

A new palaeontinid (Insecta, Hemiptera, Cicadomorpha) from the Upper Jurassic Tiaojishan Formation of northeastern China and its biogeographic significance

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Abstract.—*Cicadomorpha guancaishanensis* new species, of the extinct family Palaeontinidae, is described from the Upper Jurassic Tiaojishan Formation at Guancaishan, Jianping County, Western Liaoning, northeastern China. It represents the first record of Palaeontinidae from the Tiaojishan Formation and highlights the palaeodiversity of the Late Jurassic palaeontinids. *Cicadomorpha* Martynov, 1926 previously included three species with extremely limited morphological differences from the Karabastau Formation of Kazakhstan, the Glushkovo Formation, and the Ukurei Formation of Chita, Transbaikalia, and Russia, indicating a correlated stratigraphic relationship. This discovery provides new evidence that closure of the Okhotsk Ocean began in the Middle Jurassic. Thus, there is no distinct geographical barrier between the southern and northern areas of Mongolia-Okhotsk Ocean in the Late Jurassic.

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Introduction

Palaeontinoidea (Insecta: Hemiptera: Cicadomorpha) is an extinct superfamily of hemipteran insects, comprising three families (i.e., Dunstaniidae Tillyard, 1916, Mesogereonidae Tillyard, 1921, and Palaeontinidae Handlirsch, 1906). Palaeontinidae are Mesozoic cicadomorphan hoppers, superficially resembling huge moths, which existed from the Triassic (Carnian) to the Cretaceous (Aptian), distributed in Europe, Central Asia, South Africa, China, South Korea, and Australia, especially in the Northern Hemisphere (Riek, 1976; Shcherbakov and Popov, 2002; Menon et al., 2005; Wang et al., 2007; Nam et al., 2017; Szwed, 2018; Chen et al., 2019; Li et al., 2019). The striking features of Palaeontinidae are the presence of a large body covered with numerous hairs; a small head with an extremely long rostrum reaching the end of the abdomen, which is suitable for sucking juice from a macrophyte; a wide pronotum and mesonotum; broad wings armed with dark bands to avoid predators; and a fully developed nodal line on the forewing, similar to that of tettigarctids (Carpenter, 1992; Chen et al., 2016; Nam et al., 2017). Palaeontinids flourished during the Jurassic and the Early Cretaceous and became extinct in the middle Cretaceous, likely owing to the food crisis and emergence of various insectivorous mammals and birds in the Early Cretaceous (Menon et al., 2005; Wang et al., 2008).

The first unequivocal palaeontinid in China was reported by Hong (1982) on the basis of an isolated hindwing. Palaeontinidae have a rich fossil record in northern China, including 57 species within 22 genera from the Early Jurassic to the Early Cretaceous. They have been reported from the Lower Jurassic Badaowan Formation of Karamai, Xinjiang, northwestern China; the Middle–Upper Jurassic Longmen Formation (= Jiulongshan Formation) of North Hebei, the Middle–Upper Jurassic Haifanggou Formation of West Liaoning, and the Daohugou beds (Haifanggou Formation), Inner Mongolia; and the Lower Cretaceous Chijinqiao Formation of Gansu and the Yixian Formation of Hebei, Liaoning, and Inner Mongolia (Fig. 1) (Wang and Ren, 2009; B. Wang et al., 2009; Chen et al., 2016). Among them, 17 genera and 42 species were collected from the Middle–Upper Jurassic of northeastern China, belonging to the ‘early assemblage’ of the Yanliao biota. Here we report a new species of Palaeontinidae from the Upper Jurassic Tiaojishan Formation of Guancaishan—*Cicadomorpha guancaishanensis* new species—representing the first fossil record of palaeontinids in the ‘late assemblage’ of the Yanliao biota and the third insect species described from the Tiaojishan Formation.

Geological settings

The new fossil palaeontinid preserved in black shale was collected by one of us (CC) in 2013 from the Upper Jurassic Tiaojishan Formation, at the upper layer of the lacustrine deposit at Guancaishan, near Muyingzi Village, Shapai Township, Jianping County, Chaoyang City, Liaoning Province, northeastern

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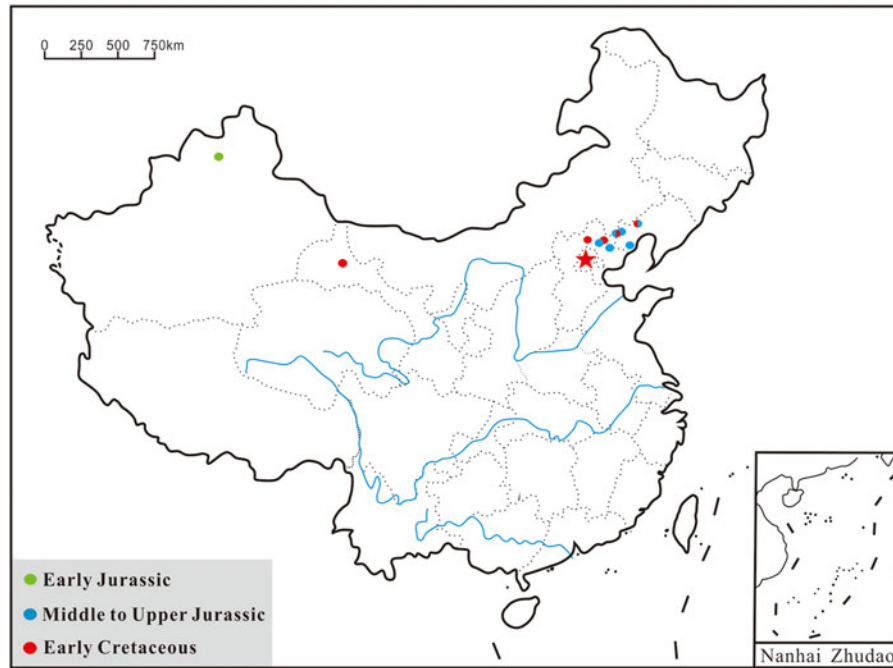


Figure 1. Distribution of Mesozoic palaeontinids in China.

China (Fig. 2). This deposit can be generally assigned within the Linglongta beds, which are the lacustrine interbedded clastic silts of the large scale andesite of the Tiaojishan Formation mainly occurring in western Liaoning, northern Hebei, and western Beijing, including several exceptional fossil localities such as Daxishan, Nanshimen, Bawangou, and Fanzhangzi (Huang, 2015, 2016; Huang et al., 2018a). The Linglongta biota contains numerous well-preserved fossils, e.g., insects, bivalves, conchostracans, ostracods, gastropods, charophytes, pollen, and spores (Duan et al., 2009; Huang, 2016; Huang et al., 2018a), as well as diverse vertebrate fossils including fishes (Huang, 2015), salamanders (Gao and Shubin, 2012; Wang et al., 2015; Jia and Gao, 2016, 2019), pterosaurs and their eggs (e.g., Lü, 2009; Lü et al., 2010, 2011; X. Wang et al., 2009; Wang et al., 2010; Cheng et al., 2012; Yang et al., 2019), feathered dinosaurs (e.g., Hu et al., 2009; Xu et al., 2011; Godefroit et al., 2013a, b), and mammals (e.g., Meng et al., 2006; Luo et al., 2011; Yuan et al., 2013; Zhou et al., 2013; Bi et al., 2014). However, the fossil insects from the Linglongta biota are poorly known. Only two species (i.e., *Omma daxishanense* Cai and Huang, 2016 and *Sinothemis difficilis* Huang, Cai, and Nel, 2018b) have been formally described from Daxishan and Guancaishan, respectively. Huang et al. (2018a) illustrated abundant fossil insects with at least 16 orders from various localities of the Linglongta beds including Daxishan, Guancaishan (Muyingzi Village), and Zhuanshanzi (Nanshimen Village).

Until now, the successive deposit of Yanliao biota contains both Daohugou and Linglongta beds only known from Guancaishan and Nanshan localities (Fig. 2). The Guancaishan deposits include the lower tuffaceous shale layers that have yielded very rich insects, bivalves, plants, and abundant salamanders (Gao and Shubin, 2012; Wang et al., 2015), and the higher black insect layers (Fig. 2; Huang et al., 2018a), which are separated by a layer of intrusive rocks. The volcanic ash

layer is located ~ 1 m above the fossil insect bedding plane dated as 157.3 ± 1.5 Ma (SIMS U-Pb zircon age), indicating the age of the fossil layer close to the boundary of Oxfordian and Kimmeridgian (i.e., 157.3 ± 1.0 Ma; Huang, 2016).

Material and methods

The fossil specimen (NIGP 168220) was carefully prepared using a sharp knife under a stereo microscope. A photograph of general habitus was taken using a Canon EOS 5D Mark II camera with a Canon 100 mm macrolens. Photomicrographs were made using a Zeiss Discovery V16 stereoscope, in some cases moistened with 70% ethanol. The raw digital images were processed with Helicon Focus 6 software, and all images were modified and arranged in Adobe Photoshop CS6. Line drawings were prepared using a binocular Olympus SZX7 microscope and were modified with CorelDRAW X7 graphic software.

Wing venation terminology and cell nomenclature follow B. Wang et al. (2009), Nel et al. (2012), and Bourgoïn et al. (2015). All measurements are given in mm.

Repository and institutional abbreviation.—The specimen is deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGP).

Systematic palaeontology

- Suborder Cicadomorpha Evans, 1946
- Superfamily Palaeontinoidea Handlirsch, 1906
- Family Palaeontinidae Handlirsch, 1906
- Genus *Cicadomorpha* Martynov, 1926

Type species.—*Cicadomorpha punctualata* Martynov, 1926.

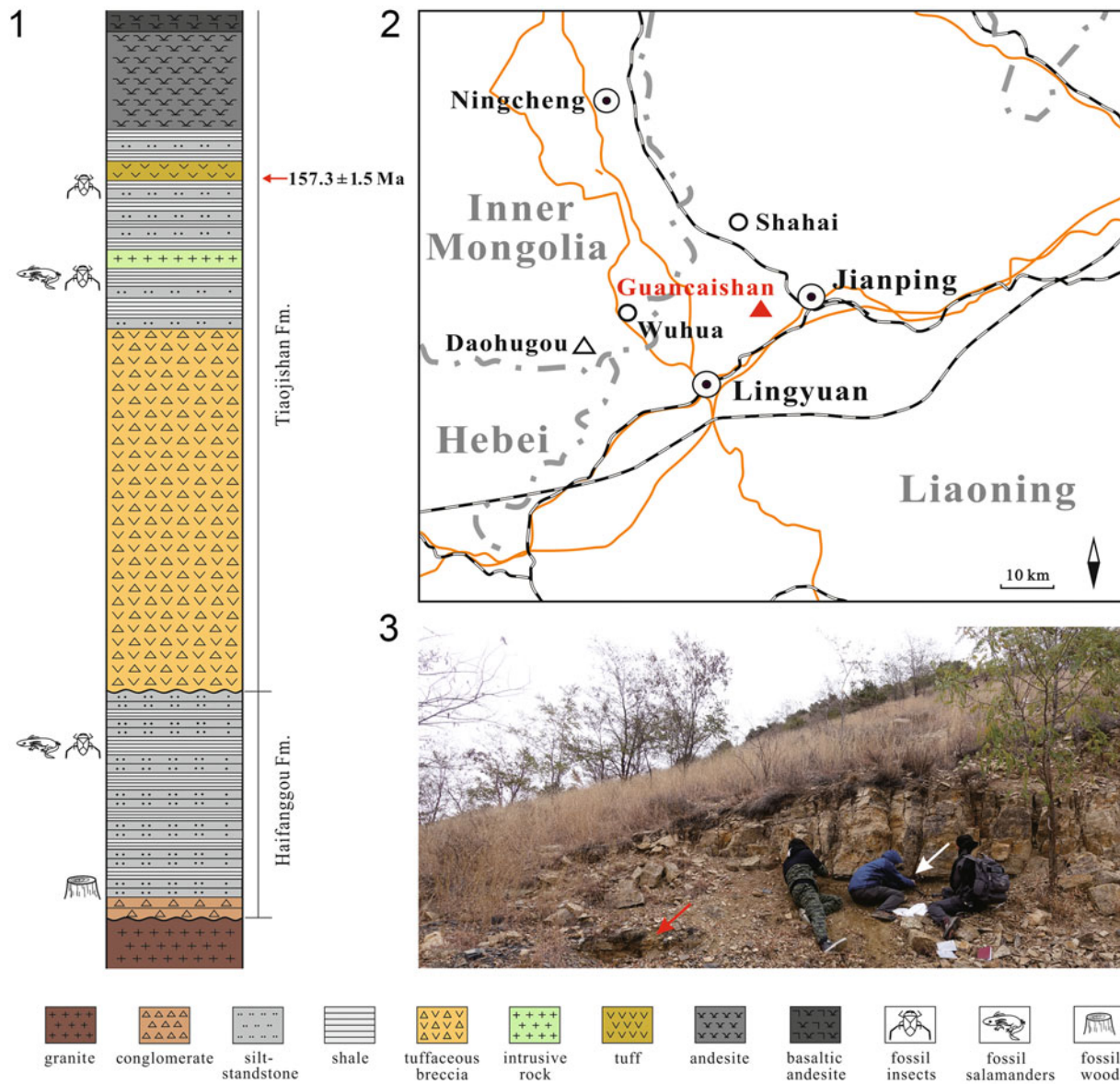


Figure 2. (1) Stratigraphic column for the Tiaoishan Formation at Guancaishan, Jianping County, Liaoning Province, northeastern China; (2) map showing the Guancaishan locality; (3) the outcrop of the fossil, red arrow indicating the black shales from which the fossil was collected, and the white arrow indicating the volcanic ash layer slightly above the black shale.

Other species.—*Cicadomorpha milva* Shcherbakov, 1988 and *C. parula* Shcherbakov, 1988.

Cicadomorpha guancaishanensis new species

Figures 3–4

Holotype.—NIGP 168220 (a, b), including part and counterpart, a nearly complete adult male with wings extended; stored at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China.

Diagnosis.—Wings with distinct color bands and suborbicular spots; tegmen with Pc + CP emitting seven branches intersecting costal area; MP bifurcate, situated slightly after bifurcation point of CuA; MP₁₊₂ as long as MP₃₊₄; cross vein mp-cua with short, wedge-shaped vein; mp₄-cua curved

mediad; Pcu fused with A1 distinctly basad of bifurcation of MP; A1 nearly straight; hind wings with cross vein ir much longer than ScP + RA₁.

Occurrence.—Upper Jurassic Tiaoishan Formation at Guancaishan near Muyingzi Village, Jianping County, Chaoyang City, Liaoning Province, China; early Late Jurassic, near boundary of Oxfordian and Kimmeridgian.

Description.—Body (Figs. 3.1, 4.1) ~32.1 mm length and 14.8 mm in width, with a pair of fore wings and hind wings, lacking only the legs.

Head small (Fig. 3.2), length ~3.3 mm, width ~5.9 mm, rounded apically; compound eyes large, ovoid, positioned laterally; postclypeus swollen, 1.13 mm long, 0.55 mm wide; anteclypeus less swollen, nearly half length of postclypeus;

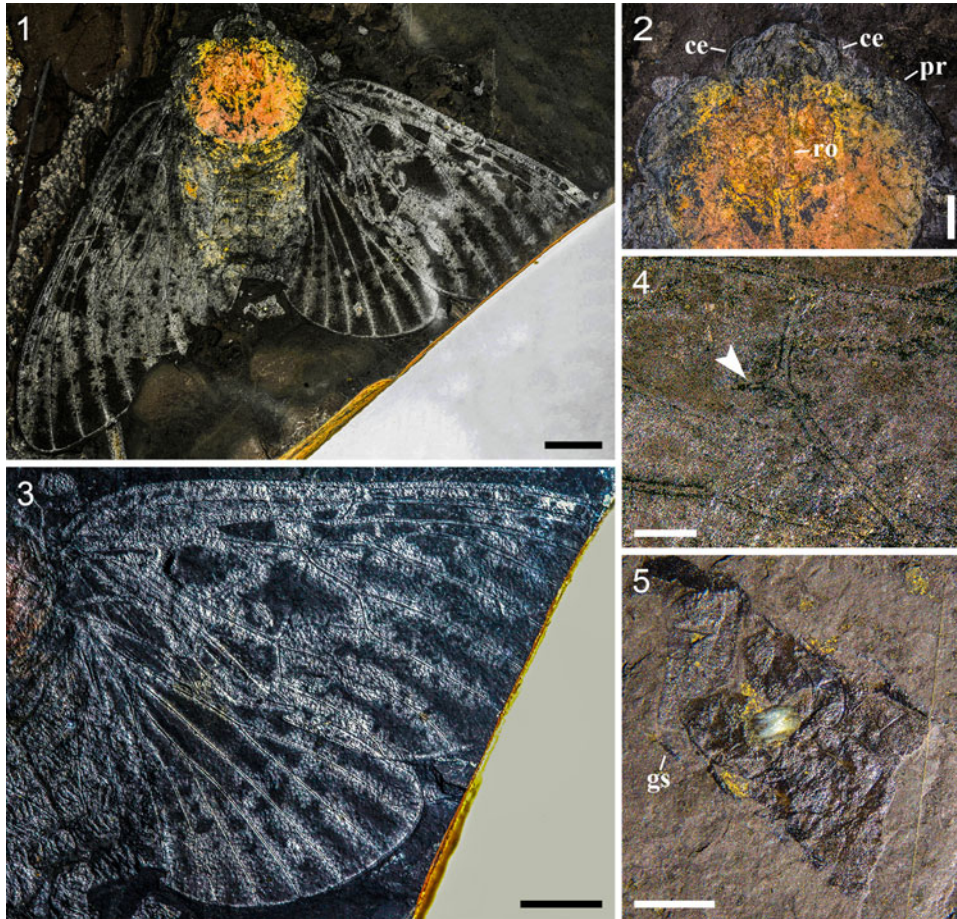


Figure 3. *Cicadomorpha guancaishanensis* n. sp. from the Upper Jurassic Tiaojishan Formation at Guancaishan: (1) holotype (NIGP 168220), male, showing general habitus moistened with 70% ethanol; (2–5) enlargements of (1), showing details of: (2) head and pronotum, moistened with 70% ethanol; (3) right tegmen; (4) discal cell and cross vein mp-cua; and (5) genitalia. ce = compound eye; gs = genital style; pr = pronotum; ro = rostrum. Scale bars = 1 mm (4, 5); 2 mm (2, 3); 6 mm (1).

clypellus triangularly elongated; rostrum long, as preserved ~3.1 mm, extending beyond thorax. Pronotum rounded (Fig. 3.2), nearly 2.3 times wider than head; anterior edge concave medially; anterolateral angles of pronotum notably expanded. Thorax partly obscured by extended mesonotum.

Tegmen subtriangular (Figs. 3.3, 4.2), 39.8 mm long, 12.6 mm wide, with length/width ratio ~3.2; tegmen armed with colored bands from base to end, dotted with suborbicular spots of varying sizes; costal margin slightly arched at base, then nearly straight; anteroapical angle rounded; posteroapical angle 148°; posteroapical margin slightly curved; postclavial margin almost straight, with position of bend connected with nodal line; basal cell wide; vein Pc + CP slightly curved, ending at level of nodal indentation, emitting seven branches intersecting costal area, these branches dispersed in increasing distance from each other; stem ScP separated from common stem R + MP at base, with terminal ScP obscure; stem R slightly curved, branching into RA and RP distinctly basad of nodal line, reaching one-third of tegmen length; RA and RP simple, with cross vein ir absent; RP connected with MP₁; cross vein mp-cua segmenting discal cell, distinctly curved with short, wedge-shaped vein (Fig. 3.4), tapering toward end of tegmen; stem MP with four branches, branching into MP₁₊₂ and MP₃₊₄ slightly basad of nodal line and slightly

after bifurcation of CuA; MP₁₊₂ as long as MP₃₊₄; cross vein im absent; mp₄-cua curved mediad; CuA dispersed from stem CuA + CuP reaching 0.14 of tegmen length, branching into CuA₁ and CuA₂ reaching 0.38 of tegmen length; basal of CuA₂ along posterior end of nodal line; CuP curved at base, then nearly straight; Pcu fused with A₁ distinctly basad of bifurcation of stem MP, reaching one-quarter of tegmen length; A1 nearly straight.

Hind wings oval (Figs. 3.3, 4.3), ~25.4 mm long, with length/width ratio 1.7, dotted with colored bands and irregular suborbicular spots; costal margin distinctly arched; costal area long, almost half length of wing, with length/width ratio ~5.2; stem ScP + RA branching into ScP + RA₁ and RA₂, reaching 0.44 of wing length, connecting with stem RP + MP by cross vein ir; RA₂ short; cross vein ir long, ~2.7 times longer than ScP + RA₁; RP fused with MP₁ for considerable distance before separating; MP with four branches, with MP₁ and MP₂ almost straight, MP₃₊₄ branching MP₃ and MP₄ at same level of bifurcation of ScP + RA; cross vein mp-cua short; stem CuA branching into CuA₁ and CuA₂, reaching 0.30 of wing length; peripheral membrane narrow.

Abdomen with seven visible segments, clothed with dense hairs; pygofer short, wide, slightly longer than preceding abdominal sternite (Fig. 3.5).

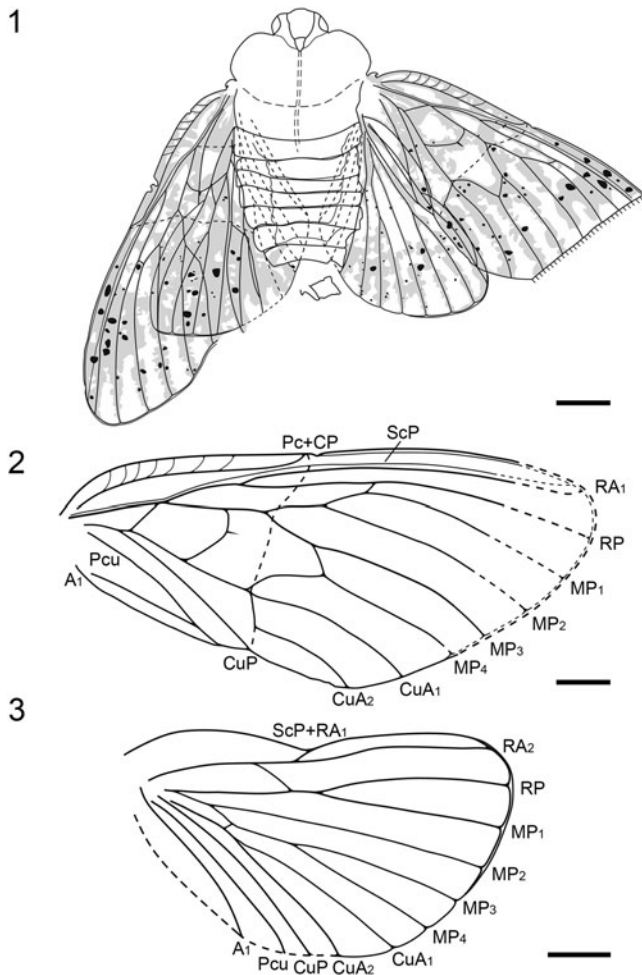


Figure 4. Line drawings of *Cicadomorpha guancaishanensis* n. sp., holotype (NIGP 168220): (1) general habitus; (2) forewing; and (3) hind wing. A = anal vein; CP = costa posterior; CuA = cubitus anterior; CuP = cubitus posterior; MP = median posterior; Pc = precosta; Pcu = postcubitus; RA = radius anterior; RP = radius posterior; ScP = subcosta posterior. Scale bars = 4 mm (2, 3); 6 mm (1).

Etymology.—The species name is from Guancaishan, indicating the type locality of the species.

Remarks.—The new species distinctly differs from the type species, *Cicadomorpha punctualata* from Kazakhstan, by following characters of the tegmen: (1) tegmen length near 40 mm (near 54 mm in *C. punctualata*); (2) stem R slightly shorter than stem MP (extremely short in *C. punctualata*); (3) MP branching into MP_{1+2} and MP_{3+4} slightly after bifurcation of CuA (branching distinctly basad of bifurcation of CuA in *C. punctualata*); and (4) cross vein mp_4 -cua long and curved (absent in *C. punctualata*).

The new species is distinguished from other species of *Cicadomorpha* from Chita, Transbaikalia by following characters: (1) Pc + CP of tegmen emitting seven branches intersecting the costal area (ScP emitting three or four branches in *C. milva* and *C. parula*); (2) tegmen with MP branching into MP_{1+2} and MP_{3+4} slightly after bifurcation of CuA (MP branching basad of bifurcation of CuA in *C. milva* and *C. parula*); (3) tegmen with MP_{1+2} as long as MP_{3+4} (slightly longer than MP_{3+4} in *C. milva*;

nearly two times longer than MP_{3+4} in *C. parula*); (4) cross vein mp -cua of tegmen with a short, wedge-shaped vein (short vein absent in *C. milva* and *C. parula*); (5) cross vein mp_4 -cua of tegmen curved mediad (straight in *C. parula*); (6) tegmen with Pcu fused with A1 distinctly basad of bifurcation of MP (Pcu fused with A1 at same level of bifurcation of MP in *C. milva*; A1 isolated in *C. parula*); and (7) hind wings with cross vein $ir \sim 2.7$ times as long as ScP + RA_1 (ir not longer than ScP + RA_1 in *C. milva* and *C. parula*).

Discussion

Martynov (1926) erected the genus *Cicadomorpha* and the single species *C. punctualata* based on an incomplete specimen from Kazakhstan. Shcherbakov (1988) placed two species in *Cicadomorpha* (*C. milva* and *C. parula*) from Chita, Transbaikalia, Russia. *Cicadomorpha guancaishanensis* n. sp. from the Upper Jurassic Linglongta beds can be firmly assigned to *Cicadomorpha*. The new species is more similar to *C. milva* from Chita than other species in terms of morphological characters, e.g., size of body and wings, stem MP of forewing distinctly longer than MP_{1+2} and MP_{3+4} , cross vein mp_4 -cua of forewing curved mediad, and Pcu fused with A1. It is notable that all species of *Cicadomorpha* show extremely limited morphological differences. Therefore, these might indicate the biostratigraphic correlation of some well-known fossil localities: the Tiaojishan Formation (Yanliao area, northeastern China), the Karabastau Formation (Karatau, Kazakhstan), and the Glushkovo and the Ukurei Formations (Chita, Transbaikalia, Russia). There is some dispute about the ages of the Karabastau Formation, the Glushkovo Formation, and the Ukurei Formation. It has been suggested that the age of the Karabastau Formation is Middle–Late Jurassic (e.g., Kirichkova and Doludenko, 1996; Zhang, 2015); the age of Glushkovo Formation and the Ukurei Formation are poorly constrained, suggested as Late Jurassic (Sinitisa, 1993), Early Cretaceous (Sinitshenkova, 2005), or perhaps at the Jurassic/Cretaceous boundary (Rasnitsyn and Quicke, 2002).

Our discovery provides new evidence suggesting that all of the above units are Late Jurassic, which is consistent with previous studies (e.g., Ponomarenko et al., 2009; Sinitisa, 2016). The geological range of the Tiaojishan Formation was limited to 161–153 Ma by recent analyses based on isotope dating (Huang, 2019), which is obviously different from the view that the age of the Tiaojishan Formation is the Middle Jurassic (Deng et al., 2003, 2017; Duan et al., 2009). Isotope dating of the volcanic ash layer at Guancaishan ~ 1 m above the fossil palaeontinid layer yielded an age of 157.3 ± 1.5 Ma (SIMS U–Pb zircon age), which is close to the boundary of Oxfordian and Kimmeridgian (157.3 ± 1.0 Ma; Huang, 2016). Therefore, this study provides a relative age for the other three well-known localities, indicating that the insect probably lived during the early Late Jurassic.

The Late Jurassic (Tithonian) palaeontinids from Solnhofen, Germany and the Cretaceous palaeontinids constitute a monophyletic group, representing the late stage of palaeontinid evolution with the following combination characters: (1) forewing trigonal; (2) costal area and claval reduced; (3) veins RA, RP, and MP originating at a common point; (4) length of the hind wing nearly one half that of the forewing; and (5) RP of hind wing often fused with MP_1 (B. Wang et al., 2009).

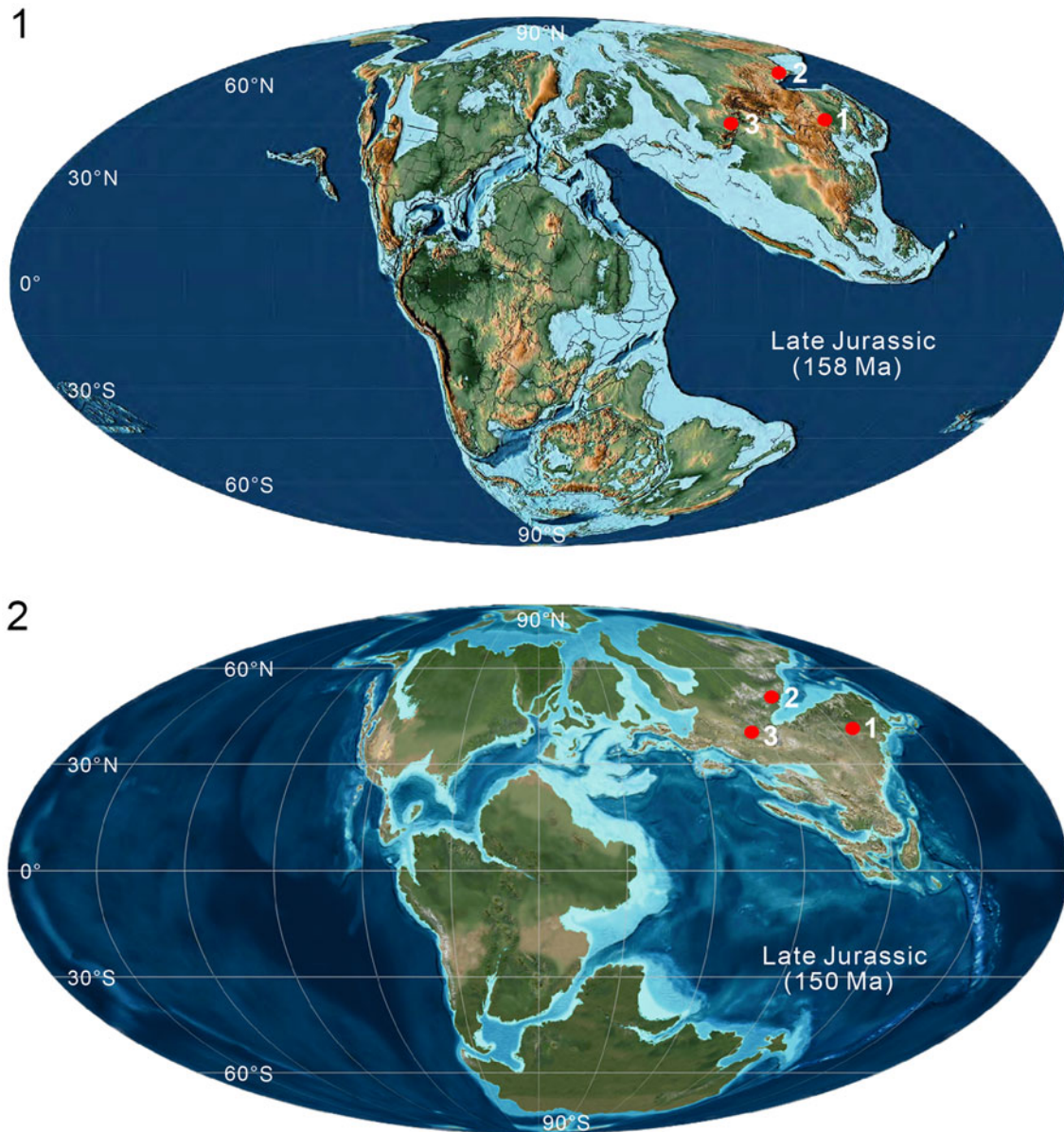


Figure 5. Palaeogeographic distribution of *Cicadomorpha* during the Late Jurassic: (1) global palaeogeographic reconstruction, 158 Ma (after Scotese, 2014); (2) global palaeogeographic reconstruction, 150 Ma (after <https://www2.nau.edu/rcb7/>). 1 = Guancaishan, Liaoning Province, China; 2 = Karatau, Kazakhstan; 3 = Chita, Transbaikalia, Russia.

Cicadomorpha completely differs from the Solnhofen palaeontinids and Cretaceous palaeontinids, but shares similarities with *Palaeontiondes* Martynov, 1937 and *Daohugoucossus* Wang, Zhang, and Fang, 2006 from the Middle–Upper Jurassic Haifanggou Formation at Daohugou, Inner Mongolia, northeastern China in having similar subtriangular forewings, costal area and claval wide, cross vein mp-cua segmenting the discal cell, and hind wing relatively large. However, *Cicadomorpha* differs from *Palaeontiondes* and *Daohugoucossus* by two distinct characters: costal area with some intersecting branches and cross vein r-m of hind wing absent, and RP fused with MP₁ for a considerable distance. The cross vein r-m of the hind wing is present in Dunstaniidae and Mesogereonidae, and some genera of Palaeontinidae, e.g., *Suljuktocossus* Becker-Migdisova, 1949, *Ningchengia*

B. Wang et al., 2009, and *Palaeontinodes*, but it is absent from most Cretaceous palaeontinids (B. Wang et al., 2009).

Cicadomorpha appears to be descended from the early assemblage of the Yanliao biota (e.g., Daohugou) by sharing some groups, and then migrating throughout Eurasia in the Late Jurassic, suggesting their adaptability to surroundings to some extent. The age difference between the core fossil layers of the Daohugou and the Linglongta assemblages is < 5 Ma. Until now, no species common to both assemblages have been discovered, because of the strong tectonic deformation and the large-scale volcanic activity that occurred (Yanshan Movement, Phase A2), resulting in the ecosystem of Daohugou area being seriously collapsed (Huang, 2015; Huang et al., 2018a).

Biogeographic implications

Siberia and Mongolia were separated by an enormous gulf in the Paleopacific, called the Mongolia-Okhotsk Ocean, which is located in the northern part of the Mongolian-North China Block, dated from the Triassic to the Jurassic (Zonenshain et al., 1990; Huang, 2019). The Siberia Plate began a southward subduction and closure of the Mongolia-Okhotsk Ocean, to produce the Mongol-Okhotsk fold belt (Zorin, 1999; Kravchinsky et al., 2002). There is much debate about the beginning of the closure of the Mongolia-Okhotsk Ocean. Available data suggest that the closure of the Mongolia-Okhotsk Ocean occurred during the Middle–Late Jurassic (Zonenshain et al., 1990; Kravchinsky et al., 2002; Tomurtogoo et al., 2005; Huang, 2019), although paleomagnetic studies have indicated that it was completely closed by the Early Cretaceous (~130 Ma; Zhao et al., 1990; Enkin et al., 1992; Gilder and Courtillot, 1997; Metelkin et al., 2007). A regional unconformity below the Tiaojishan Formation of Yanliao area, China, formed at 161 Ma (Huang et al., 2018a; Huang, 2019). There is also a regional unconformity below the Toutunhe Formation—the Junggar Basin in northwestern China (correlated to the Tiaojishan Formation)—and the age of the bottom of the Toutunhe Formation is ~161.2 Ma (Fang et al., 2015). Huang (2019) suggested that a widespread unconformity in northern China is indicative of the Yanshan Movement, Phase A2, related to the closure of the Mongolia-Okhotsk Ocean. The closing of the Mongolia-Okhotsk Ocean probably occurred before the Yanshan Movement, Phase A1 (~168 Ma). The ancient landform north and northeast of the Yanliao area is uplift, and then a set of complex conglomerates is rapidly denuded.

All species of *Cicadomorpha* are confined to Eurasia (Fig. 5). During the early Late Jurassic, *C. punctulata* from Kazakhstan was located in the western Okhotsk Ocean, *C. milva* and *C. parula* from Chita, Transbaikalia were located in the north Okhotsk Ocean, and the new species from Guancaishan, northeastern China was located in the southern Okhotsk Ocean (Fig. 5). Considering the limited flight capacity of these early cicada-like insects, it was almost impossible to cross the vast ocean, and the similarities between the new species and *C. milva* from Chita instead of *C. punctulata* from Kazakhstan indicate that a biological connection emerged between Chita and northeastern China. Our discovery, therefore, inclines toward the global palaeogeographic reconstruction of Scotese (2014; Fig. 5.1), and provides new evidence indicating that the closure of the Okhotsk Ocean began in the Middle Jurassic.

Acknowledgments

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