# First North American occurrence of hairy cicadas discovered in the Cenomanian (Late Cretaceous) of Labrador, Canada

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We report the discovery of *Maculaferrum blaisi* gen. et sp. nov, the first occurrence of the family Tettigarctidae, informally known as hairy cicadas, in North America. *Maculaferrum blaisi* is part of a new collection assembled during recent fieldwork in the Redmond Formation, Labrador, Canada, near Schefferville. It consists in a single isolated forewing whose venational characters allow a classification to Tettigarctinae at the subfamily level. Classification at a higher level remains uncertain since it displays a combination of characters supposedly unique to tribes Protabanini, Meunierini, and Tettigarctini. Thus, this discovery adds credence to suggestions of a revision of the definitions of these tribes since they seem to be based on many convergent or plesiomorphic characters. Remnants of a spotted pattern on the wing membrane and probable setae along some veins are also preserved. Observations of the holotype's fine anatomical characters have been facilitated by the use of Reflectance Transformation Imaging (RTI), an emerging method for the visualization of compression and impression fossils. Considering that the estimated age of the Redmond Formation is the Cenomanian (Late Cretaceous), the discovery of *M. blaisi* contributes to a very recent expansion of the tettigarctid fossil record that fills a gap between Early Cretaceous and Cenozoic genera. It suggests that hairy cicadas maintained a global distribution and thrived in a variety of climate regimes well into the Late Cretaceous, and that their competitive exclusion by singing cicadas occurred definitely closer to the end of the Cretaceous, or even during the Cenozoic. This discovery is only the start of a thorough description of the recently expanded entomofauna in the Cretaceous of Labrador.

Key words: Insecta, Cicadoidea, Tettigarctidae, Cretaceous, Cenomanian, Redmond Formation, North America.

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## Introduction

Tettigarctidae (hairy cicadas) were the dominant family within Cicadoidea for much of the Mesozoic (Shcherbakov 2009; Moulds 2018). They are distinguished from sister family Cicadidae (modern singing cicadas) by a greatly expanded pronotum covering much of the mesonotum, forewings with a conspicuous nodal line, a posterior radial sector (RP) emerging closer to the wing base than to the node, all anal veins running separately, male genitalia with styles, hind coxae overhanging the abdomen, the presence of tarsal empodia, absence of tympana, and a nervous system with separated thoracic ganglia (Evans 1941; Moulds 1990, 2005). Another distinctive tettigarctid character is the presence of rudimentary tymbals that produce low-intensity, substrate-transmitted acoustic signals, instead of well-developed tympanal auditory organs that lead to loud airborne calls characteristic of singing cicadas (Claridge et al. 1999).

Today, Cicadidae number nearly 2900 species worldwide (Bartlett et al. 2018) as a result of a radiation that probably occurred in the Palaeogene (Kaulfuss and Moulds 2015), while Tettigarctidae are represented by only two species of *Tettigarcta* White, 1845: *T. crinita* Distant, 1883 in southeastern Australia, and *T. tomentosa* White, 1845 in Tasmania. Both species are restricted to cool subalpine forests to which they are adapted with dense insulating hairs, and have a nocturnal habit unique among extant cicadoids (Claridge et al. 1999; Shcherbakov 2009). This is a very specialized lifestyle in a far more restricted range than that occupied by this once diverse family in the Mesozoic (Boulard and Nel 1990; Zeuner 1944). While the diet of tettigarctids shifted from gymnosperm to angiosperm herbivory, likely in response to the floral turnover that occurred in the middle of the Cretaceous, cicadids seem to have appeared at the peak of this angiosperm radiation and retained them as hosts throughout their history (Labandeira 2014). This may have conferred cicadids a competitive advantage resulting in the displacement of tettigarctids from most of their original range until a single lineage remained in biogeographical isolation in southern Australia (Zeuner 1944; Wang and Zhang 2009).

Until recently, the tettigarctid fossil record contained 29 genera and 46 species spread into subfamilies Cicadoprosbolinae and Tettigarctinae (Moulds 2018; Fu et al. 2019; Jiang et al. 2019; Lambkin 2019). The oldest members of the family are *Mesodiphthera grandis* Tillyard, 1919, *Tardilly prosboloides* (Tillyard, 1922) and *Tardilly dunstani* (Tillyard, 1922) from the Norian (Late Triassic) of Dinmore, Queensland, Australia. The youngest is *Paratettigarcta zealandica* Kaulfuss and Moulds, 2015 from the early Miocene of Hindon Maar, New Zealand. The Jurassic has the highest tettigarctid diversity of any period, although it is restricted to Laurasia and represented largely by species from the Yanliao (Daohugou) Biota (Moulds 2018). Some of these reached far larger body sizes than modern species (Chen and Wang 2016), while others had already evolved patterns of disruptive colouration (Chen et al. 2016; Zheng et al. 2016) and dense body hairs that were initially thought to be unique to modern *Tettigarcta* (Liu et al. 2016). The known family diversity decreases in the Early Cretaceous, but has a more global distribution, with the first occurrences in former Gondwanan landmasses: *Architettix compacta* Hamilton, 1990 and *Tettagalma striata* Menon, 2005 from the Crato Formation of Brazil, and *Magrebarcta africana* Nel, Zarbout, Barale, and Philippe, 1998 from the Duriet Formation of Tunisia. Not a single hairy cicada was known from the Late Cretaceous until the discovery of three new species in the earliest Cenomanian amber deposits of Kachin, Myanmar: *Cretotettigarcta burmensis* Fu, Cai, and Huang, 2019, *Vetuprosbole parallelica* Fu, Cai, and Huang, 2019, and *Hpanraais problematicus* Jiang, Chen, Jarzembowski, and Wang, 2019. Their unique location and relatively ancestral character states supported the hypothesis of southeast Asia as a Late Cretaceous tropical refuge based on the occurrence of other rare insect taxa.

In this paper, we report the discovery of *Maculaferrum blaisi* gen. et sp. nov., the first tettigarctid known from North America. It was found during a recent expedition to the Redmond no.1 mine, located in Labrador, Canada, near Schefferville. This abandoned iron ore mine contains lacustrine deposits that represent the only known exposures of Cretaceous rocks in the entire Quebec-Labrador Peninsula (Blais 1959; Dorf 1967). The expedition led to the discovery of more fossil leaf morphotypes and potentially new insect species. *Maculaferrum* is the first of these newly discovered insects to be formally described.

*Institutional abbreviations.*—MNHN, Muséum national d'histoire naturelle, Paris, France; MPE, Musée de paléontologie et de l'évolution, Montreal, Canada; NMV, National Museums Victoria, Melbourne, Australia; RMIP, Redpath Museum, Invertebrate Palaeontology, Montreal, Canada.

*Other abbreviations.*—A, anal vein; a, apical cell; av, ambient vein; bc, basal cell; C, costa; Cu, cubitus; CuA, cubitus anterior; CuP, cubitus posterior; M, media; $M_{1+2}$, two anterior branches of M; $M_{3+4}$, two posterior branches of M; m, medial cross vein; mc, medial cell; m-cua, mediocubital cross vein; RA, radius anterior; RP, radius posterior; r, radial cross vein; r-m, radio-medial cross vein; Sc, subcosta; u, ulnar cell.

*Nomenclatural acts.*—This published work and the nomenclatural acts it contains have been registered in ZooBank: urn:lsid:zoobank.org:pub:914D1FF0-AA2F-4BBB-945F-0BDD5E822AAA

# Geological setting

The Redmond no.1 mine is located at coordinates of 54°41' N and 66°45' W, Labrador, Canada, 16 km south southeast of Schefferville (Fig. 1). This site remains the only known exposure of the Redmond Formation, a basin surrounded by Palaeoproterozoic rocks that was 1524 m long, 508 m wide, and up to 183 m deep when first surveyed in 1957 before becoming out of geological context due to mining activities (Blais 1959). Apart from carbonized wood fragments of cupressacean affinity, the fossils found in this basin were restricted to impressions in a 1.5 m thick bed composed of a hard, very fine-grained, evenly laminated ferruginous argillite of umber colour (Blais 1959; Dorf 1967). The uncovered palaeoflora comprised a few fern, conifer, and lycopod specimens, dominated by angiosperm tree leaves that enabled palaeobotanist Erling Dorf to produce a Cenomanian age estimate based on biostratigraphic correlation and to suggest a warm temperate and fully humid climate for the region (Dorf 1959). The insect discoveries were scarce, but still led to the description of five unique and well-preserved specimens: the raphidiopteran *Alloraphidia dorfi* Carpenter, 1967, the hodotermitid *Cretatermes carpenteri* Emerson, 1967, the protocoleopteran *Labradorocoleus car-*
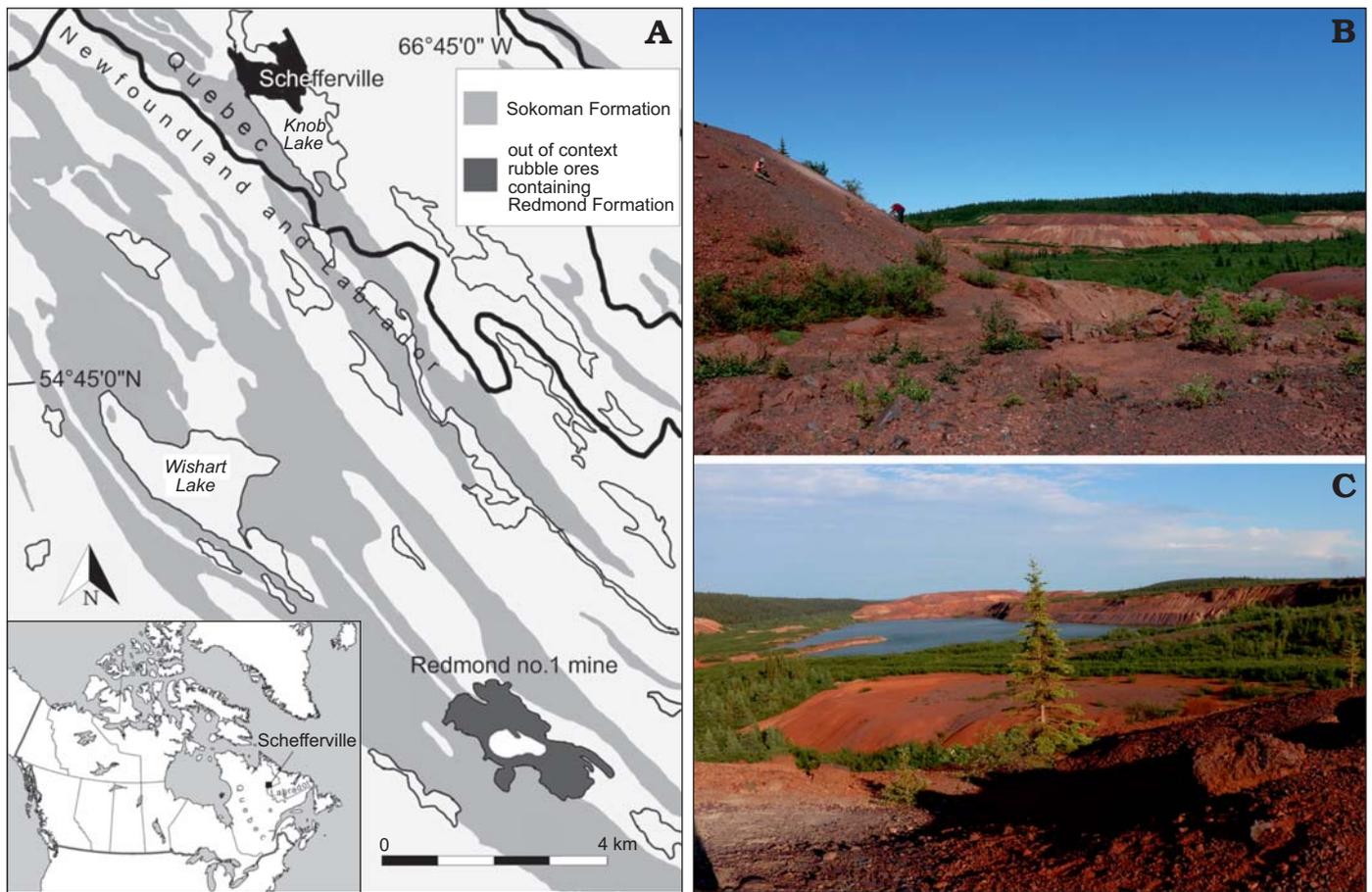
Fig. 1. Geographical location and geological setting of the Cenomanian (Late Cretaceous) Redmond Formation. **A**. Location of the Redmond Formation near Schefferville in Labrador, Canada (54°41'N, 66°45'W). Exposures of the Sokoman Formation based on Conliffe (2016). **B**. Prospecting along the spoil pile to the west of the Redmond no. 1 mine, where the specimen was discovered. **C**. Southeast facing view of the mine from the top of the western spoil pile. The open-pit mine is now flooded by groundwater.

*penteri* Ponomarenko, 1969, the (possibly) myrmeleontid *Palaeoleon ferrogeneticus* Rice, 1969, and the phasmatodean *Palaeopteron complexum* Rice, 1969. In addition, a few isolated blattodean wings (Dorf 1967), some elytra assigned to water beetles (Schizophoridae), and two elytra assigned respectively to Cupedidae and to the haliplid *Peltodytes* sp. (Ponomarenko 1969) have also been mentioned. Despite this meagre collection, the occurrence of taxa rarely preserved in the insect fossil record suggested that many more awaited discovery in the Redmond Formation.

The site was not explored until an expedition by the Musée de paléontologie et de l'évolution (MPE) in summer 2013, by which time mining activities had fragmented the Redmond Formation into small flat claystone rocks scattered among rubble piles (Fig. 1). In August 2018, the first author set out on a longer expedition organized jointly by the Redpath Museum and the MPE. The discovery of yet more fossil leaves in these two expeditions led to an absolute palaeoclimate estimate that encompassed the entire known angiosperm flora, and that confirmed Dorf's (1959) initial relative palaeoclimate and dating hypotheses (Demers-Potvin and Larsson 2019). This fieldwork also led to a

significant expansion of the known entomofauna from the site, including the discovery of near-complete nymphs and aquatic coleopterans that strengthened the initial hypothesis of a lacustrine depositional setting (Blais 1959; Dorf 1959; Demers-Potvin and Larsson 2019).

Among the diverse terrestrial entomofauna preserved in the Redmond Formation was a rare representative of Tettigarctidae. The sole specimen was found on a small thin slab (~6 × 10 × 0.7 cm) of argillite of burgundy colour enriched in iron oxide, among similar pieces of float. Amid this recently assembled entomofauna, we have looked for hind wings that could potentially belong to this genus or a relative within the family, but the most similar ones clearly belonged to leafhoppers (Cicadomorpha: Cicadellidae).

## Material and methods

The slice of argillite in which the specimen was found was cut to a 3 × 3 cm square using a Lortone lapidary trim saw, Model FS8. The specimen was drawn and photographed at the Centre de recherche sur la Paléobiodiversité et les

Paléoenvironnements (MNHN). A draft drawing was done with a microscope equipped with a camera lucida (Zeiss SteREO Discovery V8 stereomicroscope equipped with a pair of W-PL 10 × / 23 eye pieces, a Plan Apo S 1.0 × FWD objective; all from Zeiss). The drawing was finalized with Adobe Illustrator CC 2019 using the draft drawing and photographs.

A Reflectance Transformation Imaging (RTI) file was built out of a set of photographs to enhance the 3D contrasts in the impression fossil that facilitate its observation, and to produce composite photographs of superior quality. Photographs were taken using a Canon EOS 5D Mark III digital camera with a Canon MPE-65 macro lens (without polarizing filters). The photographs were taken under a Portable Light Dome, optimized and processed using Adobe Camera Raw and Adobe Photoshop CC 2019, and compiled into an RTI file using the RTI Builder software v. 2.0.2 (freely available under GNU license, using the HSH fitter; see Béthoux et al. 2016; RTI 2019 for more details). We provide the RTI file along with viewer software and instructions (see Supplementary Online Material available at http://app.pan.pl/SOM/app65-Demers-Potvin_etal_SOM.pdf). The photographs of RMIP 2018.18.24 included in this paper have all been extracted from the RTI files.

The forewing representing *Maculaferrum blaisi* gen. et sp. nov was also compared with those of the only two extant species of hairy cicadas, *Tettigarcta crinita* and *Tettigarcta tomentosa*. Habitus and individual forewing photographs were taken for specimens of each species (*T. crinita*: one male [NMV HEM5660]; *T. tomentosa*: one male [NMV HEM472] and one female [NMV HEM476]) with a Nikon D5300 enhanced with an AF-S Micro Nikkor 105 mm macro lens in the Entomology collections of NMV. ~20 images per view were taken and subsequently stacked and optimized using Adobe Photoshop CC 2018. The wing venation terminology follows that of Moulds (2005). Vein M in this terminology is equivalent to vein MP, as MA is always totally fused with RP, which is a synapomorphy of Hemiptera (Kukalová-Peck 1991; Nel et al. 2012, 2013; Bourgoin et al. 2015).

# Systematic palaeontology

Order Hemiptera Linnaeus, 1758

Suborder Cicadomorpha Evans, 1946

Superfamily Cicadoidea Latreille, 1802

Family Tettigarctidae Distant, 1905

Subfamily Tettigarctinae Distant, 1905

Tribe Protabanini Hong, 1982 (?)

Genus *Maculaferrum* nov.

*Zoobank LSID:* urn:lsid:zoobank.org:act:6EDDA824-816B-4AE5-AE3B-2975E12D5AA2

*Type species*: *Maculaferrum blaisi* sp. nov.; by monotypy, see below.

*Etymology*: From Latin *macula*, spot; referring to the apparent spotted

pattern observed on parts of the wing membrane, and *ferrum*, iron; referring to the high iron content that confers the matrix a distinctive reddish colour.

*Diagnosis.*—As for the type species.

## *Maculaferrum blaisi* sp. nov.

Figs. 2, 3, 4A.

*Zoobank LSID:* urn:lsid:zoobank.org:act:8F96A300-25A5-4F3E-BCFC-B5171A85A11D

*Etymology*: In reference to Roger A. Blais, who undertook the initial survey of the Redmond Formation in 1957.

*Holotype*: RMIP 2018.18.24 (part), impression of a single isolated forewing either ripped in half or folded onto itself so that the middle area is hidden from view. The basal part consists in the majority of the pre-nodal area, and the apical part consists in the vast majority of the post-nodal area.

*Type locality*: Redmond no. 1 mine, near Schefferville, Labrador, Canada.

*Type horizon*: Redmond Formation, Cenomanian, Late Cretaceous.

*Diagnosis.*—In general view, forewing similar to forewing of Protabanini fossils, *Tettagalma striata* Menon, 2005 from the Aptian Crato Formation of Brazil and *Protabanus chaoyangensis* Hong, 1982 from the Jiulongshan Formation, Liaoning, China. Costal cell narrower basally than basal cell (as in *Tettagalma*; in *Protabanus* costal cell about as wide as basal cell); single terminal RP longer than cell a6 (as in *Protabanus*; in *Tettagalma* cell u3 distinctly shorter than cell a6); apical portion of stem CuA basad of nodal line minimally curving mediad (as in *Protabanus*; in *Tettagalma* this section of stem CuA is distinctly curved mediad); $CuA_2$ with a sharp uniform curve apically (contrary to at most faint apical curves in *Protabanus* and *Tettagalma*). Specimen also resembling some Meunierini, viz. *Meuniera haupti* Piton, 1936 from the Palaeocene quarry of Menat, France, and members of Tettigarctini such as extant *Tettigarcta* spp. from southern Australia, due to M and CuA joined by a m-cua cross vein at the apical extremity of the basal cell and $CuA_2$ running along nodal line up to clavus apex. However, it differs from Meunierini due to stem M forking closer to nodal line than to wing base; it also differs from Tettigarctini due to forking of RA not level with cross vein r and $CuA_2$ curving towards apex instead of base. Uniform curvature of $CuA_2$ seems apomorphic for *Maculaferrum* gen. nov. Round darker markings in apical cells, less distinct rounded spots in ulnar cells; appendix with minuscule striae (corrugations) exceeding ambient vein; punctate pattern on basal portion of forewing.

*Description.*—Total forewing length estimated at 20–23 mm; maximal forewing width 7.5 mm. Marginal membrane (appendix) present along entire margin apical of $RA_1$ to 1A terminal apex; ambient vein perfectly visible, criss-crossed by minuscule striae, from $RA_2$ to $CuA_2$ (Figs. 2, $3A_1$, $A_2$); post-claval membrane present, narrow. Rows of tubercles present along segments of longitudinal veins, each projecting perpendicular to vein (Fig. $3A_3$). Only short segment of the nodal line appears visible, parallel to $CuA_2$ (Fig. 3B). Round to oblong patches present in apical cells a1 to a8 and postnodal
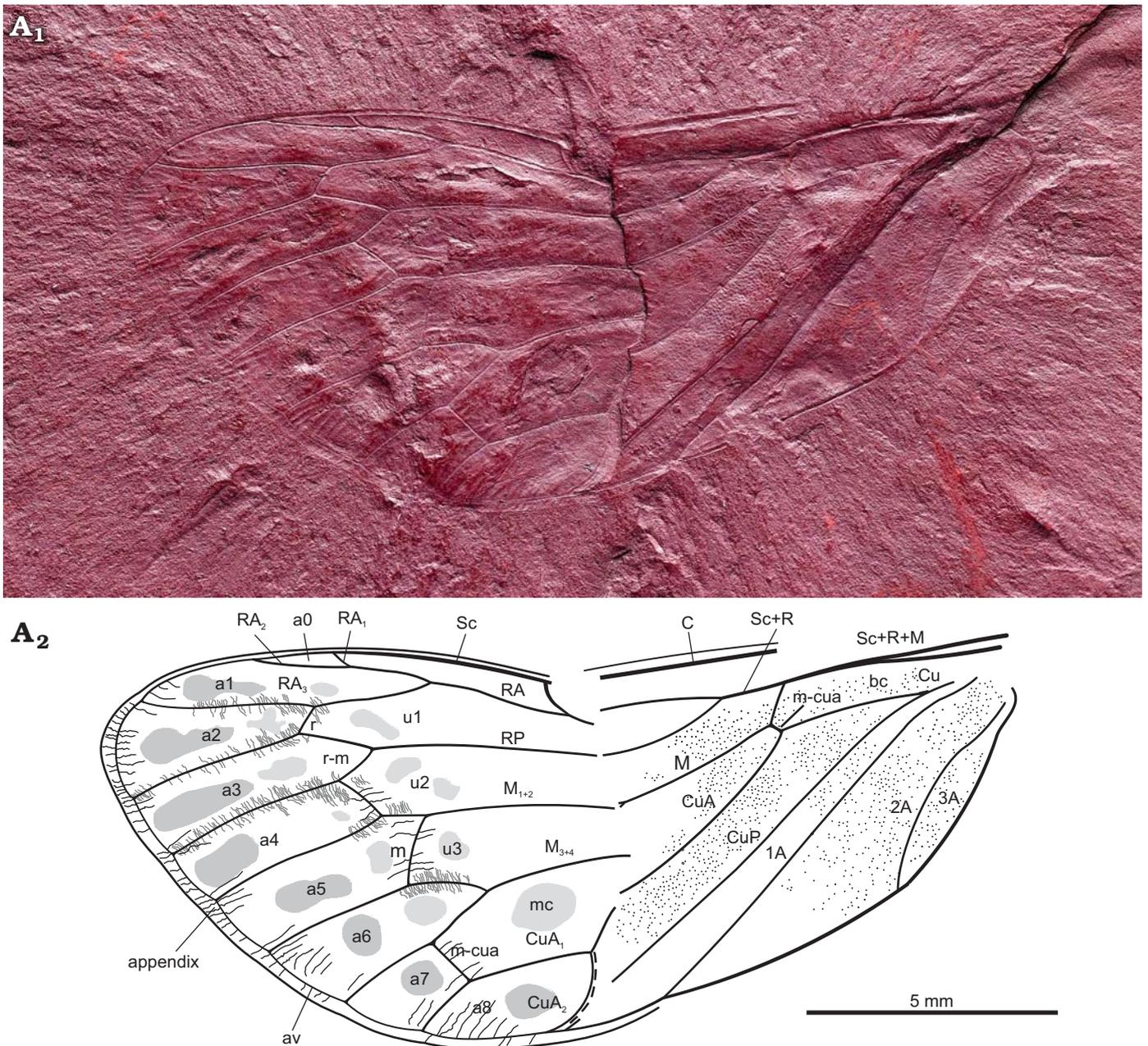
Fig. 2. Hairy cicada *Maculaferrum blaisi* gen. et sp. nov. (holotype RMIP 2018.18.24) from the Cenomanian (Late Cretaceous) Redmond Formation, Labrador, Canada. Habitus photograph ($A_1$), extracted from the RTI file (downloaded from http://culturalheritageimaging.org/Technologies/RTI/ on 31 July 2019; see SOM) and interpretative line drawing ($A_2$). Wing venation terminology after Moulds (2005). Abbreviations: A, anal vein; a, apical cell; av, ambient vein; bc, basal cell; C, costa; Cu, cubitus; CuA, cubitus anterior; CuP, cubitus posterior; M, media; $M_{1+2}$, two anterior branches of M; $M_{3+4}$, two posterior branches of M; m, medial cross vein; mc, medial cell; m-cua, mediocubital cross vein; RA, radius anterior; RP, radius posterior; r, radial cross vein; r-m, radio-medial cross vein; Sc, subcosta; u, ulnar cell. Black lines, striae along wing apex; grey lines, tubercles along apical vein segments; dashed line, visible portion of nodal line.

portion of ulnar cells u1 to u3 and medial cell, closer to cross veins (Figs. 2, 3C). Punctate pattern observed on much of pre-nodal area but absent from post-nodal area (Figs. 2, 3D).

Costal area of forewing straight at base, increasingly curved apically, apex relatively sharply curved, claval margin straight, apex of clavus slightly exceeding half of forewing length. Costal margin thick, veins of costal complex flattened to level of nodus. Stem vein Sc tightly adjoined and subparallel to stem R+M, fused with R+M

merely apicad of apex of basal cell. Stem Sc+R short, about ¼ of length of basal cell, forked distinctly basad of nodal line and M forking; branch of Sc+R subparallel to costal margin, its prenodal section about 3 times as long as stem Sc+R; terminal Sc short, oblique, diverged slightly apically of nodal line. Branch RA forked at basal half of membrane, with three terminals: branch $RA_{1+2}$ slightly sinuous, $RA_1$ short, oblique, $RA_2$ subparallel to forewing anterior margin, $RA_1$ and $RA_2$ terminal apices distinctly basad of forewing
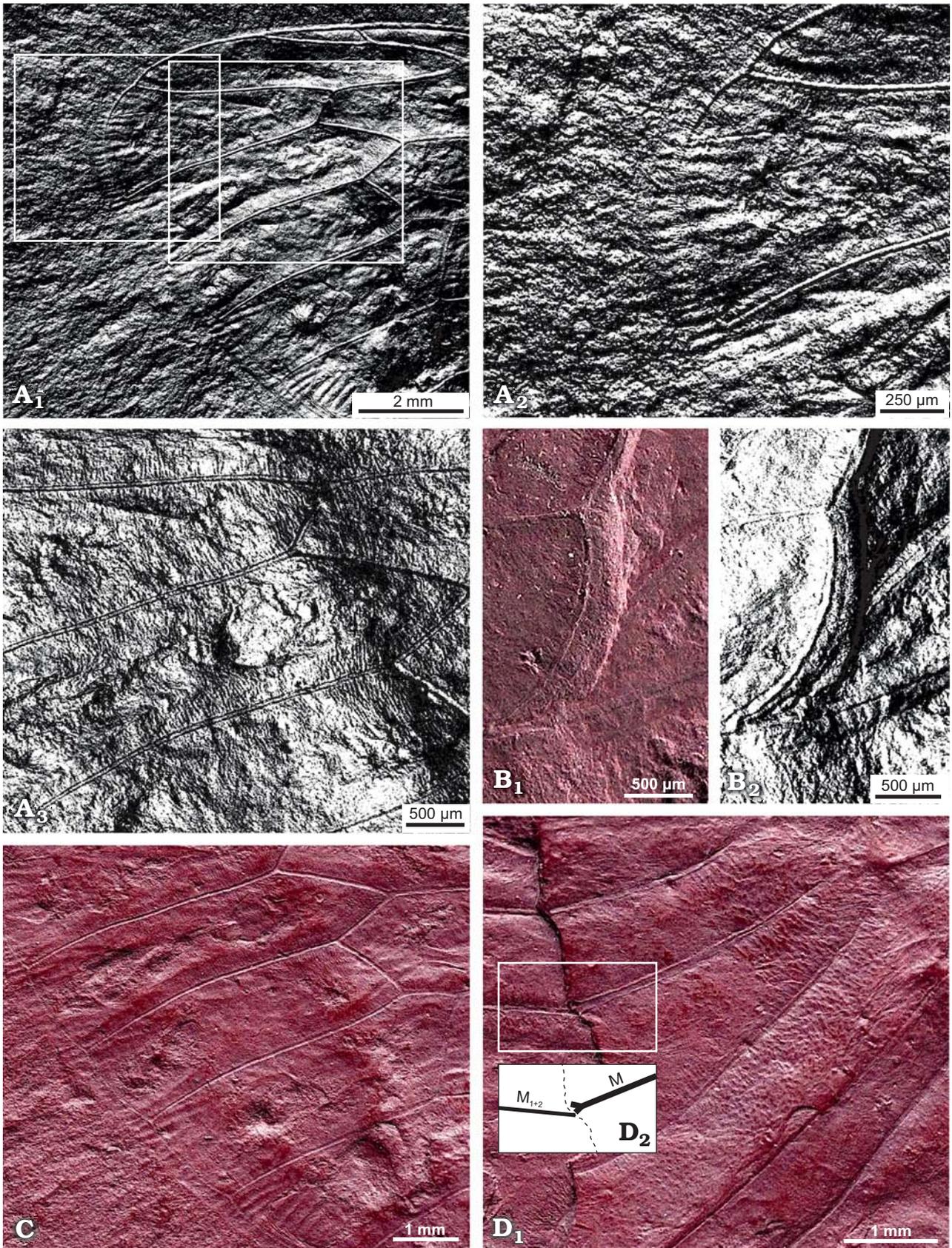
Fig. 3. Photomicrographs highlighting specific characters of the forewing of hairy cicada *Maculaferrum blaisi* gen. et sp. nov. (holotype, RMIP 2018.18.24) from the Cenomanian (Late Cretaceous) Redmond Formation, Labrador, Canada, extracted from the RTI file (see SOM). **A**. Highlights on striae along ambient vein and tubercles along longitudinal veins. Apical portion of the forewing, striae crossing ambient vein either side of apex, under specular →

apex; $RA_3$ reaching ambient vein slightly basad of forewing apex; RP forked from Sc+R basad of 0.3 of forewing length, reaching ambient vein with single terminal slightly basad of forewing apex. Stem M forked close to nodal line level (Fig. $3D_2$, not clearly preserved), branch $M_{1+2}$ forked apicad of branch $M_{3+4}$ forking and apicad of RA forking; $M_{3+4}$ forked basad of RA forking. Stem CuA leaving basal cell distinctly curved at base, then arcuate, geniculately bent posteriad at nodal line, forked at level of nodal line; branch $CuA_1$ much longer than branch $CuA_2$, subparallel to branch $M_{3+4}$, then bent to ambient vein, to reach it at level of RA forking. CuP and claval fold straight, reaching margin merely basad of nodal line; 1A slightly sinuate, subparallel to CuP; 2A arcuate, relatively short; 3A fused to basal margin of forewing. Cross vein r slightly apicad of terminal $RA_1$; cross vein r-m oblique, at level of terminal $RA_1$; cross vein m oblique, connecting $M_{1+2}$ with terminal $M_3$, slightly basad of terminal $RA_1$; basal cross vein m-cua very short, connecting stem M with stem CuA at posterior apical corner of basal cell; apical cross vein m-cua oblique, connecting terminal $M_4$ with $CuA_1$ distinctly basad of terminal $RA_1$, basad of half of $M_4$ length, apicad of half of $CuA_1$ length. Basal cell about 4 times as long as wide, subrectangular. Costal cell about as wide as basal cell. Prenodal portion of cell u1 shorter than postnodal portion. Prenodal portion of cell u3 short (not clearly preserved). Cell a7 significantly shorter than other apical cells. Cell a8 slightly shorter than adjoining postnodal portion of cell mc.

*Remarks.*—During fossilization, the forewing was broken along the nodal line, and portions partly overlap. It means that much of the area surrounding the nodal line is not clearly preserved. It is very difficult to see the position of the branching of M into $M_{1+2}$ and $M_{3+4}$, but it seems to be very close to the margin of the preserved basal portion of the forewing. Considering the incomplete state of the specimen, a reconstruction of the entire forewing is presented alongside wings of living relatives *Tettigarcta crinita* and *T. tomentosa* (Fig. 4).

*Stratigraphic and geographical range.*—Type locality and horizon only.

# Discussion

*Maculaferrum blaisi* gen. et sp. nov. belongs to family Tettigarctidae based on the following characters: costal cell present, about as wide as basal cell; branch RP arising basally, closer to base than to node; 1A separated from CuP, veins 2A and 3A separated at least at base; nodal line distinct; clavus exceeding half of forewing length; basal portion of forewing punctate. It can be placed further in subfamily Tettigarctinae based on the following characters (Shcherbakov 2009): basal cell wide, not narrowed to apex; costal cell relatively narrow (only slightly narrower than intercubital area); forewing apex sharply curved; very short basal m-cua closing basal cell; apical cell basad of $CuA_2$ either very narrow or absent (in the case of this new genus); apex of clavus slightly exceeding half of forewing length. The latter character is also found in some taxa placed in Cicadoprosbolinae and could not be diagnostic; further analyses are necessary to assess the importance of this feature. In addition, *M. blaisi* seems to share with other members of Tettigarctinae a cross vein r closer to the wing apex than to the nodal line. This character cannot be observed directly in the specimen since the nodal line is not preserved for most of the wing's width, so it is only implied here (see Remarks; Figs. 2 and 4). *M. blaisi* can be assigned to tribe Protabanini based on the following characters (Shcherbakov 2009): presence of very short basal m-cua closing basal cell; cross vein r reclined; anteriormost apical cell (a0, between $RA_1$ and $RA_2$) narrow triangular; distal section of CuA geniculately bent at nodal line, prolonged by $CuA_2$; nodal line at or beyond mid-wing; forking of stem M far closer to nodal line than to wing base, implied due to lack of preservation of nodal line (see Fig. 4). Only the a0 cell character seems truly unique to Protabanini, while the other characters can also be observed on numerous members of Cicadoprosbolinae, such as *Architettix compacta* Hamilton, 1990 (Architettigini; Aptian, Crato Formation, Brazil), Turutanoviini, species of the genus *Sanmai* Chen, Zhang, Wang B., Zheng Y., Wang X., and Zheng X., 2016, *Hirtaprosbole erromera* Liu, Li, Yao, and Ren, 2016, *Shuraboprosbole daohugouensis* Wang and Zhang, 2009, *Tianyuprosbole zhengi* Chen, Wang B., Zhang, and Wang X., 2014 (all from the Callovian/Oxfordian [Middle/Late Jurassic] Daohugou Formation of northeastern China); and Cicadoprosbolinae genera unassigned to tribes, *Vetuprosbole* and *Hpanraais* (both from earliest Cenomanian [Late Cretaceous] Kachin amber of Myanmar). *Maculaferrum blaisi* gen. et sp. nov. also shares with the aforementioned Jurassic taxa Sc+R significantly shorter than Sc+RA, and m-cu connecting $CuA_1$ to $M_4$. It seems to share with members of Protabanini a stem M curving mediad just before bending geniculately along the nodal line. In this respect, M curves relatively minimally in this new genus (as in *Protabanus chaoyangensis* Hong, 1982 or *Sunotettigarcta kudryashevae* Shcherbakov, 2009) instead of curving sharply (as in *Tettagalma*). However, even this character is present in some Cicadoprosbolinae, most notably *Hpanraais*.

enhancement rendering mode ($A_1$). Emphasis on the apex, with striae particularly visible on the apicalmost segment of the ambient vein, under specular enhancement rendering mode ($A_2$). Longitudinal veins RP, $M_1$ and $M_2$ ($A_3$); note rows of tubercles emerging perpendicular to veins, under specular enhancement rendering mode. **B**. Posteriormost segment of nodal line between $CuA_2$ and post-burial fracture, running subparallel to both structures ($B_1$); image under specular enhancement rendering mode ($B_2$). **C**. Round to oblong patches arranged in a row near apical edge of apical cells. Second row of smaller patches visible in basal part of apical cells. **D**. Emphasis on part of the pre-nodal area featuring a punctate pattern; forking point of vein M (into $M_{1+2}$ and $M_{3+4}$) highlighted in inset ($D_1$); interpretative drawing ($D_2$). Abbreviations: CuA, cubitus anterior; M, media; RP, radius posterior.
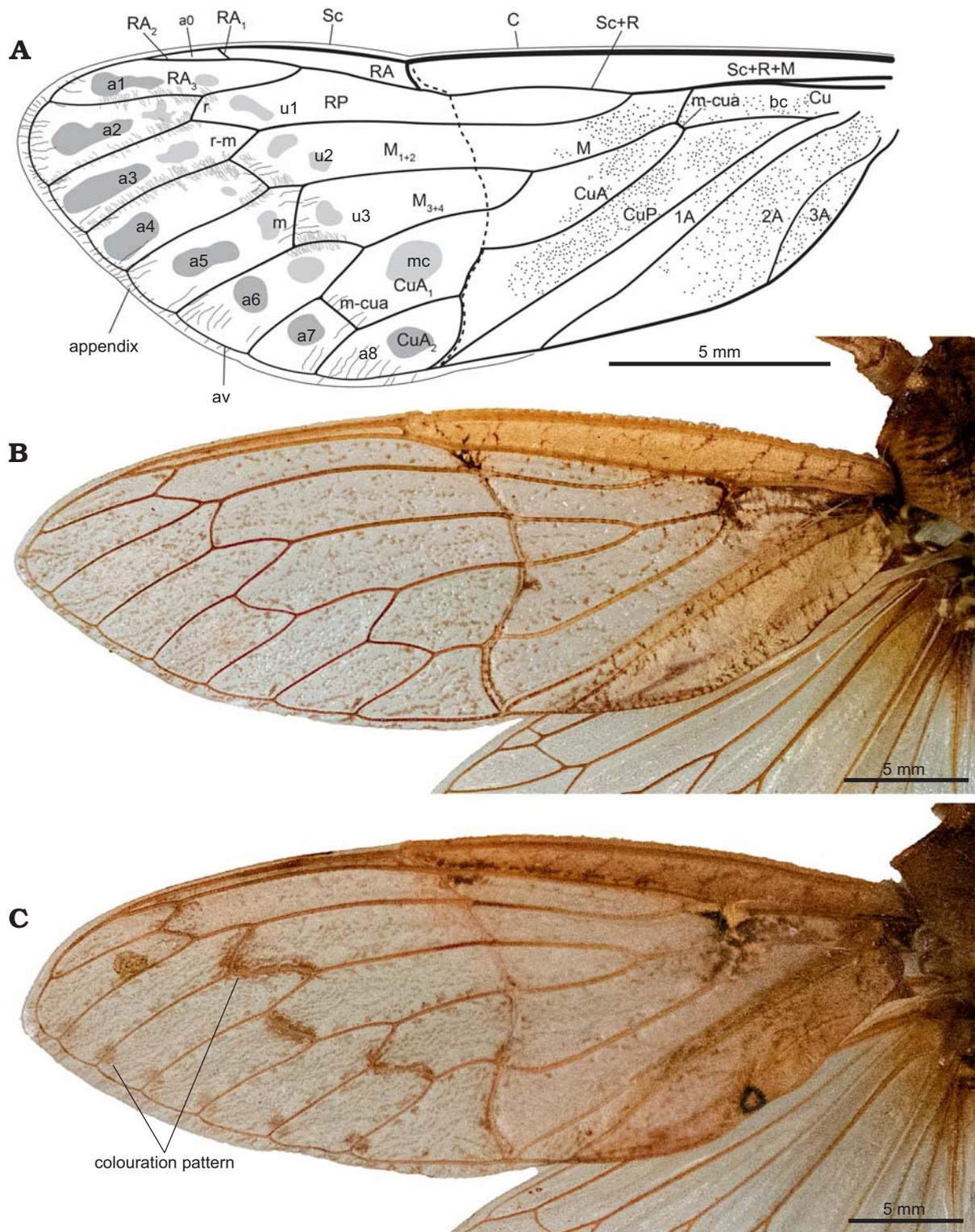
Fig. 4. Comparison of hairy cicada *Maculaferrum blaisi* gen. et sp. nov. (holotype RMIP 2018.18.24) from the Cenomanian (Late Cretaceous) Redmond Formation, Labrador, Canada, with forewings of extant relatives (B, C). **A**. Interpretative drawing of *M. blaisi* gen. et sp. nov. (holotype RMIP 2018.18.24) in pre-burial state, based on extant and extinct relatives. **B**. Left forewing of male *Tettigarcta crinita* Distant, 1883 from southern Victoria, Australia; NMV HEM5660 in dorsal view. **C**. Left forewing of female *Tettigarcta tomentosa* White, 1845 from Tasmania, Australia; NMV HEM476 in dorsal view. Note colouration pattern on post-nodal half: round patches near junction of terminal longitudinal veins with ambient vein, a larger darker round patch in cell a2, smaller irregular patches along more basal segments of longitudinal veins, and large oblong to irregular patches along cross veins and short segment of $M_1$. Abbreviations: A, anal vein; a, apical cell; av, ambient vein; bc, basal cell; C, costa; Cu, cubitus; CuA, cubitus anterior; CuP, cubitus posterior; M, media; $M_{1+2}$, two anterior branches of M; $M_{3+4}$, two posterior branches of M; m, medial cross vein; mc, medial cell; m-cua, mediocubital cross vein; RA, radius anterior; RP, radius posterior; r, radial cross vein; r-m, radio-medial cross vein; Sc, subcosta; u, ulnar cell.
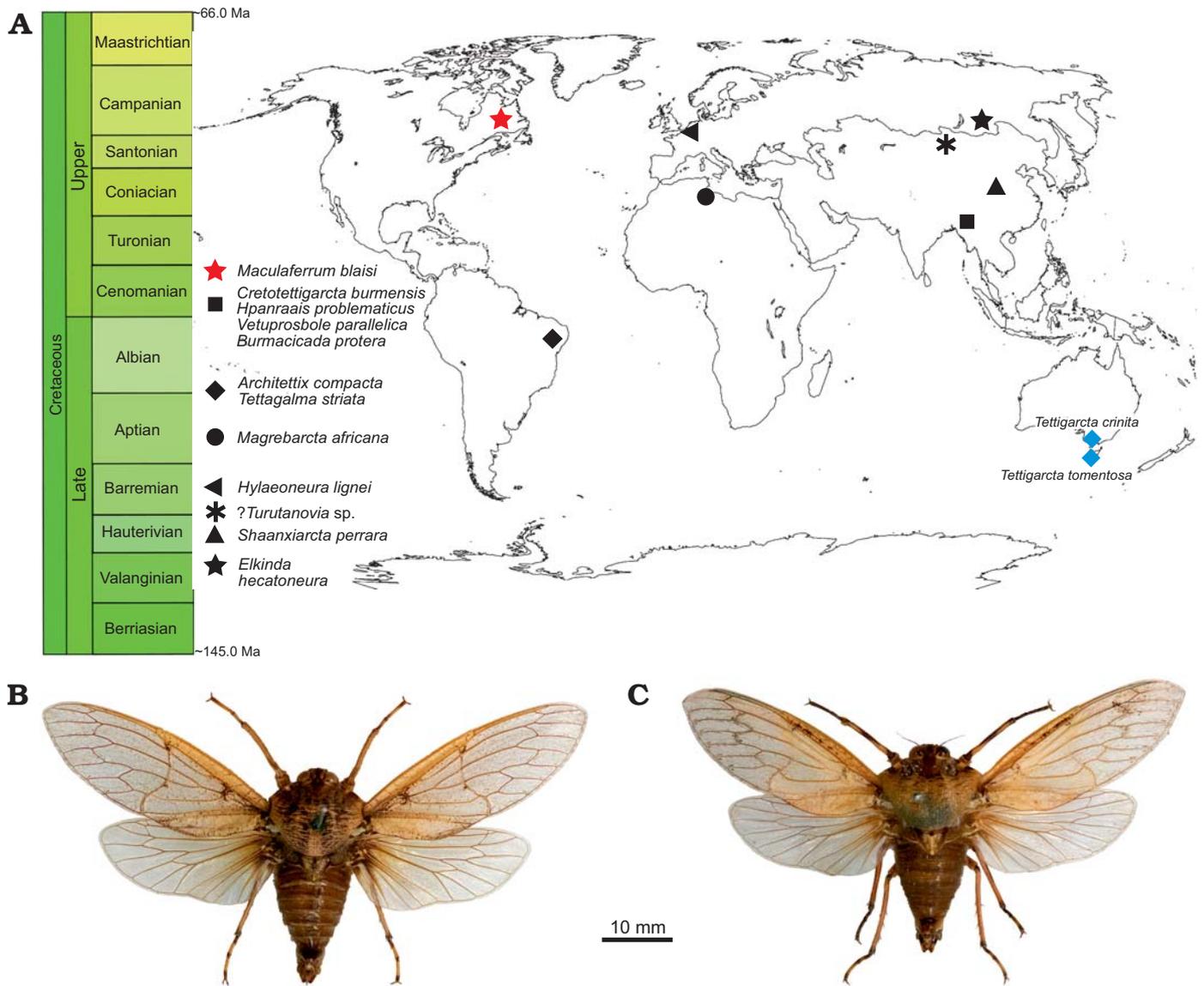
Fig. 5. **A**. Spatial and geographical distribution of cicadoid occurrences in the Cretaceous (red star, black shapes) compared with extant tettigarctids (blue diamonds). **B**. Habitus photograph of male *Tettigarcta crinita* Distant, 1883 from southern Victoria, Australia; NMV HEM5660 in dorsal view. **C**. Habitus photograph of male *Tettigarcta tomentosa* White, 1845 from Tasmania, Australia; NMV HEM472 in dorsal view. Fossil occurrences retrieved from the Paleobiology Database (Czaplewski 2019).

Several features observed on the specimen seem to exclude it from Protabanini, as originally defined (Shcherbakov 2009). These are M and CuA joined by a m-cua cross vein in the apical extremity of the basal cell (instead of cross-joining at that extremity) and $CuA_2$ running along nodal line up to clavus apex (instead of a divergence of the distal section of $CuA_2$ from the nodal line). These traits are more characteristic of taxa classified in Meunierini (such as *Meuniera haupti* Piton, 1936) and Tettigarctini (such as *Tettigarcta*). The new genus and species shares with Meunierini a forking of RA level with a forking of $M_{1+2}$ (Shcherbakov 2009). However, it differs from Meunierini due to the forking of stem M at unequal distances from the wing base and nodal line, and it differs from Tettigarctini due to the forking of RA not level with cross vein r (Shcherbakov 2009) and

$CuA_2$ curving towards the apex instead of the base (Fig. 4). Consequently, *Maculaferrum blaisi* gen. et sp. nov. presents a combination of characters supposedly diagnostic of Protabanini, Meunierini, and Tettigarctini. Thus, its affinities to a particular tribe within Tettigarctinae remain obscure, and a similar condition has been noted in its contemporary *Cretotettigarcta burmensis* (Fu et al. 2019). Together, these recently described genera could contribute to a revision of the definitions of tribes within Tettigarctinae (such as Protabanini), since they seem based on many convergent or plesiomorphic characters.

**Interpretation of spotted and filamentous patterns on the wing membrane**.—The presence of minuscule tubercles along the veins suggests that setae or bristles were
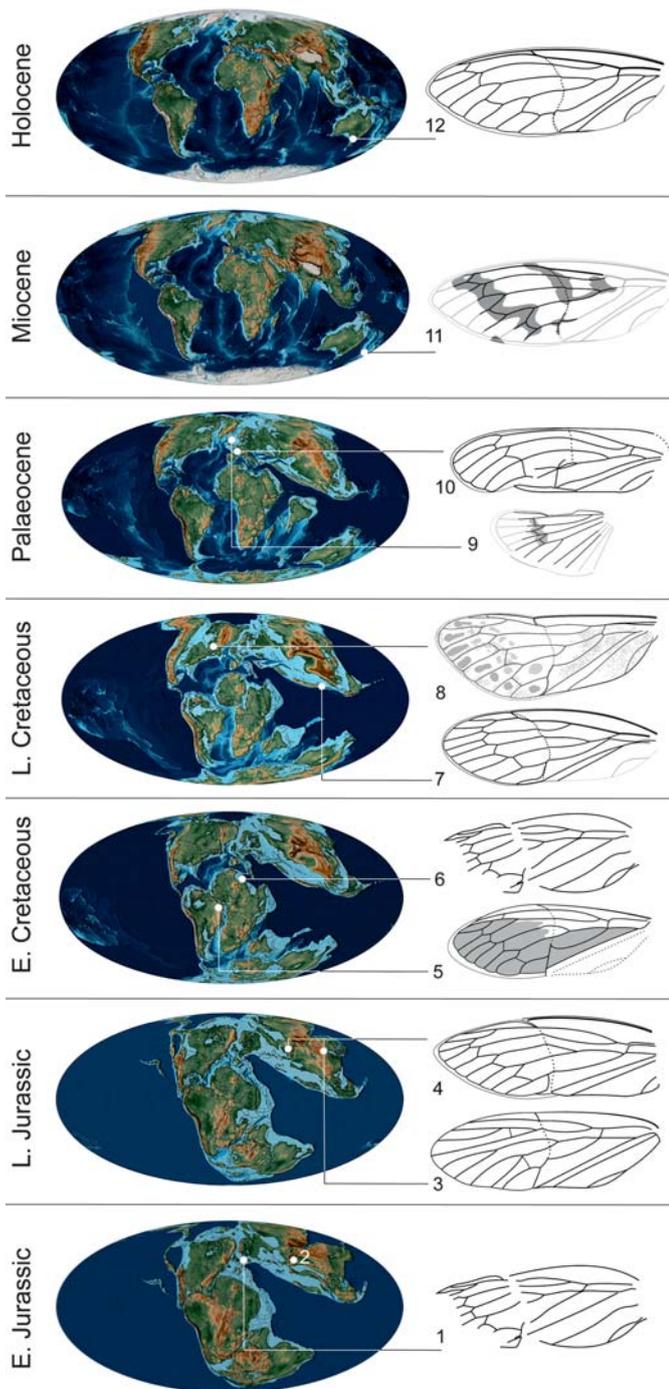
present on the forewing of *Maculaferrum blaisi* gen. et sp. nov. (Fig. 3A$_3$). Such setae are preserved in extant relative *Tettigarcta*. They have also been observed in extinct relatives (not ascribed to tribes) preserved in Cenomanian (Late Cretaceous) Kachin amber of Myanmar, e.g., *Hpanraais*, *Cretotettigarcta*, and *Vetuprosbole*. It must also be noted that the clear delineation between a punctate pattern on the pre-nodal area and a smoother pattern on the post-nodal area is very similar to that observed in *Tianyuprosbole* (Chen et al. 2014).

The presence of patches on the apical portion of the forewing of *Maculaferrum* probably does not result from taphonomical bias. Instead, they may indicate a spotted pattern that was actually present on the wing. However, since *Maculaferrum* is represented by an impression fossil, the origin of this pattern is far more nebulous than in a compression fossil, and the lack of distinct pigmentation means that the wing's original colouration pattern may not be fully preserved. This means that any interpretation of this observation must be treated with extreme caution. Spotted patterns are occasionally observed in some *Tettigarcta* individuals, although they are found along the veins and seem less extensive than in *Maculaferrum* (Fig. 4). Of the limited sample of *Tettigarcta* individuals available for this study, such a pattern was only found on the female *T. tomentosa* (Fig. 4C). A future study could aim to compare wing colouration patterns more systematically between sexes among both extant species. Similar patterns are also infrequently present among extant singing cicadas Cicadidae (Distant 1889, 1914; Emery et al. 2017). Lighter spots in cells on a dark background are present in species of the genus *Ambragaeana* (Gaeanini) Chou and Yao, 1985. Darker spots on a transparent background, but distributed on veins and adjoining cells, are present in *Kamalata pantherina* Distant, 1889 (Cicadini); more irregular patches on veins and adjoining portions of cells are also present in other Cicadini (Distant 1889, 1912). In contrast, cryptic colouration or patterns of disruptive colouration (speckles and longitudinal stripes) are frequently observed in extinct Tettigarctidae, such as in *Liassocicada* Bode, 1953, *Sunotettigarcta kudryashevae*, *Sanmai*, and *Maculaprosbole* Zheng, Chen, and Wang, 2016 from the Jurassic, or the Miocene *Paratettigarcta* Kaulfuss and Moulds, 2015. Cryptic and disruptive colouration are recognized as defense mechanisms for avoiding predation

Fig. 6. Tettigarctinae occurrences through time. 1, *Liassocicada antecedens* Bode, 1953 from Early Jurassic Posidonia Shale Formation, Germany (drawing from Nel et al. 1998); 2, *Kisylia psylloides* Martynov, 1937 from Early Jurassic Kisyl-Kiya, Kyrgyzstan; 3, *Protabanus chaoyangensis* Hong, 1982 from the Callovian/Oxfordian (Middle/Late Jurassic) Jiulongshan Formation, China; 4, *Sunotettigarcta* (represented by drawing of *Sunotettigarcta kudryashevae* Shcherbakov, 2009) from Late Jurassic Karatau, Kazakhstan; 5, *Tettagalma striata* Menon, 2005 from the Aptian (Early Cretaceous) Crato Formation, Brazil; 6, *Magrebarcta africana* Nel, Zarbout, Barale, and Philippe, 1998 from the Aptian (Early Cretaceous) Duriet Formation, Tunisia; 7, *Cretotettigarcta burmensis* Fu, Cai, and Huang, 2019 from the Cenomanian (Late Cretaceous) Hukawng Valley, Myanmar; 8, *Maculaferrum blaisi* gen. et sp. nov. (holotype RMIP 2018.18.24) from the Cenomanian (Late Cretaceous) Redmond Formation, Labrador, Canada; 9, *Eotettigarcta scotica* Zeuner, 1944 from the Palaeocene Isle of Mull, UK (only known from a partial hind wing); 10, *Meuniera haupti* Piton, 1936 from the Palaeocene Menat quarry, France; 11, *Paratettigarcta zealandica* Kaulfuss and Moulds, 2005 from the Miocene Hindon Maar, New Zealand; 12, *Tettigarcta crinita* Distant, 1883 from southern Victoria, Australia (extant). The classification of *Liassocicada ignota* Brodie, 1845 within Cicadoprosbolinae introduces uncertainty about the affinities of *L. antecedens* to Tettigarctinae (Shcherbakov 2009). Drawings not to scale; 1, 4, 6, 7, 9–11, mirrored to facilitate comparison with *Maculaferrum*. Fossil occurrences retrieved from the Paleobiology Database (Czaplewski 2019). Palaeogeographical maps from Scotese (2001).

(Quicke 2017), and the fossil record shows that they evolved in Tettigarctidae during much of their history.

**Palaeobiogeographical and palaeoclimate considerations**.—The preservation state of *Maculaferrum blaisi* gen. et sp. nov. does not provide any insight into aspects of tettigarctid biology, such as hair density or feeding apparatus, as in other members of the family (Hamilton 1990; Li et al. 2012; Chen et al. 2014; Fu et al. 2019). However, its contribution to our understanding of tettigarctid biogeography cannot be overstated. The unique geographical distribution of *Maculaferrum* strongly supports its new genus status based on the anatomical diagnosis outlined above. Tettigarctids were already known to have a global distribution during the Cretaceous ranging from Eurasia to South America, and this discovery finally confirms that their range extended to North America (Fig. 5). The fact that *Maculaferrum* only represents the first occurrence of this family on this continent demonstrates how rare tettigarctids can be in the Cretaceous hemipteran fossil record. Most continents have only one or two known fossils representing this family (Hamilton 1990; Nel et al. 1998; Menon 2005; Kaulfuss and Moulds 2015); they are conspicuously absent from a number of well-sampled Lagerstätten, such as the Jehol biota (Fu et al. 2019), Koonwarra (Shcherbakov 2009), or the spatially and temporally close New Jersey amber (Grimaldi et al. 2000). In the Lagerstätten that do contain them (such as the Yanliao biota or the Crato Formation, see Hamilton 1990; Li et al. 2012; Chen et al. 2016), species are only ever represented by one or two specimens, and their occurrence is not clearly correlated with preservation potential. Not a single species was known in the form of amber inclusions until 2019, and these occurrences are all reported from the Hukawng Valley, a single exceptional locality in Myanmar (Fu et al. 2019; Jiang et al. 2019). In contrast, the only tettigarctids known from Africa and New Zealand, and now North America, consist in isolated fragmentary wings (Nel et al. 1998; Kaulfuss and Moulds 2015). Taphonomical bias may explain this situation more than any rarity in the Cretaceous biocoenoses since tettigarctids have a life history that would make them less likely to fossilize as part of Lagerstätten than lacustrine or riparian insects.

How does this discovery contribute to our understanding of cicadoid eco-evolutionary trends throughout the Cretaceous? At the time of Moulds' (2018) review of cicadoid diversity, seven tettigarctid species were known from the Early Cretaceous, and none from the Late Cretaceous. One year later, four species (including *Maculaferrum blaisi* gen. et sp. nov.) are known from the Late Cretaceous, from very distant localities (Fig. 5). If the relative dating of the Redmond Formation is accurate, it would be of a similar age to the reasonably constrained Hukawng Valley of Myanmar, the only other Cenomanian locality to have produced tettigarctids (Shi et al. 2012; Fu et al. 2019; Jiang et al. 2019). These new discoveries suggest that the decline in tettigarctid diversity was not as abrupt as first envisioned.

They do not completely refute the hypothesis of competitive displacement by Cicadidae (Wang and Zhang 2009), but suggest a shift in its timing towards the Cenozoic, or at least nearer the end of the Cretaceous, especially now that *Burmacicada protera* Poinar and Kritsky, 2012 is assigned to Tettigarctidae instead of Cicadidae (Moulds 2018; Chen et al. 2019a, b). The discovery of *Maculaferrum* also leads us to doubt Fu et al.'s (2019) hypothesis on southeast Asia as a tropical refuge for tettigarctids during the Cenomanian. It may be supported for more specialized taxa because of their unique occurrence in an environment that is exceptionally humid compared with localities that experienced a more seasonal tropical climate (Spicer et al. 1996; Grimaldi et al. 2002; Hay and Flögel 2012). However, our discovery demonstrates the occurrence of tettigarctids at a higher latitude that experienced a warm temperate to subtropical climate with a significant seasonality (Demers-Potvin and Larsson 2019), and suggests that the versatility demonstrated by the diverse Jurassic record in this family extended at least into the beginning of the Late Cretaceous. Conversely, it also confirms their presence in another habitat experiencing milder conditions than their extant relatives' current refuge (Claridge et al. 1999). Considering the evidence for Mesozoic tettigarctids living in tropical to subtropical environments, this family constitutes yet another example of an insect group for which uniformitarian assumptions based on the natural history of modern species cannot be applied to extinct relatives.

At a higher taxonomical level, the discovery of *Maculaferrum blaisi* gen. et sp. nov. offers more insight on the biogeography of its subfamily. Jurassic taxa assigned to Tettigarctinae were distributed in Europe, as well as central and northeastern areas of Asia (Kazakhstan and northeastern China) (Martynov 1937; Bode 1953; Hong 1983). In the Early Cretaceous, members of this subfamily are only found in northern Africa and eastern South America (Nel et al. 1998; Menon 2005). The discovery of *Maculaferrum* extends the Late Cretaceous record of Tettigarctinae from the West Burma Block to northern areas of North America. The spatiotemporal distribution of the known fossil record of Tettigarctinae suggests a dispersal of the subfamily over its history in two possible scenarios: either an expansion of the range, or a retreat of the group from warm areas of Europe and/or central and eastern Asia towards equatorial Africa, South America and the West Burma Block, then to slightly cooler areas at higher latitudes during the Cenozoic (Fig. 6). Considering that the North Atlantic Ocean was opening during the Late Cretaceous, the presence of *Eotettigarcta scotica* Zeuner, 1944 in the Palaeocene Isle of Mull deposits, Scotland, could be explained by a dispersal across the Thulean Land Bridge, which is considered to have been the most important path of interchange for temperate biota in the earliest span of the Eocene (Sanmartín et al. 2001; Archibald et al. 2011). Alternatively, a vicariance hypothesis cannot be ruled out considering that the oldest known tettigarctids

existed in Australia likely before the breakup of Pangaea (Lambkin 2019), and that this same landmass is now home to the family's only extant representatives (Moulds 2005). Such a small sample size stretched over a ~200 Ma fossil record may restrict our ability to precisely elucidate the biogeographical patterns of tettigarctids.

## Conclusions

The discovery of *Maculaferrum blaisi* gen. et sp. nov. finally confirms the presence of the once-widespread cicada family Tettigarctidae in North America and contributes to filling a Late Cretaceous gap in the fossil record of hairy cicadas. The erection of a new genus is strongly supported by distinctive forewing venational characters and a unique geographical distribution. This is the most recently described member of Tettigarctinae to display a combination of venational characters supposedly diagnostic of tribes Protabanini, Meunierini and Tettigarctini. Consequently, it supports the hypothesis according to which the definitions of these taxa are based on many convergent or plesiomorphic characters, and that they should be revised accordingly. It also leads us to propose the hypothesis that tettigarctids were still thriving at least at the start of the Late Cretaceous, and that their competitive displacement by singing cicadas occurred at least later than the Cenomanian. Additionally, the relatively high palaeolatitude of the locality of this new genus supports a hypothesis of shifts in the extent of the world distribution of Tettigarctinae throughout the lineage's history. More fossil discoveries are necessary to refine these ecological and biogeographical hypotheses. Together with a more thorough study of wing venation patterns and variability among the extant *Tettigarcta* species, they should also contribute to refining the taxonomy of this family. The small number of known Late Cretaceous, and more precisely Cenomanian, sites means that it remains difficult to determine whether the abundance of rare occurrences in the Redmond entomofauna is caused by taphonomical bias or a biogeographically significant phenomenon. *Maculaferrum* is the first hemipteran described from Labrador's Redmond Formation, and represents the beginning of a renewed scientific interest in this unique and remote Cretaceous locality. Further descriptions of this recently expanded palaeocommunity, and its eventual comparison with the relatively spatially and temporally close assemblage in New Jersey amber, may provide insight on this matter on a more continental scale.

## Acknowledgements

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SUPPLEMENTARY ONLINE MATERIAL FOR

# First North American occurrence of hairy cicadas discovered in a Cenomanian (Late Cretaceous) from Labrador, Canada

Alexandre V. Demers-Potvin, Jacek Szwedo, Cassia P. Paragnani, and Hans C.E. Larsson

**Supplementary Online Material**

A Reflectance Transformation Imaging (RTI) file along with viewer software and instructions available at

http://app.pan.pl/SOM/app65-Demers-Potvin_etal_SOM/ReadMe.txt

http://app.pan.pl/SOM/app65-Demers-Potvin_etal_SOM/1_softwares_set/RTIbuilder_2_0_2_MacOs.dmg
http://app.pan.pl/SOM/app65- Demers-Potvin_etal_SOM/1_softwares_set/RTIbuilder_2_0_2_setup_WinOs.exe
http://app.pan.pl/SOM/app65- Demers-Potvin_etal_SOM/1_softwares_set/RTIViewer-1.1.0_MacOs.dmg
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