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ABSTRACT

The neuropteran *Moltenopsychops magnus* n. gen., n. sp. (Osmylopsychopidae Martynova, 1949) is described from the Late Triassic of the Molteno Formation (South Africa) based on an incomplete forewing. The new taxon bears strong resemblance to *Petropsychops* Riek, 1956, from the Upper Triassic of Australia, in having a peculiar configuration of the median vein (M) in relation to the first branch of the radial sector (Rs1), forming together a single, anteriorly pectinate unit. The tribe Petropsychopsini n. tr. is newly erected to encompass the two genera. *Moltenopsychops magnus* n. gen., n. sp. is the first species of Triassic Neuroptera to be reported from the African continent. The finding further highlights the similarity between South African and Australian Triassic insect faunas and, more generally, complements our knowledge of the diversity of Gondwanan Neuroptera in the Mesozoic.

KEY WORDS
Osmylopsychopidae,
fossil insect,
South Africa,
new tribe,
new genus,
new species.

RÉSUMÉ

Une espèce nouvelle d'Osmylopsychopidae (Neuroptera, Insecta) de la Formation de Molteno souligne les liens entre les sites du Trias du Gondwana méridional.

Le neuroptère *Moltenopsychops magnus* n. gen., n. sp. (Osmylopsychopidae Martynova, 1949) est décrit du Trias supérieur de la Formation de Molteno (Afrique du Sud) sur la base d'une aile antérieure incomplète. Ce nouveau taxon présente une forte ressemblance avec *Petropsychops* Riek, 1956, du Trias supérieur d'Australie, par une configuration particulière de la nervure médiane (M) par rapport à la première branche du secteur radial (Rs1), formant ensemble une seule unité antérieurement pectinée. La tribu Petropsychopsini n. tr. est nouvellement constituée pour englober les deux genres. *Moltenopsychops magnus* n. gen., n. sp. est la première espèce de neuroptère triasique signalée sur le continent africain. Cette découverte souligne la similitude entre les faunes d'insectes triasiques sud-africaines et australiennes et, plus généralement, complète nos connaissances sur la diversité des neuroptères gondwaniens au Mésozoïque.

MOTS CLÉS
Osmylopsychopidae,
insecte fossile,
Afrique du Sud,
tribu nouvelle,
genre nouveau,
espèce nouvelle.

INTRODUCTION

The order Neuroptera Linnaeus, 1758 is one of the earliest lineages of holometabolous insects, with the earliest remains dating back from the Early Permian (Ponomarenko 2002) and is estimated to have been already present during the Carboniferous (Vasilikopoulos *et al.* 2020). During the Permian period, the group was not insignificant in number. For example, it makes up to 5.9% of all fossil insects collected at the Upper Permian Isady locality (European Russia), ranking fifth among insect orders (Aristov *et al.* 2013). However, the diversity of Permian Neuroptera at the family level was low. The 62 species and 25 genera described so far for the Permian all belong to the single family Permithonidae Tillyard, 1922 (Prokop *et al.* 2015), except for *Archeosmylus pectinatus* Riek, 1953 from the Upper Permian of Australia ,which belongs to the Archeosmylidae Riek, 1953.

Diversification at the family level increased during the Triassic period, when some of the recent families of Neuroptera appeared, such as Psychopsidae Handlirsch, 1906 and Berothidae Handlirsch, 1906 (Khramov 2023; Lambkin 2014), as well as the first representatives of recent neuropteran super-families Osmyloidea Leach, 1830 and Ithonoidea Newman, 1853 (Khramov *et al.* 2024). The Triassic was also the time when some typical Mesozoic families appeared, such as the Osmylopsychopidae Martynova, 1949 (Lambkin 2014), one of the most diverse and abundant groups of extinct Neuroptera. At the same time, families of Permian origin, the Permithonidae and Archeosmylidae, co-existed with these new lineages (Khramov 2024; Montagna *et al.* 2024) and subsequently went extinct by the Jurassic. In sum, the Triassic marked a transition from comparatively uniform Permian faunas to more diverse Mesozoic and Cenozoic assemblages.

To gain a more detailed picture of this transitional stage, it is crucial to broaden the geographical scope of the Triassic record of the order. So far, Triassic Neuroptera have only been recorded from two continents, Australia and Eurasia. The richest and most abundant (but still understudied) assemblage of Triassic Neuroptera comes from the Madygen locality (Kyrgyzstan, Central Asia; Khramov 2023, 2024). Two other important sources of Triassic Neuroptera are various localities in Queensland (Australia; Lambkin 1988, 1992, 2014, 2024; Riek 1955, 1956; Tillyard 1917, 1919, 1922, 1923) and the Ominé locality (Momonoki Formation ; Khramov *et al.* 2024). Isolate findings of Triassic Neuroptera have been reported also from France, China and Switzerland (Ellenberger *et al.* 1952, Hong 1980, Montagna *et al.* 2024). In the present paper, we add to this list a new Triassic Neuroptera site in South Africa, namely the Molteno Formation. This unit is the lowest part of the Upper Triassic-Lower Jurassic Stormberg Group, which covers portions of the Eastern Cape Province of South Africa in the Karoo basin (Chima *et al.* 2018). The Molteno Formation, up to 600 m thick, extends over an area roughly 400 km north to south and 200 km west to east. Fossils from the Molteno Formation, primarily consisting of plants and insects, have been collected from 69 sites scattered across the region (Anderson *et al.* 1998). The Molteno Formation was deposited in braided river channels and consists of different types of sediments, including conglomerates, sandstones, siltstones, mudstones as well as coal seams (Anderson *et al.* 1998; Chima *et al.* 2018). It yielded more than 2000 fossil insects, which are most abundant in laminated shales deposited in the floodplain lakes (Anderson *et al.* 1998). Among them, only three belong to the Neuroptera, one of them being the focus of the current account.

MATERIAL AND METHODS

The fossil specimen PRE/F/21985 newly described herein (Fig. 1) was collected from the lacustrine deposits at Aasvöelberg (Aas) 411 site, located in the north-central part of Eastern Cape Province, 50 km southwest of the town of Molteno (South Africa), and belonging to the Molteno Formation. It is estimated to be Carnian in age based on plant macrofossils (Anderson *et al.* 1998; Anderson & Anderson 2023). The fossiliferous horizon at Aas 411 is two-meter thick, consisting of highly baked yellowish-grey rhythmically bedded and thinly laminated shales (Labandeira *et al.* 2018; Scott *et al.* 2004). Fossil insects are diverse at Aas 411, numerically dominated by Coleoptera Linnaeus, 1758 and Blattodea Latreille, 1810 (Labandeira *et al.* 2018; Scott *et al.* 2004). The specimen is housed at the Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg (South Africa).

Photographs of this specimen were taken using a Canon EOS 5D Mark III equipped either with a 50 mm (general view; Fig. 1A) or a MP-E 65 mm (details; Fig. 1C) macro lens (all Canon, Tokyo, Japan). Obtained photographs were optimized using Adobe Photoshop CS6 (Adobe Systems, San Jose, CA, USA). Additionally, a draft drawing was prepared with the aid of a Zeiss SteREO Discovery V8 Stereomicroscope equipped with a pair of W-PL 10x/23 eye pieces, a Plan Apo S 1.0x FWD objective, and a drawing tube (Jena, Germany). A vector drawing (Fig. 1B) was produced using Adobe illustrator CS6 (Adobe Systems, San Jose, CA, USA) based on a working document composed of a scan of the draft drawing and multiple photographs as original data layers.

To conduct our comparative analysis, we also relied on four new photographs of the holotype of *Petropsychops superbus* Riek, 1956 [of both positive and negative imprints; housed at the Geosciences Collection, Queensland Museum, Brisbane (Australia); specimen number UQ C2135-6; Fig. 2A] made on request by G. Thompson (Queensland Museum) using a Canon 5DS equipped with a MP-E 65 mm macro lens. Each photograph was the outcome of the stacking of 11 source images (produced with the Zerene Stacker software) and further edited with Adobe Photoshop and Topaz AI Sharpening. The apical fragment of the specimen was re-adjusted digitally. A vector drawing was produced as specified above, based on a working document composed of the 4 new photographs and a scan of the drawing of the specimen by Lambkin (2014: fig. 9) as data layers.

Venation terminology and abbreviations follow Peng *et al.* (2016; and see reference therein for alternative homologies and terminology), as follows.

Abbreviations

AA	anterior analis;
CuA	anterior cubitus;
CuP	posterior cubitus;
M	media;
R1	first branch of the radius;
Rs	sector of the radius;
Rs1	first posterior branch of Rs;
Sc	subcosta.

SYSTEMATIC PALEONTOLOGY

Class INSECTA Linnaeus, 1758
Order NEUROPTERA Linnaeus, 1758
Family Osmylopsychopidae Martynova, 1949
Subfamily uncertain

Petropsychopsini n. tr.

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Type genus. — *Petropsychops* Riek, 1956, by present designation.

Composition. — Type genus and *Moltenopsychops* n. gen.

Diagnosis. — Rs1, rs_1-m (if present) and M forming an anteriorly pectinate unit; M richly branched; most of proximal branches of Rs deeply forked.

Remarks

Both genera assigned to the proposed new tribe share a unique configuration of Rs1 and M, not observed among other Neuroptera, including the Osmylopsychopidae. While M (MP under alternative homologies) has two main stems, is not particularly branched, and is completely independent from the Rs in typical members of this family (Khramov & Makarkin 2015; Peng *et al.* 2016), this vein, in the Petropsychopsini n. tr., is multi-branched and forms, together with the rs_1-m cross-vein and the posterior-most branch of Rs (Rs1), a single anteriorly pectinate unit. The posterior-most main branch of Rs1 is connected via a short cross-vein (rs_1-m) with M (or, possibly, is briefly fused with it; see below) before the first medial bifurcation, and Rs1 and M are both anteriorly pectinate. As a consequence, Rs1, rs_1-m (if present) and M form a single, consistently anteriorly pectinate 'unit' (thereafter referred to as the 'Rs1/rs_1-m/M unit'). In the case of *Moltenopsychops* n. gen., the rs_1-m cross-vein is very short, giving an impression of a near complete fusion of Rs1 and M.

The unusual configuration of M and the posterior-most branch of Rs was noted by Lambkin (2014) in *Petropsychops*, who regarded it as an autapomorphy of this genus. The discovery of another genus sharing this trait justifies the erection of a taxon of higher rank. Given that the systematics of Osmylopsychopidae has not yet been developed, the appropriate rank of the new taxon comprising both genera is not entirely clear. We tentatively treat it as a tribe. Although the tribal rank is seldom applied in palaeoentomology, it appears to constitute a practical compromise, in view of both the limited number of included taxa and our incomplete knowledge of the relationships among Osmylopsychopidae genera. Future research may demonstrate the need to elevate it to subfamily rank.

It must finally be noticed that the two genera also share a richly branched M, a trait acquired independently in several groups of broad-winged Neuroptera, such as Kalligrammatidae Handlirsch, 1906 (Yang *et al.* 2011: fig.5; Yang *et al.* 2014) and some Psychopsidae, e.g. *Gigantopsychops* Peng, Makarkin & Ren, 2015, from the Middle Jurassic of China, and the extant Australian *Megapsychops* Tillyard, 1919 (Peng *et al.* 2016; New 1988). Fore- and hindwings of some Mesozoic Kempyninae Carpenter, 1943 (1913) (Osmylidae Leach, 1815), more elongate than kalligrammatid and psychopsoid wings, but also with dense venation, likewise demonstrate the multiplication of branches of M (Khramov *et al.* 2019). However, M does not form an association with Rs1 in these lacewings. The Rs1/rs-m/M anteriorly pectinate unit present in *Moltenopsychops* n. gen. and *Petropsychops* resulted in a pattern looking like a "mirrored" Rs (excluding Rs1) and probably served to enhance the wing mechanical properties.

Genus *Moltenopsychops* n. gen.

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Type species. — *Moltenopsychops magnus* n. gen., n. sp.; monotypic genus.

ETYMOLOGY. — From the name of the geological formation it was yielded from, and *-psychops*, a traditional ending of psychopsoid generic names; gender masculine.

DIAGNOSIS. — Area between anterior wing margin and Sc very broad, tapering gradually; multiple cross-veins present between Sc veinlets; area between Sc and RA not particularly broad; Rs1 with 2 main forks before its posterior-most branch connects with M (via the rs_1-m cross-vein); rs1-m cross-vein very short; occurrence of multiple, well-organized gradate series of cross-veins, especially in the wing distal half.

REMARKS

Moltenopsychops n. gen. can be assigned to the psychopsoid family Osmylopsychopidae based on dense venation, forked Sc veinlets and multi-branched Rs1. Within this group, the new genus shares with the monotypic genus *Petropsychops* Riek, 1956, from the Upper Triassic of Denmark Hill and Mount Crosby (Australia; Fig. 2; and see original description, Jell [2004], and Lambkin [2014]), the very distinctive 'Rs1/rs_1-m/M anteriorly pectinate unit' (see diagnosis of the proposed new tribe).

Moltenopsychops n. gen. can be distinguished from *Petropsychops* by a much broader area between the anterior wing margin and Sc (in particular in the basal quarter of the wing). Because hindwings commonly have a costal area narrower than that of the forewing in Neuroptera, it may have been conceived that the holotype of *Petropsychops* (Fig. 2), preserving this area, may be a hindwing. However, CuA is clearly convex in the corresponding wing (Lambkin 2014), while it is expected to be concave in a neuropteran hindwing (Makarkin *et al.* 2009; and see Shi *et al.* 2012). Therefore, the holotype of *Petropsychops* is likely a forewing, and this trait appears adequate to distinguish the two genera. In addition, the Sc-R1 area is comparatively wider in *Petropsychops*. Also, in *Moltenopsychops* n. gen., Rs1 has 2 main forks before its posterior-most branch connects with M, while *Petropsychops* displays 3 such main forks (Fig. 2C; and possibly one more, if one considers that its posterior-most branch is briefly fused with M, see Fig. 2D and below), despite a smaller size. *Moltenopsychops* n. gen. displays long gradate series of cross-veins in the radial and medial areas. In contrast, cross-veins in *Petropsychops* are distributed more irregularly, and may form, at best, loose gradate series in the distal half (Lambkin 2014; Fig. 2). Altogether, the erection of a new genus is well supported.

The length of the rs_1-m cross-vein, as identified herein (green arrows on Figs 1C, 2C), significantly differs in the two genera. It must be acknowledged, however, that it cannot be definitely ruled out that, in *Petropsychops*, the presumed rs_1-m cross-vein is actually a part of the posterior-most branch of Rs1, which would then be briefly fused with M (Fig. 2D). If so, the two genera would nonetheless differ in how M and Rs1 connected, via a short rs_1-m cross-vein in *Moltenopsychops* n. gen. (Fig. 1C) or through a brief fusion of the posterior-most branch of Rs1 with M in *Petropsychops* (Fig. 2D). For the paucity of available material, the variability of this trait remains difficult to appreciate. Also, in the preserved parts of the antero-distal, apical and posterior areas in the vicinity of wing margin, *Petropsychops* displays, between branches of the main veins, longitudinal bulges of the membrane (not represented on Fig. 2B), not uncommon among extant and fossil large-sized Neuroptera (AK and OB, pers. obs. 2025). Such structures are not present in what is preserved of the forewing of the type-species of *Moltenopsychops* n. gen., but it is because the corresponding areas are entirely missing in the available material.

Moltenopsychops magnus n. gen., n. sp.
(Fig. 1)

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TYPE MATERIAL. — **Holotype**. **South Africa** • 1 right forewing; Eastern Cape Province; Stormberg Group, Molteno Formation, Aasvoëlberg 411 site; Late Triassic, Carnian; PRE/F/21985 (University of the Witwatersrand, Evolutionary Studies Institute; positive ('a') and negative ('b') imprints; Fig. 1).

ETYMOLOGY. — From '*magnus*', 'large' or 'great' in Latin, referring to the size of the species.

TYPE LOCALITY AND STRATIGRAPHY. — Aasvoëlberg 411 site, Molteno Formation; Carnian, Late Triassic (Anderson *et al.* 1998; Anderson & Anderson 2023).

ETYMOLOGY. — By monotypy, as for the genus.

DESCRIPTION

Forewing

Length as preserved 34 mm, estimated complete length about 50-55 mm, width as preserved 28 mm; area between anterior wing margin and Sc very broad (as preserved, 6.5 mm at its broadest); with few exceptions, Sc veinlets terminally forked, some deeply divided; in the area between anterior wing margin and Sc, cross-veins more numerous in proximal part, with some veinlets connected by 2-5 cross-veins, some arranged in short, gradate series of 5-7 elements; no obvious cross-vein preserved in the Sc-R1 area; in the R1-Rs area, first cross-veins very oblique; Rs (excluding Rs1) posteriorly pectinate, with at least 13 main branches; Rs1 anteriorly pectinate, with three main branches, with the 2nd branch bifurcated close to its base and extensively branched, and the 1st and 3rd ones bifurcated more distally, almost at the same level; stem of M long and stout before its connection with the rs_1-m cross-vein (indicated by a green arrow on Fig. 1B,C), which is very short; M anteriorly pectinate, with at least 12 main anterior branches (in addition to its main stem), some of them secondarily branched, but not close to their base (except for the 6th branch and, slightly more distally, for the 5th branch); branches of Rs1 and M similarly bent downward and forming a consistently anteriorly pectinate unit occupying a narrow, triangle-shaped area; at least 8 long gradate series of cross-veins present, in the radial and median areas, mostly parallel to each other, except for the 4th and 5th series, converged at the level of the 2nd branch of Rs; distinction between CuA and CuP branches hampered by incomplete preservation of the corresponding area; anal veins not preserved.

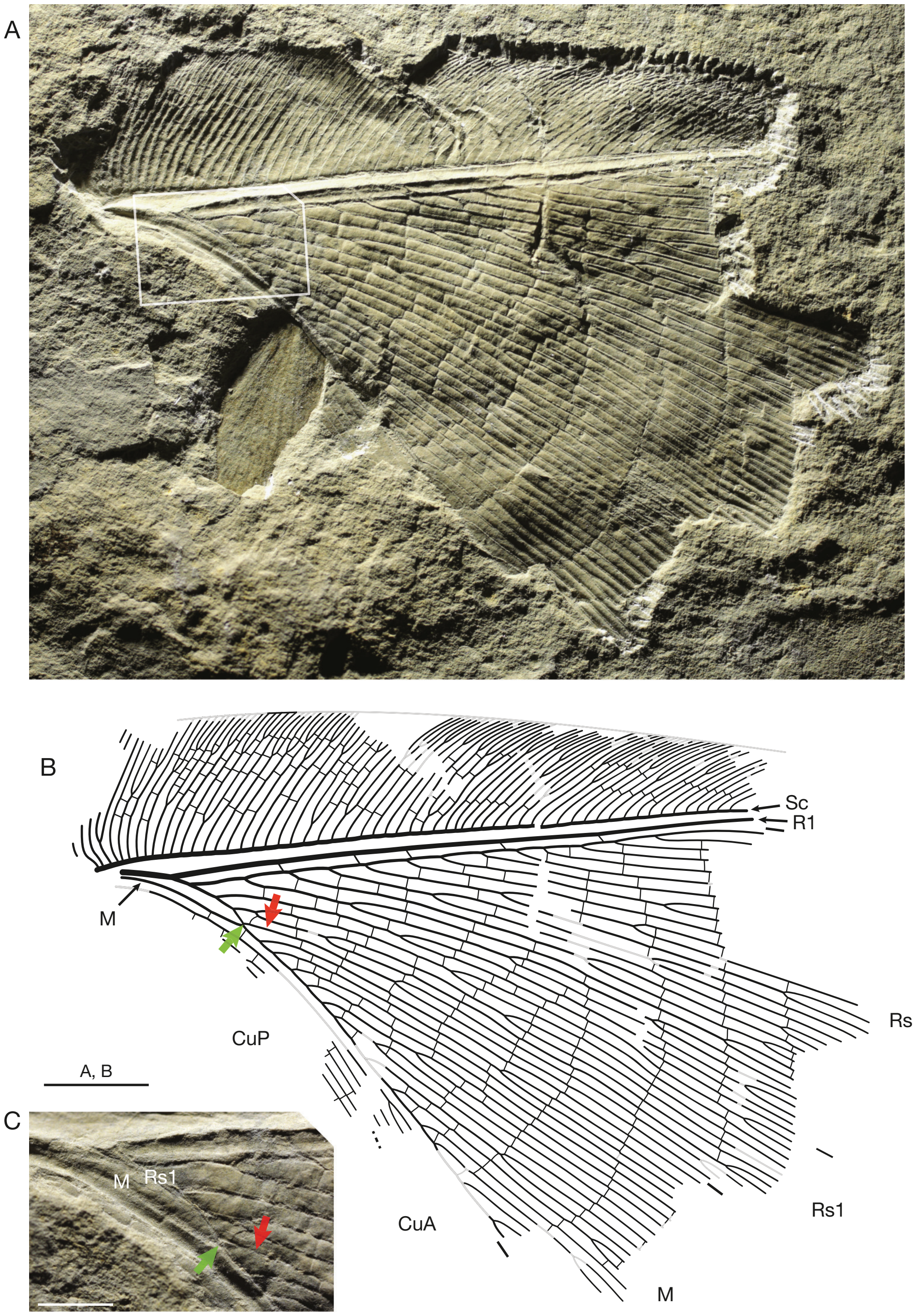

FIG. 1. — *Moltenopsychops magnus* n. gen., n. sp. (Osmylopsychopidae), holotype PRE/F/21985, right forewing (Molteno Formation; Upper Triassic; South Africa): **A**, **B**, overview; **A**, photograph (positive imprint); **B**, interpretative drawing (green arrow, rs_1-m cross-vein; red arrow, Rs1 posterior-most branch); **C**, detail of the rs_1-m cross-vein and surrounding structures, photograph (positive imprint; location as shown on **A**; large arrows, as in **B**). Scale bars: A, B, 5 mm; C, 2 mm. Photographs and drawing: O. Béthoux.

DISCUSSION

As already noted by Riek (1974) and further exemplified recently (Béthoux & Anderson 2021, 2023, Tierney *et al.* 2020), the insect fauna from the Molteno Formation (South Africa), of Carnian age (Anderson & Anderson 2023), stands in close relationship to those from Australian localities from Denmark Hill and Mount Crosby (Australia), of Norian age (Raven *et al.* 2015), but also from that from the Anisian Gayndah Formation (Lambkin 2024), although the latter is less well-sampled. Similarity between these assemblages is not unexpected, as they were located in southern Gondwana, at a similar latitudinal range, within the same floristic sub-province (Anderson & Anderson 1993, Kustatscher *et al.* 2018; among others). *Moltenopsychops*

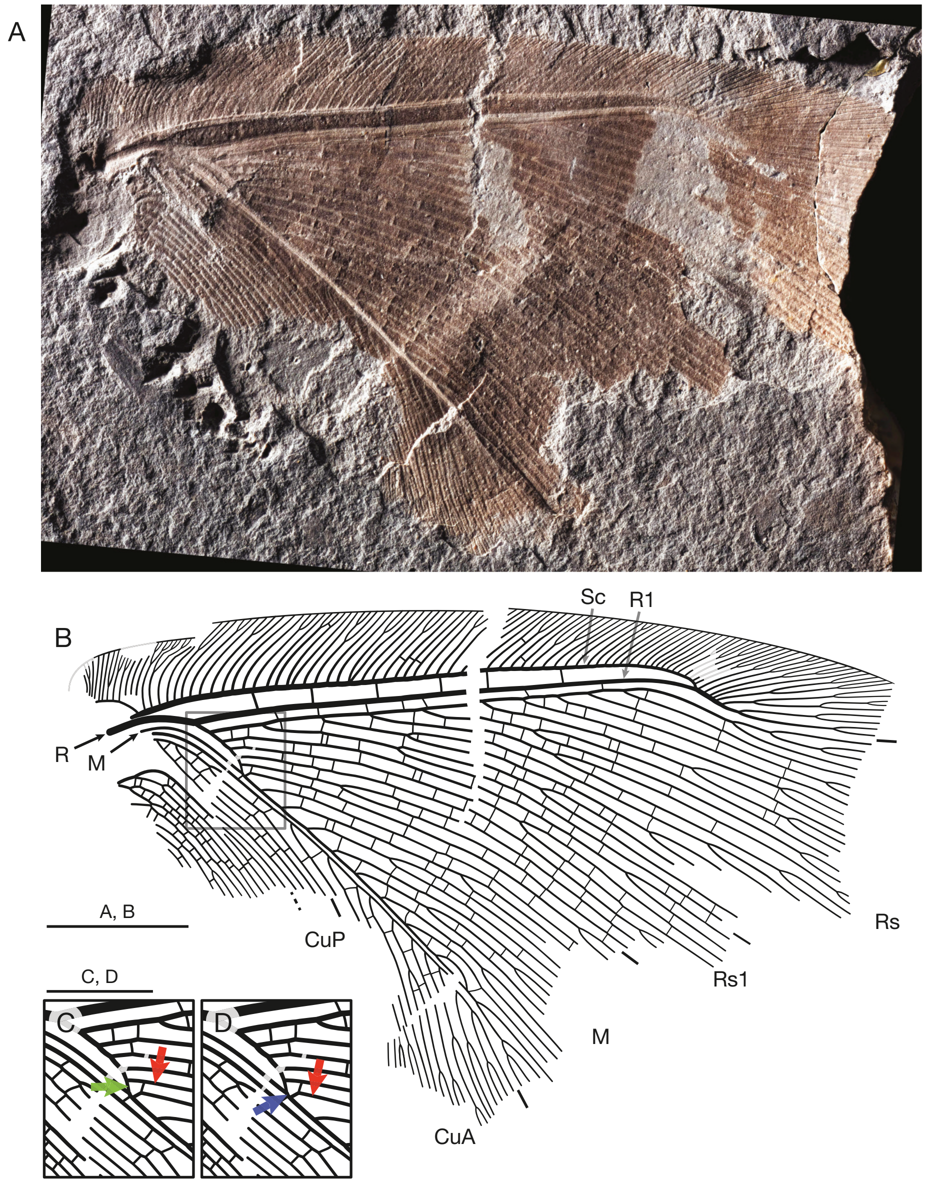

Fig. 2. — *Petropsychops superbus* Riek, 1956 (Osmylopsychopidae), holotype UQ C2135-6, left forewing (Denmark Hill; Upper Triassic; Australia), overview: **A**, photograph (negative imprint, with apical fragment re-adjusted digitally; **B**, interpretative drawing, assuming the occurrence of a rs_1-m cross-vein (as in **C**); **C**, **D**, detail of the rs_1-m cross-vein and surrounding structures (location as shown on **B**; green arrow, rs_1-m cross-vein; red arrow, Rs1 posterior-most branch; blue arrow, fusion of Rs1 posterior-most branch and M); **C**, favored interpretation; **D**, alternative interpretation. Scale bars: A, B, 5 mm; C, D, 2.5 mm. Photograph: © Queensland Museum, Geoff Thompson, reproduced with permission; drawings: O. Béthoux.

magnus n. gen., n. sp. the first Triassic and, to our knowledge, the first Mesozoic species of Neuroptera to be described from Africa, provides additional evidence of these close ties. Indeed, the closest known relative of the new taxon is the monotypic genus *Petropsychops*, known by incomplete wings from Denmark Hill and Mount Crosby (Lambkin 2014; and references therein).

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