

First records of Geinitziidae (Insecta: Grylloblattida) from the Upper Triassic of Argentina (Mendoza)

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A new grylloblattid (*Permoshurabia argentina* sp. nov.: Geinitziidae) is described and illustrated from the Upper Triassic of Argentina. The material represents the first record of this family from Argentina and expands the geographic distribution of this group during the Triassic.

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THE SMALL Grylloblattidae or Grylloblattodea order (extant representatives are referred to as ‘living fossils’ and have relictual distributions) is one of the least diverse extant insect groups (with 29 species and five genera grouped into the single extant family Grylloblattidae; Jarvis & Whiting 2006). More than 44 families have been described from the fossil record, which extends back to the early Late Carboniferous (Storozhenko 1992, 1997, Vrsansky *et al.* 2001). During the Permian, grylloblattids were the most abundant and diverse insect group and were the ancestral stock of all other perlideans (stoneflies, webspinners and earwigs; Rasnitsyn & Quicke 2002). By the end of the Early Permian to the beginning of the Middle Permian they reached their heyday (Aristov 2005). However, the diversity of the order decreased at the end of the Middle to Late Permian. Four of the 11 Late Permian families became extinct during this interval, resulting in a minimum diversity during the Early Triassic (Aristov *et al.* 2009). However, some Permian families reappeared in the Middle to Late Triassic indicating the existence of Early Triassic ghost lineages.

Triassic (or latest Permian) grylloblattids (represented by wings and fragments of pronota) in Asia were the most abundant and diverse, and occur in various deposits (Table 1; Storozhenko 2002, Aristov 2005, Aristov *et al.* 2009, Aristov *et al.* 2011, Bashkuev *et al.* 2012). They are also assigned to various families: Megakhosaridae Sharov, 1961, Blattogryllidae Rasnitsyn, 1976, Gorochoviidae

Storozhenko, 1998, Madygenophlebiidae Storozhenko, 1992, Mesorthopteridae Tillyard, 1922, Tunguskapteridae Storozhenko & Vrsansky, 1995, Chaulioditidae Handlirsch, 1906 and Geinitziidae Handlirsch, 1906 (Storozhenko 1993, Aristov *et al.* 2011). In Gondwana, only Mesorthopteridae and Geinitziidae have been recorded (in Australia and South Africa). In Argentina, the only previous fossil record of the order is a grylloblattid aquatic nymph, *Triasseuryptilon acostai* Marquat, 1991 that was found in the Potrerillos Formation (Upper Triassic), Agua de las Avispas locality, south of the Cerro Cacheuta, Cuyana Basin (Mendoza Province). This nymph was initially classified as Miomoptera but was later transferred to Atactophlebiidae (Storozhenko 1997). Aristov (2004) questioned the position of *Triasseuryptilon* within this latter family and order based on the absence of characters shared by other nymphs of Atactophlebiidae. The taxon had an elongate body with the tibiofemoral joint directed inwards similar to plecopterans. Aristov *et al.* (2006) revised the nymphs of fossil grylloblattid insects that resemble *Kirkorella* Zalessky, 1939 (based on the presence of paranota on the abdominal tergites), but noted that the Argentinean specimen is most similar to stonefly nymphs (differing in having abdominal paranota). Therefore, its position remains uncertain.

Here we describe a new specimen belonging to Geinitziidae (Grylloblattida) from the early Late Triassic of Argentina. This material represents the first confident record of this family for the country and expands the known geographic distribution of the group during the Triassic.

Age	Country	Locality/Formation/Basin/Region
Early Triassic	Russia	Babii Kamen' locality, Mal'tseva Formation, Kuznetsk Basin, Kemerovo region; Anakit and Tura localities, Chichikan and Agitkan formations, respectively; and Khungtukun-2 and Lower Lyulyukta-1; Pirda and Kholokit formations, respectively; Krasnoyarsk region; Nedubrovo and Yontala localities, Vokhma Formation, Vologda region; Tikhvinskoe locality, Rybinsk Formation, Yaroslavl' region
	Mongolia	Yamaan-Us locality, Yamaan-Us Formation, Gobi-Altai Province
Early or Middle Triassic	Germany	Gödevitz locality, Saxony Anhalt; Bremke locality, Lower Saxony
	Spain	Port de Estellencs locality, Mallorca
Middle Triassic	China	Nanshenghu locality, Guizhou Province
	France	Vosgues locality, Grès à Voltzia Formation; Alsace and Lorraine (Anisian)
	Germany	Gambach, Lengfurt and Hammelburg localities in Lower Franconia, Schwarza locality in Thuringia; Gambach locality in Bavaria; Jena Formation
		Russia
Late Triassic	Kyrgyzstan	Madygen locality, Madygen Formation, Osh region
	Argentina	Agua de las Avispas locality, Potrerillos Formation, Cuyana Basin, Mendoza Province
	South Africa	Kapokraal, Tina Bridge, Nieuwjaars Spruit and Fletcher localities, Molteno Formation, Karoo Basin, Eastern Cape Province and Orange Free State
		Australia
	Kazakhstan	Kenderlyk and Kyzyltam localities, East-Kazakhstan and Almaty regions; Tologoi and Kol'djad formations.
	Ukraine	Garazhovka locality; Kharkiv region, Protopivka Formation
	Japan	Omine locality; Carnian, Momonoki Formation

Table 1. Records of grylloblattids in the Triassic.

Material and methods

The studied fossil was collected from the Potrerillos Formation (lower Upper Triassic), in Quebrada del Durazno locality, south of Cerro Cacheuta, Cuyana Basin, Mendoza Province, Argentina (Fig. 1).

The Potrerillos Formation is characterized by fluvial conglomerates at the base, intercalated with light-greenish cross-bedded sandstones and light tuffaceous sandstones of perennial braided river origin. These fluvial deposits grade basinwards to greenish grey, laminated siltstones and sandstones that are interbedded with black bituminous shales and tuffs, which are associated with high-sinuosity river systems. These facies are laterally interfingering with, and covered by, widespread lacustrine black shales of the Cacheuta Formation. The Potrerillos Formation is dated to the Ladinian–Carnian. Fossil beds containing insects occur in the uppermost parts of the formation and are, thus, of Carnian age (for more stratigraphic information see Lara & Wang 2016). The Potrerillos Formation fossil record includes 11 orders and 29 species of insects (Table 2) that belong to hemipterans (the dominant forms), blattids, coleopterans, odonatans, plecopterans, mecopterans, orthopterans, grylloblattids, miomopterans, dipterans and hymenopterans (Lara *et al.* 2015, Lara 2016).

Recently, the Quebrada del Durazno locality (33°04'74"S/69°07'18"W; Fig. 1; Potrerillos Formation) has yielded several hundred insect specimens and become one of the most important Triassic insect sites in South America and the Southern Hemisphere. The fossil insects have been assigned to 11 species and six

orders based on more than 13 specimens collected. However, Lara (2016) recently reported that eight orders, 40 species and over 90 specimens have been collected in this area. The insect fossils are preserved in siltstone beds and black shales and/or coal levels bearing spinicaudatans and well-known plant remains of the *Dicroidium* Flora. These beds were deposited in water bodies or semi-permanent swamps with abundant roots within deltaic settings.

Insect fossils at Quebrada del Durazno are numerically dominated by sclerotized forewings of hemipterans, with less abundant membranous forewings, nymphs of odonatans, elytra of coleopterans, membranous forewings of mecopterans, orthopterans, dipterans, grylloblattids and miomopterans. The insects are fragmentary or, in a few cases, articulated and preserved as impressions of wings, parts of bodies and complete bodies. Most of the groups derive from terrestrial habitats (adult stages), however, aquatic forms (immature stages) are also present, albeit less abundant. The assemblage is characterized by a high degree of sclerotization of forewings that survive the various stages of transport before reaching the depositional sites (Lara & Zavattieri 2014, Lara 2016).

The studied specimen, IANIGLA-PI 1029, is held in the collection of the Instituto Argentino de Nivología, Glaciología y Ciencias Ambientales (IANIGLA-CCCT-CONICET), Mendoza City. The specimen was examined using an Olympus SZ51 stereomicroscope and photos were taken using an Olympus SP-350 digital camera. Line drawings were prepared on photographs using CorelDraw 16 image-editing software.

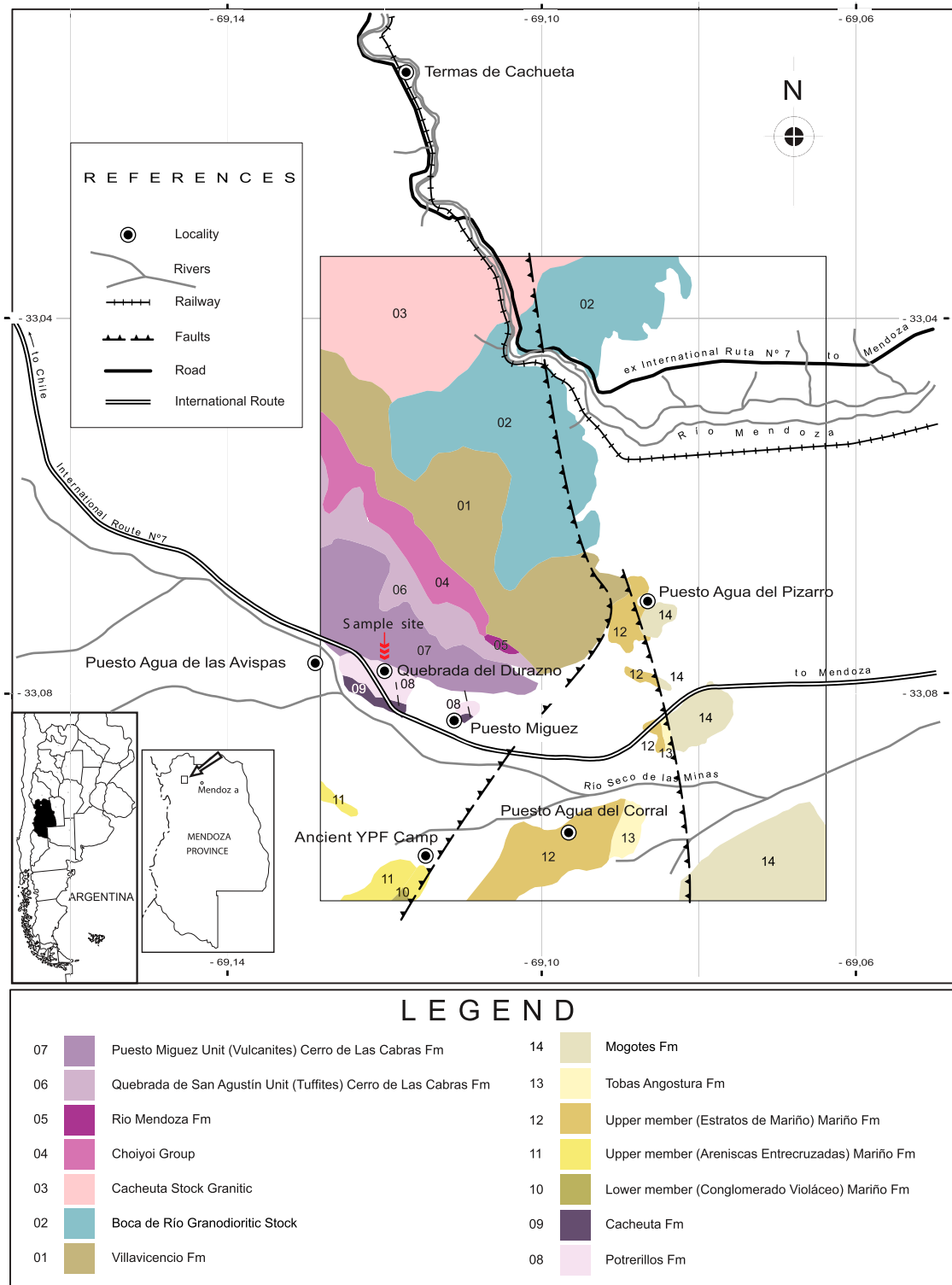


Fig. 1. Geological map of the southern Cerro Cacheuta area showing the fossiliferous locality at Quebrada del Durazno, Cuyana Basin, Mendoza Province, Argentina (modified from Gallego *et al.* 2011).

Systematic palaeontology

Order GRYLLOBLATTIDA Walker, 1914
 Suborder GRYLLOBLATTINA Walker, 1914
 Family GEINITZIIDAE Handlirsch, 1906
 Subfamily GEINITZIINAE Zeuner, 1937

Permoshurabia Aristov, 2009

Type species. *Permoshurabia mesenensis* Aristov, 2009 from the Middle Permian (Biarmanian) of the Mezen district, Arkhangelsk oblast, Russia.

Other included species. *Permoshurabia komi* Aristov, 2015 and *Permoshurabia kungurica* Aristov & Rasnitsyn, 2015 from the Lower Permian of Vorkuta and Tshekarda localities (Russia), respectively.

Orders	Species	Locality	Locality
Orthoptera	<i>Notopamphagopsis bolivari</i>	Quebrada del Durazno, south of the Cerro Cacheuta, Cuyana Basin	Cabrera 1928
	<i>Notopamphagopsis?</i> sp. 1	As above	Martins-Neto <i>et al.</i> 2008
	<i>Elcana?</i> <i>argentina</i>	Puesto Miguez, south of the Cerro Cacheuta, Cuyana Basin	Cockerell (in Wieland 1926)
Hemiptera	<i>Gallegomorphoptila acostai</i>	Quebrada del Durazno, south of the Cerro Cacheuta, Cuyana Basin	Martins-Neto <i>et al.</i> 2003, Martins-Neto & Gallego 2006
	<i>Argentinocicada magna</i>	As above	Martins-Neto & Gallego 1999
	<i>Argentinocicada minima</i>	As above	Martins-Neto & Gallego 1999
	<i>Potrerillia nervosa</i>	As above	Martins-Neto & Gallego 1999
	<i>Cacheutacicada kurtzae</i>	As above	Martins-Neto <i>et al.</i> 2008
	<i>Duraznoscarta ramosa</i>	As above	Lara & Wang 2016
	<i>Argentinoscytina clara</i>	Puesto Miguez, south of the Cerro Cacheuta, Cuyana Basin	Lara & Wang 2016
	Gen. <i>et</i> sp. indet.	As above	Lara & Wang 2016
	<i>Tipulidites affinis</i>	As above	Wieland 1925, 1926, Martins-Neto <i>et al.</i> 2003
Miomoptera	<i>Miomina mendocina</i>	Quebrada del Durazno, south of the Cerro Cacheuta, Cuyana Basin	Martins-Neto & Gallego 1999
Coleoptera	<i>Argentinosyne duraznoensis</i>	As above	Martins-Neto <i>et al.</i> 2008
	<i>Delpuentesyne menendezii</i>	Quebrada del Puente, Cerro Bayo, Cuyana Basin	Martins-Neto <i>et al.</i> 2007
Diptera	<i>Trihennigma zavattierii</i>	Puesto Miguez, south of the Cerro Cacheuta, Cuyana Basin	Lara & Lukashevich 2013
Mecoptera	<i>Argentinopanorpa miguezii</i>	Quebrada del Durazno, south of the Cerro Cacheuta, Cuyana Basin	Lara <i>et al.</i> 2015
	<i>Tipuloidea rhaetica</i>	Puesto Miguez, south of the Cerro Cacheuta, Cuyana Basin	Wieland 1925, Tillyard 1926, Martins-Neto <i>et al.</i> 2003
Blattodea	<i>Potrerilloblattla stipanicici</i>	Quebrada del Puente, Cerro Bayo, Cuyana Basin	Martins-Neto & Gallego 2007
	<i>Delpuenteblattla dangeloi</i>	As above	Martins-Neto & Gallego 2007
	<i>Lariojablatta neiffi</i>	As above	Martins-Neto & Gallego 2007
	<i>Anablatta compacta</i>	As above	Martins-Neto & Gallego 2007
Hymenoptera	<i>Potrerilloxyela menendezii</i>	Puesto Miguez, south of the Cerro Cacheuta, Cuyana Basin	Lara <i>et al.</i> 2014
Plecoptera	<i>Gondwanoperlidium argentinorum</i>	As above	Pinto & Purper 1978
	<i>Gondwanoperlidium mendozensis</i>	As above	Pinto & Purper 1978
	<i>Platyperla marquarti</i>	As above	Gallego <i>et al.</i> 2011
Grylloblattida	<i>Triasseuryptilon acostai</i>	Agua de las Avispas, south of the Cerro Cacheuta, Cuyana Basin	Marquat 1991, Storozhenko 1997
	<i>Permoshurabia argentina</i>	Quebrada del Durazno, south of the Cerro Cacheuta, Cuyana Basin	Lara & Aristov, this paper
Odonata	<i>Triassothemis mendozensis</i>	Agua de las Avispas, south of the Cerro Cacheuta, Cuyana Basin	Carpenter 1960, Nel <i>et al.</i> 2002

Table 2. Triassic insects of the Potrerillos Formation, Cuyana Basin, Mendoza Province (Argentina).

Permoshurabia argentina Lara & Aristov sp. nov. (Figs 2, 3)

2012 Lara *et al.*, fig. 6D.

Etymology. From the nation of origin.

Holotype. IANIGLA-PI 1029a-part and 1029b-counterpart of forewing.

Locality, unit and age. Quebrada del Durazno locality, southern flank of Cerro Cacheuta, southern end of the Precordillera, Cuyo Basin, Mendoza Province, Argentina; upper part of the Potrerillos Formation; early Late Triassic (Camian).

Diagnosis. Middle-sized insects. In forewing, the costal area near RS base is about twice as wide as the subcostal one. SC terminating beyond mid-length of wing, R with only a few branches. RS dichotomous, originating in basal third of wing, and rather distal branching. MA branching in distal third of wing, MP near middle of wing. CuA₁ with at least two branches, possibly three.

Description. Membranous forewing, partially preserved (Figs 2, 3). The anterior margin of the forewing is slightly convex. The costal area near the RS base is about twice as wide as the subcostal area. Sc with 10 veinlets that are both simple and forked, each

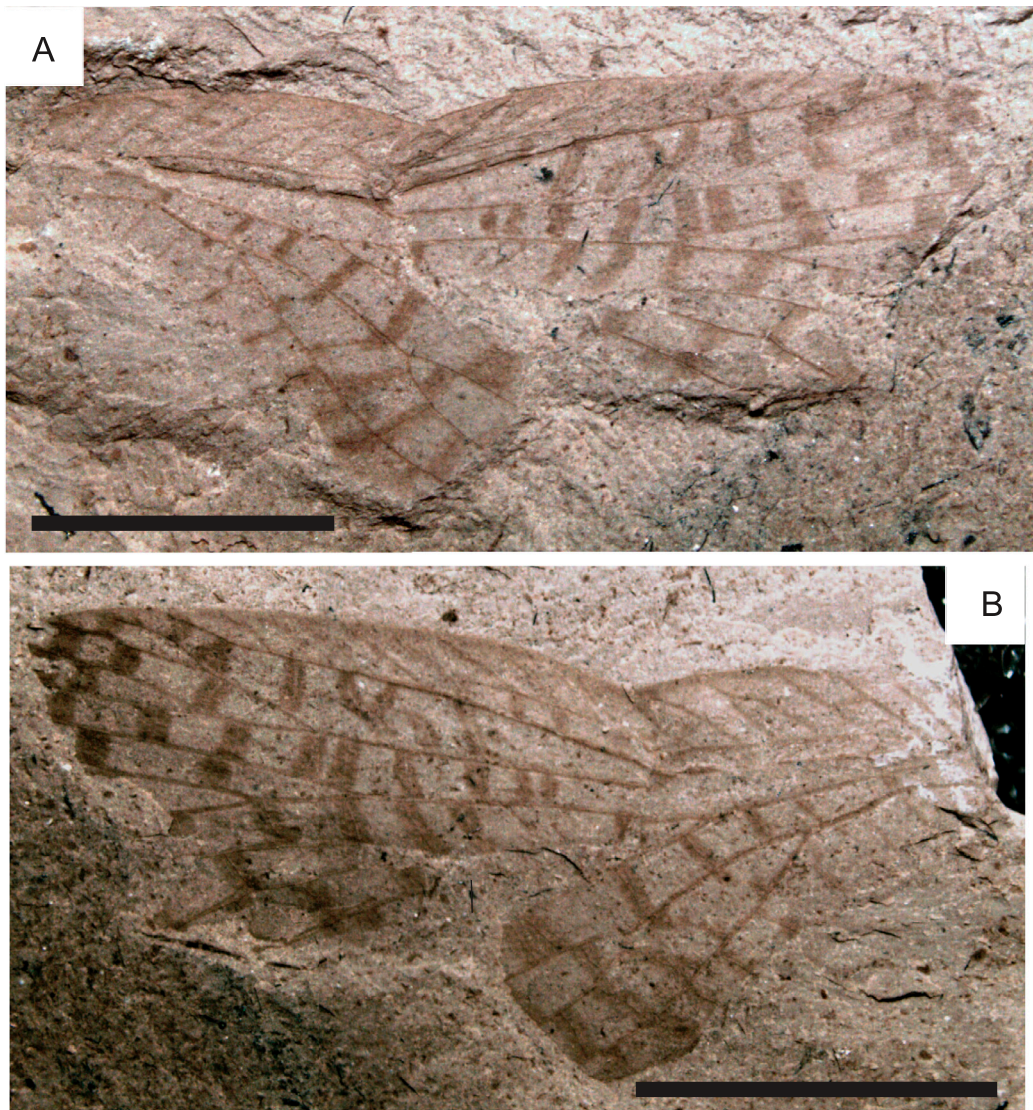


Fig. 2. *Permoshurabia argentina* sp. nov., holotype IANIGLA-PI N° 1029: **A**, photograph of part; **B**, photograph of counterpart. Scale bars = 5 mm.

originating beyond mid-length of wing. R irregularly branching into four forebranches. RS originating before middle of the wing, forking dichotomously, with four branches. M divided into MA and MP branches proximal of the base of RS. MA with three branches and MP with three branches partially preserved. Cu S-like, bent before forking into CuA₁ and CuA₂ proximal to base of the wing. CuA₁ with two branches preserved and its terminal branch ending in the distal quarter of the wing. CuA₂ simple, sinuous and curved. Wide field developed between CuA₁ and CuA₂. Crossveins mainly simple or Y-shaped. Dark coloration pattern consisting of bands along the crossveins. The damage to the forewing is probably a consequence of transport and/or biological activity (post-mortem modifications).

Measurements (in millimetres). Forewing length 15.53, width 6.59, length/width ratio 2.35.

Discussion

Permoshurabia argentina Lara & Aristov sp. nov. is assigned to Geinitziidae based on its short SC and R, RS directed to the anterior margin of the wing, M divided into MA and MP before the RS base, CuA divided into branching CuA₁ and simple CuA₂, and dark bands along the crossveins.

The extinct Geinitziidae Handlirsch, 1906 had a wide geographic and stratigraphic distribution and representatives had a general appearance similar to extant cockroaches. The family includes 10 genera, recorded from the Early Permian to Late Jurassic of Europe, Asia, Australia, South Africa and Argentina (Cui *et al.* 2012). In the Triassic, geinitziids were represented by 14 species belonging to *Shurabia* Martinov, 1937, *Geinitzia* Handlirsch, 1906, *Fletchitzia* Riek, 1976 and *Permoshurabia* Aristov, 2009 (Fig. 4; Aristov *et al.* 2009).

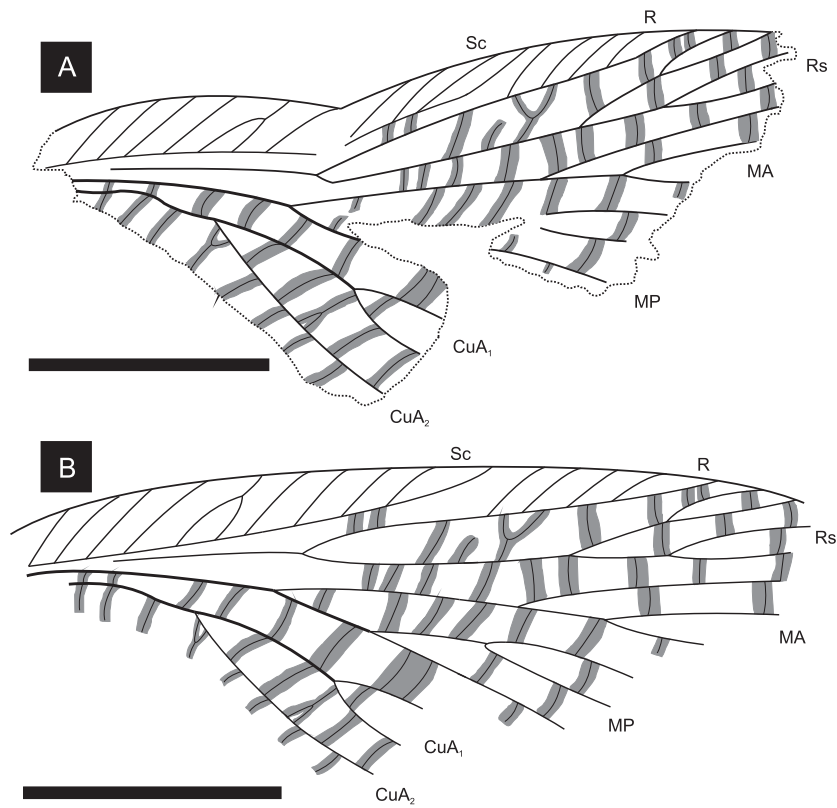


Fig. 3. *Permoshurabia argentina* sp. nov., holotype IANIGLA-PI N° 1029: **A**, line drawing; **B**, reconstruction of forewing. Scale bars = 5 mm.

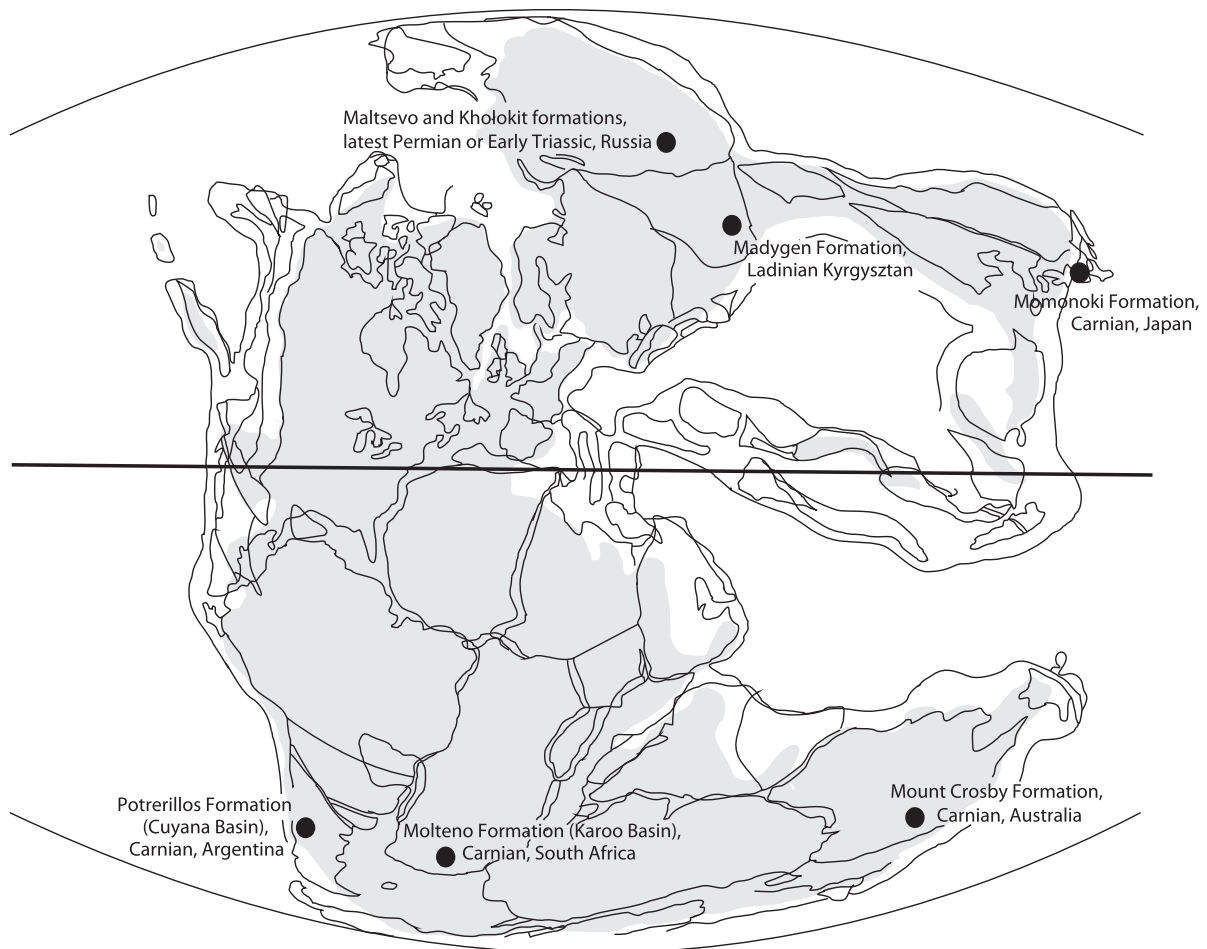


Fig. 4. Distribution map of Geinitziidae during of the Triassic.

The new species can be assigned to *Permoshurabia* Aristov, 2009 based on its dichotomous RS with four branches and CuA₁ with two branches (a unique combination in geinitziids; Aristov 2009, 2015). *Geinitzia aristovi* Cui, Storozhenko & Ren, 2012 and *Shurabia grandis* (Huang & Nel, 2008) from the Jurassic of China have the same RS arrangements but differ by having shorter SC and, hence, more branches between SC and R.

Permoshurabia argentina sp. nov. is closely related to *P. komi* Aristov, 2015 (Ufimian of Komi-Permyak Autonomous District, Russia), in having a short SC (ending before the distal third of the wing), R with four fore branches, and a dichotomizing RS with four branches. The new species differs from *P. komi* as the RS originates in the basal third of the wing and vein M branches distally into MA and MP (near the base of RS). In addition, veins MA and MP each have three or more branches. In *P. komi*, vein RS begins in the basal quarter of the wing, M also divides into MA and MP in the basal quarter of the wing (near the first fork of CuA), and MA and MP have two branches (Aristov 2015).

The new species of geinitziid, *Permoshurabia argentina* sp. nov., occurs in continental sediments of Argentina and represents the first record of an adult specimen grylloblattid from the Triassic of South America. Tentatively placed in *Permoshurabia* Aristov, 2009, it represents the first record globally of this genus in the Triassic, and provides additional evidence for the cosmopolitan distribution of the order during the Triassic and close faunal relationships between Laurasia and Gondwana during the Mesozoic.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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