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The first 'Grylloblattida' of the family Liomopteridae from the Middle Permian in the Onder Karoo, South Africa (Insecta: Polyneoptera)

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KEY WORDS
Insecta,
Polyneoptera,
Middle Permian,
Karoo Supergroup,
Gondwana,
new genus,
new species.

ABSTRACT
Here we describe a new genus and four new species of the extinct 'Grylloblattida': Liomopteridae Sellards, 1909: *Liomopterum connexus* Cawood & Nel, n. sp., *Liomopterum daenerys* Cawood & Nel, n. sp., *Colubrosopterum karooensis* Cawood & Nel, n. gen., n. sp., and *Paraliomopterum* sp. The fossil wings were collected from a new Middle Permian locality near Sutherland, Northern Cape, South Africa, with the horizon close to the Ecca-Beaufort Group contact in the southern Karoo Basin.

MOTS CLÉS
Insecta,
Polyneoptera,
Permien moyen,
'Karoo Supergroup',
Gondwana,
genre nouveau,
espèces nouvelles.

RÉSUMÉ
Les premiers 'Grylloblattida' de la famille Liomopteridae du Permien moyen du Onder Karoo, Afrique du Sud (Insecta: Polyneoptera).
Nous décrivons un nouveau genre et quatre espèces nouvelles de 'Grylloblattida' Liomopteridae Sellards, 1909 : *Liomopterum connexus* Cawood & Nel, n. sp., *Liomopterum daenerys* Cawood & Nel, n. sp., *Colubrosopterum karooensis* Cawood & Nel, n. gen., n. sp., et *Paraliomopterum* sp. Ces fossiles ont été collectés dans un nouveau gisement du Permien moyen près du Sutherland, « Northern Cape », Afrique du Sud, non loin du contact « Ecca-Beaufort » dans le bassin du sud Karoo.

INTRODUCTION

Although the extant order Grylloblattodea Walker, 1914 contains only the extant family Grylloblattidae Walker, 1914 with five genera, its alleged fossil record 'Grylloblattida' comprises at least 50 extinct families of winged insects (Bai *et al.* 2010). The Grylloblattidae is currently considered the sister group of the Mantophasmatodea Zompro, Klass, Kristensen & Adis, 2002 (Wipfler *et al.* 2019). The exact relationships among the extant Grylloblattidae and the late Palaeozoic and Mesozoic taxa currently attributed to the 'Grylloblattida' remain unclear. Originally, Rasnitsyn (1976) grouped the Mesozoic family Blattogryllidae Rasnitsyn, 1976 with Grylloblattidae on the basis of a series of unpolarised and probably plesiomorphic characters (Bai *et al.* 2010). Later, various authors added new extinct families to the set 'Grylloblattida', again without phylogenetic argument. The only phylogenetic analysis of the 'Grylloblattida' (including the fossil taxa) was made without a real outgroup, on the basis of *a priori* polarisations of the characters (Storozhenko 1998). Thus the monophyly of the 'Grylloblattida' (including the fossil taxa) is not demonstrated and the group is not supported by any apomorphy. It could be paraphyletic or even polyphyletic. The removal of some 'grylloblattid' families and their transfer into the clade Paoliida illustrate this hypothesis (Prokop *et al.* 2014). The oldest fossils attributed to the 'Grylloblattida' date back to the late Carboniferous period (Aristov 2009; Wipfler *et al.* 2014). 'Grylloblattida' apparently formed a significant component of the global Permian insect palaeofauna in lowland habitats, as evidenced by the abundance and high diversity of fossilized specimens described in the literature (see Fossilworks database).

At a finer scale, the Middle Permian Gondwanan fossil record of terrestrial organisms is sparse, especially for insects (Schlüter 2003). Upper and lower Permian 'grylloblattidan' specimens are plentiful, but the Middle Permian fossil records of 'Grylloblattida' are limited to Eurasia (Russia and Europe) (Riek 1973; Aristov 2009).

Four families of 'Grylloblattida' have been previously recorded from the Permian of South Africa, all from the upper Permian of South Africa, in the Normandien Formation (formerly the Estcourt Formation; Beaufort Group, Karoo Supergroup) and stratigraphic equivalents in the KwaZulu Natal Province. Seven species of Liomopteridae Sellards, 1909 have been recorded at localities including Mooi River, Mount West, Emakwezini Railway Station, Lidgetton, Kwa Yaya, and Bulwer (Riek 1973, 1976; Aristov *et al.* 2009; Aristov & Mostovski 2013). One species of Megakhosaridae Sharov, 1961 is described from the Mooi River locality (Riek 1976); two species of Skaliciidae Kukalova, 1964 are described from the Lidgetton and Mount West localities (Aristov & Mostovski 2013); and one species of Chaulioditidae Handlirsch, 1906 has been described from the Kwa Yaya locality (Aristov *et al.* 2009).

'Grylloblattidan' wing fossils were recently excavated at a new fossil locality near Sutherland in the Northern Cape, within the uppermost Waterford Formation, Ecca Group, Karoo Supergroup, and are probably of early Wordian Age. These 'grylloblattidan' wings represent the first recorded from the Middle Permian of Gondwana.

MATERIAL AND METHODS

Locality

To date, about 30 wing fragments attributable to the 'Grylloblattida' have been recognised from the Onder Karoo locality near Sutherland. Six specimens with well-preserved venation were selected for study, attributed to three genera, all in the Liomopteridae Sellards, 1909. The Onder Karoo locality is approximately 40 km from Sutherland. Although it is currently mapped within the uppermost Waterford Formation, Ecca Group, it probably lies at the Ecca-Beaufort group contact (M. Day and B. S. Rubidge, ESI, University of the Witwatersrand; pers. comm.).

Geological setting

The deposits at the Onder Karoo site are olive-grey, fine-grained and finely laminated mudrock and siltstone, indicating deposition in a low-energy setting such as a lake. The fossils are all impressions. Considering the regional geological context, including uranium-lead (U-Pb) dates obtained from volcanic ashes in the nearby Ouberg Pass (Lanci *et al.* 2013; Day *et al.* 2022), the fossils are probably Middle Permian (Wordian) in age, dating to approximately 268 Mya.

Processing of material

Standard excavation techniques using geological hammers and chisels were used to excavate the fossils. The material was bulk-collected and large numbers of specimens were collected for ecological studies. The material used for this research

TABLE 1. — Comparison of 11 characters between the type specimen of *Liomopterum connexus* Cawood & Nel, n. sp., *Liomopterum daenerys* Cawood & Nel, n. sp. and genera of Liomopteridae. States in **bold** would exclude *L. connexus* Cawood & Nel, n. sp. from the relevant genus. Abbreviations: **N**, no; **Y**, yes; *, missing on holotype (Fig. 3). Other abbreviations: see Material and methods.

Character	*Liomopterum connexus* Cawood & Nel, n. sp.	*Liomopterum daenerys* Cawood & Nel, n. sp.	*Liomopterum* Sellards, 1909	*Micropermula* Storozhenko, 1992	*Mioloptoides* Riek, 1976	*Semopterum* Carpenter, 1950	*Fumopterum* Kukalova, 1964	*Liomopterella* Sharov, 1961	*Climaconeurites* Sharov, 1961	*Abashevia* Sharov, 1961	*Mongolopermula* Storozhenko, 1992	*Khosara* Martynov, 1937	*Mioloptera* Riek, 1973	*Liomopterites* Sharov, 1961	All other liomopterid genera
RA and RP uniquely shaped	N	N	N	**Y**	–	–	–	–	–	–	–	–	–	–	–
Area between RA and RP broad	Y	Y	Y	–	N	N	–	–	–	–	–	–	–	–	–
RP branching reduced	Y	Y	Y	Y	–	–	**N**	**N**	**N**	Y	Y	Y	Y	Y	**N**
RP and M not anastomosed	Y	Y	Y	–	–	–	–	–	N	–	–	–	–	–	–
MA with only three branches	Y	N	Y	–	–	–	–	–	–	N	–	–	–	–	–
MA simple	N	N	N	–	–	–	–	–	–	–	Y	–	–	–	–
MP forked twice	Y	?*	Y	–	–	–	–	–	–	–	–	N	–	–	–
Cu with long stem	N	N	N	–	–	–	–	–	–	–	–	–	Y	–	–
Area between CuA and CuP broad	Y	Y	Y	–	–	–	–	–	–	–	–	–	N	N	–

is housed in the fossil collections of the Albany Museum, Makhanda, South Africa. Photographs of each specimen were taken using a Nikon D5000 camera mounted onto a Zeiss Discovery V8 microscope. Low-angle lighting was used to highlight surface relief of the impressions, with a polarised filter to reduce glare. Images were photographed at multiple lighting angles to recover as much detail as possible. Photographs were taken at the highest resolution possible and edited with GIMP v2.8. The specimens were identified to genus-level using their wing venation, following the wing venation nomenclature of Carpenter (1950) and Storozhenko (1998).

ABBREVIATIONS

CuA	cubitus anterior;
CuP	cubitus posterior;
M	median;
MA	median anterior;
MP	median posterior;
ScP	subcosta posterior;
RA	radius anterior;
RP	radius posterior.

SYSTEMATIC PALAEONTOLOGY

Class INSECTA Linnaeus, 1758
Order 'GRYLLOBLATTIDA' Walker, 1914

Family LIOMOPTERIDAE Sellards, 1909

DIAGNOSIS (translated from Storozhenko 1998: 136). — Forewing membranous, small to medium sized; ScP terminating in apical third of wing; costal area with numerous transverse veins, with little branching or cell formation; CuA divided into two main branches, CuA_1 weakly curved distally and not parallel to posterior wing margin, with at least two terminal branches, CuA_2 always simple; area between CuA and CuP broad; CuP simple; no anastomosis between M and Cu, and M and RP; apical part of wing acuminate; ScP sclerotised, weakly curved distally; RP with weak branches.

Genus *Liomopterum* Sellards, 1909

Liomopterum connexus Cawood & Nel, n. sp.
(Figs 1; 2)

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DIAGNOSIS. — Forewing venation characters only. RP with reduced number of branches; RP branches distally fused and weak; RP and M without anastomosis; MA with three branches; area between RA and RP broad; Cu with rather short stem; area between CuP and CuA broad.

HOLOTYPE. — AM11016 (an isolated forewing impression, Fig. 1); stored in the fossil collection at the Albany Museum, Makhanda, South Africa.

TYPE LOCALITY AND FORMATION. — Onder Karoo locality near Sutherland, Northern Cape, South Africa; Middle Permian (early Wordian), uppermost Waterford Formation, Ecca Group, Karoo Supergroup.

ETYMOLOGY. — From Latin *connexus* (joined, connected) referring to the distal fusion of RP.

REFERRED MATERIAL. — Two other specimens AM11252 and AM11318 are attributed to the same species because the shared preserved parts are identical to those of the holotype (Fig. 2).

DESCRIPTION

Forewing with only extreme base and apex, and anal areas missing; wing 19.0 mm long, 7.5 mm wide; membranous and bare, apical part not strongly widened; double rows of cells absent; crossveins simple throughout. Anterior margin convex; costal area (between C and ScP) twice as wide as subcostal area, with transverse veinlets and few crossveins between them; ScP sclerotized, terminating at distal third of wing; few crossveins between ScP and R; RA weakly curved with six-seven short anterior branches; origin of RP proximal to basal third of wing; RP with two weak distal branches fused together distally; area between RA and RP broad, with a series of parallel transverse

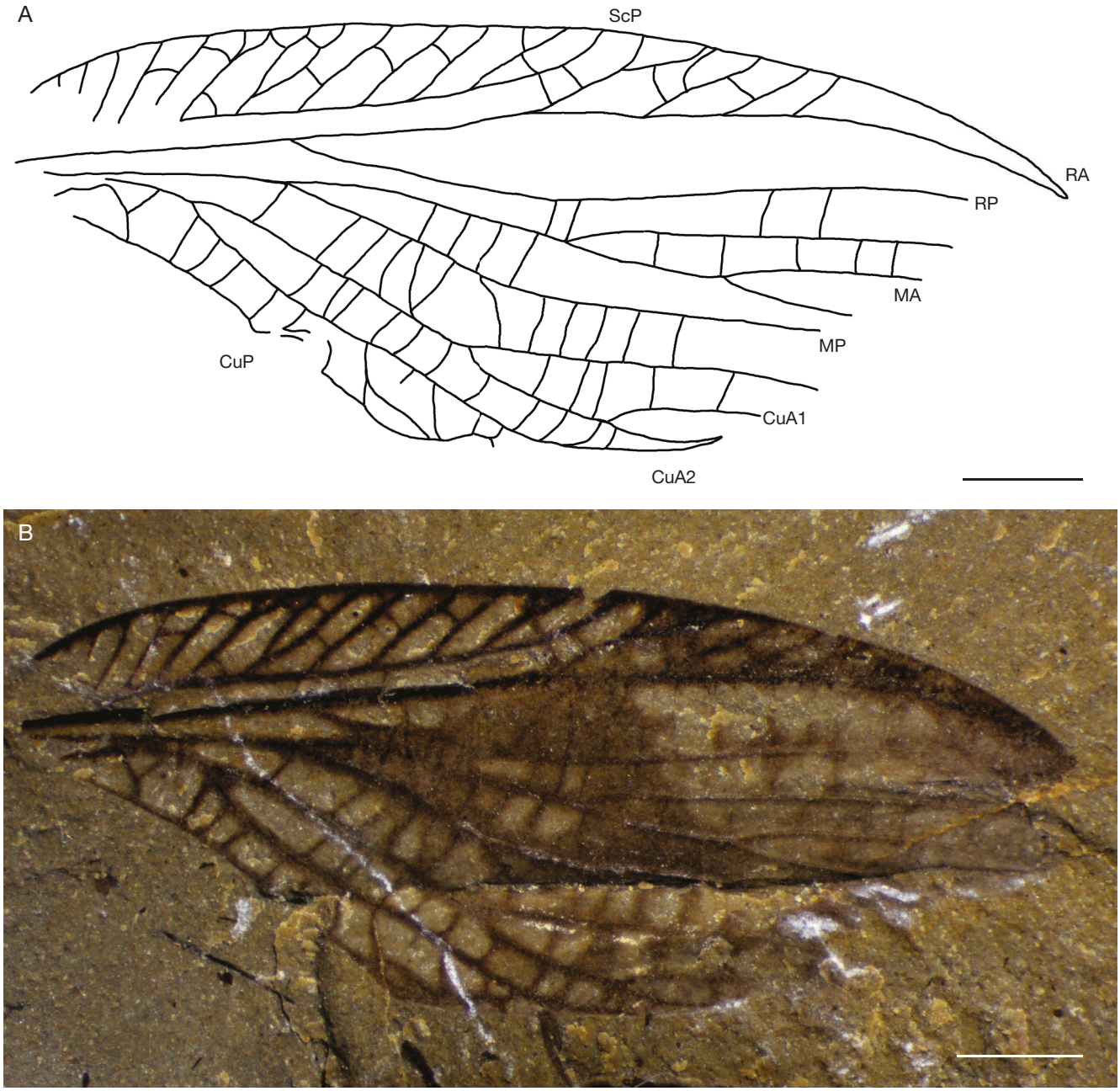

Fig. 1. — *Liomopterum connexus* Cawood & Nel, n. sp., holotype AM11016: **A**, drawing; **B**, photograph. Abbreviations: see Material and methods. Scale bars: 2 mm.

veinlets; R, M and Cu separated during all of their course; RP and M, and M and Cu, without anastomosis; M with two main branches proximal to base of RP; MA with three distal anterior branches; area between M and CuA broad, with a series of parallel transverse veinlets; CuA not parallel to posterior wing margin distally; CuP and CuA separating near wing base, area between them broad with parallel crossveins; CuA divided into CuA_1 and CuA_2 proximal to origins of M and R; CuA_1 with two branches; CuA_2 and CuP simple (Figs 1; 2).

Notes (Table 1)

Liomopterum connexus Cawood & Nel, n. sp. is placed in the Liomopteridae because of its general similarity with the taxa in this family, as no synapomorphy is known to define this group. *Liomopterum connexus* Cawood & Nel, n. sp. has reduced branching of RP, which excludes it from *Climaconeurites* Sharov, 1961, *Fumopterum* Kukalova, 1964, *Liomopterella* Sharov, 1961, and all of the other liomopterid genera except *Abashevia* Sharov, 1961, *Khosara* Martynov, 1937, *Liomopterites* Sharov, 1961, *Liomopterum*, *Micropermula* Storozhenko, 1992, *Mioloptera* Riek, 1973, and *Mongolopermula* Storozhenko, 1992. The absence of anastomosis between RP and M also excludes *Climaconeurites*. *Liomopterum connexus* Cawood & Nel, n. sp. differs from *Liomopterites* in having a broad area between CuP and CuA. *Abashevia* is excluded because of the presence of only three branches of anterior branch of M in

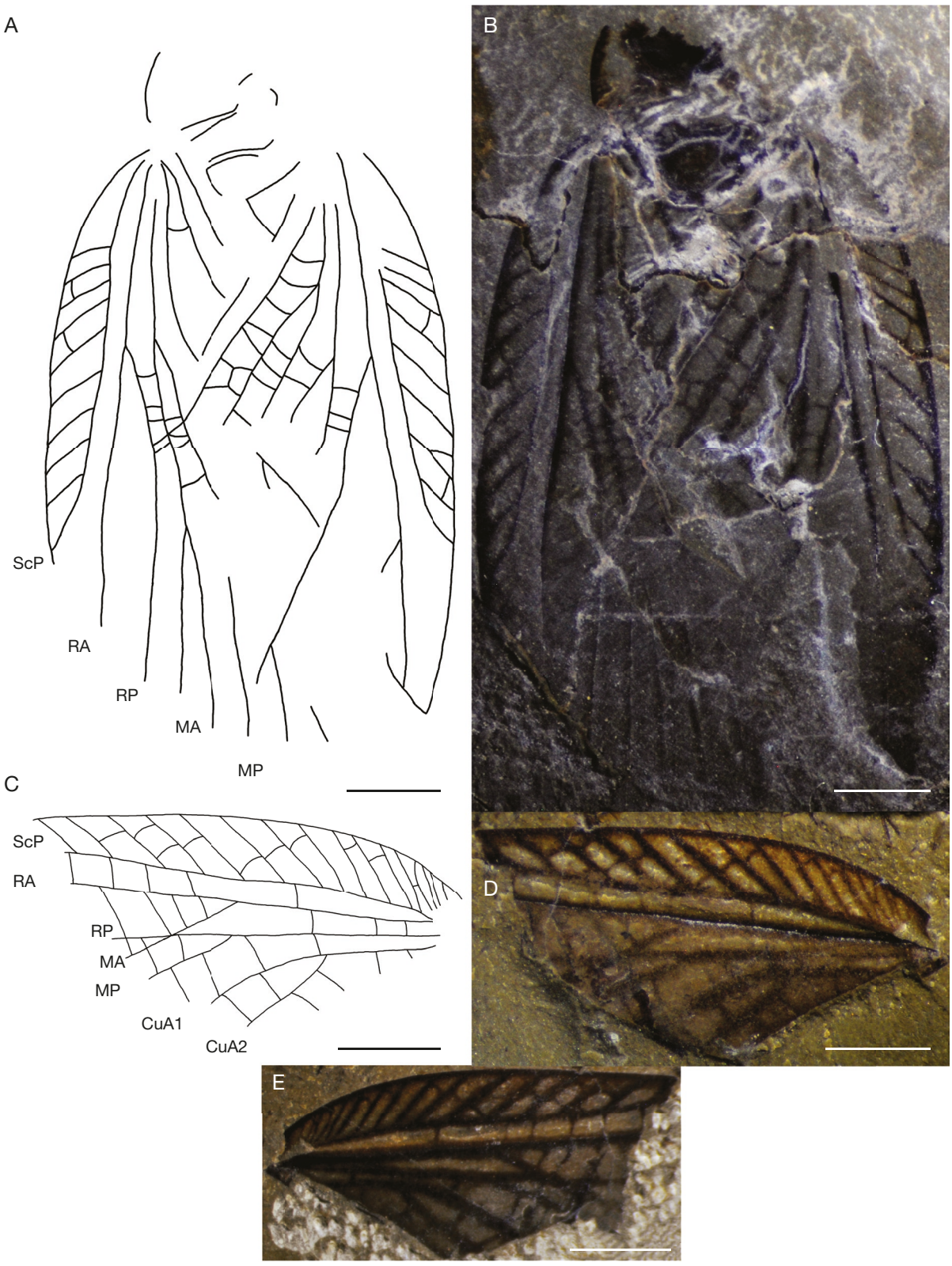

FIG. 2. — *Liomopterum connexus* Cawood & Nel, n. sp., other specimens: **A**, **B**, AM11252, drawing and photograph; **C**-**E**, AM11318, drawing and photographs of imprint and counterimprint. Abbreviations: see Material and methods. Scale bars: 2 mm.

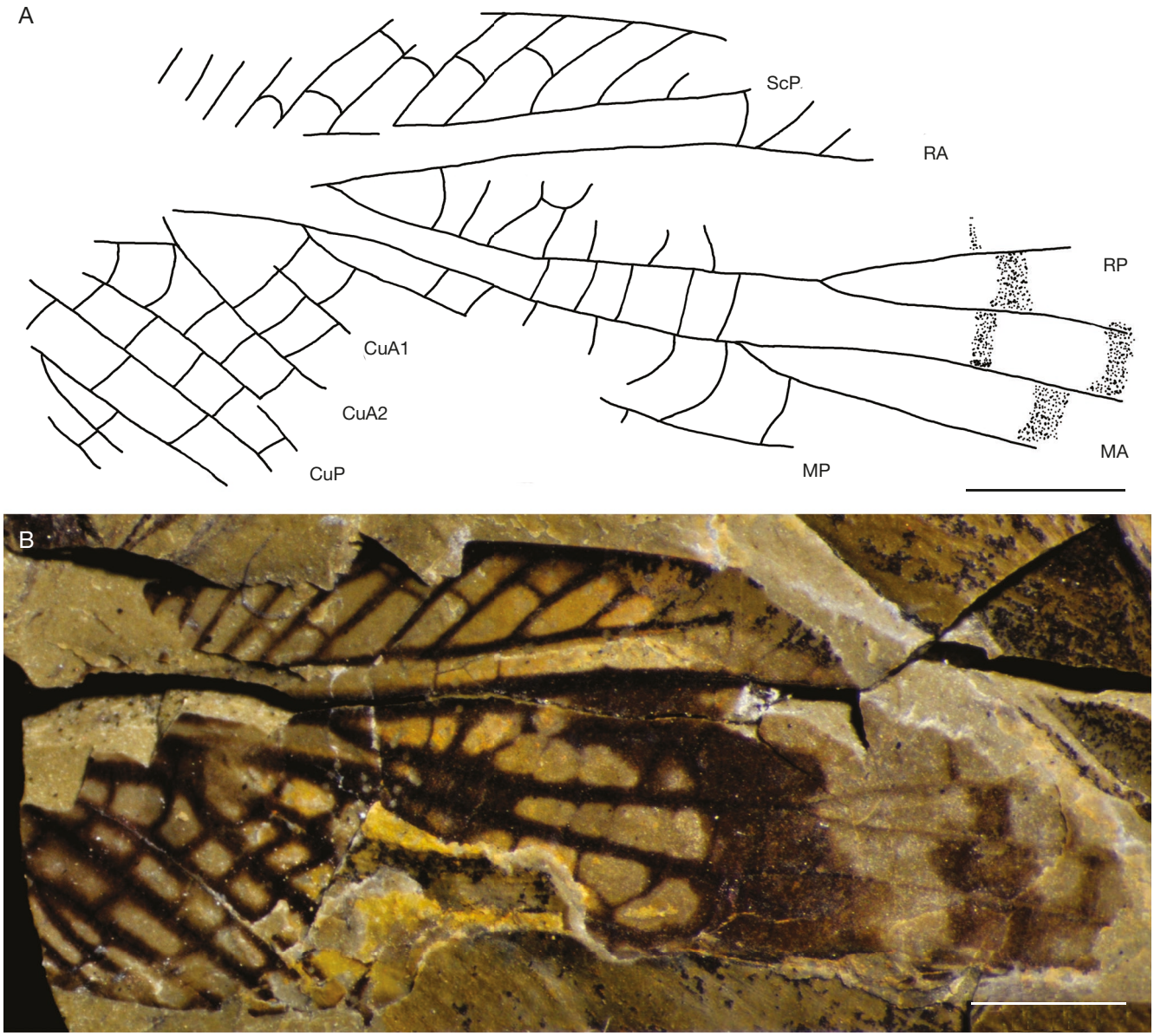

Fig. 3. — *Liomopterum daenerys* Cawood & Nel, n. sp., holotype AM11312: **A**, drawing; **B**, photograph. Abbreviations: see Material and methods. Scale bars: 2 mm.

Liomopterum connexus Cawood & Nel, n. sp.; the broad area between RA and RP excludes affinities with *Semopterum* Carpenter, 1950 and *Mioloptoides* Riek, 1976. *Khosara* is excluded because the anterior branch of M has three branches in *Liomopterum connexus* Cawood & Nel, n. sp. instead of two. Note that Aristov (2020) described a new species, *Khosara ultima* Aristov, 2020, on the basis of an incomplete forewing with only the distal parts of M, RP, and MA. *Mongolopermula* has a simple MA, unlike *Liomopterum connexus* Cawood & Nel, n. sp. *Mioloptera* has a stem of Cu distinctly longer than in *Liomopterum connexus* Cawood & Nel, n. sp. *Micropermula* has a very particular shape of RA and RP and a narrow area between CuP and CuA. The wing venation of *Liomopterum connexus* Cawood & Nel, n. sp. strongly resembles that of the type genus *Liomopterum*. The distally fused weak RP branches differ from the other species of this genus.

Liomopterum daenerys Cawood & Nel, n. sp. (Fig. 3)

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Diagnosis. — Forewing characters only. MP incomplete; area between CuP and CuA broad; origin of CuA_2 rather distal; costal area broad; MA with only one fork; radial and medial areas with a double row of sigmoidal cells; some crossveins S-shaped; median and distal parts of wing with parallel series of dark patches.

Holotype. — AM11312 (forewing impression), stored in the fossil collection at the Albany Museum, Makhanda, South Africa (Fig. 3).

Type locality and stratum. — Onder Karoo locality near Sutherland, Northern Cape, South Africa; Middle Permian (early Wordian), uppermost Waterford Formation, Ecca Group, Karoo Supergroup.

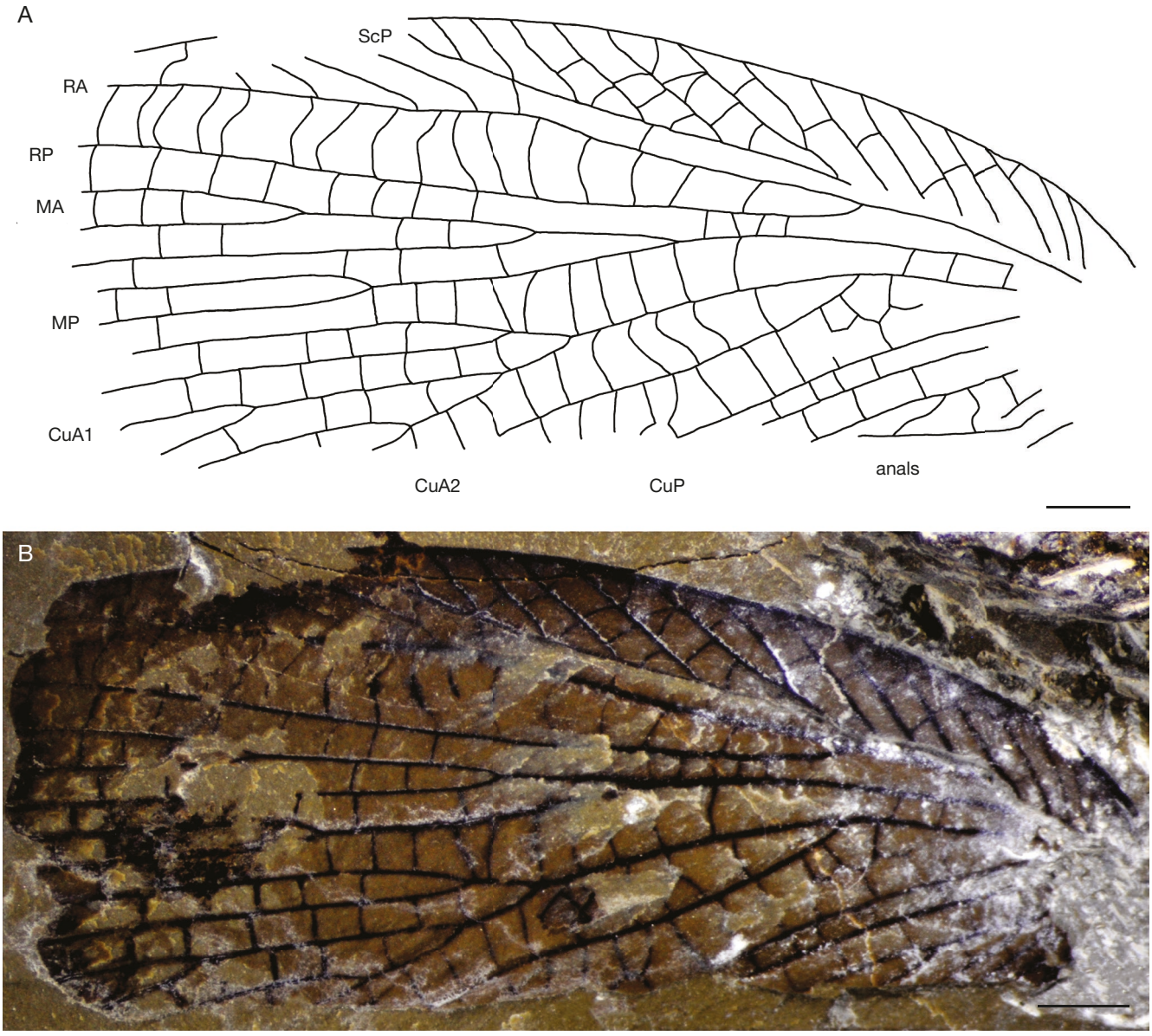

Fig. 4. — *Colubrosopterum karooensis* Cawood & Nel, n. gen., n. sp., holotype AM11389: **A**, drawing; **B**, photograph. Abbreviations: see Material and methods. Scale bars: 2 mm.

Etymology. — From Daenerys Targaryen (*daenerys*), a strong female lead in George R.R. Martin's *Game of Thrones; A Song of Fire and Ice*. The name can be interpreted as 'God is my judge in my destruction' or 'God is my judge of my excellent purpose', a mix of Hebrew and Greek.

Description

A well preserved yet fragmented forewing, with distal part of Cu and apex missing. Preserved part 15 mm long, 6.5 mm wide; costal area with a series of simple transverse veinlets sometimes connected by crossveins, three times as wide as subcostal area; ScP ending at distal third of wing with a weak curve; crossveins present between ScP and R; R straight; area between RA and RP broad, with a double row of cells; RP origin proximal to basal third of wing; RP with two branches; M divided into two branches proximal to origin of RP; MA with two main branches; a double row of cells between MA and MP; area between M and CuA broad, with a series of parallel transverse veinlets; CuA divided into CuA_1 and CuA_2 near its base; CuA_2 simple; CuP simple; area between CuA and CuP broad; coloration preserved as three-four parallel dark patches (Fig. 3).

Notes

Taxonomically important structures of this tegmen are missing, especially the distal parts of RA, MP and CuA_1. Nevertheless, it resembles *Liomopterum* due to the broad area between RA and RP, and RP with only one fork, broad area between CuA and CuP, and origin of CuA_2 rather distal. It differs from *L. connexus* Cawood & Nel, n. sp. due to its broad costal area and MA with only one fork. Crossveins are more numerous in this specimen than in *L. connexus* Cawood & Nel, n. sp., and a double row of cells is present in the radial and medial

TABLE 2. — Comparison of six characters between the type specimen of *Colubrosopterum* n. gen. and genera of Liomopteridae. States in **bold** would exclude *Colubrosopterum karooensis* Cawood & Nel, n. gen., n. sp. from the relevant genus. Abbreviations: **N**, no; **Y**, yes. Other abbreviations: see Material and methods.

Character	*Colubrosopterum* Cawood & Nel, n. gen.	*Paraliomopterum* Sharov, 1961	*Liomopterum* Sellards, 1909	*Micropermula* Storozhenko, 1992	*Mongolopermula* Storozhenko, 1992	*Khosara* Martynov, 1937	*Mioloptera* Riek, 1973	*Abashevia* Sharov, 1961	*Liomopterites* Sharov, 1961
RP simple	Y	**N**	**N**	**N**	**N**	**N**	**N**	**N**	**N**
M forked well after origin of RP	Y	–	N	–	–	–	N	–	–
MA simple	N	–	–	Y	Y	–	–	–	–
CuA_1 with a single fork	N	–	–	–	–	Y	–	–	–
CuA_2 rather distal	Y	–	–	–	–	–	Y	Y	–

areas, with crossveins defining sigmoidal cell shapes. Some crossveins are S-shaped and the presence of a series of parallel, dark patches is a further diagnostic feature.

Colubrosopterum Cawood & Nel, n. gen.

urn:lsid:zoobank.org:act:54391D50-3B52-4951-AEE6-FF5B2785C877

DIAGNOSIS. — Costal area three times as wide as subcostal area, RP weakly curved and simple; fork of M distal to that of the origin of RP; CuA_1 with at least six branches, area between CuA_2 and CuP broad, numerous S-shaped crossveins (Fig. 4).

TYPE SPECIES. — *Colubrosopterum karooensis* Cawood & Nel, n. sp.

ETYMOLOGY. — From Latin *colubrosus* (winding) referring to the S-shaped veins in the wing, and the genus *Liomopterum (-opterum). Pterum* from the Greek *pteron* (*pterov*) for wing. Gender masculine.

Colubrosopterum karooensis Cawood & Nel, n. gen., n. sp. (Fig. 4)

urn:lsid:zoobank.org:act:9ACA81CB-6DE7-4864-A5BA-CE9C54BF0B98

DIAGNOSIS. — As for genus.

HOLOTYPE. — AM11389 (forewing impression), stored in the fossil collection at the Albany Museum, Makhanda, South Africa (Fig. 4).

TYPE LOCALITY AND FORMATION. — Onder Karoo locality near Sutherland, Northern Cape, South Africa; Middle Permian (early Wordian), uppermost Waterford Formation, Ecca Group, Karoo Supergroup.

ETYMOLOGY. — After the type locality Onder Karoo.

DESCRIPTION

A nearly complete forewing with only the apex and part of the anal area missing. Wing 22.0 mm long and 10.5 mm wide; anterior margin of wing convex; costal area with forking transverse veinlets and crossveins linking them, three times as wide as subcostal area; apex of ScP at distal third of wing; few crossveins present between ScP and R; RA weakly curved with several anterior branches; RA branches dichotomising; origin of RP proximal to basal quarter of wing; RP simple; area between RA and RP with S-shaped crossveins; M divided into two main branches, branching distal to base of RP; MA forking slightly more proximally than MP; MA with three branches; MP with two branches; area between M and CuA broad; CuA and CuP separating near wing base; CuA divided into CuA_1 and CuA_2 proximal to mid wing; CuA_1 with at least six branches, approximately parallel to posterior wing margin; area between CuA_1 and CuA_2 with a double row of cells; CuA_2 simple; area between CuA and CuP broad, with a double row of cells; CuP simple; numerous S-shaped crossveins; coloration is represented as spots (Fig. 4)

NOTES (Table 2)

This fossil belongs to a group of genera with RP reduced (i.e., with fewer than three branches and two forks), viz. *Abashevia*, *Micropermula*, *Khosara*, *Mongolopermula*, *Mioloptera*, *Liomopterites*, and *Liomopterum.* It differs from *Liomopterum* in having the fork of M in a distal position, well after the origin of RP. *Micropermula* is based on a hindwing that, unlike our fossil, has a simple MA. The forked MA also excludes *Mongolopermula*. *Khosara* has a CuA_1 with a simple fork, unlike our fossil. *Liomopterites* has a narrower area between CuA_2 and CuP. Our fossil shares with *Mioloptera* and *Abashevia* the rather distal position of CuA_2. It differs from all of them except the upper Permian South African genus *Mioloptera* in the broader area between CuA_2 and CuP. *Colubrosopterum* Cawood & Nel, n. gen. differs from AM11265 (provisionally assigned to *Paraliomopterum* Sharov, 1961) in the simple RP, a character also seen in *Liomopterum connexus* Cawood & Nel, n. sp.. Nevertheless, the first fork of M in our fossil is comparatively in a very distal position, well after the base of RP, and this warrants its allocation to a new genus and species.

Genus *Paraliomopterum* Sharov, 1961

?*Paraliomopterum* sp. (Fig. 5)

TYPE LOCALITY AND FORMATION. — Onder Karoo locality near Sutherland, Northern Cape, South Africa; middle Permian (early Wordian), uppermost Waterford Formation, Ecca Group, Karoo Supergroup.

MATERIAL. — AM11265 (forewing with costal area and wing apex missing), stored in the fossil collection at the Albany Museum, Makhanda, South Africa.

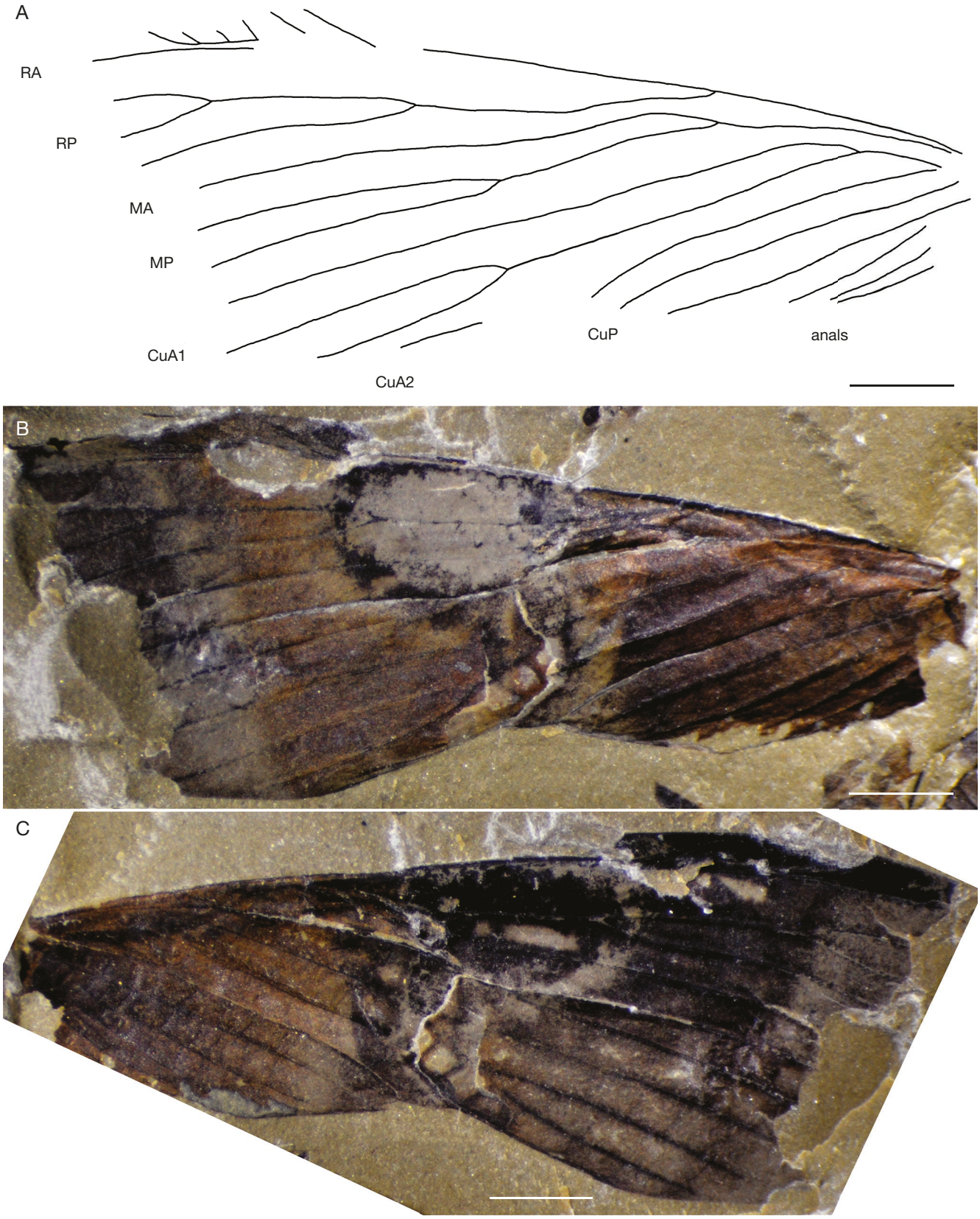

FIG. 5. — *Paraliomopterum* sp., AM11265, forewing: **A**, drawing; **B**, photograph of imprint; **C**, counterimprint of **B**. Abbreviations: see Material and methods. Scale bars: 2 mm.

TABLE 3. — Comparison of characters between specimen AM11265 attributed to ?*Paraliomopterum* sp. and genera of Liomopteridae. States in **bold** would exclude specimen AM11265 from the relevant genus. Abbreviations: **N**, no; **Y**, yes.

Character	*Liomopterum connexus* Cawood & Nel, n. sp.	*Liomopterum daenerys* Cawood & Nel, n. sp.	*Colubrosopterum* Cawood & Nel, n. gen.	specimen AM11265	*Paraliomopterum* Sharov, 1961	*Micropermula* Storozhenko, 1992	*Expartalioma* Aristov, 2004	*Khosara* Martynov, 1937	*Mioloptera* Riek, 1973	*Mongolopermula* Storozhenko, 1992	*Abashevia* Sharov, 1961	*Liomopterites* Sharov, 1961	All other liomopterid genera
RA and RP uniquely shaped	N	N	N	N	N	**Y**	N	N	N	N	N	N	N
RP simple, < three long branches	N	N	**Y**	N	N	N	N	N	N	N	N	N	N
RP branching reduced	**Y**	**Y**	**Y**	N	–	Y	–	**Y**	**Y**	**Y**	**Y**	**Y**	N
M forked well after origin of RP	N	N	**Y**	N	–	–	–	–	N	–	–	–	–
MA simple	**N**	**N**	**N**	Y	Y	Y	**N**	–	–	Y	–	–	–
MP forked twice	Y	Y	Y	Y	**N**	Y	**N**	**N**	Y	Y	Y	Y	–
CuA_1 with a simple fork	N	**Y**	N	N	**Y**	N	N	**Y**	N	N	N	N	–
Area between CuA_2 and CuP not narrow	Y	Y	Y	N	Y	–	N	–	Y	–	N	N	–

DESCRIPTION

Preserved part of wing 16.0 mm long, 9.0 mm wide; RA weakly curved and apparently simple; origin of RP proximal to basal third of wing; RP with three branches; area between RA and RP broad; M divided into two main branches proximal to origin of RP; MA simple; MP with two branches; area between M and CuA broad; CuA and CuP separating close to wing base; area between CuA and CuP narrow; CuA divided into CuA_1 and CuA_2; CuA_1 and CuA_2 branch proximally; CuA_1 with three branches; CuA_2 apparently simple (Fig. 5).

NOTES (Table 3)

AM11265 differs strongly from the taxa described above in the following characters: RP has at least three long branches; CuA_1 has long branches; and the area between CuA and CuP is narrow. It corresponds to a different genus from the other species found at the site. It shows some similarities with the genus *Expartalioma* Aristov, 2004 in the branching of RP and CuA, and the narrow area between CuA and CuP. The main difference is the simple MA in our fossil while it has numerous branches in *Expartalioma*. *Paraliomopterum* could better fit with our fossil for the same characters as above including a simple MA (Storozhenko 1998; Aristov 2004, 2019). The difficulty is that the material currently attributed to *Paraliomopterum* consists of incomplete tegmina (Storozhenko 1998; Aristov 2004, 2019), thus their exact patterns of venation remain partially conjectural. *Paraliomopterum rectum* Aristov, 2004 was revised by Aristov (2019) who attributed to this species wings with three branches of MA and of MP and incomplete wings in which it is not possible to determine the number of branches of main veins. *Paraliomopterum alium* Aristov, 2004 is based on an incomplete wing in which the number of branches of main veins is unknown. *Paraliomopterum paulum* Storozhenko, 1991 is based on a specimen in which MA and MP are simple (but incomplete) (Storozhenko 1991, 1998). *Paraliomopterum karaungirense* Storozhenko, 1991 is based on a hind wing, hardly comparable to the preceding forewings.

We provisionally attribute our fossil to the genus *Paraliomopterum* and not create a new genus, because we prefer to avoid increasing the current taxonomic confusion.

CONCLUSION

We are aware that the assignment of these new species to genera is tentative because the limits and variations in the branching patterns of the main veins remain very poorly investigated among the fossil 'Grylloblattida'. The attribution of a wing to one genus rather than another is mainly a question of personal opinion because of the current lack of phylogenetic analysis of the 'Grylloblattida'. For instance, some genera are separated by authors on the basis of having four branches of CuA vs three, which remains a rather weak character. Nevertheless, with these discoveries, we demonstrate that the Middle Permian diversity of the South African 'Grylloblattida' was significant, with taxa closely related to forms known from the northern part of Pangea. It is not surprising to find many 'grylloblattidan' wing fragments assignable to the family Liomopteridae because it is the largest family within the 'Grylloblattida', consisting of over 45 genera (Storozhenko 1997; Aristov 2004; Fossilworks database site at http://fossilworks.org/bridge.pl). Liomopterids are also the most abundant and diverse 'grylloblattidans' at Permian localities globally (Aristov 2004).

These new taxa confirm that current knowledge of the Permian entomofaunas from the southern part of this supercontinent remains quite poor. Future discoveries in the Middle Permian of South Africa would add valuable knowledge to the entomofaunas of this period. Despite the incompleteness of these wings, the exquisite preservation of the structures and colour patterns show that the outcrop is very promising for this endeavour.

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