Planthoppers (Insecta: Hemiptera: Fulgoromorpha: Fulgoroidea: Surijokocixiidae) of the Queensland Triassic

Kevin J. LAMBKIN

Honorary Research Fellow, Biodiversity and Geosciences Program, Queensland Museum, PO Box 3300, South Brisbane, Qld 4101, Australia. Email: megapsychops@bigblue.net.au

Citation: Lambkin, K.J. 2020. Planthoppers (Insecta: Hemiptera: Fulgoromorpha: Fulgoroidea: Surijokocixiidae) of the Queensland Triassic. *Memoirs of the Queensland Museum-Nature*. 60: 123–131. Brisbane. ISSN 2204-1478 (Online), ISSN 0079-8835 (Print). Accepted: 12 March 2020. First published online: 4 June 2020.

https://doi.org/10.17082/j.2204-1478.62.2020.2019-04

LCID urn:lsid:zoobank.org:pub:24C5EB15-59A9-4631-B624-8CB06AD4004A

ABSTRACT

The suborder Fulgoromorpha, highly diverse and speciose today, was a minor component of the Cicadomorpha-dominant hemipteran fauna of the Queensland Triassic known only from five tegmen specimens of three species in three genera of the extinct family Surijokocixiidae: *Tricrosbia minuta* Evans, 1971, and *Crosbixius carsburgi* gen. et sp. nov., from the Late Triassic (Norian) Mount Crosby Formation of the Ipswich Coal Measures, and *Karesmina punicea* gen. et sp. nov. from the Middle Triassic (Anisian) Esk Formation. The Surijokocixiidae are otherwise known from four Permian genera from Russia and unnamed Triassic species from Kyrgyzstan and China. *Tricrosbia* Evans, 1971, is distinguished from other genera of the family by its simple MP1+2, and the very shallow fork of CuA. *Crosbixius* is similar to the Permian *Surijokocixius* Becker-Migdisova, but differs in the costal space of equal width along its entire length, the more basal fork of ScP+RA and RP, and mp-cu running between MP and CuA1 rather than MP3+4 and CuA1. *Karesmina* is distinguished by its larger size (tegmen length 9 mm, < 6 mm in the others), backwardly inclined ir, and peculiar structure of RP and MP1+2. *Tricrosbia* and *Crosbixius* were the last of the Surijokocixiidae which were extinct by the end of the Triassic, succeeded in the Jurassic by a more diverse and modern looking fulgoromorph fauna, dominated by numerous species of the extinct Fulgoridiidae. Confirmation of the presence of the Surijokocixiidae in the Mount Crosby Formation adds another family to the Ipswich Coal Measures hemipteran fauna, a transition insect fauna typical of the Triassic, with a mix of survivors from the Permian which did not last beyond the Triassic (Dunstaniidae, Scytinopteridae, Surijokocixiidae) or Jurassic (Dysmorphoptilidae), peculiar Triassic endemics (Chiliocyclidae, Mesogereonidae, Ipsviciidae), the newly emerged Hylicellidae which survived until the Cretaceous, and lastly more modern forms, Archijassidae, the earliest record of the extant Membracoidea, and Tettigarctidae, the hairy cicadas, which still exist today.

❑ *Insecta, Hemiptera, Fulgoromorpha, Fulgoroidea, Surijokocixiidae, Tricrosbia, Mount Crosby Formation, Esk Formation, fossil insects.*

Triassic sedimentary formations of south-eastern Queensland have yielded a numerous and diverse hemipteran fauna comprising Cicadomorpha (including Scytinopteroidea), Sternorrhyncha and Heteroptera (Jell 2004). Thus far however, just one specimen has been recorded of the diminutive *Tricrosbia minuta* Evans, 1971, the only representative of the highly diverse extant suborder Fulgoromorpha, the planthoppers (Szwedo 2018). Through patient and persistent field work at two Triassic fossil insect sites in south-eastern Queensland, local enthusiast Allan Carsburg has collected three additional fulgoromorph tegmen specimens – a second specimen of *T. minuta* and a specimen of an undescribed species from the Mount

Crosby Formation, and a specimen of another undescribed species from the Esk Formation. A search of the collections of the Queensland Museum has also revealed a second specimen of the same undescribed Mount Crosby species. The two new species are described, and *T. minuta* is redescribed herein.

The three species belong to the extinct fulgoromorph family Surijokocixiidae, established by Shcherbakov (2000) for the Permian *Surijokocixius* Becker-Migdisova, 1961, *Scytocixius* Martynov, 1937, *Boreocixius* Becker-Migdisova, 1955, (Russia) and the Triassic *Tricrosbia* Evans, 1971, (Queensland). Shcherbakov (2016) added the Russian Permian *Paraprys* Aristov and Rasnitsyn, 2014, to the family's inventory; unnamed specimens of the family have also been recorded from the Triassic of Kyrgyzstan (Shcherbakov 2011) and China (Zheng *et al*. 2018). The surijokocixiids were quite small plant-hoppers, with tegmina usually less than 6 mm long, the new Esk species being the exception at about 9 mm. The family is characterised by a tegmen 'usually coriaceous with membrane smooth, costal area broad, precostal carina wide, C slightly angulate near base, R and CuA deeply forked, M at least twice forked, *cup-pcu* absent, Pcu+A1 joining claval suture' (Shcherbakov 2004). While the fulgoromorph affinities of the Surijokocixiidae are generally accepted, there are different views on its position within the Fulgoromorpha. Shcherbakov (1996, 2004, 2016) has proposed placement of Surijokocixiidae in the Fulgoroidea, as that superfamily's most primitive family, arguing that these 'Permian [and Triassic] planthoppers are already cixiid-like, similar to living ones enough to be included in Fulgoroidea' (Shcherbakov 2004). On the other hand, Szwedo *et al*. (2004), Bourgoin and Szwedo (2008) and Szwedo (2018) have proposed that the family is sufficiently distinct to warrant allocation to its own fulgoromorph superfamily, Surijokocixioidea, separate from the Fulgoroidea. The superfamily classification of Shcherbakov (1996, 2004, 2016) has been adopted herein.

THE FOSSIL LOCALITIES

The four Mount Crosby Formation specimens examined herein were collected at Mount Crosby Fossil Insect Localityies; locality B, a water pipeline cutting near Allawah Road, at -27.552° 152.782°, and Locality C, a gully running into the Brisbane River, at -27.550° 152.769° (details in Tindale 1945, Allen 1961). The two localities are in the vicinity of the suburb of Mount Crosby, approximately 10 km north of the town of Ipswich in south-eastern Queensland.The Mount Crosby Formation lies near the base of the Ipswich Coal Measures (Purdy and Cranfield 2013) which have been dated as Late Triassic (Norian) (Raven *et al*. 2015). The Esk Formation fossil insect site is in pinkish siltstone of the Middle Triassic (Anisian) Esk Formation (Purdy 2013) exposed near 5 Mile Creek on the western shore of Lake Wivenhoe in south-eastern Queensland, at -27.309° 152.521°. The only ones described thus far are a species of Titanoptera (Jell & Lambkin 1992), and two insects Hemiptera: Scytinopteridae (Lambkin 2016).

MATERIALS AND METHODS

All specimens examined are single tegmina. Specimens with both part and counterpart have an a/b number, otherwise only the part is present. The length was measured from the base of R to the apex of the tegmen, and the width from the costal margin in a perpendicular line to the apex of the clavus. Venational and other tegminal terminology follows that of Bourgoin *et al*. (2015), including the use of the term 'peripheral membrane' for the 'special and very narrow marginal area, extending from the nodus to the apex of the clavus' (Bourgoin *et. al*. 2015). The only exception is that I have used the term precostal carina for the ventrally-expressed carina along the costal margin and converging with it near the node (Shcherbakov 2016). The abbreviations used are as follows: bc, basal cell; pc, precostal carina; pm, peripheral membrane; ScP, subcosta posterior; R, radius; RA, radius anterior; RP, radius posterior; MP, media posterior; CuA, cubitus anterior; CuP, cubitus posterior; ir, crossvein between RA

and RP; rp-mp, crossvein between RP and MP; mp-cua, crossvein between MP and CuA; C1a, apical cell between ScP and RA.

The photographs were focus-stacked with Zerene Stacker software from source images taken with a Canon 5S camera on a Visionary Digital BK-Plus Lab System. For ease of comparison all specimens are illustrated as right tegmina. The original photographs of left tegmen specimens have therefore been mirrored, as indicated in the figure captions. All specimens are in the collection of the Queensland Museum, with designation QMF.

SYSTEMATICS

ORDER Hemiptera Linnaeus, 1758

SUBORDER Fulgoromorpha Evans, 1946

SUPERFAMILY Fulgoroidea Latreille, 1807

FAMILY Surijokocixiidae Shcherbakov, 2000

Tricrosbia Evans, 1971

Tricrosbia Evans, 1971: 145; Hamilton, 1992: 428; Shcherbakov, 2000: 251; Jell, 2004: 64; Szwedo *et al.*, 2004: 41.

Type species. *Tricrosbia minuta* Evans, 1971, by original designation.

Emended diagnosis. Tegmen small, less than 4 mm long, *c.* 2 times longer than wide; costal and apical margins evenly rounded; costal margin and ScP+R→ScP+RA more or less parallel, costal space therefore of equal width for entire length; fork of ScP and RA distal to level of primary MP fork; ScP and RA entering antero-apical margin; ScP more or less upright, RA slightly concave, the cell between them (C1a of Bourgoin *et al*. 2015) narrowly triangular; fork of ScP+RA and RP slightly proximal to ½ tegmen length, about midway between basal cell and fork of ScP and RA; RP with 2 branches, directed towards apical margin; *ir* not detected; one *rp-mp*, upright, between RP and MP1+2 ; MP1+2 simple, MP3+4 with 2 or 3 branches; *mp-cua* between MP3+4 and CuA1; CuA shallowly forked, nearly at apex of clavus, at same level as primary MP fork, with 2 short, more or less straight parallel branches, directed towards postero-apical margin.

Notes. The diagnosis is based on an analysis of the descriptions and figures of three of the previously described genera of the family, *Surijokocixius*, *Scytocixius* and *Boreocixius* (Martynov 1937, Rohdendorf *et al*. 1961, Becker-Migdisova 1962) The fourth genus, *Parapryg*, is too poorly preserved and documented to be included in the analysis (Shcherbakov 2016). *Tricrosbia* is clearly distinct from the three genera in the position of the fork of ScP+RA and RP (much more distal in *Surijokocixius* and *Scytocixius*, but much more basal (just beyond basal cell) in *Boreocixius*), the simple MP1+2 (at least 2-branched in the others), and the very shallow fork of CuA, at the same level as the primary MP fork (much deeper in the others, at around ½ tegmen length, far basal to the primary MP fork). Additionally it differs from *Surijokocixius* in the costal space of equal width over its entire length rather than expanded basally, the much smaller C1a cell, and the more or less straight branches of CuA (strongly curved posteriorly in *Surijokocixius*); from *Scytocixius* in the much smaller C1a cell; and from *Boreocixius* in ScP and RA entering the antero-apical rather than the anterior margin, RP with 2 rather than 3 branches, the presence of *rp-mp*, and the more or less straight branches of CuA (at least CuA1 strongly curved in *Boreocixius*).

Tricrosbia was considered by Evans (1971) as Fulgoroidea, by Hamilton (1992) as Cicadomorpha: Hylicellidae, and by Jell (2004) as Fulgoridae. Shcherbakov (2000) agreed with Evans on the fulgoroid affinities of the genus and included it in his newly established family Surijokocixiidae within the Fulgoroidea. Szwedo *et al.* (2004) listed *Tricrosbia* under Surijokocixiidae, and with Bourgon and Szwedo (2008) and Szwedo (2018) placed the family in its own fulgoromorph superfamily, Surijokocixioidea.

Tricrosbia minuta Evans, 1971
(Fig. 1)

Tricrosbia minuta Evans, 1971: 267; Jell, 2004: 64, one unnumbered fig.; Lambkin, 2019a: 392–393.

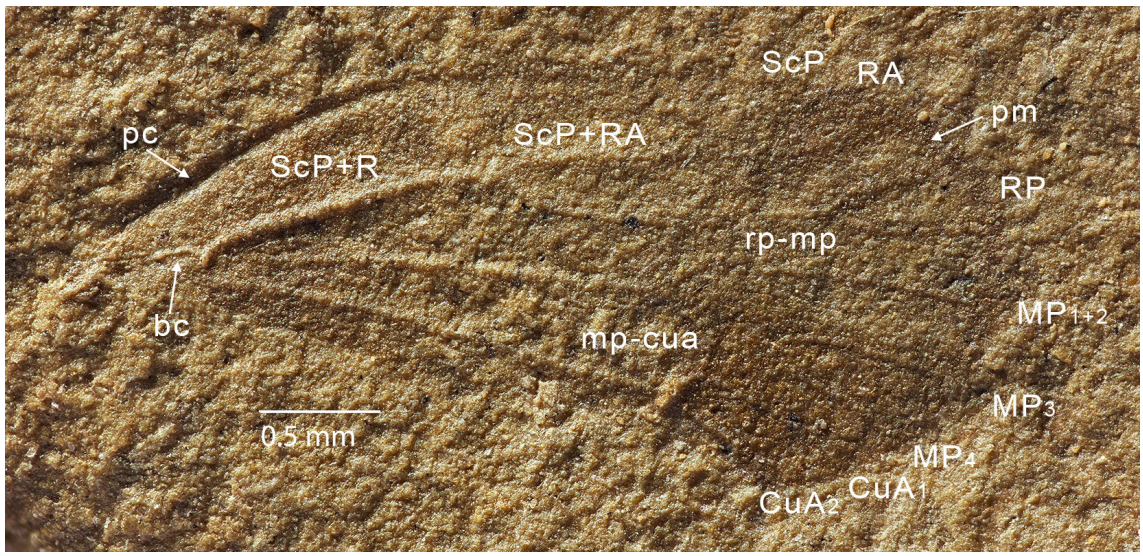

FIG. 1. *Tricrosbia minuta* Evans, 1971, QMF60132. bc, basal cell; pc, precostal carina; pm, peripheral membrane.

Material examined. Holotype tegmen QMF6520, Mount Crosby Formation, Fossil Insect Locality C. One other tegmen, QMF60132, Mount Crosby Formation, Fossil Insect Locality B, collected by Allan Carsburg. Late Triassic (Norian).

Description. Tegmen 3.4 (holotype), 3.8 mm long, 1.8 mm wide (only measurable in QMF60132); MP3+4 with 2 branches in QMF60132, 3 in holotype; clavus preserved in holotype only, Pcu+A1 directed towards apex; typical fulgoroid post-nodal peripheral membrane clearly developed; membrane (post-nodal area of tegmen) darkly shaded, corium pale.

Notes. Evans' holotype tegmen is fairly well preserved, and even though it has a glob of resin covering the antero-medial area, much of the marginal venation is still visible. In considering Evans' illustration (Evans 1971, fig. 1), however, it should be noted that the base of the tegmen is not preserved, and that neither the oblique inter-radial crossvein, nor the long crossvein between MP and CuA could be detected in the present study.

Crosbixius gen. nov.

Type species. *Crosbixius carsburgi* sp. nov.

Etymology. The generic name, which is masculine, is a combination of 'Crosb' from Mount Crosby, and 'ixius', part of the standard generic root 'cixius'.

Diagnosis. Tegmen small, less than 6 mm long, *c.* 2.5 times longer than wide; costal margin evenly rounded, apical margin somewhat truncate postero-apically; costal margin and ScP+R→ScP+RA more or less parallel, costal space therefore of equal width for entire length; fork of ScP and RA distal to level of primary MP fork; ScP and RA entering antero-apical margin; ScP fairly upright, slightly curved, RA markedly concave, C1a cell broadly ovate; fork of ScP+RA and RP slightly proximal to ½ tegmen length, about midway between basal cell and fork of ScP and RA; RP simple, directed towards apical margin; *ir* short, forwardly inclined; one *rp-mp*, upright, between RP and MP1+2 ; MP1+2 with 2 branches, MP3+4 with 3; *mp-cua* between MP and CuA1; CuA deeply forked, at *c.* ½ tegmen length, well before apex of clavus and primary MP fork, with 2 long parallel branches curved towards posterior margin.

Notes. *Crosbixius* is quite similar to the Russian Permian genus *Surijokocixius* differing only in the costal space of equal width over its entire length rather than expanded basally, the more

basal fork of ScP+RA and RP, and *mp-cua* running between MP and CuA1, rather than MP3+4 and CuA1. It differs from *Scytocixius* in these same three characters, and also in having a branched rather than simple MP3+4, and curved, rather than straight branches of CuA. It differs from *Boreocixius* in the more distal fork of ScP+RA and RP, ScP and RA entering the antero-apical rather than the anterior margin, the broader C1a cell, a simple rather than 3-branched RP, and five rather than seven MP branches; and from *Tricrosbia* in its larger size, differently shaped C1a cell, presence of *ir*, simple RP, 2-branched rather than simple MP1+2, and the deeply forked CuA with curved branches.

Crosbixius carsburgi sp. nov.
(Fig. 2)

Material examined. Holotype tegmen QMF60133, Mount Crosby Formation, Fossil Insect Locality B, collected by Allan Carsburg. Paratype tegmen QMF6978a/b, same locality. Late Triassic (Norian).

Description. Tegmen 5.7 mm long, 2.4 mm wide (both specimens); clavus not preserved; typical fulgoroid post-nodal peripheral membrane clearly developed; base of costal space, base of CuA1 cell, around most veins, and two indistinct posteriorly convergent fascia on the membrane darkly shaded.

Notes. The specific name honours Allan Carsburg of Brisbane who collected the holotype.

Karesmina gen. nov.

Type species. *Karesmina punicea* sp. nov.

Etymology. The generic name is a combination the given names Karen and Jasmine, the spouse and daughter of the collector Allan Carsburg, and is feminine.

Diagnosis. Tegmen larger, *c.* 9 mm long, *c.* 2.5 times longer than wide; apical margin somewhat truncate antero-apically; costal margin and ScP+R→ScP+RA apparently more or less parallel, base of costal space not preserved; fork of ScP and RA at about same level as primary MP fork; ScP and RA entering antero-apical margin; ScP forwardly inclined, fairly straight, RA slightly concave, directed apically, C1a cell broadly triangular; fork of ScP+RA and RP slightly proximal to ½ tegmen length, about midway between basal cell and fork of ScP and RA; RP apparently with 2 branches, directed towards apical margin; *ir* long, backwardly inclined; two apparent *rp-mp*, the proximal one strongly backwardly inclined, between RP and MP1+2 which is deflected anteriorly at this point; the apparent distal *rp-mp* very short, between ?RP2 and MP1 which is also deflected anteriorly; MP1+2 with 3 branches, MP3+4 with 2; *mp-cua* between MP3+4 and CuA1; CuA deeply forked, at *c.* ½ tegmen length, well before apex of clavus and primary MP fork, with 2 long branches curved towards posterior margin and convergent apically.

Notes. As evident in Fig. 3, the tegmen of the type species is indistinctly preserved (? and possibly deformed) in the area of MP1+2 and the distal section of RP. The interpretation of the veins and crossveins in this area can therefore only be considered as tentative. The backwardly inclined vein between RP and MP1+2 is in the same position as the single *rp-mp* in other surijokjocixiids (for example, *C. carsburgi*, see Fig. 2A), and has therefore been interpreted as this crossvein. *Karesmina* gen. nov. differs from all other known surijokocixiids in its larger size (tegmen length 9 mm, length no more than 6 mm in the others), truncate antero-apical margin, long, backwardly inclined *ir*, and peculiar structure of RP and MP1+2.

Karesmina punicea sp. nov.
(Fig. 3)

Material examined. Holotype tegmen QMF60134a/b, Esk Formation, near 5 Mile Creek on the western shore of Lake Wivenhoe, south-eastern Queensland, collected by Allan Carsburg. Middle Triassic (Anisian).

Description. Tegmen fragment 6.4 mm long (indicating a total length of *c.* 9 mm), 4.2 mm wide; clavus not preserved; typical fulgoroid post-nodal peripheral membrane preserved around antero-apical margin; any colour pattern apparently not preserved (darker areas in Fig. 3 are shadows).

FIG. 2. *Crosbixius carsburgi* gen. *et* sp. nov.; **A**, holotype QMF60133; **B**, paratype QMF6978a (mirrored).

Notes. The specific name is the Latin adjective for pink and refers to the colour of the siltstone in which the type specimen is preserved.

DISCUSSION

While just a few fossil Hemiptera have been found in the Esk Formation, over the last 100+ years hundreds of Hemiptera specimens have been collected from the Mount Crosby Formation and the nearby Late Triassic Blackstone Formation (Lambkin 2019a). The finding of only five specimens of Fulgoromorpha in that time demonstrates their rarity, consistent with Shcherbakov's (2004) observation that the Fulgoromorpha were a minor component of the pre-Jurassic hemipteran fauna. Notwithstanding this rarity, the five specimens represent three species in three genera, suggesting at least some

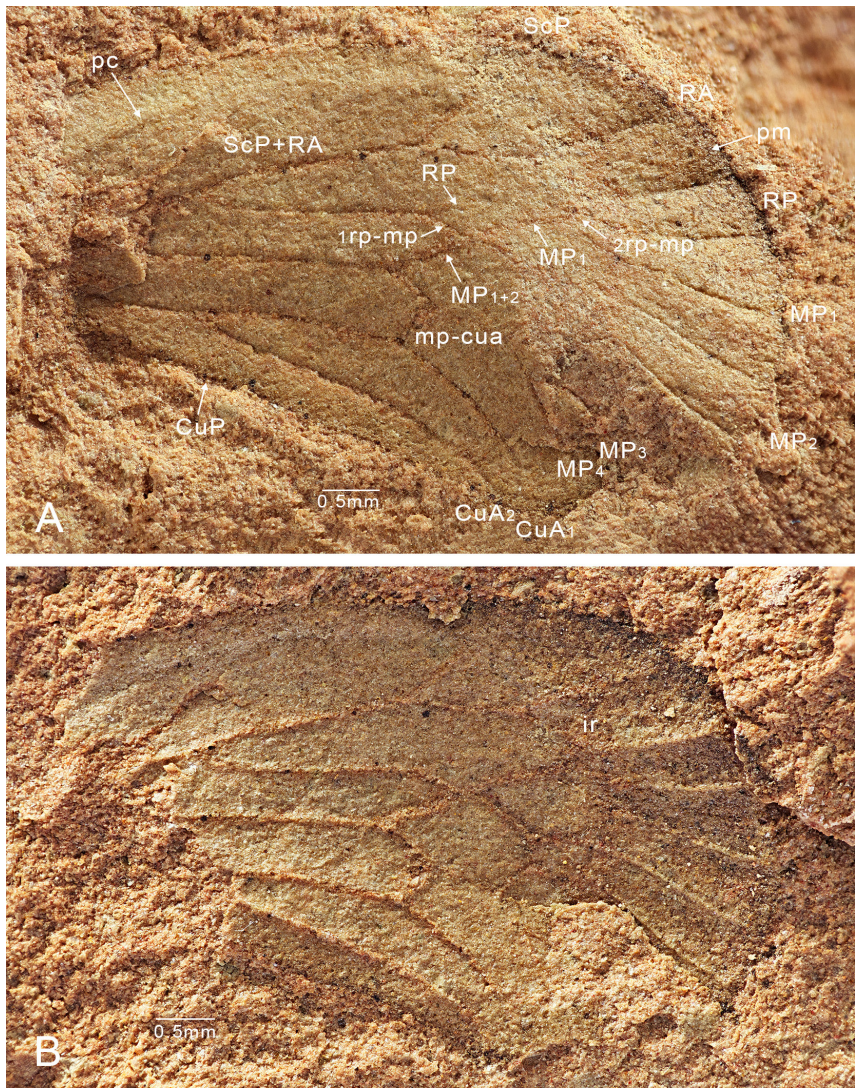

FIG. 3. *Karesmina punicea* gen. et sp. nov. holotype; **A**, QMF60134a (part) (mirrored); **B**, QMF60134b (counterpart), to show ir.

diversity in the fulgoromorph fauna of the Queensland Triassic.

The surijokocixiids were extinct by the end of the Triassic, succeeded in the Jurassic by a much more diverse fulgoromorph fauna, dominated by numerous species of the extinct Fulgoridiidae (Li *et al*. 2011, Szwedo *et al*. 2011). *Tricrosbia* and *Crosbixius* from the Late Triassic (Norian) (~227 – ~208.5 Ma) (International Chronostratigraphic Chart v.2019/5) Mount Crosby Formation were the last of the surijokocixiids. The earliest records of the family, and therefore the oldest fulgoroids, were *Surjokocixius* and *Scytocixius* from the Middle Permian and *Boreocixius* and *Paraprys* from the Late Permian of Russia (Shcherbakov 2008a, 2016). The other Triassic records of the family were from older deposits than

Mount Crosby. The Madygen Formation of Kyrgyzstan (Shcherbakov 2011) has been dated as mid-Triassic (late Ladinian–early Carnian, 237 ± 2 Ma) (Voigt *et al*. 2017), the insect-bearing layer of the Tongchuan Formation of China as Middle Triassic (late Ladinian, 238 – 237 Ma) (Zheng *et al*. 2018), and the Esk Formation (*K. punicea* herein) as Middle Triassic (Anisian, 247.2 – ~242 Ma).

Confirmation of the presence of the Surijokocixiidae in the Mount Crosby Formation adds another family to the Late Triassic (Norian) Hemiptera '*Auchenorrhyncha*' from the long-known and well-collected Mount Crosby and Blackstone formations of the Ipswich Coal Measures. Even though the family composition of the two formations differs, probably due to habitat difference (Lambkin 2019a), the fauna as a whole is a classic transitional insect fauna typical of the Triassic (Shcherbakov 2008b, Zheng *et al*. 2018), with a mix of survivors from the Permian which did not last beyond the Triassic (Dunstaniidae, Scytinopteridae, Surijokocixiidae) or Jurassic (Dysmorphoptilidae), peculiar Triassic endemics (Chiliocyclidae, Mesogereonidae, Ipsviciidae), the newly emerged Hylicellidae which survived until the Cretaceous, and lastly the more modern forms, Archijassidae, the earliest record of the extant Membracoidea (Shcherbakov 2012), and Tettigarctidae, the hairy cicadas, which still exist today (Lambkin 2019b).

ACKNOWLEDGEMENTS

I am very grateful to Allan Carsburg of Brisbane who kindly allowed me to examine his Mount Crosby and Esk specimens. I am indebted to Geoff Thompson of the Queensland Museum who took the excellent photographs, and to my daughter, Jennifer Negline, who prepared the plates. Kristen Spring and Deb Lewis of the Queensland Museum were, as always, unfailingly helpful in allowing access to specimens in their care.

LITERATURE CITED

Allen, R.J. 1961. The Kholo Sub-group of the Ipswich Coal Measures. *Geological Survey of Queensland Publication* **300**: 1–14.

Becker-Migdisova, E. E. 1962. Superorder Rhynchota. Insects with proboscis. Pp 216–317. *In* Rohdendorf, B.B. (ed.) *Fundamentals of Paleontology, vol. 9, Arthropoda, Tracheata, Chelicerata*. (Akademiya Nauk SSSR, Moscow). [In Russian; English translation 1991, Smithsonian Institution Libraries and The National Science Foundation, Washington, DC].

Bourgoin, T. & Szwedo, J. 2008. The 'cixiid-like' fossil planthopper families. *Bulletin of Insectology* 61: 107–108.

Bourgoin, T., Wang, R-R., Asche, M., Hoch, H., Soulier-Perkins, A., Stroiński, A., Yap, S. & Szwedo, J. 2015. From micropterism to hyperpterism: recognition strategy and standardized homology-driven terminology of the forewing venation patterns in planthoppers (Hemiptera: Fulgoromorpha). *Zoomorphology* **134**: 63–77 https://doi.org/10.1007/s00435-014-0243-6.

Evans, J.W. 1971. Some Upper Triassic Hemiptera from Mount Crosby, Queensland. *Memoirs of the Queensland Museum* **16**: 145–152.

Hamilton, K.G.A. 1992. Lower Cretaceous Homoptera from the Koonwarra Fossil Bed in Australia, with a new superfamily and synopsis of Mesozoic Homoptera. *Annals of the Entomological Society of America* **85**: 423–430 https://doi.org/10.1093/aesa/85.4.423.

Jell, P.A. 2004. *Fossil insects of Australia. Memoirs of the Queensland Museum* **50**: 1–124.

Jell, P.A. & Lambkin, K.J. 1992. Middle Triassic orthopteroid (Titanoptera) insect from the Esk Formation at Wivenhoe Dam. *Memoirs of the Queensland Museum* **33**: 258.

Lambkin, K.J. 2016. Revision of the Scytinopteridae (Hemiptera: Cicadomorpha: Scytinopteroidea) of the Queensland Triassic. *Zootaxa* **4117**: 580–590 https://doi.org/10.11646/zootaxa.4117.4.9.

Lambkin, K.J. 2019a. Revision of *Mesothymbris* Evans, 1956, from the Late Triassic of Mount Crosby, Queensland (Hemiptera: Cicadomorpha: Hylicelloidea: Hylicellidae). *Zootaxa* **4629**: 389–396 https://doi.org/10.11646/zootaxa.4629.3.6.

Lambkin, K.J. 2019b. *Mesodiphthera* Tillyard, 1919, from the Late Triassic of Queensland, the oldest cicada (Hemiptera: Cicadomorpha: Cicadoidea: Tettigarctidae). *Zootaxa* **4567**: 358–366 https://doi.org/10.11646/zootaxa.4567.2.8.

Li, S., Szwedo, J., Ren, D. & Pang, H. 2011. *Fenghuangor imperator* gen. et sp. nov. of Fulgoridiidae from the Middle Jurassic of Daohugou Biota (Hemiptera:

Fulgoromorpha). *Zootaxa* **3094**: 52–62 https://doi.org/10.11646/zootaxa.3094.1.4.

Martynov, A.V. 1937. Permian fossil insects from Kargala and their relationships. *Trudy Paleontologischeskogo Instituta Akademii Nauk SSSR* **7**: 1–92. [In Russian, with English summary]

Purdy, D.J. 2013. Esk Basin. Pp 387–391. *In* Jell, P. A. (ed.) *Geology of Queensland*. (Geological Survey of Queensland: [Brisbane]).

Purdy, D.J. & Cranfield, L.C. 2013. Ipswich Basin. Pp 391–396. *In* Jell, P.A. (ed.) *Geology of Queensland*. (Geological Survey of Queensland: [Brisbane]).

Raven, R.J., Jell, P.A. & Knezour, R.A. 2015. *Edwa maryae* gen. et sp. nov. in the Norian Blackstone Formation of the Ipswich Basin – the first Triassic spider (Mygalomorphae) from Australia. *Alcheringa* **39**: 259–263 https://doi.org/10.1080/03115518.2015.993300.

Rohdendorf, B.B., Becker-Migdisova, E.E., Martynova, O.M. & Sharov, A.G. 1961. Paleozoic insects of Kuznetsk Basin. *Trudy Paleontologischeskogo Instituta Akademii Nauk SSSR* **85**: 1–705. [In Russian]

Shcherbakov, D. E. 1996. Origin and evolution of the Auchenorrhyncha as shown by the fossil record. Pp 31–45. *In* Schaefer, C.W. (ed.), *Studies on Hemipteran Phylogeny*. (Entomological Society of America, Lanham, Maryland).

Shcherbakov, D.E. 2000. Permian faunas of Homoptera (Hemiptera) in relation to phytogeography and the Permo-Triassic crisis. *Paleontological Journal* **34**: 251–267.

Shcherbakov, D.E. 2004. On Permian and Mesozoic Fulgoroidea. Pp 68–70. *In* Kerzhner, I. M. (ed.) *Third European Hemiptera Congress Abstracts*. (Russian Academy of Sciences: St. Petersburg).

Shcherbakov, D.E. 2008a. On Permian and Triassic insect faunas in relation to biogeography and the Permian–Triassic crisis. *Paleontological Journal* **42**: 15–31.

Shcherbakov, D.E. 2008b. Insect recovery after the Permian/Triassic crisis. *Alavesia* **2**: 125–131 https://doi.org/10.11646/zootaxa.2836.1.1.

Shcherbakov, D.E. 2011. New and little-known families of Hemiptera Cicadomorpha from the Triassic of Central Asia – early analogs of treehoppers and planthoppers. *Zootaxa* **2836**: 1–26.

Shcherbakov, D.E. 2012. More on Mesozoic Membracoidea (Homoptera). *Russian Entomological Journal* **21**: 15–22 https://doi.org/10.15298/rusentj.21.1.02.

Shcherbakov, D.E. 2016. On the taxonomic position of the genus *Parapryg* (Homoptera, Fulgoroidea) and classification of Protorthoptera and related groups. *Paleontological Journal* **50**: 412–413 https://doi.org/10.1134/S0031030116040110.

Szwedo, J. 2018. The unity, diversity and conformity of bugs (Hemiptera) through time. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **107**: 109–128 https://doi.org/10.1017/S175569101700038X.

Szwedo, J., Bourgoin, T. & Lefebvre, F. 2004. *Fossil planthoppers (Hemiptera: Fulgoromorpha) of the world An annotated catalogue with notes on Hemiptera classification*. (Studio 1: Warsaw).

Szwedo, J., Wang, B. & Zhang, H.-C. 2011. An extraordinary Early Jurassic planthopper from Hunan (China) representing a new family Qiyangiricaniidae fam. nov. (Hemiptera: Fulgoromorpha: Fulgoroidea). *Acta Geologica Sinica* **85**: 739–748 https://doi.org/10.1111/j.1755-6724.2011.00479.x.

Tindale, N.B. 1945. Triassic insects of Queensland. 1. *Eoses*, a probable lepidopterous insect from the Triassic beds of Mount Crosby, Queensland. *Proceedings of the Royal Society of Queensland* **56**: 37–46.

Voigt, S., Buchwitz, M., Fischer, J., Kogan, I., Moisan, P., Schneider, J. W., Spindler, F., Brosig, A., Preusse, M., Scholze, F. & Linnemann, U. 2017. Triassic life in an inland lake basin of the warm-temperate biome – the Madygen Lagerstätte (southwest Kyrgyzstan, Central Asia). Pp 65–84. *In* Fraser, N.C. & Sues, H.D. (eds) *Terrestrial conservation Lagerstätten: windows into the evolution of life on land*. (Dunedin Academic Press: Edinburgh).

Zheng, D., Chang, S-C., Wang, H., Fang, Y., Wang, J., Feng, C., Xie, G., Jarzembowski, E. A., Zhang, H. & Wang, B. 2018. Middle-Late Triassic insect radiation revealed by diverse fossils and isotopic ages from China. *Science Advances* **4**(9): 1–7 https://doi.org/10.1126/sciadv.aat1380.