

ANTHRACOBLATTINA MENDESI PINTO ET SEDOR (BLATTODEA, PHYLOBLATTIDAE): THE MOST COMPLETELY PRESERVED SOUTH AMERICAN PALAEOZOIC COCKROACH

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ABSTRACT – An abundant and diverse fossil record, encompassing some specimens with exceptional preservation, identifies the Campáleo outcrop in the earliest Permian marine Lontras Shale of the Paraná Basin, in the northern uplands of State of Santa Catarina, Brazil as a Carboniferous-Permian *fossilagerstätte*. Among others, a relatively rich entomofauna was recently discovered in pyrite-rich black shales, yielding several exceptionally preserved, partly pyritized, body fossils of ‘cockroachoid’ (Blattodea) insects. Some of these were identified as *Anthracoblattina mendesi* Pinto & Sedor, which is revised here in a preliminary comparison with all Palaeozoic related species known thus far from South America. Based on these new finds, *A. mendesi* becomes the most complete Palaeozoic blattoid described so far from South America. Several sub-complete individuals provide additional information about the anatomy of Late Palaeozoic blattoids, in general. The new finds demonstrate that the genus *Anthracoblattina* is not only a common and typical component of the Euramerican Late Pennsylvanian/early Permian entomofauna, but was also present in the South American Gondwana entomofauna. It is hypothesized that *Anthracoblattina* immigrated from Euramerica into this part of Gondwana during a climate amelioration event during the course of the Late Paleozoic Ice Age (LPIA), as it is indicated by the transgressive marine Lontras Shale.

Key words: Blattodea, taxonomy, Itararé Group, Paraná Basin, South America, Carboniferous-Permian.

RESUMO – Um registro fóssil abundante e diverso, compreendendo espécimes com preservação excepcional, identifica o afloramento Campáleo, posicionado no Folhelho Lontras (Permiano inferior da Bacia do Paraná) na região do Planalto Norte de Santa Catarina, Brasil, como um *fossilagerstätte* do contato Carbonífero-Permiano. Dentre outros fósseis, uma entomofauna relativamente rica foi recentemente encontrada nos folhelhos negros ricos em pirita deste afloramento contendo vários fósseis parcialmente piritizados e excepcionalmente preservados de corpos de Blattóides (antecessores paleozoicos das baratas atuais) que foram identificados como a espécie *Anthracoblattina mendesi* Pinto & Sedor, aqui revisada em uma comparação preliminar com todos os Blattodea sul-americanos até então conhecidos. Baseado nestes novos achados, *A. mendesi* se tornou a espécie de blatódeos paleozoicos mais completa da América do Sul. Vários indivíduos subcompletos provêm informações adicionais sobre a anatomia dos blatódeos do Paleozoico. Os novos achados demonstram que o gênero *Anthracoblattina* não é apenas um componente comum e típico do Pennsylvaniano Superior/Permiano inferior da Euramérica, como também é presente na entomofauna da Gondwana Sul-Americana. Levanta-se a hipótese de que o gênero *Anthracoblattina* imigrava da Euroamérica para esta porção do Gondwana durante os eventos de melhoramento climático durante o curso da Era Glacial do Neopaleozoico, LPIA (*Late Paleozoic Ice Age*), como indicado pelo evento transgressivo do Folhelho Lontras.

Palavras-chave: Blattodea, taxonomia, Grupo Itararé, Bacia do Paraná, América do Sul, Carbonífero-Permiano.

INTRODUCTION

The first Brazilian insect fossil described was *Phyloblatta oliveirai* Carpenter, 1930, later transferred to the genus *Anthracoblattina* by Schneider (1983a). It was collected in the municipality of Teixeira Soares, State of Paraná, from the Carboniferous-Permian Teixeira Soares Shale, which belongs to the Itararé Group of the Paraná Basin. From the same site *Phyloblatta roxoi* Petri, 1945, *P. pauloi* Mezzalana, 1948, *P. sommeri* Pinto & Purper, 1979, and *Anthracoblattina langei* Pinto & Purper, 1979 were also collected.

In addition to those five species from the Teixeira Soares Shale, throughout South America, only three other species of the order Blattodea are known. Two of them, *Archangelskyblatta vishniakovae* Pinto, 1972a, and *Anthracoblattina archangelskyi* Pinto & Mendes, 2002, were collected in the Early Permian Rio Genoa Formation of the Tepuel-Genoa Basin, Chubut Province, southern Argentina. A further species, *Anthracoblattina mendesi* Pinto & Sedor, 2000, comes from the Lontras Shale, uppermost Campo Mourão Formation, Itararé Group of the Paraná Basin. The type locality of this species is situated in the municipality of Mafra, State of Santa Catarina, about 100 km away from Teixeira Soares town.

The fossil occurrences from Mafra town were first discussed in Woodworth's (1912) expedition report, but they were already known since 1908 from Euzébio P. de Oliveira's expedition (Oliveira, 1930). Details on the fossil content of the Lontras Shale from Mafra were first published by Ruedemann (1929) and by Carvalho *et al.* (1942), who reported palaeoniscoid fishes, fish coprolites, plant remains, and the brachiopods *Orbiculoidea guaraunensis* Oliveira, 1930 and *Langella imbituvensis* Oliveira, 1930.

More than one century after these early reports, palaeontological research in the Mafra region have disclosed several other fossil occurrences, mostly in the Lontras Shale. In the 1990s the Campáleo outcrop (Figures 1-3) was discovered. This fossil site in the Lontras Shale is characterized by an extremely high palaeodiversity found in a thin package of black silty argillite (Scomazzon *et al.*, 2013; Iannuzzi *et al.*, 2014; Ricetti *et al.*, 2014). From the same site, during a fieldtrip in 1997, the first specimens of *Anthracoblattina mendesi* were recovered. More recently, about 150 insect specimens were obtained from the bottom of the 1.1 m thick shale. Among those, 18 specimens were identified as Blattodea, all of them related herein to *A. mendesi*. Those specimens have preserved various additional details that provide us with a better understanding

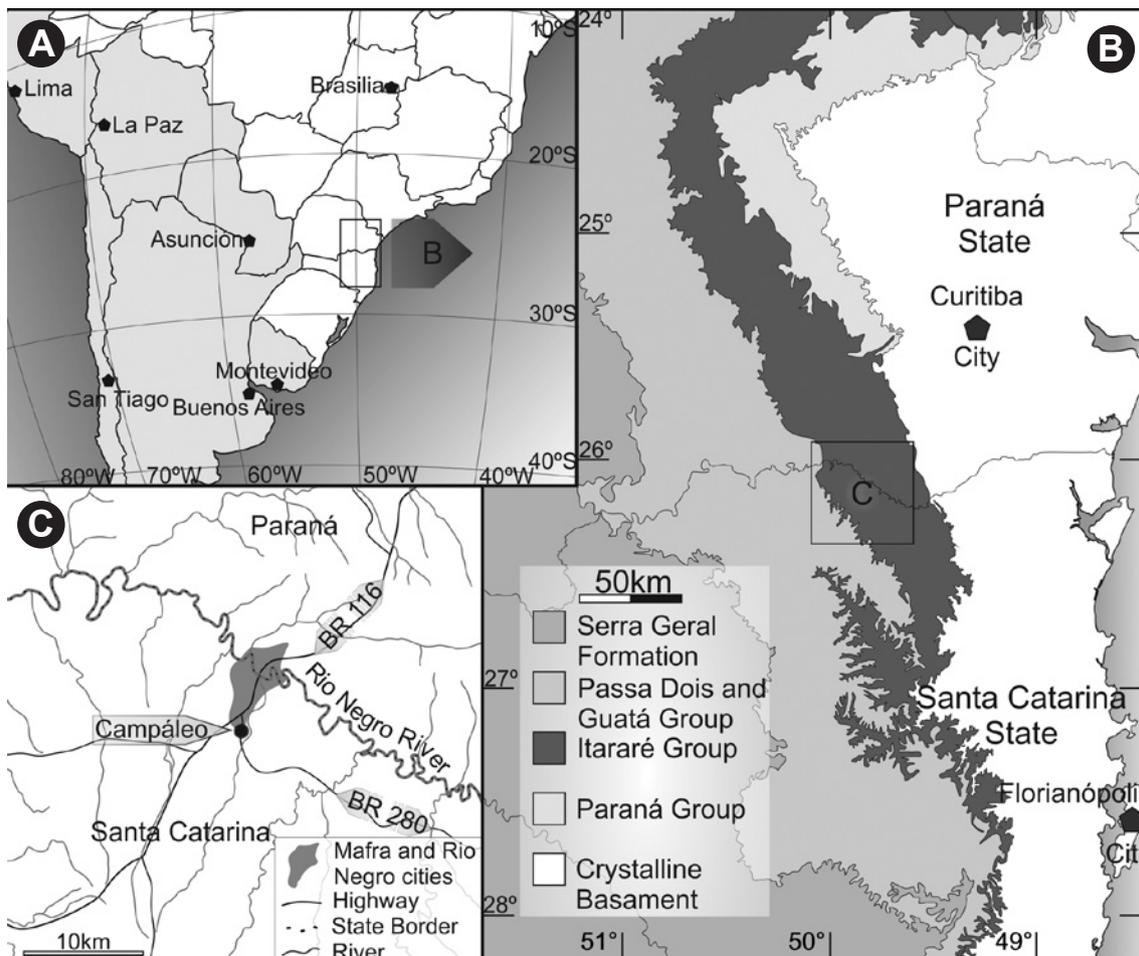


Figure 1. Location map of the Campáleo outcrop. **A**, South America with the position of the study area; **B**, simplified geological map of the Paraná Basin; **C**, location of the Campáleo outcrop in the State of Santa Catarina, Brazil.

of the morphology of this species, which can be considered as the most complete South American Palaeozoic cockroach described so far. The primary goal of our study is a detailed description of this *Anthracoblattina* species, to provide a basis for the revision of the single and not-so-well-preserved type specimens of the *Anthracoblattina* species, as well as for the revision of the type specimens of several *Phyloblatta* species so far described from South America. Some of the latter are most likely synonymous with *Anthracoblattina*.

GEOLOGICAL AND PALAEONTOLOGICAL SETTINGS

The Paraná Basin and Itararé Group

The Paraná Basin is an intracratonic basin on the South-American platform, covering ca. 1,600,000 km² in southern Brazil and central Uruguay, eastern Paraguay and northeastern Argentina (Figure 1). In the east, it is bordered erosionally as a result of crustal uplift during the opening of the Atlantic. In this way, exposed Palaeozoic rocks form an almost north-south extending belt from State of São Paulo in Brazil to Uruguay (Milani *et al.*, 2007). Milani *et al.* (1998) subdivided the basin fill into six second-order depositional supersequences, ranging from Upper Ordovician to the Upper Cretaceous. Here, we focus on the base third supersequence of Milani *et al.* (1998), the Gondwana I Supersequence, which spans the Carboniferous–Triassic interval (Figure 2).

In the Paraná Basin the shift from the Late Palaeozoic Ice Age (LPIA) to the Permian Greenhouse is recorded by the Itararé and Guatá groups, and encompasses a succession of glacial-to-non-glacial deposits, including both continental and marine facies, which thickness goes up to almost 2,050 m (Vesely & Assine, 2006; Holz *et al.*, 2010).

The Itararé Group was primary subdivided into the Campo do Tenente, Mafra and Rio do Sul formations by Schneider *et al.* (1974), based on surface data, and, later, into the Lagoa Azul, Campo Mourão and Taciba formations, by França & Potter (1988), based on drill cores. Weinschütz & Castro (2004, 2005, 2006) reinvestigated the Itararé Group for the Mafra region based on drill cores and outcrops. Weinschütz & Castro (2004) distinguished four sedimentary sequences and recognize, amongst regressive/transgressive cycles, three basin-wide maximum transgression events.

The second maximum transgression event is represented by silty and argillaceous sediments that are related to a proximal coastal facies of the Lontras Shale (Figures 2-3) according to Weinschütz & Castro (2005). The mudstone and siltstone package that locally composes the base of Lontras Shale has dropstone-rich varved shales on its bottom, which provides evidence of the deglaciation process during deposition of the Itararé Group (Figure 3). According to palynostratigraphic data, the Carboniferous–Permian boundary for the Paraná Basin is drawn at the base of Lontras Shale at the transition from the *Crucisaccites monoletus* to *Vittatina costabilis* palynomorph zone (Holz *et al.*, 2008; Iannuzi *et al.*, 2014).

		Geochronology		Lithostratigraphy				
Permian	Lopingian	Changhsingian	254.14±0.07	Passa Dois Supergroup	Rio do Rasto Fm.	Morro Pelado Mb.		
		Wuchiapingian	259.8±0.4					
		Guadalupian	Capitanian				265.1±0.4	
			Wordian				268.8±0.5	
	Cisuralian	Roadian	272.3±0.5		Teresina Fm.			
		Kungurian	283.5±0.6		Serra Alta Fm.			
		Artinskian	Asselian		295.0±0.18	Iratí Fm.	Assistência Mb.	Triunfo Mb.
							Taquaral Mb.	
		Sakmarian	Tubarão Supergroup		298.9±0.15	Guatá Group	Tatuí Fm.	Palermo Fm.
								Rio Bonito Fm.
	Carboniferous	Pennsylvanian	Gzhelian		303.7±0.1	Itararé Group	Taciba Fm.	Lontras Shale
			Kasimovian		307.0±0.1			
Moscovian			315.2±0.2					
Bashkirian								
				Lagoa Azul Fm.				

Figure 2. Carboniferous–Permian interval of the Gondwana I Supersequence with the stratigraphic of the Lontras Shale (Campo Mourão Formation, Itararé Group). Modified from Holz *et al.* (2010).

The Campáleo outcrop

The Campáleo outcrop is located in the urban area of the municipality of Mafra (UTM 22J 0.618.473, 7.106.243, Figures 1, 3) in the northern uplands of State of Santa Catarina (Figure 1). Geologically, it is situated in the eastern border area of the Paraná Basin, in the outcropping region of the Itararé Group (Figure 1). The Campáleo outcrop is stratigraphically positioned in the first 10 m of the Lontras Shale, which has a thickness of about 50 m in the Mafra area (Figure 3). Based on palynological data, the fossil assemblage of the Campáleo outcrop is considered to be earliest Early Permian in age, positioned immediately above the Carboniferous–Permian boundary, which is drawn at the base of the Lontras Shale (see above).

The outcrop starts with an approximately 1 m thick silty argillite bed, which is strongly bioturbated by the *Glossifungites* suite (Balistieri & Netto, 2002) (Figure 3). It is

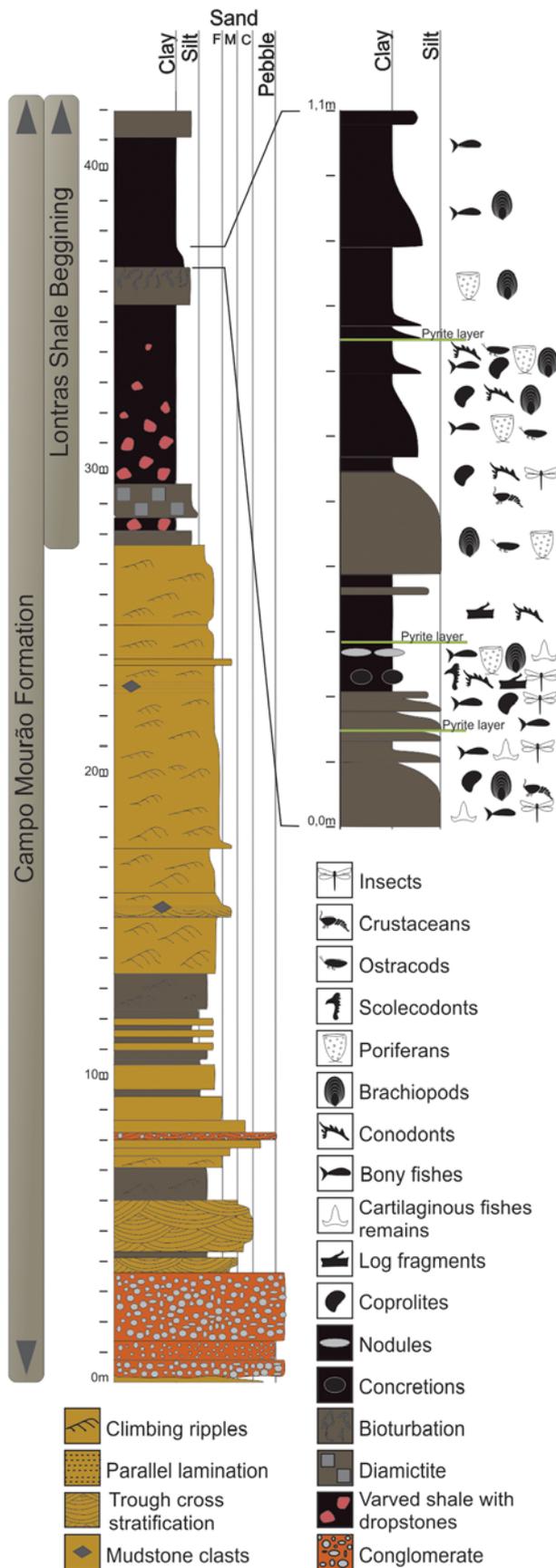


Figure 3. Lithological profile of the Campáleo section based on the TC well core, drilled at the Campáleo outcrop. Inset: detail of the very fossiliferous part of the Lontras Shale with the fossil content. Modified after Scmazzon *et al.* (2013).

followed by 1.1 m macrofossil rich black shales, which bottom is formed by a layer of siliceous-phosphatic concretion rich in carbonate and macrofossils, overlain by a bed of carbonate nodules barren of fossils. The black shales is rich in bony and cartilaginous fishes (Malabarba, 1988; Richter, 1991; Hamel, 2005), poriferans (Mouro *et al.*, 2014), conodonts (Scmazzon *et al.*, 2013; Wilner *et al.*, 2016), insects (Pinto & Sedor, 2000), and scolecodonts (Ricetti & Weinschütz, 2011), among many other fossils not described yet. From this bed, the type material of *Anthracoblattina mendesi* was recovered as well as the new insect sample described here. The black shale bed above is a much-silicified rock enriched in organic matter. It contains pyrite rich horizons, including three horizons rich in sulfur, enough to create layers of pyrite, and also framboidal pyrite and phosphatic material.

The insects were found inside the siliceous-phosphatic concretions or in the bottom-to-middle layers of the shale. When found in the shale, the specimens are usually strongly compressed and pyritized. However, small-sized insects with little compressed structures were occasionally found.

The abundant and diverse fossil record, comprising some specimens with exceptional preservation, identified the Campáleo outcrop as a Carboniferous-Permian fossiliferous site (Scmazzon *et al.*, 2013; Iannuzzi *et al.*, 2014; Ricetti *et al.*, 2014).

The fossil insect fauna of the Paraná Basin

There are a total of 24 fossil insect species so far published from Late Palaeozoic deposits of the Paraná Basin. They are summarized with their type localities in the following Table 1.

Despite this apparently good and diverse record of fossil insects, the number of findings is surprising low considering the huge outcropping area of Palaeozoic strata on the eastern border of the Paraná Basin.

MATERIAL AND METHODS

The holotype and paratype specimens of *Anthracoblattina mendesi* and 18 newly sampled specimens of this species, of which eight specimens are described here in detail, compose the base of the study. The new samples came from the type locality, the Campáleo outcrop and the type stratum, the Lontras shale, of Pinto & Sedor (2000). The Lontras Shale is very rich in pyrite, and fossils in this organic rich black shale are more or less pyritized. To prevent the alteration of the shale as well as to avoid the destruction of the fossils by pyrite oxidation, samples from the Campáleo site were stored submerged in translucent pure mineral oil. Additionally, the diffraction properties of the oil support a better visualization of the structures of fossils. For the same purpose, the fossils were moistened with ethylic alcohol at times during the beginning of our study.

The Museu de Ciências Naturais (MCN) of the Universidade Federal do Paraná (UFPR), municipality of Curitiba; State of Paraná, Brazil (acronym MCN.P.) houses the holotype and paratype of *Anthracoblattina mendesi*, while the Centro Paleontológico da Universidade do

Table 1. Fossil insect fauna from Paraná Basin.

Irati Formation		
Order	Family	Species
	Amaral Machado quarry, BR373, km 19, Piracicaba municipality, State of São Paulo	
Meganisoptera	Permaeschnidae	<i>Gondvanoptilon brasiliense</i> Rösler et al., 1981
	Outcrop at BR 290, km 185,5, Uruguaiana municipality, State of Rio Grande do Sul	
Prosbolidae	Dysmorphoptilidae	<i>Fulgoringruo kukalovae</i> Pinto, 1990 <i>Probole iratiensis</i> Pinto, 1987 <i>Probolecicada gondwanica</i> Pinto, 1987
Coleoptera	Permocupedidae	<i>Kaltanicupes ponomarenkoi</i> Pinto, 1987 <i>Protocupoides rohdendorfi</i> Pinto, 1987
Mecoptera	Permochoristidae	<i>Petromantis evansi</i> Pinto, 1972 <i>Asiachorista beckermigdisovae</i> Pinto, 1972
	Outcrop at BR 290, km 79, State of Rio Grande do Sul	
Hemiptera	Pareboridae	<i>Gondvanaptera capsii</i> Pinto & Ornellas, 1981
Neuroptera	Permithonidae	<i>Permipsythone panfilovi</i> Pinto & Ornellas, 1980
	São Borja municipality, State of Rio Grande do Sul	
Mecoptera	Permochoristidae	<i>Petromantis rieki</i> Pinto, 1972
Itararé Group		
	Boituva municipality, State of São Paulo: 2-IGG core	
Cnemidolestodea	Cnemidolestidae	<i>Irajanarkemina rodendorfi</i> Pinto & Ornellas, 1978
Eoblattida	Protophasmatidae	<i>Cacurgulopsis sanguinettiae</i> Pinto & Adami-Rodrigues, 1995 <i>Pintopinna martinsnetoi</i> Würdiger et al., 1998
Grylloblattodea	Proedischiiidae	<i>Proedischia mezzalirai</i> Pinto & Ornellas, 1978
	Jucá farm outcrop, Anitápolis municipality, State of Santa Catarina	
Cnemidolestodea	Spanioderidae	<i>Carpenteroptera onzii</i> Pinto, 1990
	Dursanal outcrop, Caçapava do Sul municipality, State of Rio Grande do Sul	
Cnemidolestodea	Spanioderidae	<i>Carpenteroptera rochacamposi</i> Pinto & Ornellas, 1978
	Taió municipality, State of Santa Catarina	
Eoblattida	Protophasmatidae	<i>Taiophlebia niloriclasodae</i> Martins-Neto et al., 2007
Upper Taciba Formation, Itararé Group		
	Teixeira Soares municipality, State of Paraná	
Blattodea		<i>Anthracoblattina oliveirai</i> Carpenter, 1930 <i>Phyloblatta roxoi</i> Petri, 1945
	Phyloblattidae	<i>Phyloblatta pauloi</i> Mezzalira, 1948 <i>Phyloblatta sommeri</i> Pinto & Purper, 1979 <i>Anthracoblattina langei</i> Pinto & Purper, 1979
Upper Campo Mourão Formation, Itararé Group		
	Campáleo outcrop, Mafra municipality, State of Santa Catarina	
Blattodea	Phyloblattidae	<i>Anthracoblatinna mendesi</i> Pinto & Sedor, 2000

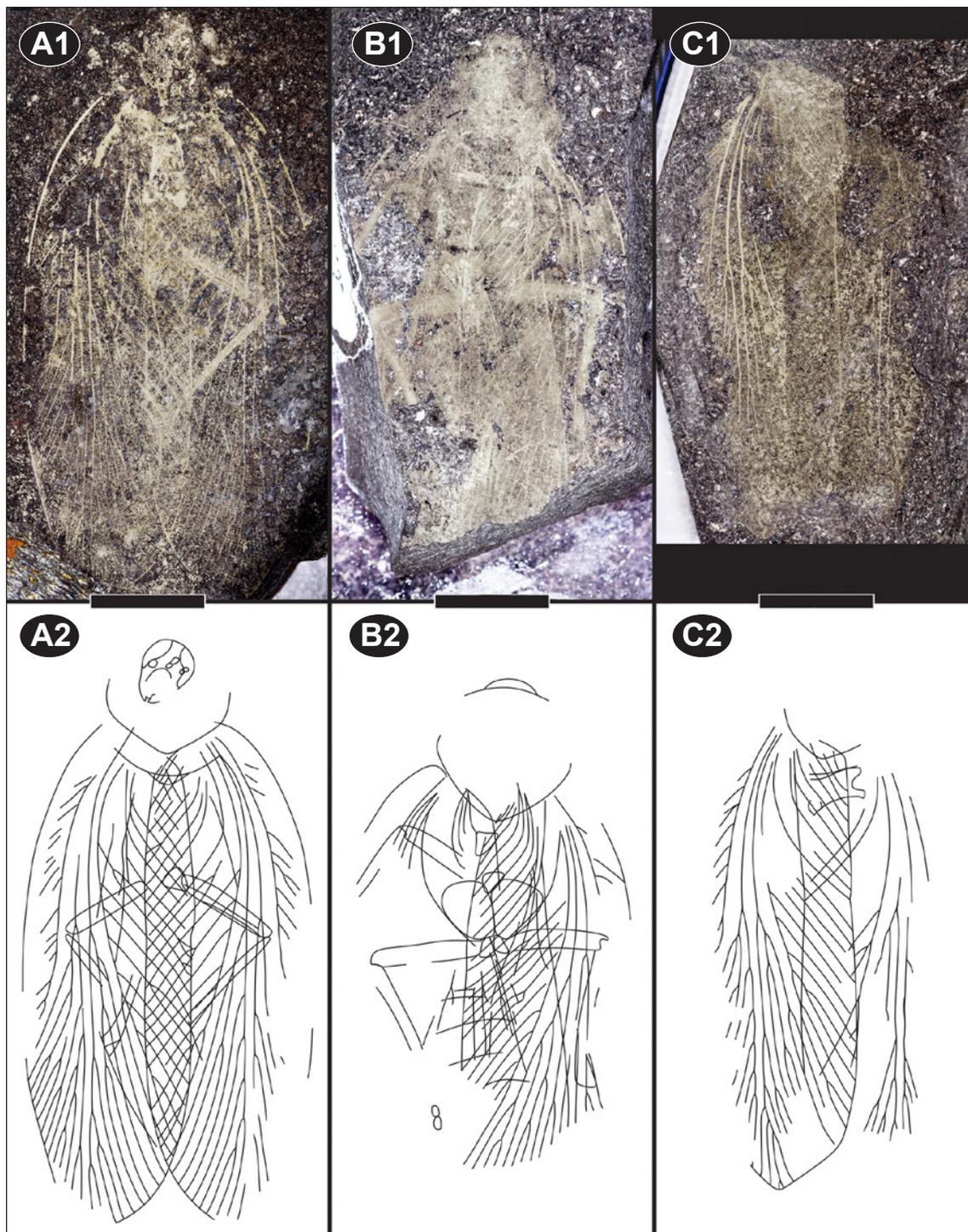


Figure 4. Best preserved specimens of *Anthracoblattina mendesi* from the Campáleo outcrop (lowermost Permian, Lontras Shale). **A1-A2**, specimen CP.I 2182; **B1-B2**, specimen CP.I 725; **C1-C2**, specimen CP/E 4387. Scale bars = 10 mm.

Contestado (**CENPALEO**), municipality of Mafra, State of Santa Catarina, Brazil (acronym CP/E) houses the 18 newly sampled specimens.

Photos were taken at the photographic laboratory of the Universidade Federal do Rio Grande do Sul (**UFRGS**) using Canon T3i camera with 70mm Sigma D6 macro lenses. The Scanning Electron Microscope analyses were made in the Microanalysis and Microscopy Center (**CMM**) of the UFRGS;

specimens were sputtered with carbon. Chemical analyses were performed using the Energy Dispersive X-Ray Spectrophotometer (**EDS**) attached to the SEM at CMM-UFRGS. Drawings based on series of high quality photographs obtained with different illumination settings, using vector image software and by direct observation with a binocular stereomicroscope.

The classification of higher taxa follows Hennig (1981) and Grimaldi (1997), *i.e.*, order Blattaria for extant cockroaches

and Blattodea or Blattoptera for paraphyletic Paleozoic cockroachoid. The wing venation nomenclature follows Lameere (1922), with the recommendations of Schneider (1984), Béthoux *et al.* (2009), and Zhang *et al.* (2013), regarding the specifics of blattoid wing venation pattern. Costal field designates the area between the anterior wing margin and the Subcosta. Wing venation abbreviations relevant to this contribution are repeated here for convenience (see Figure 5A). The anatomical terminology of the insect body (Figure 5B) follows the usual conventions (McAlpine, 1981).

SYSTEMATIC PALEONTOLOGY

The detailed reinvestigation of the type and paratype specimens of *Anthracoblattina mendesi* Pinto & Sedor (2000) has provided a perfect conformance of the species-features with the eight new specimens found at the type locality and described here (Figure 8). Minor differences in the branching pattern fall within the intra-specific variability, as discussed below. Based on the reinvestigation of the type material of Pinto & Sedor (2000), an emended diagnosis is presented here.

Class INSECTA Linnaeus, 1758
 Superorder DICTYOPTERA Latreille, 1829
 Order BLATTODEA Brunner von Wattenwyl, 1882
 Family PHYLOBLATTIDAE Schneider, 1983

Anthracoblattina Scudder, 1879

Species type. *Anthracoblattina americana* Scudder, 1879.

Anthracoblattina mendesi Pinto & Sedor, 2000
 (Figures 4-7)

Holotype. MCN.P.218a,b, part and counterpart of a fragmentary left and right forewing stored at the Museu de Ciências Naturais da Universidade Federal do Paraná (Natural Sciences Museum of Federal University of Paraná), municipality of Curitiba, State of Paraná, Brazil (Figure 8A).

Paratype. MCN.P.65a,b, part and counterpart of a fragmentary forewing stored at the Museu de Ciências Naturais da Universidade Federal do Paraná, municipality of Curitiba, State of Paraná, Brazil (Figure 8B).

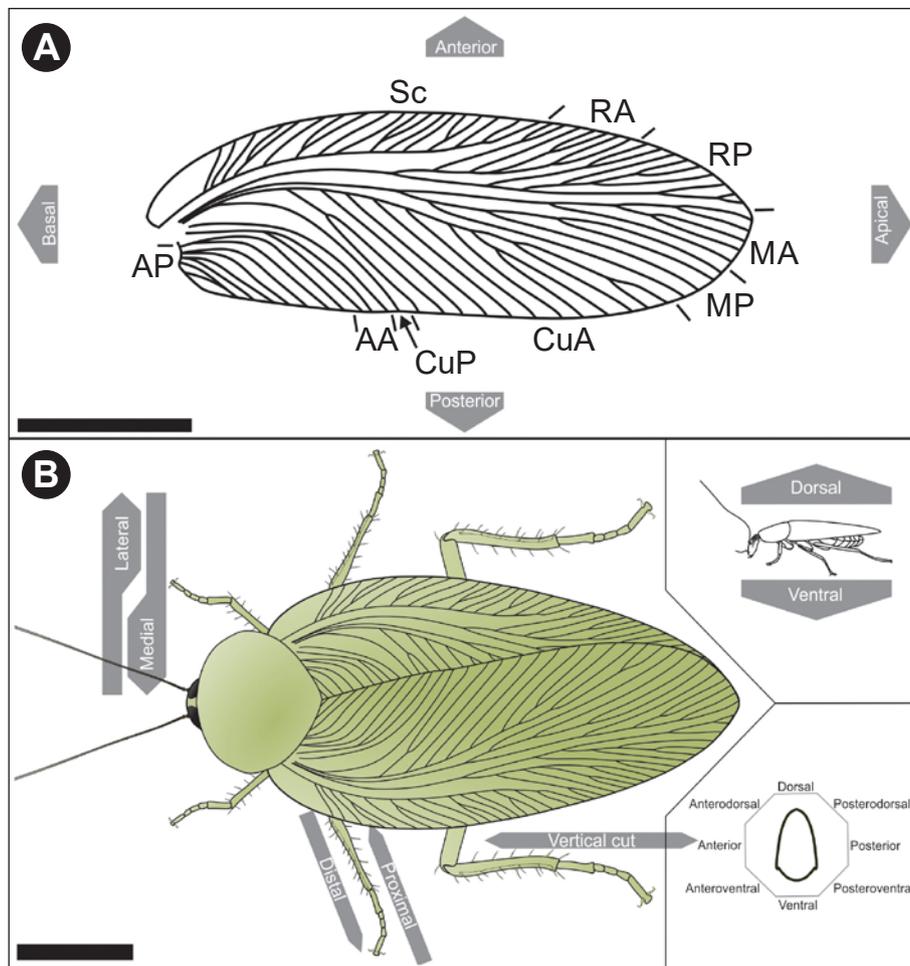


Figure 5. *Anthracoblattina mendesi* from the Campáleo outcrop (lowermost Permian, Lontras Shale). **A**, reconstruction of forewing with the terminology of the wing venation (based on a composition of specimens CP/E 3755, CP/E 4387, CP/E 8193 and CP.I 2182). **B**, life reconstruction of *A. mendesi* with terminology used in the description. **Abbreviations:** Sc, Subcosta; RA, anterior Radius; RP, posterior Radius; MA, anterior Media; MP, posterior Media; CuA, anterior Cubitus; CuP, posterior Cubitus; AA, anterior Analis; AP, posterior Analis. Scale bars = 10 mm.

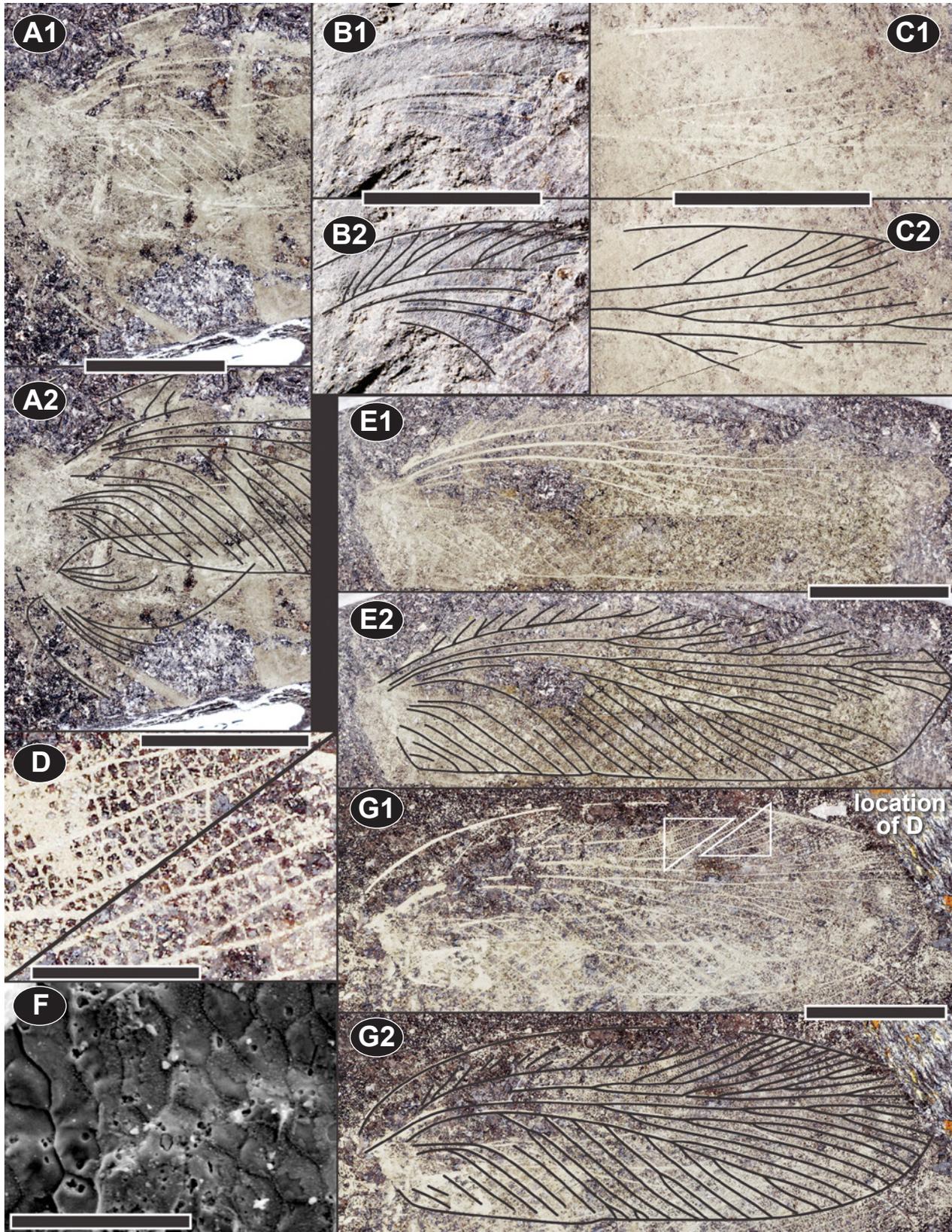


Figure 6. *Anthracoblattina mendesi* from the Campáleo outcrop (lowermost Permian, Lontras Shale), wing venation. **A1-A2**, specimen CP.I 725, left and right forewing with details of the basal portion and the analfield; **B1-B2**, specimen CP/E 3755.a, left forewing fragment, mirrored, basal portion of the Sc; **C1-C2**, specimen CP/E 8193, right forewing, detail of the R and M bifurcation; **D**, detail from G1, specimen CP.I 2182.a, typical cross venation, left in the Sc/RA area, right in the area of first RA branches close to the wing border; **E1-E2**, specimen CP/E 4387, left forewing, mirrored; **F**, SEM image of specimen CP/E 3755.a, cuticle pattern around the MP vein region; **G1-G2**, specimen CP.I 2182.a, left forewing, mirrored, with indication on the position of the enlargement reproduced in D. Scale bars: A1-A2, B1-B2, C1-C2, E1-E2, G1-G2 = 10 mm; D = 2,5 mm; F = 5 μ m.

Additional material. Eighteen specimens stored at the Centro Paleontológico da Universidade do Contestado – CENPALEO (Contestado University Paleontological center) collection, municipality of Mafra, State of Santa Catarina, Brazil; collection numbers CP/E 1027; CP/E 3385; CP/E 3386; CP/E 3580 a,b; CP/E 3668; CP/E 3755 a,b (Figures 6B1-B2, F); CP/E 4387 (Figures 4C1-C2; Figures 6E1-E2; Figures 7D1-D2); CP/E 4390; CP/E 5293; CP/E 5301; CP/E 6695 a,b (Figures 7C1-C2); CP/E 7051; CP/E 8193 a,b (Figures 6C1-C2); CP/E 8495 a,b; C.P.I 725 (Figures 4B1-B2; Figures 6A1-A2; Figures 7E1-E2); CP/E 1745 a,b; C.P.I 2142 a,b (Figures 7A1-A2, H1-H2); C.P.I 2182 a,b (Figures 4 A1-A2; Figures 6D1-D2, G1-G2; Figures 7B1-B2, F1-F2, G1-G2).

Type locality. Campaleo outcrop, UTM 22J 0.618.473, 7.106.243, road cut at km 166 of the Road BR 280, municipality of Mafra, State of Santa Catarina, Brazil.

Type stratum. Base of the Lontras Shale, Campo Mourão Formation, Itararé Group of the Paraná Basin, lowermost Permian (Asselian).

Emended diagnosis. Forewing elongated, 42.1 mm long, 3 times longer than wider. Costal field strip-like, covering about 60% of the wing length, narrower near the wing base. Sc weakly sigmoidal, with pectinate branches inclined apically, simple, bifurcated or trifurcated. R and M bifurcated into RA, RP, MA and MP, respectively, approximately at 40% of wing length. RA and RP with multiple branches; number of RP distal branches slightly higher than in RA; posterior-most RP vein reaching the wing apex at its middle. M relatively straight; MA with a relatively long basal stem; first fork of MA at about its mid-length; MP with multiple branches; number of MA and MP veins sub-equal; MA and MP covering the posterior side of the apex. Distal to its basal bending, anterior stem of CuA straight, reaching the posterior wing margin at about 80% of wing length; in its basal half, with pectinate branches, simple or forked apically, inclined; in its apical half, branches with multiple forks. CuP arcuate with a slight bending at the middle of his length. Area between CuP and first AA vein broad; AA with few branches; AP veins regularly spaced; both AA and AP veins arcuate with a slight bending (as for CuP). Cross veins (archedictyon) mesh-like reticulate, cells proximally narrow, distally wider.

Description. **Forewings:** three times longer than wide, as calculated from the (nearly) complete specimens CP/E 4387 (42.1 mm x 13.7 mm) and C.P.I 2182 (42.1 mm x 14.2 mm) (Figures 4A1-A2, C1-C2; Figures 6E1-E2, G1-G2). Costal field: Figures 4, 6. Strip-like, covering about 60% of the wing length, narrowing to the wing base (well visible in specimens CP/E 4387, C.P.I 2182 and CP/E 8495). Subcosta (Sc): (Figures 4, 6) weakly sigmoidal, branches pectinate, regularly spaced, mostly simple, in places bifurcated to trifurcated, more than twenty terminal branches reaching the anterior wing margin (well visible in specimens CP/E 4387, C.P.I 2182, CP/E 8495, CP/E 3580). Radius (R): (Figures 4, 6) besides the basal bending, nearly straight, crossing the entire length of the wing and reaching wing margin slightly above the middle of the wing apex (CP/E 4387, C.P.I 2182); first fork of R (into RA and RP) located at about 40% of wing length; branches of RA and RP

arose from the main stem mostly by simple branching and are themselves bifurcated to trifurcated, rarely simple (specimens CP/E 4387, C.P.I 2182, CP/E 3385, CP/E 8193, CP/E 3580, CP/E 3755, CP/E 8495, CP/E 3668); 6 and 8 branches of RA and RP, respectively reaching the anterior wing margin (specimen C.P.I 2182). Media (M): (Figures 4, 6) besides the basal bending, nearly straight crossing the entire length of the wing and covering the posterior side of the apex; first fork (into MA and MP) located at about 40% of wing length, immediately distal of the first fork of R (specimens C.P.I 2182, CP/E 4387, C.P.I 725, CP/E 6695, CP/E 8193, CP/E 8495, CP/E 3385) or immediately proximal to it (specimen CP/E 3580); MA usually with relatively long basal stem, as long as about half of MA length (approximately at the last third of wing length), without multiple branches, without clear branching pattern; MP with multiple branches; number of MA and MP veins sub-equal, altogether counting roughly 10. Anterior Cubitus (CuA): (Figures 4, 6) besides its basal bending, nearly straight, covering about 80% of the wing length; with pectinate branches, simple or forked apically, inclined; altogether with about 13 branches covering the posterior wing margin (specimens C.P.I 2182, CP/E 4387; C.P.I 725). Posterior Cubitus (CuP): (Figures 4, 6) arcuate with a slight bend at the middle of their length (specimens C.P.I 2182, CP/E 4387, C.P.I 725, CP/E 3755, CP/E 6695, CP/E 8193, CP/E 8495); area between CuP and first AA vein broadened. Anal field: (Figures 4, 6) anteriorly delimited by CuP (running along the claval furrow); it occupies about 35% of the wing length (specimens C.P.I 2182, CP/E 4387). Anterior Analis (AA): with few branches (about 2 or 3). Posterior Analis (AP): veins regularly spaced, number so far unknown because of incomplete preservation; both AA and AP veins arcuate with a slight bending as in CuP (specimens C.P.I 2182, CP/E 4387, C.P.I 725, CP/E 6695, CP/E 8193, CP/E 8495). AP veins may merge (specimen C.P.I 725). Cross venation (archedictyon): (Figure 6D) mesh-like reticulate, cells proximally narrow, distally wider (specimens C.P.I 2182, CP/E 3755, CP/E 3385, CP/E 6695). The specimen CP/E 3755, well preserved in a concretion, show in the SEM picture (Figure 6F) a polygonal pattern of the cuticle surface. **Hindwings:** only indistinct remains preserved (Figures 4A1-A2, B1-B2), without any remarkable characteristics worth to be described (specimens C.P.I 2182, CP/E 6695, CP/E 8495, C.P.I 725). **Head:** preserved in the specimens C.P.I 2182 and C.P.I 2142. In C.P.I 2182 (Figures 7B1-B2) 5.7 mm long and 4.5 mm wide; with dorso-laterally positioned compound eyes (CE in Figure 7B2) which are 3.2 mm long and 1.7 mm wide. Evidence of epistomal suture (ES in Figure 7B2), convex, 1.6 mm wide and 0.9 mm long. Evidence of ventral-most parts of left and right mandibles (M in Figure 7B2). Antenna (Figures 7A1-A2, B1-B2) positioned on front of the head capsule with indications of antennal sutures (AS in Figure 7B2). Scape visible on specimen C.P.I 2142 (S in Figure 7A2), subtrapezoidal, 0.4 mm long. Evidence of the Pedicel (P in Figures 7A2, B2) in specimens C.P.I 2182 and C.P.I 2142, 0.3 mm long. Incomplete Flagellum visible in both specimens (Fla in Figures 7A2, B2), eight subspherical segments in specimen C.P.I 2142 (Figure 7A2), each 0.2 mm long and 0.1 mm wide; three subspherical segments in specimen C.P.I 2182

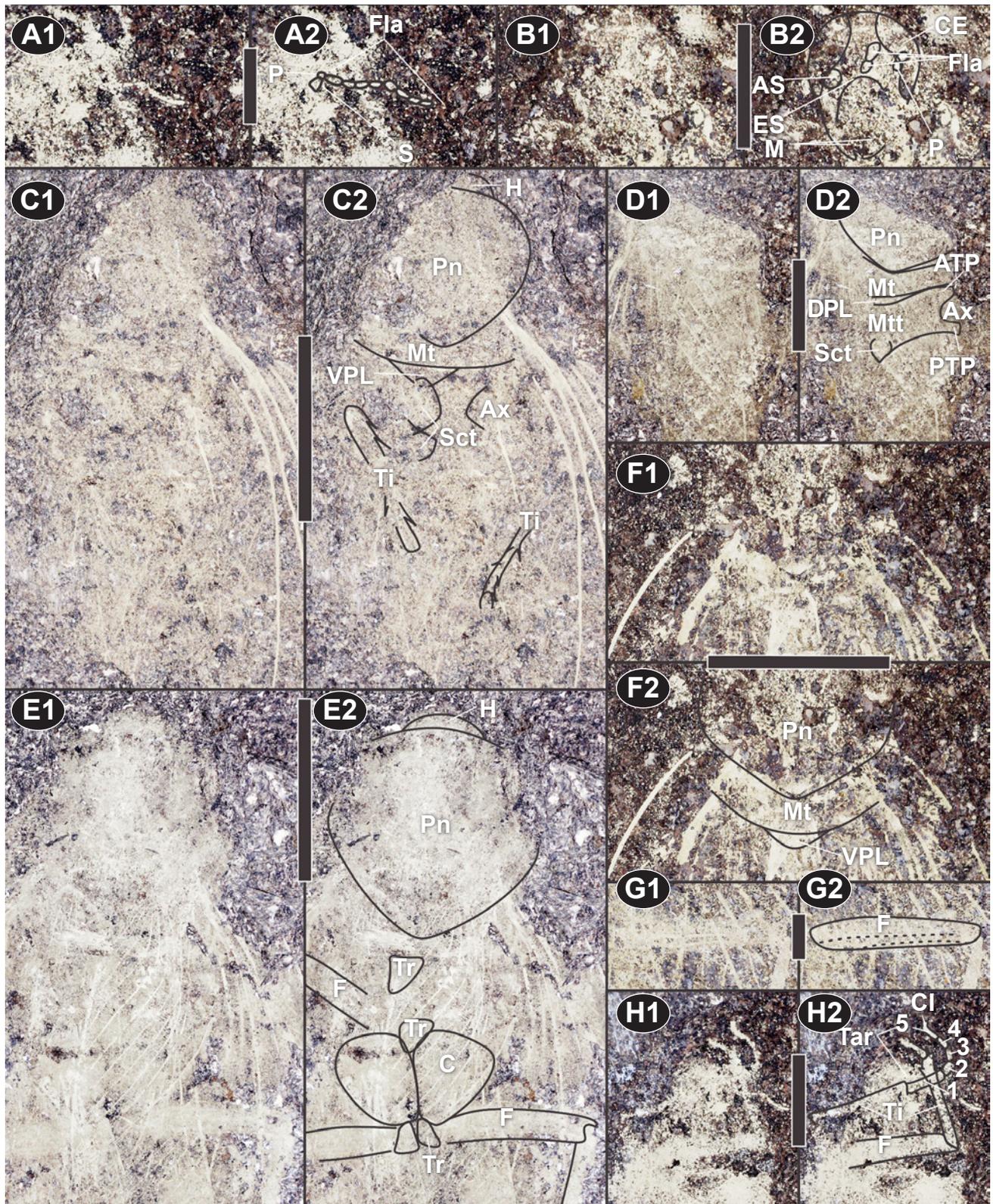


Figure 7. *Anthracoblattina mendesi* from the Campáleo outcrop (lowermost Permian, Lontras Shale), head region, thorax and legs. **A1-A2**, specimen CP.I 2142.b, details of the right antenna; **B1-B2**, specimen CP.I 2182.a, dorsal head region; **C1-C2**, specimen CP/E 6695.a, pronotum, thoracic tergites, 2nd and 3rd tibia; **D1-D2**, Specimen CP/E 4387, details of thoracic tergites; **E1-E2**, specimen CP.I 725, pronotum and anterior portion of the head, 3rd left and right coxa, trochanter and femur; **F1-F2**, specimen CP.I 2182.a, details of thoracic tergites; **G1-G2**: specimen CP.I 2182.a, details of 3rd right femur; **H1-H2**: specimen CP.I 2142.b, 1st left and right tibia and tarsus. **Abbreviations:** **AS**, antennal suture; **ATP**, anterior tergal process; **Ax**, axillary area; **C**, coxa; **CE**, compound eyes; **ES**, epistomal suture; **F**, femur; **Fla**, flagellum; **H**, head; **M**, mandible; **Mt**, mesotergite; **Mtt**, metatergite; **P**, pedicel; **Pn**, pronotum; **PDL**, post-tergal dorsal lappet; **PTP**, posterior tergal process; **PVL**, post-tergal ventral lappet; **S**, scape; **Sct**, scutellum; **Tar**, tarsi (1-5); **Ti**, tibia; **Tr**, trochanter. Scale bars: A1-A2 = 2,5 mm, B1-B2, D1-D2, H1-H2 = 5 mm, C1-C2, E1-E2, F1-F2 = 10 mm, G1-G2 = 2,5 mm.

(Figure 7B2), each in average 0.5 mm long and 0.4 mm wide. **Thorax:** pronotum preserved in specimens CP.I 2182, CP/E 6695, CP.I 725 and CP/E 4387 (Pn in Figures 7C2, D2, E2, F2), subpentagonal shaped, with most sharp angle turned posteriorly over the metatergite. In average 10 mm x 10 mm, covering almost entirely the head (specimens CP/E 6695, CP.I 725). Mesotergite partially preserved with the exception of the posterior margin, visible in specimens CP/E 6695, CP/E 4387 and CP.I 2182 (Mt in Figures 7C2, D2, F2), concave, with post-tergal dorsal lappet and post-tergal ventral lappet (VPL and DPL in Figures 7C2, D2, F2), both semicircular and contiguous to the middle posterior margin of the mesotergite, estimated size 2.1 mm x 0.5 mm in specimen CP/E 4387, and average of 3.5 mm x 1.0 mm for specimens CP/E 6695 and CP.I 2182. Metatergite observed in CP/E 4387 and CP/E 6695, anterior margin concave (Mtt in Figure 7D2). Anterior tergal process (ATP in Figure 7D2) occupies 20% (0.3 mm) of the metatergite lateral edge. Axillary area invagination measures in

specimen CP/E 4387 0.5 mm and occupies 53% (0.8 mm) of the lateral edge (Ax. in Figures 7C2, D2). Posterior tergal process (PTP in Figure 7D2) occupies 26% (0.4 mm) of the lateral edge. Posterior margin formed by two oblique convexities, joined medially, forming a “V” shaped vertex, which supports the posterior portion of scutellum (SCT in Figures 7C2, D2); anterior part of the scutellum spear-shaped with its vertex pointed anteriorly, measuring 1.5 mm x 1.0 mm (CP/E 6695), posterior part hexagone-shaped, estimated size of 0.9 mm x 1.0 mm (CP/E 4387; CP/E 6695). **Legs:** First leg pair directed anteriorly, second and third pairs posteriorly (specimens CP.I 2142, CP/E 8495, CP.I 725, CP.I 2182; Figures 4A1-A2, B1-B2, 7C1-C2, E1-E2, G1-G2, H1-H2), as in modern cockroaches. Coxa (C in Figure 7E2) triangular, 4.0 mm long (about 9% of leg length), 4.0 mm wide in its proximal portion and 2.0 mm in its distal portion (CP.I 725). Trochanter (Tr in Figure 7E2) also triangular, 1.3 mm long (about 5% of leg length) 1.1 mm wide (specimen CP.I 725). Femur (F in Figures 7E2, G2, H2), 8.25 mm x 1.65 mm (about 39% of leg length), five times longer than wide, without spines, ventrally weakly convex, dicondyl articulation (specimens CP.I 725; CP.I 2182). Tibia (Ti in Figures 7C2, H2) in average 4.3 mm long and 0.6 mm wide (about 20% of leg length), seven times and a half longer than wide, with spines visible all over its length (specimens CP/E 6695, CP.I 2142). Tarsi (Tar in Figure 7H2) 5.6 mm long and 0.6 mm wide (about 26% of leg length), composed of five tarsomeres (as in modern Blattaria; specimen CP.I 2142); 1st tarsomere 2.1 mm x 0.6 mm, 3.5 times longer than wide; 2nd tarsomere 0.7 mm x 0.6 mm, robust; 3rd tarsomere 0.9 mm x 0.5 mm, thinner than the 2nd; 4th tarsomere 0.7 mm x 0.4 mm, thinner than the 3rd; 5th tarsomere 1.2 mm x 0.4 mm, thinner than the 4th, with a 0.5 mm long claw (CL in Figure 7H2) arched in a 120° angle. **Abdomen:** indistinctly preserved in specimens CP/E 6695, CP/E 8495, CP.I 725, and CP.I 2142 (Figures 4B1-B2).

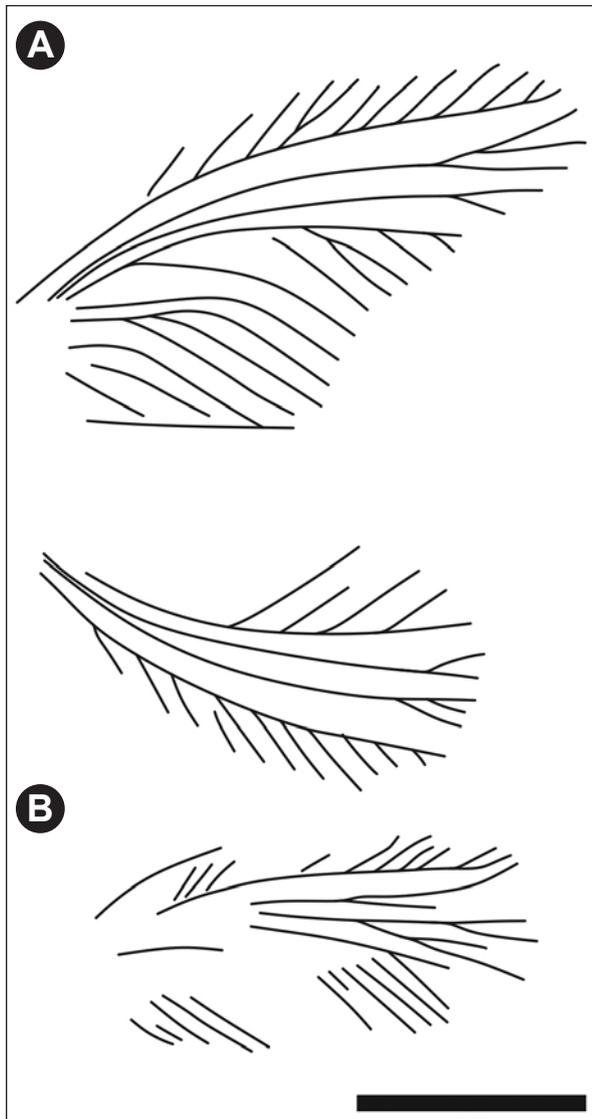


Figure 8. *Anthracoblattina mendesi* type specimens redraw; **A**, holotype MCN.P.218 a.b.; **B**, paratype MCN.P.65 a.b. Scale bar = 10 mm.

DISCUSSION

Generally, the genus *Anthracoblattina* is well established by four characteristic features observed in forewings: the distinct narrowing of the strip-like costal field near wing base, the first forks of both R and M located between the first third and the half of the wing length, the straight (*i.e.* non-sinuuous) CuA, and a broad interspace between CuP and AA (Schneider, 1983a, p. 122-134, pl. 3, fig. 2). Very similar venation patterns are known in species of the genera *Kunguroblattina* Martinov, 1930 and *Kashmiroblattina* Verma, 1967. *Kunguroblattina* is distinct from the two other genera by a costal field with a constant width (Schneider, 1983a, p. 124-125, pl. 3, fig. 3). *Kashmiroblattina* has, in contrast to the other genera, broad areas between Sc, R, M and CuA.

Much more difficult to apprehend is the classification of the *Anthracoblattina* species, as shown by Schneider (1978, 1983a,b) in the revision of European Carboniferous and Permian cockroachoids. This is due to the somewhat ‘archaic’ venation pattern, especially in regard of the broad area between CuP and AA, as well as the distinct bifurcation of R and M into two nearly equal parts, *i.e.* well-developed

RA and MA (Wei *et al.*, 2013). This ground pattern remains unaffected from the Late Pennsylvanian (Kasimovian) forms to the youngest ones, in the middle Early Permian (Artinskian). An additional issue regards the high intra-individual and intraspecific variability (shared with all Phylloblattidae). Although *Anthracoblattina* is represented in nearly all Euramerican Late Palaeozoic insect localities from North America via Morocco to Europe (*e.g.* Schneider *et al.*, 2004; Hmich *et al.*, 2006), the number of specimens known at one single locality is restricted. The exception is from the Late Pennsylvanian (Gzhelian) of Commeny (France), from which a large number of conspecific specimens are known by means of 12 forewings, two pairs of them belonging to a single individual; the high variability was figured and discussed for the *Anthracoblattina gigantea* - *Anthracoblattina ensifera* species-group by Schneider (1983b, p. 82-84, pl. 3, figs. 1-11). Bearing this in mind, a first and preliminary comparison of South American Late Palaeozoic cockroachoids will be done here based on literature and data gained from the new material of *Anthracoblattina mendesi*, as follows.

In comparison with *Anthracoblattina oliveirai*, from Teixeira Soares, the venation pattern of *A. mendesi* is quite similar. Substantial differences exist only in size; reconstructed forewing size for *A. oliveirai* is 27 mm x 13 mm, while *A. mendesi* is 42 mm x 14 mm. Even if forewing size could considerably vary within one species (up to 65 % in the extant *Periplaneta americana* Linnaeus, 1758), *A. mendesi* could be regarded as different from *A. oliveirai*. *Phyloblatta roxoi* is a hindwing bearing the general problem that isolated hindwings could not be assigned with certainty because most species are known from, and identified based on forewings. *Phyloblatta pauloi* Mezzalana, 1948 is a strongly deformed fragment of a forewing; without better-preserved material, it must remain a *nomen dubium*. *Phyloblatta sommeri* Pinto & Puper, 1979 is clearly a phylloblattid forewing, but because of its fragmentary preservation, it is difficult to compare with any other well-determined genus or species. The small sized forewings (20 mm x 8 mm) of *Archangelskyblatta vishniakovae* was assigned to *Kashmiroblatta* by Schneider (1983a) because of the broad fields between Sc, R, M and CuA, but based on figures in Pinto (1972a,b) only; a reinvestigation of the type specimen is necessary. *Anthracoblattina langei*, a forewing fragment, may be identical with *A. mendesi*; the investigation of the type specimen will bring clarity. The genus determination of *Anthracoblattina archangelskyi* is correct, but a reinvestigation of the type specimen is necessary for detailed comparisons.

CONCLUSIONS

Based on the data presented above, *Anthracoblattina mendesi* is the most complete Palaeozoic blattoid described so far from South America. Several nearly complete individuals, with complete bodies and attached wings, deliver additional information on the morphology of Late Palaeozoic cockroachoids in general. The unusual preservation of the partly pyritized insect fossils allow the description of many

details, as *e.g.* the morphology of the legs, which compare functionally completely with the cursorial legs (*i.e.* adapted for fast running) of modern roaches (only arolium hooks have not been found). Parts of the head are preserved, such as the filiform antennae, and indications of large compound eyes situated at the dorso-lateral surface of the head. Triangular structures at the anterior border of the head are interpreted as remnants of strong mandibles. Future investigations of pyritized body parts with more sophisticated techniques and additional finds from the ongoing excavation of the Lontras Shale fossilagerstätte will significantly increase the knowledge of the palaeobiology of fossil Blattodea. The new finds of well-preserved and clearly determinable forewings of *A. mendesi* demonstrate that the genus *Anthracoblattina* is not only a common and typical component of the Euramerican Late Pennsylvanian/early Permian entomofauna, but also represented in the Gondwana entomofauna. It is hypothesized that *Anthracoblattina* immigrated from Euramerica into this part of Gondwana during a climate amelioration event in the course of the LPIA, as it is indicated by the presence of diamictites underlying (Campo Mourão Formation) and overlying (Taciba Formation) the transgressive marine Lontras Shale as appointed by Weischütz & Castro (2005, 2006).

ACKNOWLEDGMENTS

The author's special thanks go to I.D. Pinto (*in memory*) for a life dedicated to the study of fossil arthropods, and for his assistance in beginning of this study, providing data from his previous studies. S.G. Lucas is thanked for improvement of the English of parts of the manuscript. Thanks go to M. Fritsch for helpful discussions and for providing laboratorial assistance. G.R. Pires Moreira is thanked for discussions on anatomy, O.A. Ricetti Junior for collaborative discussions and field support, L.F. Lopes for the photography, and V. Greinert for enthusiastic fossil collecting, providing the base for this publication. Both the reviewers, O. Bethoux and C. Brauckmann, have greatly improved the manuscript, special thanks for that. The authors thank the National Council of Technological and Scientific Development (CNPq) for the grant provided to R. Iannuzzi (PQ 309211/2013-1). J.W. Schneider acknowledges the support of the German Research Foundation (DFG), grants DFG Schn 408/21 and DFG Schn 408/22. This publication aims to contribute to IGCP 630 "Permian-Triassic climatic and environmental extremes and biotic response" as well as to the tasks of the "Late Pennsylvanian - Permian - Early Triassic Non-Marine - Marine Correlation Working Group" of the International Subcommittee on Carboniferous, Permian and Triassic stratigraphy.

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Received in January, 2016; accepted in June, 2016.