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The first palaeontinid from the Late Jurassic of Australia (Hemiptera, Cicadomorpha, Palaeontinidae)

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Palaeontinidae, an extinct group of large arboreal insects, has the most diverse record among the Mesozoic Hemiptera, but only a few taxa have been reported from the Southern Hemisphere. Herein, *Talbragarocossus jurassicus* Chen, Beattie & Wang gen. et sp. nov., one of the earliest representatives of ‘late’ Palaeontinidae, is described and illustrated from the Upper Jurassic Talbragar Fossil Fish Bed in New South Wales, Australia. This new taxon constitutes the first representative of Palaeontinidae in Australia and the first Jurassic example in Gondwanaland, providing significant distributional and stratigraphic extensions to the family.

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Key words: Hemiptera, Palaeontinidae, Australia, Late Jurassic, new taxon

WITH nearly 100 species attributed to more than 40 genera, Palaeontinidae is now considered to have the most diverse fossil record among families of Mesozoic Hemiptera (Fossilworks 2018). This arboreal cicadomorph group was originally regarded as the earliest Lepidoptera, and then transferred to the ‘Homoptera’ by Tillyard (1921) (Wang *et al.* 2009, Chen *et al.* 2016, Li *et al.* 2019a, 2019b). Palaeontinids are commonly large, with the forewing greater than 80 mm long in some species (i.e., *Eoiocossus* spp.) (Wang *et al.* 2006, Wang *et al.* 2007). They are robust, moth-like, hairy like the relic modern hairy cicada *Tettigarcta* and probably also crepuscular (Shcherbakov & Popov 2002). The large palaeontinids have an extremely long rostrum, even extending beyond the end of the abdomen for some Late Jurassic and Cretaceous examples, indicating that these extinct insects might have been primarily xylem feeders, like modern singing cicadas (Novotny & Wilson 1997).

Few palaeontinids are known from the Triassic (Nam *et al.* 2017), but they prospered in the Jurassic with numerous records from around the world. They became extinct in the mid-Cretaceous; the youngest assemblage being from the Albian Crato Formation of

Brazil. Recently, these Mesozoic insects were divided into two groups based on fore- and hind wing characters: the ‘early’ Palaeontinidae mostly lived in the Jurassic and have elliptical forewings and large hind wings; whereas, the ‘late’ Palaeontinidae lived mostly during the Cretaceous and had triangular forewings and hind wings of diminished size (Wang *et al.* 2009, 2010). The evolutionary trend of wings from the ‘early’ to ‘late’ Palaeontinidae is argued to reflect remarkable innovations in the flight mechanism and a significant improvement in flight capability (Wootton & Kukalová-Peck 2000, Wang *et al.* 2009).

Palaeontinids are well documented from Mesozoic strata with only a few, however, recorded in the Southern Hemisphere including one taxon (*Fletcheriana magna*) from the Upper Triassic Molteno Formation of South Africa (Riek 1976) and four genera from the Lower Cretaceous Crato Formation of Brazil (Menon *et al.* 2005, 2007). *Talbragarocossus jurassicus* Chen, Beattie & Wang, gen. et sp. nov. described and illustrated herein, constitutes the first palaeontinid record from Australia and the first representative of Palaeontinidae from the Jurassic of Gondwana. Moreover, it significantly extends the geographic and stratigraphic range of Palaeontinidae. This taxon is probably one of the earliest ‘late’ Palaeontinidae, and is significant in

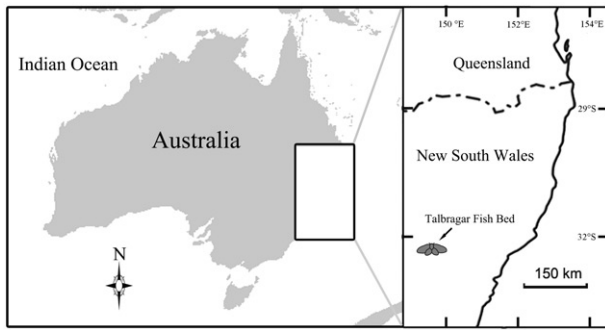


Fig. 1. Collection location of the holotype of *Talbragarocossus jurassicus* gen. et sp. nov.

understanding the evolution, biodiversity, palaeobiogeography and radiation of the family.

Material and methods

One fossil palaeontinid is reported herein from the Talbragar Fossil Fish Bed of central New South Wales, Australia (Fig. 1). The bed is renowned for its abundant fossils, such as numerous fishes, plants and arthropods (Beattie & Avery 2012, McLoughlin *et al.* 2015, Frese *et al.* 2017). Radiometric dating of zircon crystal inclusions indicated that this rock unit was deposited at 151.55 ± 4.27 Ma (Bean 2006), a Kimmeridgian–Tithonian (Late Jurassic) age (Cohen *et al.* 2018). The general paucity of Jurassic insect sites in the Southern Hemisphere is well documented (Beattie & Avery 2012). The Talbragar Fossil Fish Bed has been one of most important Jurassic deposits in Gondwana for aquatic and terrestrial insects. The entomofauna of the Talbragar Fossil Fish Bed is strongly dominated by Hemiptera, but only one presumed hemipteran species (*Griphologus lowei*) with an uncertain taxonomic placement has been described to date (Etheridge & Olliff 1890, Beattie & Avery 2012, Moulds 2018). The new genus and species reported herein, attributed to Palaeontinidae, are the first certain representative of Hemiptera. The insect fossil described herein was examined and photographed using a Canon PowerShot A630. Illustrations and line drawings were prepared with software programs CorelDraw 12.0 and Adobe Photoshop CS3. All measurements were made in the software ImageJ 1.42q (Wayne Rasband; National Institutes of Health, Bethesda, MD, USA).

There is no consensus on Cicadomorpha venation terminology and vein homology; various authors have used different schemes and interpretations (e.g., Emeljanov 1987, Hamilton 1992, Pulz & Carvalho 1998). Nel *et al.* (2012) proposed a new interpretation of wing venation for all Paraneoptera, assuming that CuA becomes fused with the M+R stem at the wing base and is connected with CuP by a specialized cross-vein *cua-cup*, which is remarkably different from the traditional interpretations (Chen *et al.* 2015, 2017). The venation terminology used herein is slightly modified

from Nel *et al.* (2012). The first longitudinal vein on the clavus was treated as an open problem by Nel *et al.* (2012). We tentatively treat this longitudinal vein as Pcu rather than A₁. An additional point is that the complete fusion of MA with R in Paraneoptera results in only MP being present; thus we treat the independent medial vein as MP instead of M (Nam *et al.* 2017).

Systematic palaeontology

Order HEMIPTERA Linnaeus, 1758

Superfamily PALAEONTINOIDEA Handlirsch, 1906

Family PALAEONTINIDAE Handlirsch, 1906

Talbragarocossus Chen, Beattie & Wang gen. nov.

Type species. *Talbragarocossus jurassicus* Chen, Beattie & Wang, sp. nov.

Etymology. Named after the type locality, Talbragar, and ‘cossu’, a common suffix for palaeontinid genera. Gender: masculine.

Diagnosis. Forewing with anterior margin nearly straight; nodal indentation weak; wing apex acute; costal area reduced, narrow; ScP fused with R just beyond basal cell, independent in prenodal area and terminating at wing tip; Hind wing about half length of forewing; costal area long and narrow; R bifurcating into RA and RP far away from nodal indentation; RP fused with MP₁ for a long interval.

Remarks. *Talbragarocossus* gen. nov. is distinctly different from the Triassic and early Middle Jurassic ‘early’ Palaeontinidae in possessing forewings with a nearly straight costal margin, narrow and strongly reduced costal area, acute wing apex, and small hind wings with the position of the bifurcation of R and MP near the wing base. This new genus is similar to Late Jurassic *Cicadomorpha* from Kazakhstan and Siberia in possessing forewings with the nearly straight anterior margin, the membrane stained with some irregular longitudinal stripes, somewhat reduced prenodal area, and an acute wing apex, but it differs from the latter in having forewings lacking cross-vein *mp-cua* in the discal cell, and with the ScP terminating at the wing tip in the postnodal area and without veinlets. It is also similar to the Late Jurassic Palaeontinidae (*Eocicada*, *Prolystra* and *Archipsyche*) from Solnhofen in possessing forewings with a reduced prenodal area and acute wing apex, but it differs from the latter in having vein ScP independent in the postnodal area and terminating at the wing tip, the bifurcation of R being far away from the division of R+MP, MP₁₊₂ and MP₃₊₄ bifurcating almost at the same level, and CuA bifurcating beyond its junction with cross-vein *mp₄-cua*. Additionally, *Talbragarocossus* gen. nov. differs from the Cretaceous ‘late’ Palaeontinidae in having

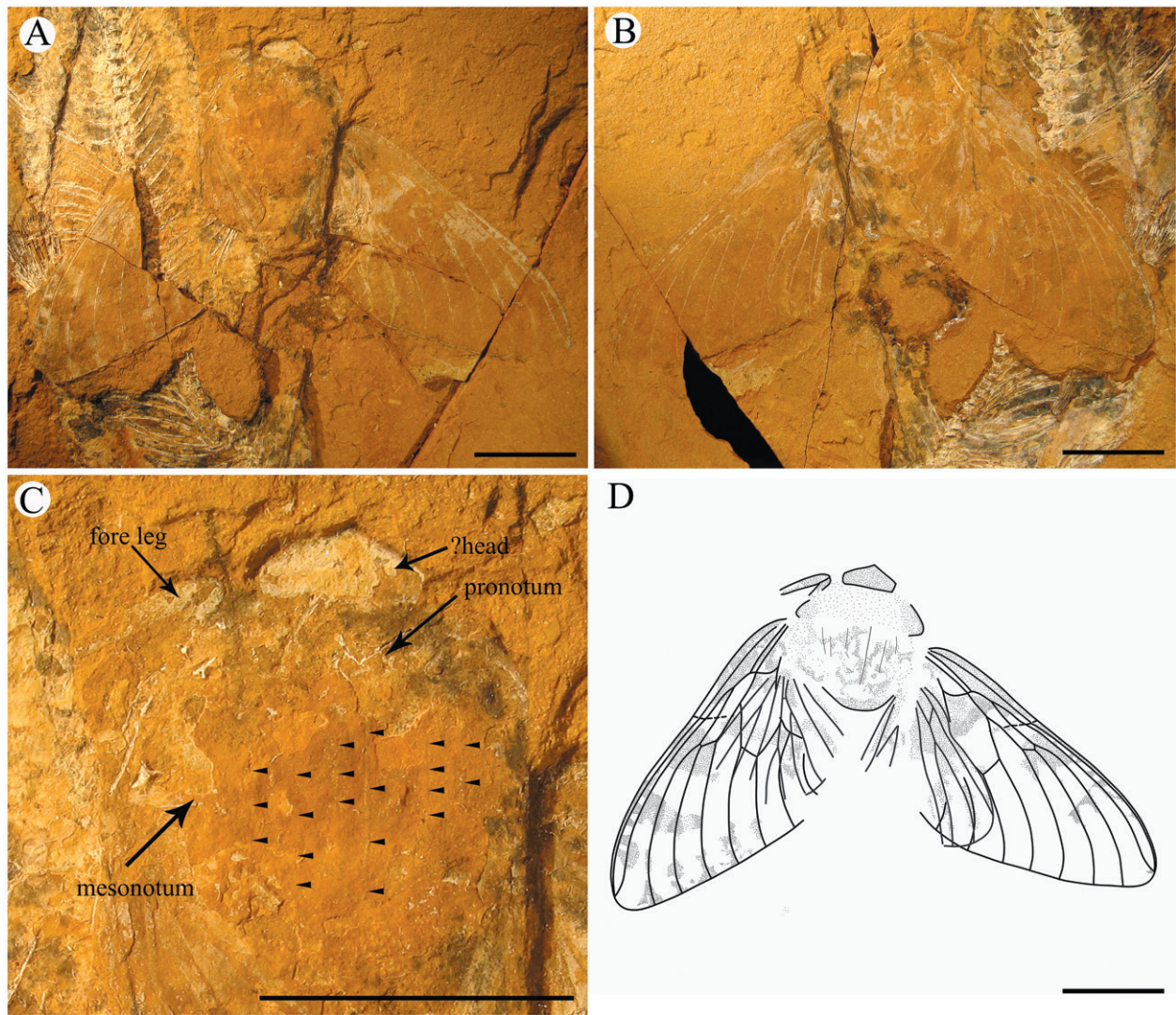


Fig. 2. *Talbragarocossus jurassicus* gen. et sp. nov. **A**, Photograph of the holotype F.136849; **B**, Photograph of the counterpart of the holotype; **C**, Enlargement of the head and thorax of the holotype; **D**, Illustration of the holotype based on part and counterpart specimens. Scale bars = 10 mm.

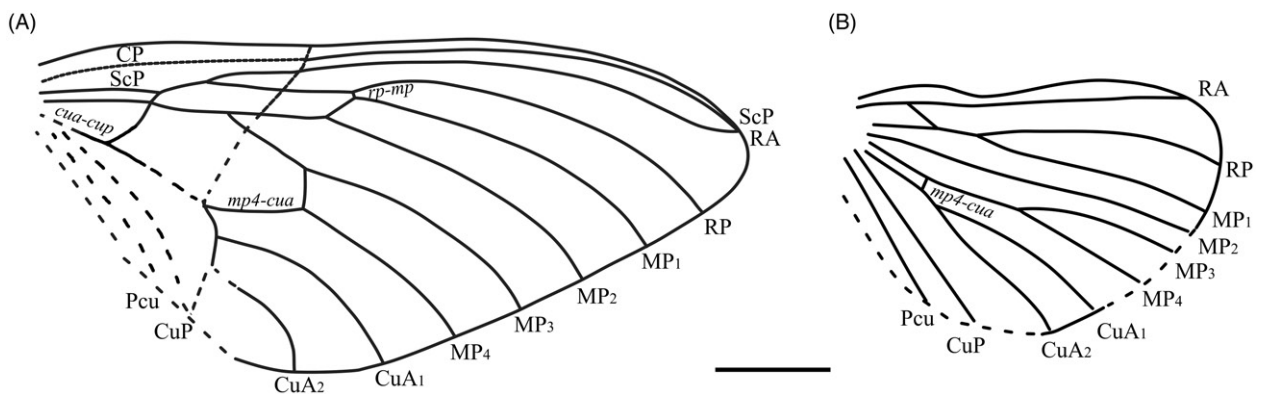


Fig. 3. Line drawings of the wings of *Talbragarocossus jurassicus* gen. et sp. nov. **A**, Forewing; **B**, Hind wing. Scale bar = 5 mm.

forewings with the position of the bifurcation of R closed to nodal line and hindwings having cross-vein *mp4-cua*.

Talbragarocossus jurassicus Chen, Beattie & Wang sp. nov. (Figs 2,3)

Etymology. The species name is a reference to the Jurassic age of the fossil.

Holotype. F.136849, part and counterpart; an insect with four wings and body preserved; housed in the Australian Museum, Sydney, Australia.

Unit and locality. Purlawaugh Formation, Upper Jurassic; Talbragar, New South Wales, Australia.

Diagnosis. Forewing about 34 mm long and 16 mm wide, with length/width ratio about 2.1; stem R long, branching into RA and RP basad of nodal line; MP branching into MP₁₊₂ and MP₃₊₄ basad of nodal line; CuA branching into CuA₁ and CuA₂ far away from its connection with cross-vein *mp₄-cua*. Hind wing with nodal indentation notable, at basal 0.37 of wing length; CuA strongly curved at its junction with cross-vein *mp₄-cua*, branching into CuA₁ and CuA₂ basad of nodal indentation.

Description. Body structures partly preserved. Head(?) much smaller than thorax, 5.4 mm wide. Pronotum 11.8 mm long, nearly twice as wide as long; lateral angles acute, not distinctly expanded. Mesonotum large, well developed, with several sparse extremely slender longitudinal carinae. Fore leg partly preserved with fore tibia slender and covered with dense tiny bristles.

Forewing about 34 mm long and about 16 mm wide, with length/width ratio about 2.1. Anterior margin nearly straight; outer margin oblique and nearly straight. Wing membrane stained with some irregular longitudinal stripes. Nodal indentation very weak, at about basal two-fifths of wing length. Nodal line partly preserved, weak and traceable as crease. Prenodal area distinctly reduced. Wing apex acute. Costal area reduced, very narrow, with length/width ratio about 5.6. Basal cell oblique, about one-fifth of wing length. Discal cell oblique, moderate, about one-quarter of wing length. CP straight. ScP fused with R just beyond basal cell, separating from ScP+RA at nodal line, independent in prenodal area and terminating at wing tip. R+MP+CuA long, parallel to ScP, branching into R, MP and CuA at tip of basal cell. Stem R long, branching into RA and RP basad of nodal line, and just basad of bifurcation of MP; RP strongly curved at its connection with cross-vein *rp-mp*. MP branching into MP₁₊₂ and MP₃₊₄ basad of nodal line; MP₁₊₂ and MP₃₊₄ bifurcating almost at the same level; MP₁ and MP₄ geniculate at their junctions with cross-veins *rp-mp* and *mp₄-cua*, respectively. CuA gravitating

towards wing base at base, geniculate at its connection with cross-vein *cua-cup*, and then nearly straight, branching into CuA₁ and CuA₂ far away from its connection with cross-vein *mp₄-cua*.

Hind wing 16.8 mm long, about half length of forewing. Nodal indentation notable, at basal 0.37 of wing length. Costal area long and narrow, with length/width ratio about 6.8; costal margin smoothly curved. R bifurcating into RA and RP at wing base and far away from nodal indentation; RP fused with MP₁ for a long interval. MP₁, MP₂ and MP₃₊₄ separating from stem MP at wing base; MP₃₊₄ connected to CuA by cross-vein *mp₄-cua*. Stem CuA strongly curved at its junction with cross-vein *mp₄-cua*, branching into CuA₁ and CuA₂ basad of nodal indentation. Pcu nearly straight.

Discussion

The 'late' Palaeontinidae appeared as early as the Late Jurassic, and evolved some key adaptive innovations in the wings to improve flight ability and thereby alleviate intense predation pressures from newly evolved insectivorous animal groups (Menon & Heads 2005, Menon *et al.* 2007, Wang *et al.* 2010). Just a few palaeontinids have been recorded from Late Jurassic strata (Table 1) with the Jurassic 'late' Palaeontinidae only known from the Tithonian of Germany, represented by *Eocicada microcephala* Oppenheim, 1885, *Prolystra lithographica* Oppenheim, 1885 and *Archipsyche eichstattensis* Handlirsch, 1906 (Wang *et al.* 2010). *Talbragarocossus* gen. nov. has the forewing with a reduced prenodal area, acute wing apex and long and straight outer margin, and also possesses hind wings of diminished size, indicating that the new Kimmeridgian–Tithonian genus is likely a representative of the early 'late' Palaeontinidae. These taxa from Germany and Australia suggest that the 'late' Palaeontinidae radiated rapidly after the group's derivation from the 'early' Palaeontinidae and widely prevailed in the Late Jurassic.

Palaeontinidae was represented by high taxonomic diversity and morphological disparity in the Middle Jurassic, especially in the Yanliao Biota (Wang *et al.*

Table 1. Geographic and stratigraphic distribution of palaeontinid genera and species in the Late Jurassic.

Unit, age and locality	Taxa and references
Solnhofen Fm., Tithonian; Solnhofen, Bavaria, Germany	<i>Eocicada microcephala</i> Oppenheim, 1885; <i>Prolystra lithographica</i> Oppenheim, 1885; <i>Archipsyche eichstattensis</i> Handlirsch, 1906 (Oppenheim 1885, Handlirsch 1906, Wang <i>et al.</i> 2010)
Glushkovo Fm., Tithonian; Daya locality, Chita, Russia Ukurei Fm., ?Tithonian; Shev'ya site, Chita, Russia	<i>Cicadomorpha milva</i> Shcherbakov, 1988 (Shcherbakov 1988) <i>Cicadomorpha parula</i> Shcherbakov, 1988 (Shcherbakov 1988)
Purlawaugh Fm., Kimmeridgian–Tithonian; Talbragar, New South Wales, Australia	<i>Talbragarocossus jurassicus</i> gen. et sp. nov. (this paper)
Karabastau Fm., Oxfordian–Kimmeridgian; Karatau-Karabastau, Chimkent, Kazakhstan	<i>Cicadomorpha punctulata</i> Martynov, 1926 (Martynov 1926)

2009, Chen *et al.* 2014, 2016). In the Late Jurassic, however, their diversity reduced sharply: the ‘early’ Palaeontinidae with elliptical or subtriangular forewings almost vanished and only *Cicadomorpha* spp. with somewhat triangular forewings persisted in Kazakhstan and Siberia (Table 1; Shcherbakov 1988). Although *Cicadomorpha* spp. bear somewhat triangular forewings, their hind wings are longer than half the forewing length, suggesting that they might not have been outstanding flyers compared with the ‘late’ Palaeontinidae (Wang *et al.* 2010). A significant radiation of the ‘late’ Palaeontinidae probably occurred in the Late Jurassic as mentioned above. Besides triangular forewings and diminished hind wings, the flight flexibility of the Late Jurassic ‘late’ Palaeontinidae likely improved significantly because some terminal branches of the longitudinal veins began to migrate towards the wing base (i.e., R on the forewing, R and MP on the hind wing), which is an adaptation to local torsion of the wing (Wootton & Kukalová-Peck 2000, Wang *et al.* 2009, Chen *et al.* 2016). In the Late Jurassic, paravians further radiated and diversified, resulting in the appearance of avians capable of powered flight (Xu *et al.* 2014, Brusatte 2017). Continuous predation pressures of these flying animals might have led to the sharp decline of the ‘early’ Palaeontinidae in the early Late Jurassic and, correspondingly the more adept flying ‘late’ Palaeontinidae arose and began to radiate significantly.

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Disclosure Statement

No potential conflict of interest was reported by the authors.

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