Fossil insects of the Middle Triassic Gayndah Formation of south-eastern Queensland

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ABSTRACT

The Middle Triassic (Anisian) Gayndah Formation is the northernmost unit of the Early–Middle Triassic Esk Basin of south-eastern Queensland. Fossil insects were discovered in the formation in 1962 and 90 specimens have been collected since then. Of those, the 80 specimens identifiable to Order level are mainly Hemiptera (39%) and Coleoptera (36%), with much fewer Odonata *s.l.*, Plecoptera, Neuroptera, Mecoptera and Trichoptera, and single specimens of Blattodea, Reculida, Titanoptera and ? Orthoptera. The dominance of Hemiptera and Coleoptera is likely due to the durability of their tegmina and elytra during sedimentary transport and deposition, rather than an indication of faunal composition. Faunal elements identified to family or lower level are: Reculida: *Shurabia australis* Rasnitsyn, 1982 (Geinitziidae); Plecoptera: ? *Gondwanoperlidium* spp. (Euxenoperlidae); Hemiptera: *Tennentsia evansi* Lambkin, 2015, *Dysmorphoptiloides ellisi* Lambkin, 2015, *Mesonirvana dougsmithi* sp. nov. (Dysmorphoptilidae), *Mesoscytina woodsi* Lambkin, 2016 (Scytinopteridae), Hylicellidae; Neuroptera: *Riekchotes reticulatus* gen. et sp. nov. (Ithonidae), *Lithosmylidia baronne* Lambkin, 1988, *Lithosmylidia* sp. (Archeosmylidae), *Gayndahpsychops carsburgi* Lambkin, 2014 (Osmylopsychopidae); Mecoptera: *Mesoses gayndah* Lambkin, 2014 (Mesopsychidae), *Mesochorista* sp. (Permochoristidae); Trichoptera: *Prorhyacophila colliveri* Riek, 1955 (Prorhyacophilidae). The fauna is a typical Triassic transitional one that has commonalities with the more extensively sampled and species-rich faunas of the Queensland Late Triassic insect localities at Denmark Hill, Dinmore and Mount Crosby. Exceptions are a hindwing base ascribed to the Titanoptera, an order known in Australia only from the Middle Triassic Hawkesbury Sandstone of New South Wales, and the forewing of *Riekchotes reticulatus*, the earliest and only Triassic record of the neuropteran family Ithonidae.

The Gayndah Formation, established as a formal stratigraphic unit by Cranfield (1989), is the northernmost unit of the Early–Middle Triassic Esk Basin of south-eastern Queensland (Purdy 2013). It was described in detail by Geological Survey of Queensland (GSQ) geologist Peter Ellis during his mapping of the Maryborough 1:250,000 sheet area over the period 1962–1965 (Ellis 1968). The formation comprises mostly sandstone with lesser conglomerate, siltstone, mudstone, acidic volcanics and rare thin coal beds, with a recorded maximum thickness of approximately 170 metres (Purdy 2013). It outcrops over an area of approximately 180 km^2 in the vicinity of Gayndah in the North Burnett region, but is poorly exposed due to deep weathering, low topography and much superficial cover. Based on its fossil microflora, the age of the Gayndah Formation has been estimated as early Middle Triassic (Anisian) (de Jersey 1979, Purdy 2013).

On 12 July 1962, during his mapping, Ellis collected fragmentary fossil plants and three poorly preserved fossil insects 'in grey shale interbedded in sandstone and conglomerate sequence' in a road cutting three kilometres east-north-east of Gayndah. The fossils were identified as 'Insect abdomen (Coleoptera)' (GSQ specimen F4258b), 'Insect wing (? Hemiptera)' (GSQF4259) and 'Insect wing (? Odonata)' (GSQF4260) by GSQ palaeontologist Jack Woods, who presciently observed that while the preservation of the insects was imperfect, 'their diversification suggests that the locality may be worthy of exploitation for these fossils' (Woods 1962).

THE GAYNDAH FOSSIL INSECT SITE

The collecting site discovered by Ellis is a low (maximum two metres high) cutting on the eastern side of a rise on what is now named Beronne Road at -25.615° 151.640°. The cutting extends over a length of approximately 70 metres, comprising 45 metres of horizontal conglomerate with some interbedded sandstone overlying 25 metres of horizontal mudstone/siltstone. Fossil insects occur in the lower levels of this mudstone/siltstone bed, which is the only currently recorded locality for insects in the Gayndah Formation. Insects are not common at the site — several hours of rock splitting may yield one, or on a good day, two specimens, many of which are fragmentary or otherwise poorly preserved. Except for strongly sclerotised beetle elytra and certain robust, coriaceous hemipteran tegmina, the specimens are invariably fragments of broken wings or body parts. This suggests that final deposition has only occurred after substantial sedimentary transport, during which dead insects have disintegrated into fragments. The depositional environment of the Gayndah Formation, which produced mostly barren sediments containing rare isolated fragmentary insect remains and even rarer small plant fragments, was similar to the Late Triassic Mount Crosby Formation and similarly arcane. On the other hand, the depositional environment of the other major Queensland fossil insect deposit, the Late Triassic Blackstone Formation, is more obvious. The occurrence there of occasional isolated wings and elytra among abundant and diverse *Dicroidium* flora plant fossils clearly suggests a swamp and floodplain fluvial environment where fragments of dead insects are deposited amongst the abundant remains of a rich flora.

Over many years, with the assistance of colleagues Doug Smith and Robert Knezour on several occasions, the author has assembled a collection of 87 fossil insect specimens from the Beronne Road site that, with the addition of the three found by Ellis, brings the total number to 90. Seventeen of the specimens have already been examined as part of revisional studies of the Queensland Triassic insect fauna (Lambkin 1988, 2014a, 2014b, 2015, 2016a); consequently, six species are currently known from Gayndah: the neuropterans *Lithosmylidia baronne* Lambkin, 1988 and *Gayndahpsychops carsburgi* Lambkin, 2014, the mecopteran *Mesoses gayndah* Lambkin, 2014, and the hemipterans *Tennentsia evansi* Lambkin, 2015, *Dysmorphoptiloides ellisi* Lambkin, 2015, and *Mesoscytina woodsi* Lambkin, 2016. The site is now deeply weathered and as there is little prospect of obtaining new material without major excavation, it is opportune timing to record an inventory and descriptions of the collection as it stands.

COLLECTION INVENTORY

Of the 90 specimens, only 80 can be referred to particular insect orders. The remaining 10 specimens are thorax or abdomen fragments and although most appear to be Coleoptera, they are not identifiable with any certainty. Of the 80 able to be identified to order, the majority are Hemiptera (31 specimens, 39%) and Coleoptera (29 specimens, 36%), with the remaining 25% of the sample comprising Neuroptera (seven specimens), Odonata *s.l.* (three specimens), Plecoptera, Mecoptera, Trichoptera (two specimens each), and Blattodea, Reculida, ? Orthoptera and Titanoptera (one specimen each). The dominance of Hemiptera and Coleoptera is almost certainly due to the durability of their tegmina and elytra during sedimentary transport and deposition, rather than any indication of faunal composition.

MATERIALS AND METHODS

All specimens are in the collection of the Queensland Museum (QMF), including those previously held by the Geological Survey of Queensland that retain their GSQF specimen numbers. Specimens with both part and counterpart have an a/b number, otherwise only the part is present. The venational abbreviations used are: a, arculus; Cu, cubitus; CuA, cubitus anterior; CuP, cubitus posterior; cv, costal veinlets; *ir*, interradial crossvein; M, medius; R, radius; RA, radius anterior; RP, radius posterior; *ra–rp*, crossvein between RA and RP; *rp–m*, crossvein between RP and M; Sc, subcosta; str, strigil; 1A, 2A, first and second anal veins. The photographs were taken with a Nikon D850 camera and Sigma 180 1:2.8 macro lens. For ease of comparison all wing specimens are illustrated as right wings. The original photographs of specimens of left wings have therefore been mirrored, as indicated in the figure captions. The scales on Figs 1–9 are all 2 mm.

SYSTEMATICS

Order ODONATA Fabricius, 1793 *sensu lato*

(Fig. 1A, F)

Material: Hindwing base fragment, QMF61195a/b, and two small wing fragments, QMF61196 and GSQF4260 (Woods 1962), too incomplete for further determination.

Order BLATTODEA Brunner von Wattenwyl, 1882

(Fig. 1C)

Material: Hindwing fragment, QMF61197a/b, not able to be further identified.

Order RECULIDA, Handlirsch, 1906

Family GEINITZIIDAE, Handlirsch, 1906

Shurabia Martynov, 1937

Shurabia australis Rasnitsyn, 1982

(Fig. 1D, E)

Material: Forewing fragment, QMF61198a/b.

Notes: The forewing fragment is 8.8 mm long, with the primary fork of M basally-placed near that of R, M with four main branches, CuA_1 with two branches, and CuA_2 almost parallel to the posterior margin, has a venational scheme consistent with the genus *Shurabia* (see Figs. 1C–G in Aristov et al. 2009). *Shurabia australis* was named by Rasnitsyn (1982) based on a ‘fragment of a protorthopteron’ recorded in Fig. 39 of Riek (1955) from the Late Triassic (Norian) Mount Crosby Formation, Mount Crosby, south-eastern Queensland (hereafter simply referred to as ‘Mount Crosby’). The species is the only currently recorded reculid from the Queensland Triassic. The specimen, UGQC2142 (now the holotype of *S. australis*), is poorly preserved, and the apparent absence of crossveins is a preservation artefact rather than a reality. It should also be noted that the apex of RA, illustrated by Riek as deeply dichotomously forked, could not be detected on close examination of the specimen. QMF61198a/b from Gayndah is a much better specimen that preserves the crossvein field, and although slightly smaller than the holotype (width from costal margin to CuA_1 fork 3.8 mm, compared to 4.2 mm in the holotype), compares well with *S. australis* in the form and branching relativities of its main veins, and is therefore considered conspecific.

Shurabia, the most speciose member of the Geinitziidae in the extinct order of blattid insects, the Reculida (Aristov 2015a), is first recorded from the Permian of Russia and was then widespread throughout the Triassic and Jurassic with records from Germany, Ukraine, Russia, Kyrgyzstan, Tajikistan, Mongolia, China, South Korea, Japan, South Africa and Queensland (Aristov et al. 2009, Aristov 2015b, 2022, Jouault et al. 2022). Given its almost cosmopolitan distribution in the Triassic and Jurassic, its occurrence in the Gaydah Middle Triassic is not unexpected.

Order TITANOPTERA Sharov, 1968

(Fig. 1B)

Material: Wing base fragment, QMF61200.

Notes: Based on the large size of the fragment (length 8.9 mm, suggesting a total wing length of 50–60 mm), its shape and complex fan-like venation, the specimen is tentatively identified as the base of a titanopteran hindwing, comparable to those of *Prototitan* Sharov, 1968, and *Paratitan* Sharov, 1968, from the mid-Triassic of Kyrgyzstan (Figs. 48 and 49B in Sharov 1968, Fig. 1C in Shcherbakov 2011). The only other record of the Titanoptera from Queensland was *Steinhardtia maryae* Jell & Lambkin, 1993, which has now been shown to be a leaf with venation and shape uncannily resembling the titanopteran wing. Accordingly, this specimen from Gayndah is the first record of the order from Queensland.

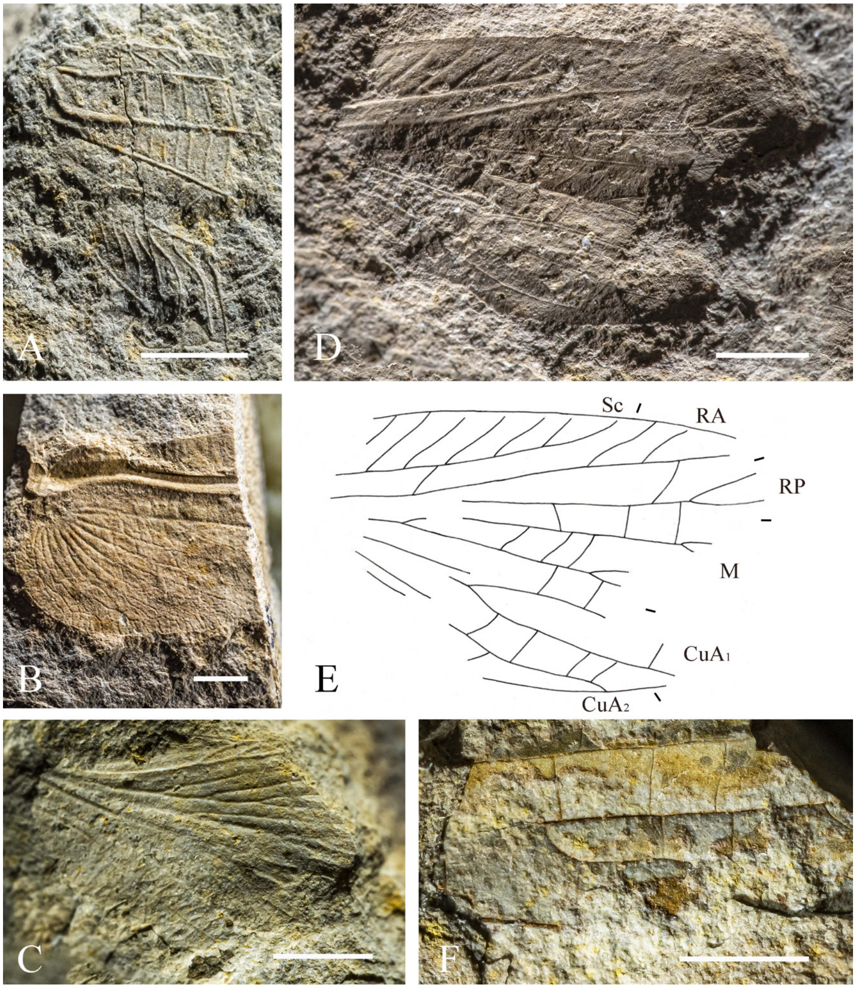

Figure 1. A Odonata *sensu lato:* QMF61195a (mirrored); **B** Titanoptera: QMF61200 (mirrored) **C** Blattodea: QMF61197a **D–E** Reculida: *Shurabia australis* Rasnitsyn, 1982: QMF61198a **F** Odonata *sensu lato:* QMF61196 (mirrored)

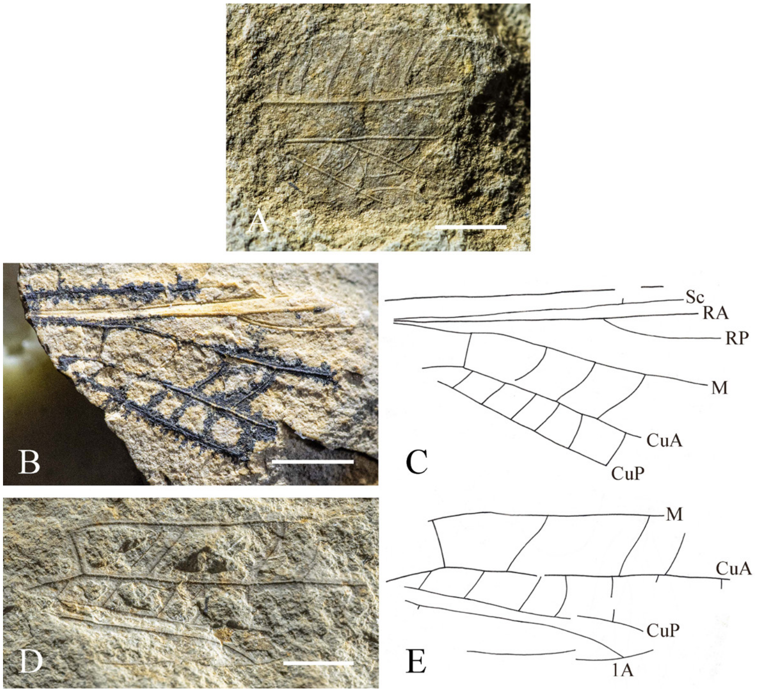

Figure 2. A ? Orthoptera: QMF61199 (mirrored) **B–E** Plecoptera: ? *Gondwanoperlidium* spp. **B–C** QMF61201a (mirrored) **D–E** QMF61202a.

? Order ORTHOPTERA Latrielle, 1793

(Fig. 2A)

Material: Wing fragment, QMF61199, not able to be further identified.

Notes: Due to the fragmentary nature of the specimen, its placement in the Orthoptera is tentative, although the pattern of venation suggests a polyneopteran insect.

Order PLECOPTERA Burmeister, 1839

Suborder ANTARCTOPERLARIA Zwick, 1969

Superfamily GRYPOPTERYGOIDEA Enderlein, 1909

Family EUXENOPERLIDAE Riek, 1976

? *Gondwanoperlidium* Pinto & Purper, 1978

? Gondwanoperlidium spp.

(Fig. 2B–E)

Material: Two forewing base fragments, QMF61201a/b, 61202a/b.

Notes: The two fragments are of wings that were quite different in size, with QMF61202a/b significantly larger. They therefore may have come from different species. Their venation, as far as is preserved, is consistent with that of the South American and Australian Triassic genus *Gondwanoperlidium*. The lack of apical areas of the wings, however, precludes generic placement with any certainty. *Gondwanoperlidium* is a southern continent Triassic genus known from three species: *G. argentinarum* Pinto & Purper, 1978 and *G. mendozensis* Pinto & Purper, 1978, from Argentina, and *G. triassicum* (Riek, 1956) from the Late Triassic (Norian) Blackstone Formation at Denmark Hill, Queensland (hereafter simply referred to as 'Denmark Hill') (Riek 1956). The latter species was originally ascribed by Riek to *Stenoperlidium* Tillyard, then transferred by Riek (1973) to *Euxenoperla* Riek, and finally to *Gondwanoperlidium* by Pinto & Purper (1978). Riek (1955) also identified a plecopteran wing fragment from Mount Crosby as possibly belonging to this genus.

Order HEMIPTERA Linnaeus, 1758

Infraorder CICADOMORPHA Evans, 1946

Superfamily PROSBOLOIDEA Handlirsch, 1906

Family DYSMORPHOPTILIDAE Handlirsch, 1906

Subfamily DYSMORPHOPTILINAE Handlirsch, 1906

Tennentsia Riek, 1976

Tennentsia evansi Lambkin, 2015
(Figs. 3A–C, 4A–D)

Material: Holotype tegmen QMF57827a/b, and 10 paratype tegmina, QMF57828a/b, 57829–57835, 57836a/b and 57837a/b, recorded by Lambkin (2015); five newly collected tegmina: QMF61203a/b, 61204a/b, 61205a/b, 61206, 61207.

Notes: Two of the new specimens, QMF61204a/b (Fig. 3A, 3B) and QMF61203a/b (Fig. 3C), with tegmen lengths of 11.6 mm and 15.5 mm respectively, extend the size range of the species, previously recorded as 16.1–19.6 mm. The largest individuals were therefore almost twice the size of the smallest. Some of the size differences could be attributed to the sex of the individual, females generally being larger than males in the Cicadomorpha. The venation of the new material is generally consistent with the original description, although both QMF61203a/b and 61204a/b show some minor variations. In 61203a/b (Fig. 3C), RP is forked rather than simple, and M_4 and the apical branch of RA_2 have end-twigs rather than being simple. In 61204a/b (Fig. 3A, 3B), the M_{3+4} fork and the apical fork of RA_2 are much shallower than previously recorded, and M_2 is forked rather than simple (Lambkin 2015).

Two of the new specimens demonstrate that the peculiar protuberances of the tegmen surface, originally recorded as three in number positioned at about ¼ length along each of M and RP and proximally on the clavus (Lambkin 2015), can also vary in number, position and degree of development. In three of the new specimens, the protuberances are similar in number, placement and degree of development to those previously recorded. Conversely, the smaller specimens QMF61203a/b and 61204a/b each have only two protuberances. Those of QMF61203a/b (Fig. 3C) are weakly developed, scarcely protrusive, and differently positioned — one on RP but placed more distally than in other specimens, and the other distally on RA_2. The two protuberances of QMF61204a/b (Fig. 3A, 3B) are in the usual positions on M and the clavus, but both are very well-developed and strongly protrusive.

QMF61204a/b, 61205a/b and 61207 demonstrate the presence of two or four well-developed triangular lobes on the hind margin of the clavus, each with a median ridge (Figs. 3A, 3B, 4A–D). These lobes were not preserved in any of the specimens recorded by Lambkin (2015). Similar prominent lobes also occur in the South African Triassic *Tennentsia protuberans*, Riek, 1976 (probably the sister species of *T. evansi*), and the Mongolian Jurassic *Dysmorphoptila notodon* Shcherbakov, 1988, while a number of other dysmorphoptilds have less prominent irregularly spaced small swellings along the hind margin of the clavus (Riek 1976, Shcherbakov 1988, Lambkin 2015). The origin and function of the lobes is unknown; presumably they interleaved when the tegmina were folded. Combined with the tegmen's colour pattern (Lambkin 2015), its bizarre shape and strange protuberances, the lobes must have produced either very effective camouflage, or a spectacular eye-catching display.

Dysmorphoptiloides Evans, 1956

Dysmorphoptiloides ellisi Lambkin, 2015

Material: Holotype tegmen QMF57823a/b (the counterpart not recorded by Lambkin 2015).

Subfamily EOSCARTERELLINAE Evans, 1956

Mesonirvana Evans, 1956

Notes: *Mesonirvana*, so far known from three species: *M. abrupta* Evans, 1956 (Mount Crosby), *M. orthoclada* (Tillyard, 1922) (Denmark Hill) and *M. dmitryi* (Lambkin, 2016) (Blackstone Formation, Dinmore, south-eastern Queensland), is one of the signature dysmorphoptilids of the Queensland Triassic (Lambkin 2016b, 2017). It is therefore not unexpected that a fourth species, with the familiar tegmen shape and lunular strigil in the basal costal space, has been found at Gayndah.

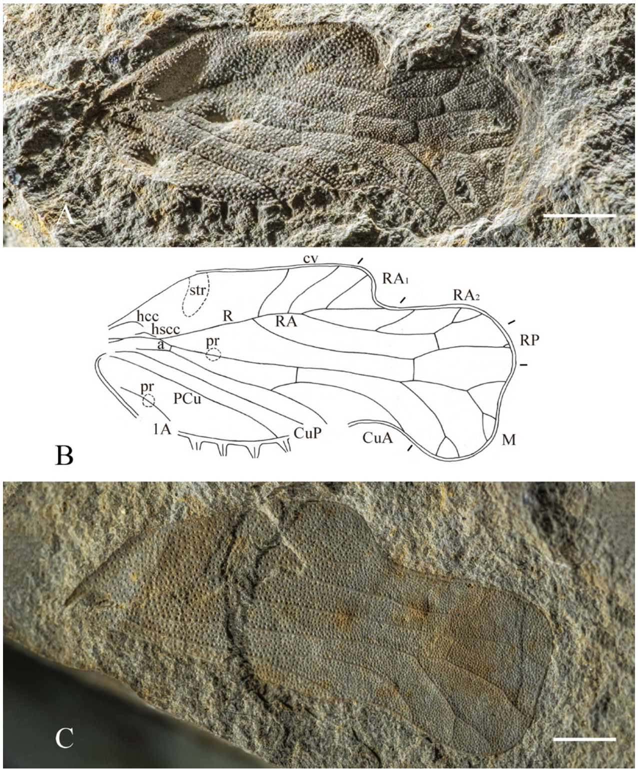

Figure 3. Hemiptera: *Tennentsia evansi* Lambkin, 2015: **A–B** QMF61204a **C** QMF61203a.

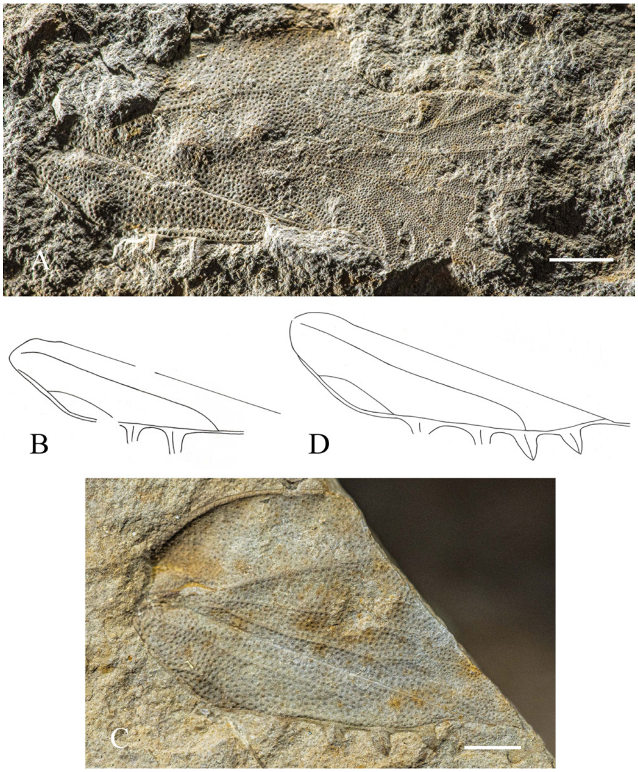

Figure 4. Hemiptera: *Tennentsia evansi* Lambkin, 2015, showing triangular lobes on hind margin of clavus: **A–B** QMF61205a (mirrored) **C–D** QMF61207 (mirrored).

Mesonirvana dougsmithi sp. nov.
(Fig. 5A, B)

Material examined: Holotype tegmen QMF61208a/b.

Description: Tegmen 16.5 mm long, 7.8 mm wide, length/width 2.1, costal margin convex (base not preserved); R without cv; primary fork of R at about clavus ½ length; stem of RA without cv; stem of RA_1 enters costal margin at about ⅔ tegmen length, with two anterior branches; RA_2 with at least three anterior branches, the 2nd branch deeply forked; RP simple, more or less straight, not obviously up-curved apically; *ra–rp* and *rp-m* not preserved; both M_1 and M_2 with deep terminal forks; distal section of M_{3+4} not preserved; *m-cu* long and gently sinuous, running to M rather than M_{3+4}; CuA deeply forked, at same level as RA fork; CuA_2 only slightly shorter than CuA_1; the possibility of a mottled colour pattern suggested by iron oxide staining.

Notes: *Mesonirvana dougsmithi* differs from its three congeners in the deep forking of CuA, at the same level as RA (well beyond the RA fork in the others) and the presence of a deep fork on M_2 (simple in the others). It also differs from *M. abrupta* in size — at 16.5 mm in length, *M. dougsmithi* is larger than any of the 16 recorded tegmina of *M. abrupta*, which have a maximum length of 12.4 mm. Compared to *M. orthoclada*, the tegmen of *M. dougsmithi* is much broader (2.1 times longer than wide) and has a convex costal margin, rather than long and narrow (2.8 times longer than wide) with an almost straight costal margin as in *M. orthoclada*. Lastly, *M. dougsmithi* also differs from *M. dmitryi* in the stem of RA_1 entering the costal margin at ⅔ rather than ½ tegmen length, and CuA_2 only slightly shorter than CuA_1 rather than much shorter as in *M. dmitryi* (Lambkin 2016b).

The holotype also preserves a fragment of the thorax that is strongly punctate. The species name honours my colleague Doug Smith, who contributed to the collection of the Gayndah specimens.

Superfamily SCYTINOPTEROIDEA Handlirsch, 1906

Family SCYTINOPTERIDAE Handlirsch, 1906

Mesoscytina Tillyard, 1919

Mesoscytina woodsi Lambkin, 2016
(Fig. 5C)

Material: Holotype tegmen QMF58698a/b, and one other tegmen, QMF58699, recorded by Lambkin (2016a); five newly collected tegmina: QMF61209a/b, 61210a/b, 61211a/b, 61212 and 61213.

Notes: The newly collected tegmina, with lengths ranging from 5.5 to 6.4 mm, give an indication of the species' size range. The holotype measurement was 5.9 mm. The venation of the new specimens is consistent with the holotype, except that in the four where it is preserved, the apical section of RP is straight and bent upwards, rather than curved downwards as in the holotype. One specimen has the apical section of RP deeply forked, and another has the anterior branch of M with a small terminal fork. Both veins are simple in the holotype.

Superfamily HYLICELLOIDEA Evans, 1956

Family HYLICELLIDAE Evans, 1956
(Fig. 5D)

Material: Three indistinctly preserved tegmina, QMF61214a/b, 61216a/b and GSQF4259 (Woods 1962).

Notes: Of the three, QMF61214a/b (length 9.0 mm) (Fig. 5D) has the venation only of the base and apex of the tegmen preserved. Although there is not much to work with, what is preserved is congruent with the venation of *Hylicella* Evans, 1956, the type genus of the Hylicellidae, namely a short lower carina at base of costal field, basal cell broad proximally then tapering distally, CuA+M and then CuA curved downward and approaching claval suture, *ir* present, RA_1 simple, RA_2 forked, RP simple, and M with four terminal branches. On these grounds, QMF61214a/b is ascribed to the Hylicellidae but is too poorly preserved to be diagnosed further. Tegmen QMF61216a/b (length 7.4 mm) has a similar shape to 61214a/b, but is much poorer and preserves only the lower costal field carina and the downward curve of M+CuA and CuA. GSQF4259 preserves only the lower costal field carina, the downward curve of M+CuA and CuA, and the proximal sections of RA and RP, which are similar to QMF61214a/b.

On these, albeit tenuous grounds, QMF61216a/b and GSQF4259 are also assigned to the Hylicellidae. GSQF4259, with length 11.6 mm, is larger than the other two and has a more broadly rounded apex, so may represent a different species.

Indeterminate CICADOMORPHA

Material: Two unidentifiable small tegmen fragments, QMF61217, 61218 and a detached clavus, QMF61219a/b.

Order NEUROPTERA Linnaeus, 1758

Family ITHONIDAE Newman, 1853 *sensu* Winterton & Makarkin, 2010

Riekchotes gen. nov.

Type species: *Riekchotes reticulatus* sp. nov.

Etymology: The generic name honours Australian entomologist Edgar Riek (1920–2016) for his ground-breaking research on the Triassic insects of Queensland.

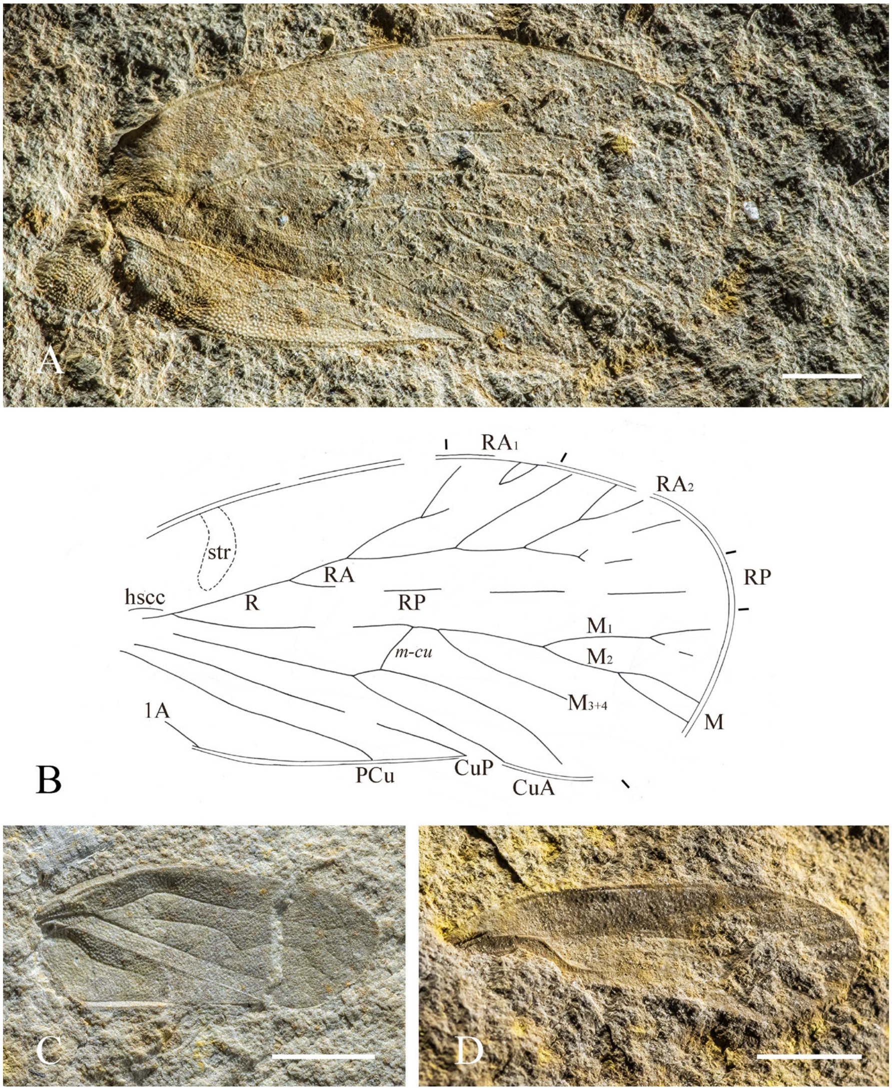

Figure 5. Hemiptera: **A–B** *Mesonirvana dougsmithi* sp. nov.: holotype QMF61208a; **C** *Mesoscytina woodsi* Lambkin, 2016: QMF61209a (mirrored) **D** Hylicellidae: QMF61214a.

Diagnosis: Forewing large, total length estimated at well over 30 mm; humeral region narrow, its costal margin somewhat sinuous; recurrent humeral vein simple, only slightly recurved with one long, simple crossvein to costal margin ; proximal cv nearly all deeply forked, distal ones appear mostly simple; *ra–rp* crossveins few in number (only two over a considerable proximal length); pectinate branches of RP extensive, in excess of the 11 preserved, kinked at crossveins; crossveins of radial field extensive, arranged in irregular gradate series.

Notes: Based on its large size, the presence of a recurrent humeral vein, the narrow humeral region, the small number of *ra–rp* crossveins, the extensive branching of RP and the irregular gradate crossvein series in the radial field, the genus is ascribed to the *Polystoechotes* genus-group of the family Ithonidae (Lambkin 1988, Xu et al. 2021). The diagnostic characters listed above, in combination, distinguish *Riekchotes* from the 20 genera assigned or attributed to the *Polystoechotes* genus-group. The extant *Polystoechotes* Burmeister, 1839, *Fontecilla* Navás, 1931, and *Platystoechotes* Carpenter, 1940, and the Eocene *Palaeopsychops* Anderson, 2001, *Polystoechotites* Archibald & Makarkin, 2006, and *Elektrithone* Makarkin et al., 2014, have a much broader humeral region and/or a more complex recurrent humeral vein with numerous crossveins to the costal margin (Archibald & Makarkin 2006, Carpenter 1940, Makarkin et al. 2014a, Oswald 1998).

The 14 remaining genera are all from the Jurassic. Of these, *Jurapolystoechotes* Ren et al., 2002, and *Puripolystoechotes* Yang et al., 2019 (known only from hindwings) and *Mesopolystoechotes* Martynov, 1937 (known only from the apical half of a fore- or hindwing) have the crossveins of the radial field limited to two regular gradate series (Martynova 1949, Ren et al. 2002, Yang et al. 2019), and *Epigambria* Handlirsch, 1939, *Polyosmylus* Ansorge, 1996, and *Rasnitsyneura* Makarkin et al., 2021, have only one gradate series (Makarkin et al. 2021). Of the remaining eight genera, *Kirgisella* Martynov, 1937, *Osmyloides* Panfilov, 1980, *Paleopterocalla* Oswald, 2007, and *Panfilovdvia* Özdikmen, 2009, are poorly preserved or not well documented, precluding a well-informed comparative analysis. What can be said, however, is that *Kirgisella*, although poorly preserved and smaller (length 20 mm), is apparently similar to *Riekchotes* in the form of the costal space, the small number of *ra–rp* crossveins, and the multitudinous branches of RP. *Osmyloides*, known only from the apical ⅔ of a fore- or hindwing, differs from *Riekchotes* in having the radial field devoid of crossveins except for one distal gradate series. *Paleopterocalla*, known only from the apical ¾ of a forewing, differs in having more numerous *ra–rp* crossveins and far fewer crossveins in the radial field, and *Panfilovdvia* differs in size (length 25 mm) and has a much narrower costal space with simple crossveins, fewer RP branches and far fewer crossveins in the radial field (Martynov 1925, Panfilov 1980).

Of the four remaining better-documented Jurassic genera — *Lichenipolystoechotes* Fang et. al., 2020, *Fuscopolystoechotes* Xu et al., 2021, *Stictopolystoechotes* Gao et al., 2023, and *Pycnopolystoechotes* Gao et al., 2023 — *Riekchotes* differs from all in its limited number of *ra–rp* crossveins and its irregular and much more extensive radial crossvein field. Additionally, *Riekchotes* is significantly larger than *Lichenipolystoechotes*, *Stictopolystoechotes* and *Pycnopolystoechotes*, which are each no more than around 27 mm long, and although of similar size to *Fuscopolystoechotes*, in addition to the *ra–rp* crossveins and radial field differences mentioned above, *Riekchotes* also differs in having a simple rather than complex recurrent humeral vein (Fang et al. 2020, Xu et al. 2021, Gao et al. 2023).

The Ithonidae is one of the oldest still extant neuropteran families and has a long and rich fossil history. Although there is a record of the Ithonoidea from the Late Triassic (Carnian) of Japan (Khramov et al. 2023), the earliest records of the Ithonidae had previously been from the Early Jurassic — *Mesopolystoechotes* from the ? Hettangian of Kyrgyzstan (Makarkin et al. 2014a), and *Epigambria*, *Polyosmylus* and *Rasnitsyneura* from the early Toarcian of Germany (Makarkin et al. 2021). The discovery of *Riekchotes* in the Gayndah Formation adds even more age to the family, extending its range back to the Middle Triassic.

Riekchotes reticulatus sp. nov.
(Fig. 6A, B)

Material: Holotype forewing fragment, QMF61220a/b.

Description: Length of fragment, 18.4 mm; middle costal crossveins forwardly curved and strongly sinuous; crossveins of proximal radial field arranged into three irregular gradate series; base of M not preserved; no indication of colour pattern.

Notes: The specific name refers to the net-like form of the radial field.

Family ARCHEOSMYLIDAE Riek, 1953

Lithosmylidia **Riek, 1955**

Lithosmylidia baronne Lambkin, 1988

Material: Holotype QMF14358 (Lambkin 1988).

Notes: No further specimens have been found since 1988. I originally considered this species as 'osmylid-like' (Lambkin 1988), and more recently Makarkin et al. (2014b), in their assessment of the several Permian and Triassic 'osmylid-like' species, have proposed that *L. baronne*, as well as the other two Triassic species of *Lithosmylidia* (*L. lineata* Riek, 1955, and *L. parvula* Riek, 1955, both from Mount Crosby) belong to the Late Permian to Late Triassic family Archeosmylidae, the likely ancestors of the Osmylidae.

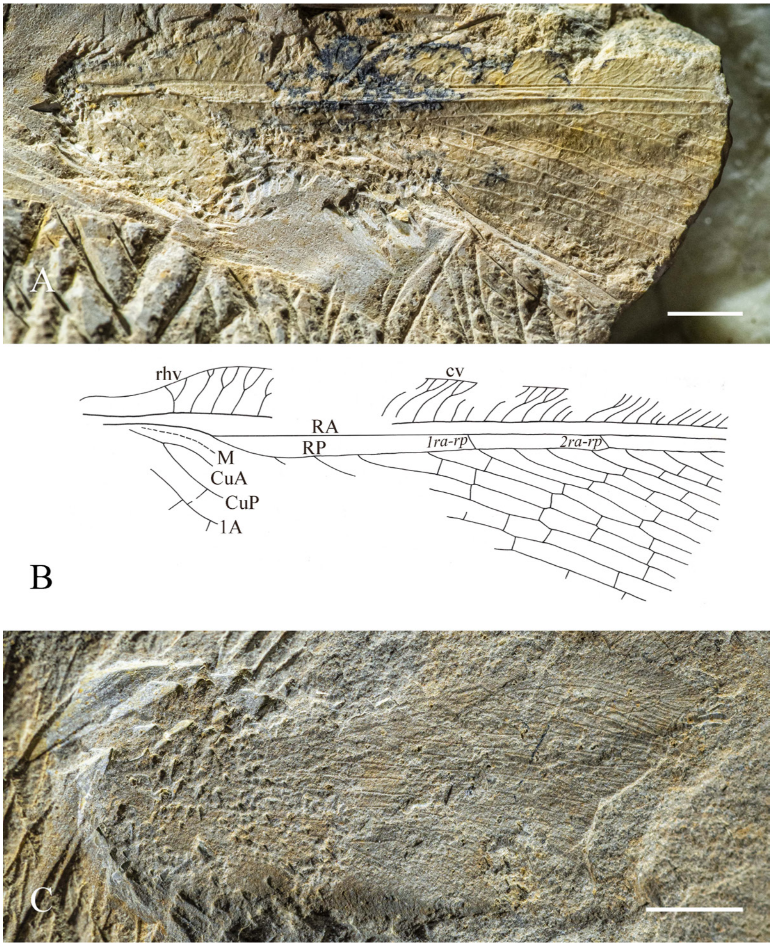

Figure 6. Neuroptera: **A–B** *Riekchotes reticulatus* gen. et sp. nov.: holotype QMF61220a **C** *Lithosmylidia* sp.: QMF61221a.

***Lithosmylidia* sp.**
(Fig. 6C)

Material: Indistinctly preserved forewing fragment, QMF61221a/b.

Notes: The fragment is similar in size to *L. baronne*, and the basic form of the terminal branches of Cu is similar to all three species of *Lithosmylidia* (and other Archeosmylidae — 'few branched, often pectinate, but [the] branches are very oblique and not as strongly pectinate as in Osmylidae' (Makarkin et al. 2014b)). From what can be made out in the specimen, the details of the branching pattern of both CuA and CuP appear to differ from those of *L. baronne* and *L. lineata*, but bear some similarity to those of the smaller species, *L. parvula*. Notwithstanding, the specimen is too poorly preserved to be adequately diagnosed, so is simply left as *Lithosmylidia* sp.

Family OSMYLOPSYCHOPIDAE Martynova, 1949

***Gayndahpsychops* Lambkin, 2014**

Gayndahpsychops carsburgi Lambkin, 2014

Material: Holotype QMF57532 (Lambkin 2014a) remains the only known specimen.

Indeterminate NEUROPTERA sp.
(Fig. 7A–D)

Material: Three imperfectly preserved forewing fragments, QMF61222a/b, 61223a/b, 61239a/b.

Notes: The three specimens are of the same species. On the basis of multiple costal veinlets, presence of a recurrent humeral vein, a multibranched pterostigma area, RP with four pectinate branches, and M extensively branched, it is considered a neuropteran, but further determination has not been possible. The small size (length *c.* 7.5 mm) and venation is suggestive of a berothid with simplified venation, similar to the Jurassic *Krokhathone* Khramov, 2015, from Kazakhstan (Fig. 2 in Khramov 2015), although Sc runs to the costal margin in the Gayndah specimens, rather than merging or at least appearing to merge with RA apically as is typical of the Berothidae.

Order COLEOPTERA Linnaeus, 1758
(Fig. 8A–G)

Material: Complete or fragmentary single elytra: QMF: 61224a/b (finely punctate), 61225 (very finely striate, L (length of elytron) 5 mm), 61226 (smooth), 61227 (strongly striate, L 1.9 mm) (Fig. 8A), 61228 (smooth), 61229 (punctate/striate, L 5.2 mm) (Fig. 8B), 61230 (punctate/striate, L 12 mm), 61231 (smooth, L 2 mm) (Fig. 8C), 61232 (faintly striate, L 3 mm), 61233 (punctate/striate), 61234 (smooth, L *c.* 2 mm), 61235 (finely striate, L 3 mm), 61236 (smooth), 61237 (striate), 61238a/b (cupedoid), 61240 (punctate/striate, L *c.* 2.5 mm), 61241 (smooth, L <2 mm), 68242 (punctate/striate, L *c.* 3 mm), 61243 (cupedoid, L <8 mm), 61215 (cupedoid, L >5 mm) (Fig. 8D). Complete or fragmentary paired elytra: 61244a/b (punctate, + whole body, antenna and part foreleg, L 10.7 mm) (Fig. 8E), 61245a/b (cupedoid, L 6.2 mm) (Fig. 8F), 61246a/b (cupedoid, + metathorax, L 10.2 mm) (Fig. 8G), 61247 (smooth, + pterothorax and abdomen), 61248 (smooth, + pronotum, L *c.* 2 mm), 61249 (smooth, + metathotrax and abdomen, L *c.* 2.5 mm), 61250 (punctate/striate), 61251 (striate, + part pronotum, L 2.5 mm), 61252 (cupedoid, + punctate abdomen, L >10.5 mm).

Notes: Based simply on surface ornamentation and size, the list suggests the presence in the fauna of possibly three cupedoid species, three species with striate elytra, two with punctate/striate elytra, one with punctate elytra, and one with smooth elytra.

Order MECOPTERA Packard, 1886

Family MESOPSYCHIDAE Tillyard, 1917

***Mesoses* Riek, 1976**

Mesoses gayndah Lambkin, 2014

Material: Holotype QMF57544 (Lambkin 2014b) remains the only known specimen.

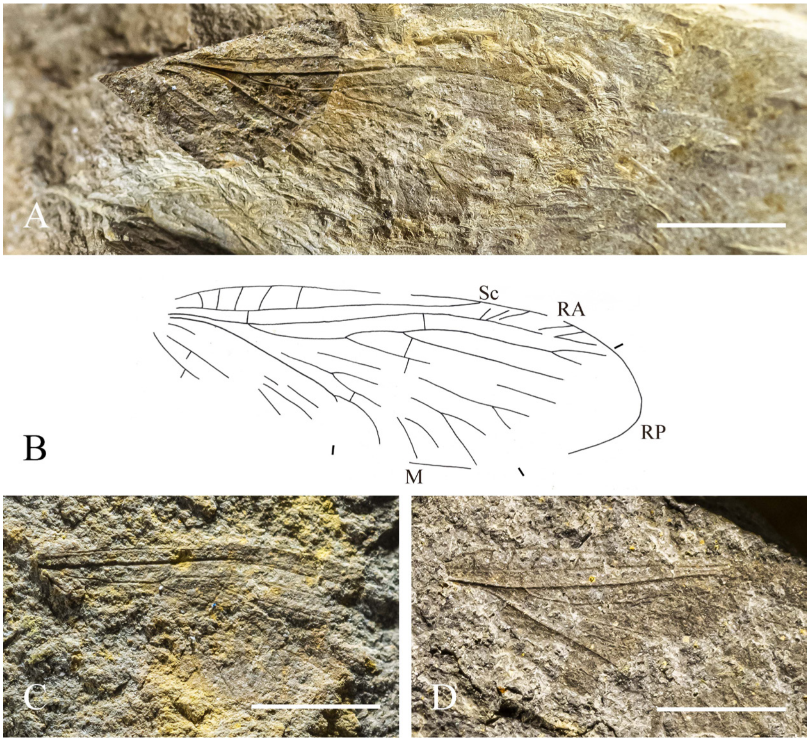

Figure 7. Neuroptera sp. indet.: **A** composite of part and counterpart (wing base) of QMF61222a/b **B** QMF61222a/b, costal space and Sc from QMF61239a/b **C** QMF61223a **D** QMF61239a.

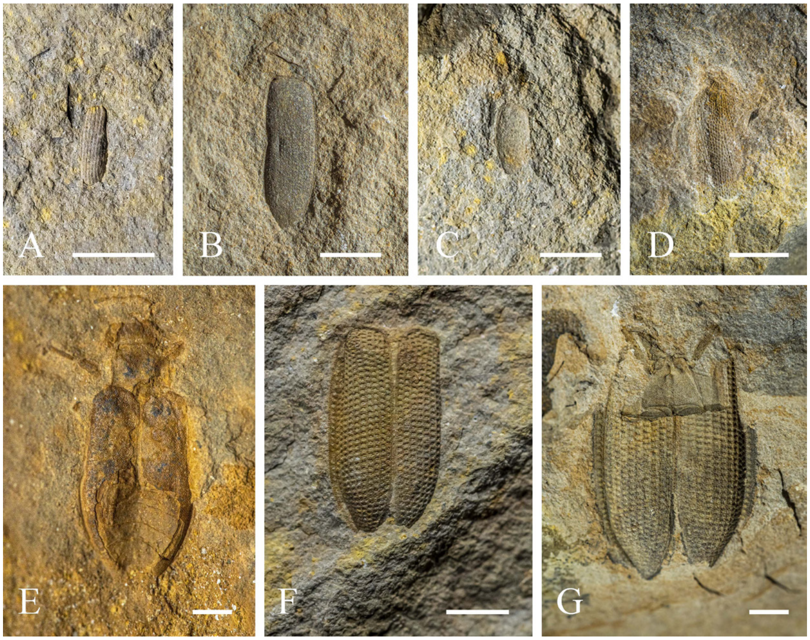

Figure 8. Coleoptera: **A** QMF61227 **B** QMF61229 **C** QMF61231 **D** QMF61215 **E** QMF61244a **F** QMF61245a **G** QMF61246a.

Family PERMOCHORISTIDAE Tillyard, 1917

Mesochorista Tillyard, 1916

Mesochorista sp.
(Fig. 9A, B)

Material: Forewing fragment, QMF61253a/b.

Notes: The specimen preserves the anterior apical quarter of a forewing, which in size and venation perfectly matches *Mesochorista proavita* Tillyard, 1916, recorded from Denmark Hill and particularly Mount Crosby where it is the most frequently collected mecopteran (Riek 1955). Notwithstanding its congruence with *M. proavita*, not enough of the wing is preserved to ascribe the fragment with certainty to that species.

Order TRICHOPTERA Kirby, 1813

Family PRORHYACOPHILIDAE Riek, 1955

Prorhyacophila Riek, 1955

Prorhyacophila colliveri Riek, 1955
(Fig. 9C, D)

Material: Incomplete forewing QMF61254, and a more fragmentary forewing, QMF61255, the latter tentatively referred to the species.

Notes: The incomplete forewing — QMF61254 (Fig. 9C, D) — is 4.1 mm long, suggesting a total length of just over 5 mm. *Prorhyacophila* and the family Prorhyacophilidae are known from three species — the genotype *P. collieri* Riek, 1955, from Mount Crosby, *P. furcata* Sukatsheva, 1973, from the Middle Triassic of Kyrgyzstan, and *P. rasnitsyni* Sukatsheva & Aristov, 2013, from the Late Permian of Russia (Riek 1955, Sukatsheva 1973, Sukatsheva & Aristov 2013).

A second Australian species, originally described as *Eocorona iani* Tindale, 1980, in the Lepidoptera, was transferred to *Prorhyacophila* by Sukatsheva (1982) based on Tindale's (1980) description and figures. A re-examination of the holotype of *E. iani* (UQC2327a/b), however, has revealed that the specimen bears little resemblance to Tindale's description and figure (Fig. 4a in Tindale 1980) — the anterior basal ¼ of the wing is lacking, only the anterior section of RP is clearly preserved and appears pectinate, M and the rest of RP in the central part of the wing are broken and overlaid and cannot be clearly identified, CuA appears to be simple, there is no jugal lobe, and importantly the anal veins are simple, not looped. The specimen is almost certainly a mecopteran, possibly a species of *Neoparachorista* Riek.

As noted by Sukatsheva & Aristov (2013) the species of *Prorhacophila* all have similar forewing venation, and are diagnosed chiefly on the relative positions of the forks of RP and M. In this character, its size and its crossvein field, QMF61254 is almost identical with *P. colliveri*, the only difference being the position of the RP_{3+4} fork — basal to (or in QMF61255 slightly distal to) RP_{1+2}, as opposed to quite distal to RP_{1+2} in the only previously recorded specimen of *P. colliveri* (Fig. 17 in Riek 1955). The position of the fork of RP_{3+4} in *P. colliveri* is, however, quite variable as revealed by a series of new specimens collected by the author at Mount Crosby. It can be quite distal to (as illustrated by Riek), just distal to, or at about the same level as that of RP_{1+2}. In light of this variability, QMF61254 and possibly also 61255 from Gayndah are referred to *P. colliveri*.

Prorhyacophila was synonymised by Ansorge (2002) with *Mesotrichopteridium* Handlirsch, 1906, from the Early Jurassic of Germany. Even though the forewings of the two genera have many resemblances, the synonymy was not adopted by Sukatsheva & Aristov (2013) nor herein, with the preference to retain *Prorhyacophila* for its Australian genotype. The phylogenetic position of the Prorhyacophilidae has also been subject to debate with Ansorge (2003) and Minet et al. (2010) arguing that the family is a stem group of the higher order group Amphiesmenoptera (Trichoptera + Lepidoptera) rather than true Trichoptera. Sukatsheva & Aristov (2013) on the other hand have maintained the Prorhyacophilidae as one of their five families of the suborder Protomeropina Tillyard, 1926, within the Tricoptera. Without any particular predilection one way or the other, the latter position has been adopted herein.

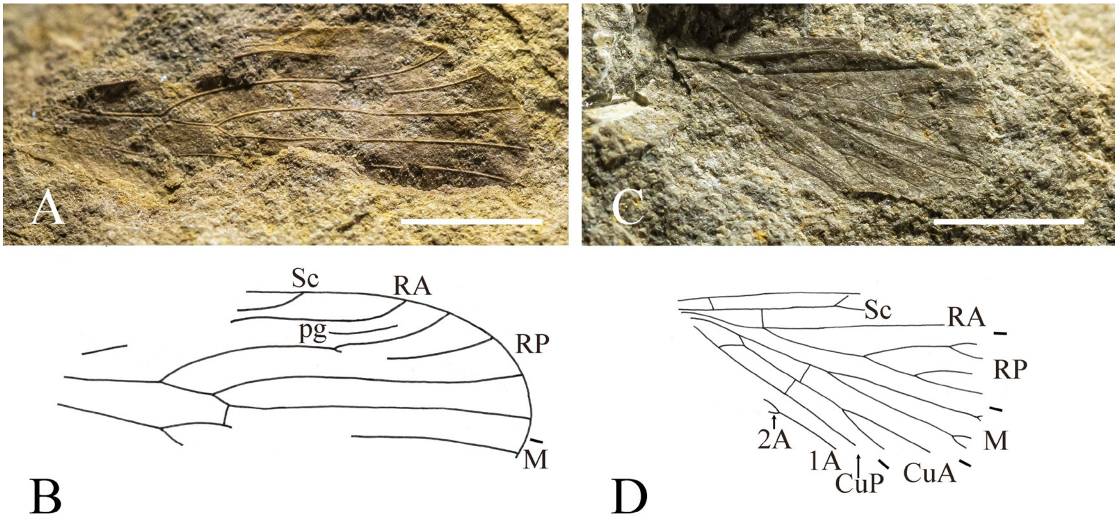

Figure 9. A–B Mecoptera: *Mesochorista* sp.: QMF61253a (mirrored) **C–D** Trichoptera: *Prorhyacophila colliveri* Riek, 1955: QMF61254 (mirrored).

INSECT BODY PARTS

Material: Thoraxes: QMF61256a/b, 61257, 61258a/b; abdomens: QMF61259a/b, 61260a/b, 61261, 61262, 61263, GSQF4258b (Woods 1962); thorax + abdomen: QMF61264.

DISCUSSION

Even though the sample is small, the insect fauna of the Middle Triassic Gayndah Formation is a typical Triassic transitional fauna (Shcherbakov 2008, Zheng et al. 2018). It shares much in common with the more extensively sampled and species-rich faunas of the Queensland Late Triassic insect localities at Denmark Hill, Dinmore and Mount Crosby — *Mesonirvana*, *Mesoscytina*, Hylicellidae and Osmylopsychopidae occur at Denmark Hill, Dinmore and Mount Crosby, *Mesochorista* at Denmark Hill and Mount Crosby, *Mesopsychidae* at Denmark Hill and Dinmore, and *Shurabia australis*, *Prorhyacophila colliveri*, *Dysmorphoptiloides* and Archeosmylidae at Mount Crosby. Two Gayndah records are, however, exceptional — a hindwing base of the Titanoptera, an order known in Australia only from the Middle Triassic Hawkesbury Sandstone of New South Wales (Jell 2004) and the forewing of *Riekchotes reticulatus*, the earliest and only Triassic record of the neuropteran family Ithonidae.

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