colina Formation (Limarino and Page 1999; Gutiérrez et al. 2006) (Fig. 1). According to Archangelsky et al. (1996), the Arroyo Totoral Formation is referred to the *Gangamopteris* Biozone of the Asselian, lower Permian, and assigned to the postglacial paleoclimatic stage with local humid conditions, subsequently changing to arid conditions during the deposition of the La Colina Formation (Limarino et al. 2014).

Fossil Locality I was established as the original stratotype (= holostatotype) for the Arroyo Totoral Formation, as defined by Andreis et al. (1984) and Cúneo (1984). The sedimentary sequence is ca. 6 m thick, and composed primarily of siltstone and claystone, representative of lacustrine facies. Intercalated within this sequence are fine- to very fine-grained sandstones deposited by suspension, and indicative of distal facies of alluvial fans. Towards the upper part of this short sequence, there is an increase of coarser, medium-grained sandstones. This suggests the development of a fluvial system with mouth bars and associated channels (Andreis et al. 1984; Cúneo 1984).

Material and methods

A single cockroachoid specimen preserved as a forewing was recovered from the “Fossil Locality I” (sensu Andreis et al. 1984) of the Arroyo Totoral Formation, south of Sierra de los Llanos (30°48'29.70"S 66°18'23.91"W), Paganzo Basin, La Rioja Province, Argentina (Fig. 1). The fossil material is preserved as a compression of a single forewing in a laminated grey shale, along with several plant remains (Fig. 2) and plant-insect interactions.

The fossil was examined using a Leica M60 stereomicroscope and photographed using a Leica DMC 2900 digital camera. Different images were obtained under a combination of brightfield and incident illumination. Line drawings were prepared from a series of photographs obtained with different illumination settings under a stereomicroscope and using CorelDrawX7 software and detailed measurements were made with ImageJ software v. 1.49.

The specimen used for this study is housed at the “Colección de Paleoinvertebrados”, Centro Regional de Investigaciones Científicas y Transferencia Tecnológica de La Rioja (CRILAR-CONICET), La Rioja Province, Argentina.

The description and nomenclature of tegmen venation is based on the system established by Comstock and Needham (1898) with its emendations by Kukulová-Peck (1983) and Lameere (1922) for R (RA and RP), M (MA and MP), and Cu (CuA and CuP), regarding the specifics of blattoid wing venation pattern (Li et al. 2018). Costal field designates the area between the anterior wing margin and the subcosta (Ricetti et al. 2016).

Systematic palaeontology

Class Insecta Linnaeus, 1758

Superorder Dictyoptera Latreille, 1829

Order Blattodea Brunner von Wattenwyl, 1882

(= Blattida Latreille, 1810 = Blattaria Latreille, 1810)

Family Phylloblattidae Schneider, 1983a

Genus *Anthracoblattina* Scudder, 1879

Type species: *Blattina spectabilis* Goldenberg, 1869; Löbejün locality, Wettin Subformation, Siebigerode Formation, Stephanian C, upper Gzhelian (upper Carboniferous), Saale Basin, Germany (Schneider et al. 2021).

Stratigraphical and geographical range.—Upper Pennsylvanian (Carboniferous) to Cisuralian (lower Permian) of Europe, North Africa (Morocco), India (Kashmir), South America (Argentina, Brazil), USA, and Russia.

Anthracoblattina macuca sp. nov.

Fig. 3

Zoobank LSID: urn:lsid:zoobank.org:act:D02460B5-C1F9-4858-9ECB-C593373B0FD1.

Etymology: In reference to the “Macuca Team”, name of the research group that participated at paleontological prospections and collections in the La Rioja Province (Argentina).

Holotype: CRI-PI 1, impression (compression) of a nearly complete single forewing.

Type locality: “Fossil Locality I” (sensu Andreis et al. 1984) of the south of Sierra de los Llanos, Paganzo Basin, La Rioja Province, Argentina.

Type horizon: Arroyo Totoral Formation, lower Lower Permian.

Material.—Type material only.

Diagnosis.—Elongated forewing, approximately 17.5 mm in length preserved (22–23 mm length estimated). Costal field elongate, narrow, wedge-shaped. Sc (pectinated) with 11 branches simple (inclined apically, parallel each other) and distal branch fork, branches arising at an angle of about 23–35° from the Sc stem, ending at anterior wing margin. R forked before to M bifurcation (distance 1.47 mm), into a two times forked RA and a multiple forked RP, terminating at the transition of the anterior wing border to the wing tip (reconstructed) (Fig. 3B). M forked into MA and MP (stem MA and MP of sub-equal length) with altogether minimally 5 preserved twigs), covering a narrow area, at the wing apex. CuA runs more or less straight toward the transition of the wing tip into the posterior wing margin. The first six posteriorly pectinate, partially forked twigs arise by branching from CuA stem. As far as preserved it follow a bifurcation. CuA altogether with about 10 branches covering the posterior wing border up into the transition to the wing tip. CuP as far as preserved in the basal part gently curved, apical part straighter. Crossveins (archedictyon) mainly straight, polygonal reticulate to anastomosing striate. Coloration monochromatic, probably pale brown.

Description.—One nearly complete isolated forewing, elongate ellipsoidal (Fig. 3), length 17.5 mm (reconstructed

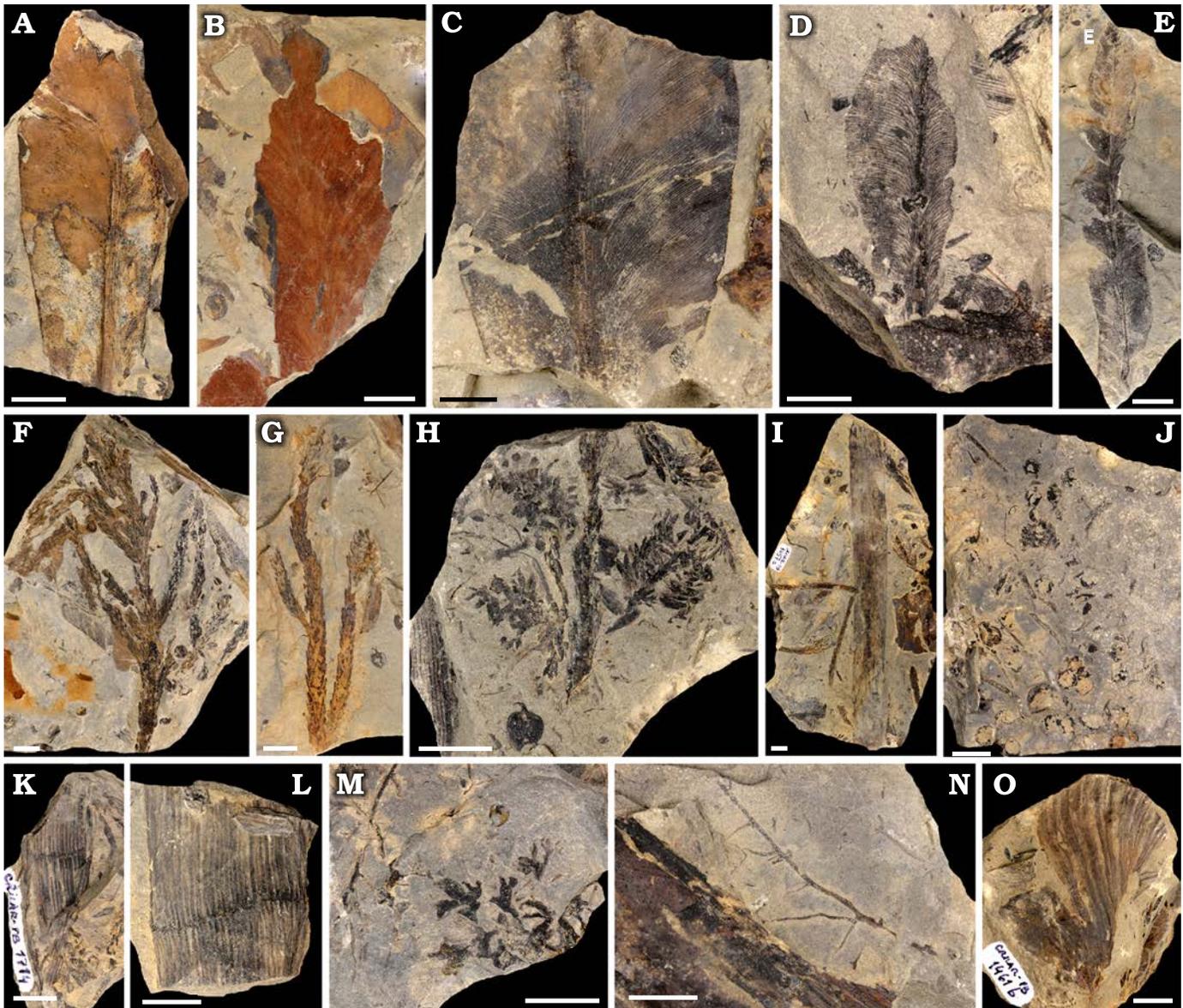


Fig. 2. Plant remains of the Arroyo Totoral Formation (Asselian–Sakmarian, lower Cisuralian, Permian), south of Sierra de los Llanos, eastern sector of the Paganzo Basin, La Rioja Province, Argentina. **A–E.** Glossterid leaves (**A**, CRILAR-PB 1479; **B**, CRILAR-PB 1483; **C**, CRILAR-PB 1539; **D**, CRILAR-PB 1519; **E**, CRILAR-PB 1949). **F–H.** Conifers leafy branches and cones (**F**, CRILAR-PB 1410; **G**, CRILAR-PB 1509; **H**, CRILAR-PB 1958). **I.** Cordaitalean leaf and conifer leafy branches (CRILAR-PB 1457). **J.** Cluster isolated seeds (CRILAR-PB 1495). **K, L.** Sphenophyte stems (**K**, CRILAR-PB 1714; **L**, CRILAR-PB 1960). **M.** Bryophyte indet and rootlets (CRILAR-PB 1590). **N.** Rootlets (CRILAR-PB 1583). **O.** ?*Barakaria* sp. (CRILAR-PB 1461). Scale bars 10 mm.

forewing size about 22–23 mm), maximum width 8.85 mm, l/w 1.97. Costal field elongate and narrow, wedge-shaped (wide at the base but narrows apically) covering about 70% of the wing length preserved, narrower toward to the apical margin. Sc, R, M, and Cu strongly sclerotized at the wing base and bifurcate posteriorly into multiple branches. Sc stem well-developed, anteriorly pectinate with 11 branches inclined apically, parallel each other, regularly spaced; nearly all branches simple (one Sc branch dichotomized), reaching the anterior of the wing tip on the anterior wing margin. R stem gently curved, nearly straight, forking into RA and RP ca. 0.56 mm distad wing base, basally fork of

M (distance 1.47 mm), into RA and RP, apparently crossing the entire length of the wing and reaching the wing margin at the transition of the anterior wing border to the wing tip. RA with at least three branches and RP with at least five branches, ending at the wing apex. M stem ca. 0.67 mm distad wing base, besides the basal bending, nearly straight, directed anteriorly, with at least five branches straight or slightly arched, and covering a narrow area (from the wing tip to the transition between wing tip and posterior wing margin). MA and MP stems of sub-equal length: 4.14 mm and 3.58 mm, respectively. CuA stem ca. 0.26 mm distad wing base, slightly sigmoidal inclined and

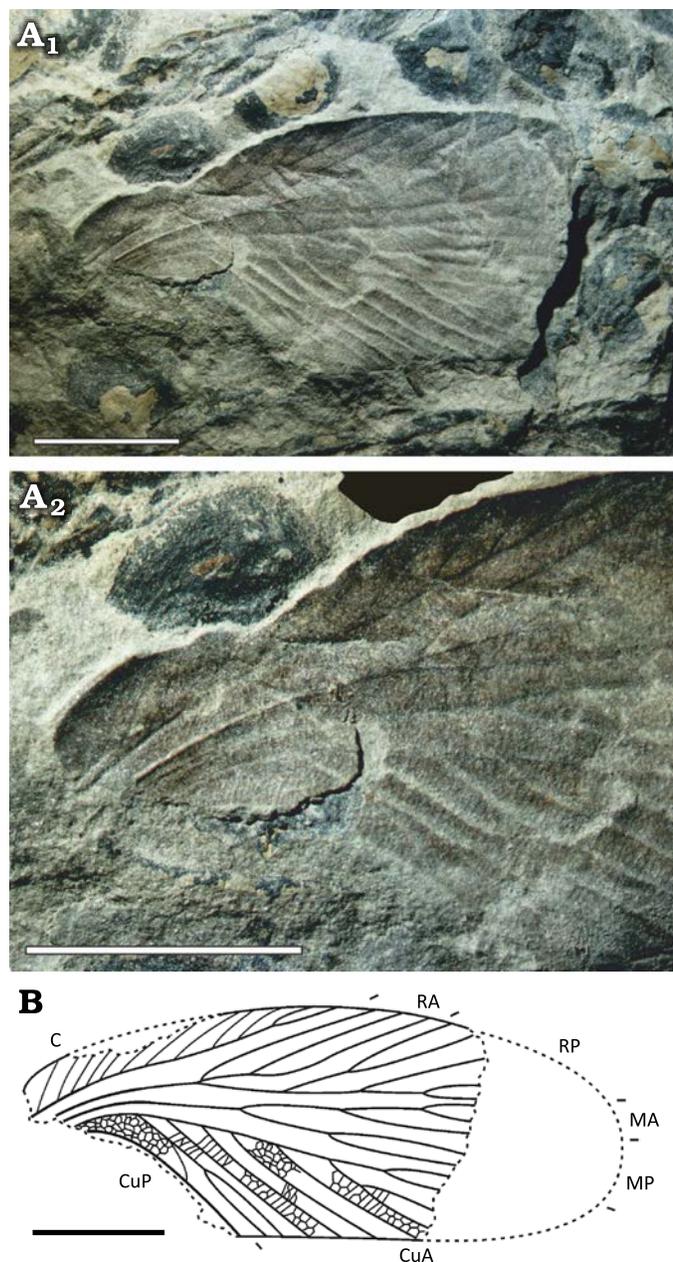


Fig. 3. Phyloblattid dictyopteran *Anthracoblattina macucai* sp. nov., Arroyo Totoral Formation (Asselian–Sakmarian, lower Cisuralian, Permian), La Rioja Province, Argentina. **A.** Photographs of the holotype (CRI-PI 1), part of the forewing (A_1), basal part of the forewing showing the crossveins (A_2). **B.** Interpretation of wing venation with veins labelled. Scale bars 2 mm. Abbreviations: C, costa; CuA/P, anterior/posterior cubitus; MA/P, anterior/posterior media; RA/P, anterior/posterior radius.

more or less straight toward the posterior wing margin; posteriorly pectinate, with seven terminal branches ending at posterior margin of wing, three being bifurcated (at least 10 branches); the first CuA branch forked followed by four simple branches and then by two forked branches. CuP simple, basal part gently curved and apical part straighter. Anal veins not preserved. Crossveins (archedictyon) observed mainly in basal and middle area of wing: straight, reticulate

to anastomosing striate. Main veins dark, appearing black when compared with rest of wing. Coloration monochromatic, probably pale brown.

Stratigraphic and geographic range.—Type locality and horizon only.

Discussion

Taxonomic implications.—Numerous cockroach-like Paleozoic and Mesozoic fossils (also called “cockroachoids”), a group well-known for its problematic taxonomy under the extant superorder Dictyoptera Leach, 1815, have been recorded in different outcrops worldwide (Legendre et al. 2015; Dvořák et al. 2022; Nel et al. 2022).

Based on the forewing venation pattern, the new species described herein, *Anthracoblattina macucai* sp. nov., shows the diagnostic characters of the family Phyloblattidae Schneider, 1983a, such as: costal field elongated and comparatively narrow apically, widened areas between the main veins (e.g., Sc, R), Sc pectinate, with branches mostly simple and nearly straight, R slightly sigmoidal divided into RA and RP, M slightly sigmoidal forked into MA and MP, twigs provide fan-like covering of the wing apex, CuA slightly curved, ends at the transition of the wing tip into the posterior wing border, CuP curved, and cross-venation anastomosing-striate to reticulate (Schneider 1983a). Phyloblattidae Schneider, 1983a, a predominantly Paleozoic “cockroachoid” group, has been recorded from strata of Pennsylvanian–Permian (late Moscovian–?Lopingian) age from Europe, North America, North Africa, Siberia, China, South America, and South Africa (Schneider 1983a; Belahmira et al. 2019; Schneider et al. 2021). However, the phyloblattids seemingly almost disappeared from the fossil record after the Permian/Triassic boundary, persisting as a reduced taxonomic group in ecosystems up to the Early Cretaceous, e.g., *Pozabudnutie antiquorum* Vršanský et al., 2023 from Cretaceous Myanmar amber (Vršanský 2003, 2010, Vršanský et al. 2023). The cockroaches Mesozoic Gondwanan localities are very sparse and do not contain phyloblattids (e.g., Vršanský 2008; Lee 2016; Martin 2020; Lara et al. 2023, Vršanský 2024).

The taxonomic position of the new Argentinian fossil under the genus *Anthracoblattina* Scudder, 1879, is supported by the shape and size of the forewing (i.e., an elongate ellipsoidal forewing, up to 50 mm length), costal field size (about 70–75% of forewing length), a distinct narrowing of the strip-like costal field, Sc with pectinate branches inclined apically (some branches forked), first forks of both R and M located between the first third and the half of the wing length, R weakly sigmoidal, with branches terminating anterior of the wing tip on the anterior wing margin, M divided behind the first fork of the R stem, branches covering an area extending from the wing tip to the transition between wing tip and posterior wing margin, CuA slightly curved at base

Table 1. A list of “cockroachoids” described from the Permian of South America.

Family	Species	Type material	Horizon	Locality	Reference
Phyloblattidae	<i>Archangelskyblatta vishniakovae</i> Pinto, 1972	BAPb 562 (positive impression), UFRGS-P-I-4202 (negative impression)	Río Genoa Formation (lower Permian), Tepuel Genoa Basin	Chubut, Argentina	Pinto 1972
Phyloblattidae	<i>Anthracoblattina archangelskyi</i> Pinto & Mendes, 2002	BAPb 640	Río Genoa Formation (lower Permian), Tepuel Genoa Basin	Chubut, Argentina	Pinto and Mendes 2002; Ricetti et al. 2016; Belahmira et al. 2019
Phyloblattidae	<i>Anthracoblattina macucaei</i> sp. nov.	CRI-PI 1	Arroyo Totoral Formation (lower Permian), Paganzo Basin	La Rioja, Argentina	this paper
Spiloblattidae	<i>Aissoblatta</i> sp.		Irati/Serra Alta formations (lower Permian), Paraná Basin	São Paulo, Brazil	Pinto 1972; Aristov et al. 2013; McLoughlin et al. 2021
Phyloblattidae	<i>Anthracoblattina oliveirai</i> Carpenter, 1930	DGM-389-I	Passinho Shales, upper section Taciba Formation (lower Permian)	Teixeira Soares, Paraná, Brazil	Carpenter 1930
Phyloblattidae	<i>Anthracoblattina langei</i> Pinto & Purper, 1979	DNPM 2981-I	Passinho Shales, upper section Taciba Formation (lower Permian)	Teixeira Soares, Paraná, Brazil	Pinto and Purper 1979
Phyloblattidae	<i>Anthracoblattina mendesi</i> Pinto & Sedor, 2000	MCN.P. 218	Lontras Shale, upper section Upper Campo Mourão Formation (Carboniferous–Permian)	Mafra, Santa Catarina, Brazil	Pinto and Sedor 2000; Ricetti 2016; Belahmira et al. 2019
Phyloblattidae	<i>Phyloblatta roxoi</i> Petri, 1945	Universidade de Sao Paulo 205 (hindwing)	Passinho Shales, upper section Taciba Formation (lower Permian)	Teixeira Soares, Paraná, Brazil	Petri 1945
Phyloblattidae	<i>Phyloblatta pauloi</i> Mezzalira, 1948	DNPM 3911-I	Passinho Shales, upper section Taciba Formation (lower Permian)	Teixeira Soares, Paraná, Brazil	Mezzalira 1948
Phyloblattidae	<i>Phyloblatta sommeri</i> Pinto & Purper, 1979	DNPM 2982-I	Passinho Shales, upper section Taciba Formation (lower Permian)	Teixeira Soares, Paraná, Brazil	Pinto and Purper 1979
Family indet.	<i>Barona arcuata</i> Calisto & Piñeiro, 2019	FC-DPI 8710	Mangrullo Formation (upper Carboniferous–lower Permian), Paraná Basin	Estancia “El Barón” locality, Cerro Largo, Uruguay	Calisto 2018; Calisto and Piñeiro 2019

then runs straight toward the posterior wing margin, basal part of CuP gently curved, apical part straighter, broad interspace between CuP and AA, and crossveins reticulate and/or anastomosing-striate (Schneider 1983a,b; Schneider et al. 2021; Ricetti et al. 2016; Belahmira et al. 2019).

Both *Phyloblatta* and *Anthracoblattina* species are difficult to distinguish due to the high degree of individual and intraspecific variability (Belahmira et al. 2019; Jörg W. Schneider personal communication 2025). In addition to this morphologic variability, *Anthracoblattina* is further complicated in taxonomic issues by the fact that it seems to be the most conservative phyloblattid genus of the late Paleozoic (Jörg W. Schneider personal communication 2025). Given the high degree of individual variability, in this paper, we prefer to attribute this specimen to a new species, *A. macucaei* sp. nov., until further well-preserved blattoid specimens become available from the Arroyo Totoral Formation, La Rioja Province, Argentina.

Comparison to other Paleozoic stem-dictyopterans records in South America.—Previous South American records of Paleozoic stem-dictyopterans come from Brazil, Uruguay, and Argentina, and are mainly referred

to family Phyloblattidae Schneider, 1983a (Table 1). In Brazil, stem-dictyopteran fossils represented by the genus *Anthracoblattina* Scudder, 1879, and *Phyloblatta* Handlirsch, 1906, were recovered from the Passinho Shale, upper section of the ?Taciba Formation (Asselian, Cisuralian, Permian) and the Lontras Shale (“Lontras Shale fossilagerstätte”), uppermost section of the Campo Mourão Formation (Pennsylvanian–Cisularian) (Table 1, Fig. 4A) (Ricetti et al. 2012, 2016; Ricetti 2016). In Uruguay, Calisto and Piñeiro (2019) described *Barona arcuata* Calisto & Piñeiro, 2019, a single left “cockroachoid” forewing from the Mangrullo Formation (Gzhelian–Asselian, Pennsylvanian–Cisularian), also considered an “ancient Konservat-Lagerstätte” in the Paraná Basin, Cerro Largo Department (Piñeiro 2004) (Fig. 4B). Furthermore, Calisto (2018) and Calisto et al. (2022) described other specimens collected in the Mangrullo Formation, some of which have also been identified as belonging to stem-Dictyoptera. In Argentina, only two species of Paleozoic “cockroachoid” were described, both from the Río Genoa Formation (lower Permian, Tepuel Genoa Basin, Chubut Province): *Anthracoblattina archangelskyi* Pinto & Mendes, 2002 (Fig. 4C) and *Archangelskyblatta vishnia-*

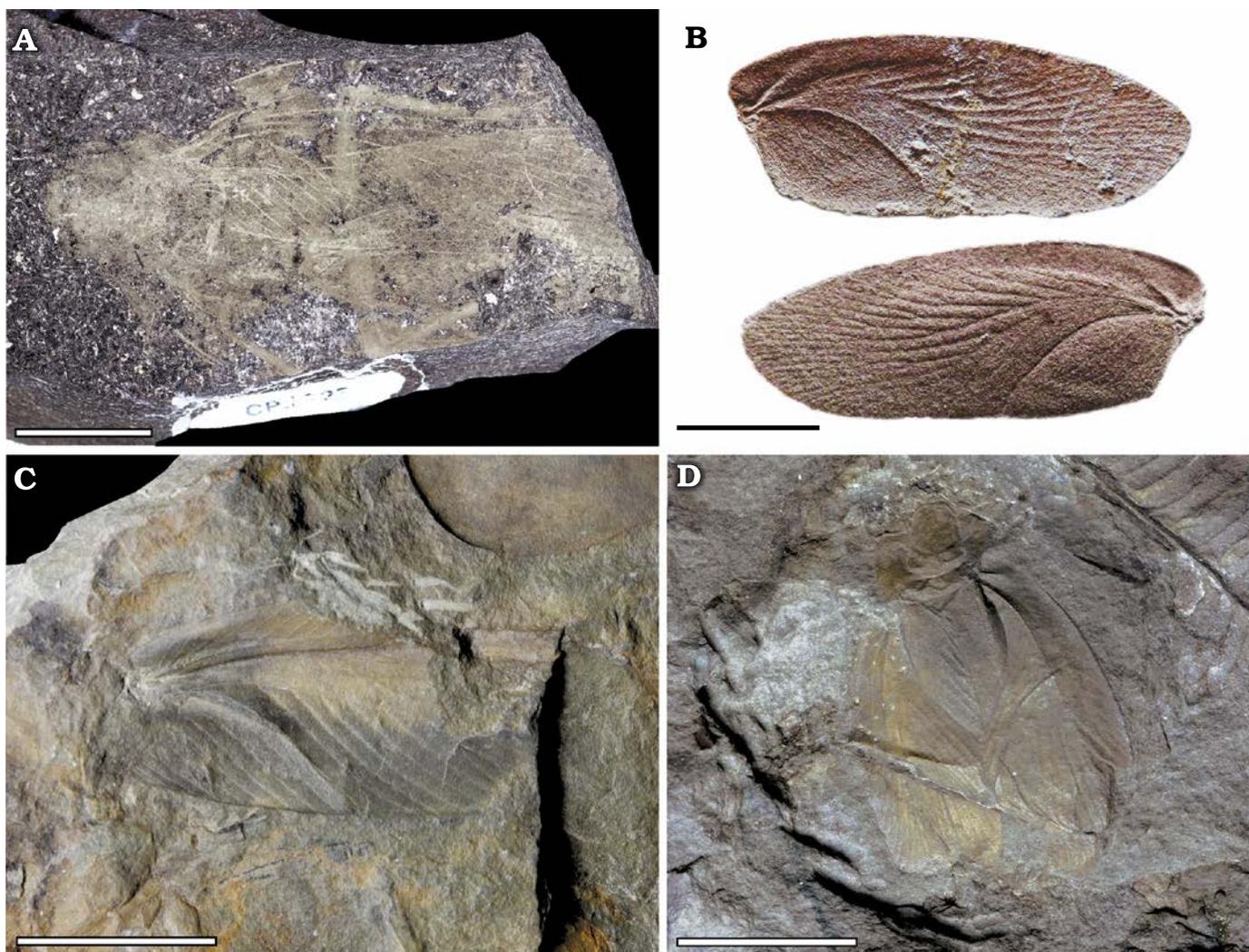


Fig. 4. Phyloblattid dictyopterans from South America. **A.** *Anthracoblattina mendesi* Pinto & Sedor, 2000 (Phyloblattidae, Dictyoptera), holotype MCN.P. 218, Lontras Shale, Campo Mourao Formation (Asselian, Cisuralian, Permian), Itararé Group, Paraná Basin, State of Santa Catarina, Brazil (photo by L.F. Pereira Lopes and J.H.Z. Ricetti). **B.** *Barona arcuate* Calisto & Piñeiro, 2019 (Family indet., Dictyoptera), holotype FC-DPI 8710, Mangrullo Formation (Gzhelian–Asselian, upper Pennsylvanian–lower Cisuralian) Paraná Basin, Cerro Largo Department, Uruguay (photo by G. Piñeiro and V. Calisto). **C.** *Anthracoblattina archangelskyi* Pinto & Mendes, 1972 (Phyloblattidae, Dictyoptera), holotype BAPb 640, Río Genoa Formation, Tepuel Genoa Basin, Chubut Province, Argentina. **D.** *Archangelskyblatta vishniakovae* Pinto, 1972 (Phyloblattidae, Dictyoptera), holotype BAPb 562, UFRGS-P-I-4202, Río Genoa Formation (Sakmarian–Artinskian?, middle Cisuralian), Tepuel Genoa Basin, Chubut Province, Argentina. Scale bars 10 mm.

kovae Pinto, 1972 (Fig. 4D) (Phyloblattidae, Dictyoptera) (Table 1) (Pinto 1972; Pinto and Mendes 2002; Ricetti et al. 2016; Lara et al. 2023).

Anthracoblattina macuca sp. nov. shows similarities with *Archangelskyblatta vishniakovae* Pinto, 1972, in the forewing size (19–20 mm vs. 20 mm) and morphology of the Sc, M, and CuA, but differs from the latter in R forking before at middle length, development of R, M forking after R, and the first branch of CuA bifurcated (Fig. 4D). Moreover, *A. macuca* sp. nov. can be distinguished from other Carboniferous–Permian South American “cockroachoid” such as *Barona arcuata* (Fig. 4B), *Phyloblatta roxoi* Petri, 1945, *Phyloblatta sommeri* Pinto & Purper, 1979, *Phyloblatta pauloi* Mezzalana, 1948 (Passinho Shale, upper section ?Taciba Formation, lower Permian, Itararé Group, Brazil; Table 1)

in the forewing size (19–20 mm vs. 22–33 mm) and scarce development of Sc, RA, RP, MA, MP, CuA.

In comparison with other Carboniferous–Permian species of *Anthracoblattina* Scudder, 1879, described from different South American outcrops (Table 1), *A. macuca* sp. nov. exhibits some morphological differences. The new species differs from *A. archangelskyi* Pinto & Mendes, 2000 (Río Genoa Formation, lower Permian, Tepuel Genoa Basin, Argentina) (Fig. 4C) by Sc branches short, first branch of RA simple, arising close to bifurcation of R, MA, and MP stems of sub-equal length, first and the two last branches of CuA forked. Likewise, *A. macuca* sp. nov. is distinguished from *Anthracoblattina mendesi* Pinto & Sedor, 2000 (Lontras Shale, Campo Mourao Formation, Asselian, Itararé Group, Paraná Basin, State of Santa Catarina, Brazil)

(Fig. 4A) in forewing size (19–20 mm vs. 42 mm), Sc shape, with 12 pectinate branches, mostly branches simple (the last branch bifurcated), R bifurcated in RA and RP distal of the M forked (1.47 mm), RA and RP with a smaller amount branches (3 and 5, respectively), RA with simple branches, stem MA shorter (vs. MA with a long basal stem), MA and MP (stems of sub-equal length) with fewer branches (3 and 2, respectively), CuA with about 10 branches covering the posterior wing margin (vs. about 13 branches in *A. mendesi*) (Ricetti 2016; Ricetti et al. 2016). Also, *A. macucai* sp. nov. can be separated from *Anthracoblattina oliveirai* Carpenter, 1930, and *Anthracoblattina langei* Pinto & Purper, 1979 (Passinho Shales, upper section ?Taciba Formation, lower Permian, Itararé Group, Brazil) in the shorter size (19–20 mm vs. 27 mm in *A. oliveirai*), Sc branches short and simple (in *A. oliveirai* and *A. langei* two bifurcated veins), RA with simple branches, the first branch of RA simple, arises close to bifurcation of R, less branches of RA (3 branches vs. 5–6 branches in *A. oliveirai* and *A. langei*) and M (5 branches vs. 7 branches in *A. oliveirai* and *A. langei*), almost similar length of MA and MP stem, distance between bifurcation of R and M, the first branch of CuA bifurcated (in *A. oliveirai* simple) (Pinto and Mendes 2002; Ricetti 2016; Ricetti et al. 2016).

Despite the comparisons of *A. macucai* sp. nov. with the above-mentioned Paleozoic stem-dictyopteran records from South America, we agree with previous statements that taxonomic redescrptions and new illustrations, including morphological notes and photographs, are needed, as noted by Ricetti (2016) and Ricetti et al. (2016).

Paleoecological and taphonomic implications.—*Anthracoblattina macucai* sp. nov. (Dictyoptera: Phylloblattidae) was recovered from the Arroyo Totoral Formation alongside a rich paleoflora, comprising glossopterids (*Gangamopteris* and *Glossopteris*), conifers (*Ferugliocladus*), cordaitaleans (*Cordaites*), sphenophytes (*Phyllothea*, *Paracalamites*), pteridosperms (*Botrychiopsis*) ginkgoaleans (*Ginkgoites*), bryophytes, abundant dispersed seeds (Fig. 2), and additional, less noticeable flora, including ferns, lycophytes, and various reproductive structures.

The state of preservation of the fossils is varied; most of the plant specimens are fairly large or complete (e.g., Fig. 2A–D), delicate (e.g., Fig. 2H, M) and articulated (e.g., Fig. 2F, G, I); although in some cases, they exhibit moderate degradation (e.g., Fig. 2D, E, H, O). This indicates a short distance of transport from the origin to deposition, suggesting the flora of the Arroyo Totoral area was growing near the water body under humid local climatic conditions. The presence of rootlets (Fig. 2N) further points to the development of paleosols and a parautochthonous assemblage. Accordingly, the flora from the Arroyo Totoral Formation is inferred to have grown at the lake’s shore, where it was later deposited in lacustrine facies (Cúneo 1984; Andreis et al. 1984; Cúneo and Archangelsky 1996).

Given the abundantly well-preserved paleoflora, and the

historical number of excavations at the site, the conspicuous lack of insects in this unit challenges our understanding. The presence of a varied paleoentomofauna living in the vegetation is inferred from the numerous plant-insect interactions registered, including generalized herbivory (Pinheiro et al. 2015), piercing and sucking, galling, and oviposition (BC unpublished data). Nonetheless, none of the herbivory traces can be attributed to *A. macucai* sp. nov., since it probably lived on the ground of vegetated areas, protected from predators and functioning as an organic-matter degrader (detritivores). However, the possibility of it having a predator role cannot be excluded (Vršanský 2024; Santos et al. 2025). Schneider (1983a) mentioned that *Anthracoblattina* Scudder, 1879, had a limited habitat preference, being more abundant in sparsely vegetated shores of lakes and seas (Belahmira et al. 2019). Regarding the oviposition traces, none were identified as exophytic. Besides, the arrangement of the observed ovipositions on sphenophyte stems and glossopterid foliage (BC unpublished data) differed from the stereotyped curved arcs that have been attributed to other Paleozoic “cockroachoids” (Laaß and Hauschke 2019), the former being likely produced by protodonatans, Protophasmatidae, or Palaeodictyoptera (i.e., Cariglino et al. 2021).

The tegmina of “cockroachoids” (as well as those of other insects, such as hemipterans and elytra beetles) represent a common element in the fossil record. The tegmina are hardened forewings with a leathery appearance, therefore having a higher preservation potential, unlike the more delicate second pair of wings (Karr and Clapham 2015). This reinforces the puzzling absence of other insect remains in the Arroyo Totoral Formation, though collection and taphonomic biases remain possible. Nonetheless, in the Lower Cretaceous Khasurtly locality (Russia), the cockroaches are completely absent despite the collection of thousands of fossil insects (Kopylov et al. 2020). Ricetti (2016) mentioned that large-winged blattoid insects such as *Anthracoblattina* Scudder, 1879, were one of the most common insects in neocarboniferous-eopermian entomofaunas, both in Euramerica and South America (Lara et al. 2023). However, when compared with other “cockroachoid” genera, *Anthracoblattina* Scudder, 1879, comprise a frequent element recorded in nearly all late Paleozoic blattoid-dominated entomofaunas (Jörg W. Schneider, personal communication 2025).

Conclusions

In this paper, *Anthracoblattina macucai* sp. nov. is described as a new species of stem-dictyopteran. The taxonomic position within family Phylloblattidae Schneider, 1983a, and the genus *Anthracoblattina* Scudder, 1879, is based on a combination of numerous characters observed from an incomplete forewing.

Anthracoblattina macucai sp. nov. (Dictyoptera: Phylloblattidae) represents the first Permian record in La Rioja

Province (Argentina), being a remarkable finding since the entomological records in South American late Paleozoic deposits are very scarce in comparison to the Northern Hemisphere. We believe that future paleontological work in this formation will greatly expand our knowledge of early insect diversity.

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