A revision of Palaeontinidae (Insecta: Hemiptera: Cicadomorpha) from the Jurassic of China with descriptions of new taxa and new combinations

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The new generic name Martynovocossus nom. nov. (Hemiptera, Palaeontinidae) is proposed as a replacement name for the preoccupied and junior homonym Pseudocossus Martynov, 1931, non Pseudocossus Kenrick, 1914, non Pseudocossus Gaede, 1933. The new genus group is redefined based on new, exceptionally preserved material including complete forewings and hindwings with colour pattern preservation. The synonymies for Martynovocossus zemcuznicovi comb. nov., M. turgaiensis comb. nov., M. strenus comb. nov., M. punctulosus comb. nov., M. bellus comb. nov. and M. ancylichenius comb. nov. are established, and the diagnostic characters for M. strenus comb. nov., M. bellus comb. nov. and M. punctulosus comb. nov. are revised. Two new species, M. decorus sp. nov. and M. cheni sp. nov., are described from the Middle Jurassic Daohugou Lagerstätte. Martynovocossus species display considerable intraspecific variation, particularly in aspects of wing size, venation and colour pattern. A key to species of Martynovocossus is presented. Copyright © 2007 John Wiley & Sons, Ltd.

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KEY WORDS Pseudocossus; Palaeontinidae; insect; homonym; Jurassic; Daohugou; China

1. INTRODUCTION

The first Palaeontinidae was recorded from the Middle Jurassic of England. It was originally regarded as the earliest Lepidoptera (Butler 1873; Handlirsch 1906–1908), and later transferred to the Auchenorrhyncha (Tillyard 1921). Subsequently, abundant palaeontinids have been reported from the Jurassic and Cretaceous of Eurasia (for details see Carpenter 1992; Wang et al. 2006a). This group first appeared in the Late Triassic, went into its most prosperous stage in the Middle Jurassic and became extinct in the mid-Cretaceous (Wang B et al. 2007a). Very recently, well-preserved fossils were discovered from the late Mesozoic of China and Brazil, and largely broadened our recognition on the Palaeontinidae (Menon and Heads 2005; Menon et al. 2005; Wang and Ren 2006, 2007; Wang et al. 2006a,b,c,d; Wang B et al. 2007a,b; Wang Y et al. 2007).

The palaeontinid genus Pseudocossus was erected by Martynov (1931) based on a forewing from the Jurassic Cheremkhovo Formation of Ust-Baley, Irkutsk and so far six species have been reported from the Lower–Middle Jurassic of Central Asia and north China (Martynov 1931; Becker-Migdisova and Wootton 1965; Zhang 1997; Wang and Ren 2006). Some specimens referred to Pseudocossus spp. were also extensively discovered from the Lower–Middle Jurassic of Siberia and Mongolia and the Late Jurassic Karabastau Formation of Southern
Kazakhstan (Shcherbakov 1985; Shcherbakov and Popov 2002). However, *Pseudocossus* Kenrick, 1914 is the available valid name of an extant genus of the Brachodidae of Lepidoptera. *Pseudocossus* Gaede, 1933 within the Cossidae of Lepidoptera is a junior homonym of *Pseudocossus* Kenrick, 1914, and has been replaced with *Zyganisus* Viette, 1951. As another junior homonym of *Pseudocossus* Kenrick, 1914, *Pseudocossus* Martynov, 1931 is also required to be substituted by a new name.

Some exceptionally preserved palaeontinids within the genus have been discovered from the Daohugou Lagerstätte and detailed observations of these specimens allow us to revise the original descriptions. Herein, two new species are described from the Middle Jurassic of Daohugou and a key to species of the genus is presented.

2. MATERIAL AND METHODS

There is no consensus on the interpretation of vein nomenclature in Palaeontinidae between Becker-Migdisova (1949), Emeljanov (1977) and Dworakowska (1988). We tentatively followed the traditional terminologies with slight modifications (Becker-Migdisova 1949; Wang et al. 2006a). Specimens were examined dry and under alcohol, using a Nikon SMZ1000 stereomicroscope and drawings were made with the aid of a camera lucida. The photographs were prepared using a NIKON D100 digital camera, and the line drawings were readjusted on photographs using image-editing software (CorelDraw 13.0 and Adobe Photoshop CS). In drawings, dashed lines denote the nodal line in the forewing, dotted lines indicate faintly seen and hypothesized missing veins and thin solid lines indicate the edges of missing or obscured regions. For the costal area (its apex is bordered with faint vein Sc) of the hindwing, the length/width ratio was measured and calculated by way of excluding the vein width.

Thirty-five specimens described here came from the Daohugou Lagerstätte (41°18’N, 119°131’E), Ningcheng County, Inner Mongolia, China. Biostratigraphic and radiometric dating methods have generated inconsistent age estimates of the Daohugou Lagerstätte (for details about the stratigraphy and biota, see Chen et al. 2005; Zhang 2006; Zhou et al. 2007). Herein, we adopt a Middle Jurassic age based on the analysis of the hymenopteran fossil assemblage (Rasnitsyn and Zhang 2004) and stratigraphic evidence (Chen et al. 2004; Chen et al. 2005; Gao and Ren 2006).

3. SYSTEMATIC PALAEONTOLOGY

Order HEMIPTERA Linnaeus, 1758
Infraorder CICADOMORPHA Evans, 1946
Superfamily PALAEONTINOIDEA Handlirsch, 1906
Family PALAEONTINIDAE Handlirsch, 1906

*Martynovocossus* Wang and Zhang, nom. nov.

1931 *Pseudocossus* Martynov, p. 94.
1956 *Pseudocossus* Martynov; Evans, p. 227.
1965 *Pseudocossus* Martynov; Becker-Migdisova and Wootton, p. 72.
1992 *Pseudocossus* Martynov; Carpenter, p. 216.
1997 *Pseudocossus* Martynov; Zhang, p. 316.
Type species

_Pseudocossus zemczuznicovi_ Martynov, 1931; by original designation.

Type horizon and locality

Cheremkhovo Formation, Lower Jurassic (Toarcian); Ust-Baley, Irkutsk.

Etymology

The new genus group is named in honour of the late Professor Andrey V. Martynov (Russian palaeoentomologist) and cossus (a generic name of Lepidoptera, also a common ending for Palaeontinidae).

Included species

Eight species: the type species _M. zemczuznicovi_ (Martynov, 1931), comb. nov.; _M. turgaiensis_ (Becker-Migdisova and Wootton, 1965), comb. nov., from the Lower–Middle Jurassic of Kazakhstan; _M. strenus_ (Zhang, 1997), comb. nov., from the Lower Jurassic of Xinjiang, China; _M. punctulosus_ (Wang and Ren, 2006), comb. nov., _M. bellus_ (Wang and Ren, 2006), comb. nov. and _M. ancylivenius_ (Wang and Ren, 2006), comb. nov., from the Middle Jurassic of Daohugou, Inner Mongolia, China; _M. cheni_ sp. nov. and _M. decorus_ sp. nov. described below.

Diagnostic characters

Forewing subtriangular and medium–large sized (length 31–78 mm); nodal indentation clear and at about basal 0.4 wing length; vein ScP subparallel to stem R + M at wing base and coalesced with branch RA; vein ScP with 4–8 veinlets; branch RA free from vein R for a short distance; crossvein r + m-cua transverse; nodal line dividing discal cell into two parts; no crossvein in discal cell.

Hindwing small (length 20–35 mm), length/width ratio about 1.4; costal area wide, maximal width in basal 1/3; nodal indentation at basal 0.4 wing length; vein Sc terminating in costal margin slightly basal of nodal indentation; branch RP fused with branch M1 for a distance; stem M branching into veins M1 and M2 + 3 + 4 at wing base; vein M3 + 4 connected with branch CuA by crossvein m-cua, and bifurcating into veins M3 and M4 at the same level of nodal indentation; vein CuA bifurcating into veins CuA1 and CuA2 distal of the level of nodal indentation; veins CuP and Pcu simple.

Remarks

Hindwings are currently only known from three species: _M. turgaiensis_, _M. punctulosus_ and _M. cheni_. However, the important basal part of the hindwing is destroyed in _M. turgaiensis_ and _M. cheni_, and so the emended diagnostic characters of the hindwing are mainly based on _M. punctulosus_.

The forewing of _Martynovocossus_ closely resembles those of _Sinopalaeocossus_ Hong, 1983 (Wang et al. 2006c) and _Eoiocossus_ Wang and Zhang, 2006 (for detailed comparison see Wang et al. 2006b,c). _Martynovocossus_ shares the similar wing shape with _Suljuktocossus_ Becker-Migdisova, 1949, but differs from the latter in the forewing with ScP veinlets. It differs distinctively from _Cicadomorpha_ Martynov, 1926 in the forewing without crossvein in the discal cell; from _Palaeontinodes_ Martynov, 1937 in the forewing with ScP veinlets and no crossvein in the discal cell; and from _Palaeocossus_ Oppenheim, 1885 in the subtriangular forewing with nodal indentation.

Based on the hindwing with vein M3 + 4 branching from stem M2 + 3 + 4, _Martynovocossus_ is attributed to the group including _Cicadomorpha_ Martynov, 1926, _Daohugoucossus_ Wang, Zhang and Fang, 2006, _Gansuocossus_ Wang, Zhang and Fang, 2006, _Palaeontinodes_ Martynov, 1931, _Shurabocossus_ Becker-Migdisova, 1949 and _Suljuktaja_ Becker-Migdisova, 1949 (Wang B et al. 2007a). The hindwing of _Martynovocossus_ is different from those of _Suljuktaja_ and _Shurabocossus_ in possessing wing shape different and vein A1 absent; from _Gansuocossus_ and _Daohugoucossus_ having wing wider, location of nodal indentation more basal, costal area wider, distal part of anterior margin straight and vein A1 absent; and from _Cicadomorpha_ in possessing wing wider and shape of costal area different (maximum width in basal 1/4–1/3 for _Cicadomorpha_). Because of the poor knowledge of...
hindwings of *Palaeontinodes*, a detailed comparison between hindwings of *Martynovocossus* and *Palaeontinodes* is impossible.

After re-examining the holotype from the Lower–Middle Jurassic of Siberia, Shcherbakov (1985) thought that *Pseudocossus mirabilis* Kolosnitsyna, 1982 was not attributed to *Pseudocossus* but more resembled *Palaeocossus*.

*Martynovocossus strenus* (Zhang, 1997) comb. nov.

1997 *Pseudocossus strenus* Zhang, pp. 316–318, figure 3.

**Holotype**

NIGP126782a,b; deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences; Badaowan Formation, Lower Jurassic; Tuzigou of Karamai, Xinjiang.

**Diagnostic characters**

Forewing medium-sized (length about 42 mm); indentation at about basal 0.42 wing length; vein ScP with about 8 veinlets; vein RA dividing from vein R at basal 0.3 wing length, tightly close to costal margin for distal half; vein RP ending in the apex; vein M distinctly geniculate at junction with crossvein m-cua; crossvein m-cua short; vein M bifurcating a little basal of the level of indentation; vein M₁+₂ bifurcating nearly at middle of wing; vein M₃+₄ bifurcating at the same level of vein M₁+₂ forking.

**Description**

Forewing with clavus and apex missing, part and counterpart, length as preserved 42.5 mm (estimated complete length about 45 mm), width 23.2 mm. Forewing subtriangular, with nodal indentation at about basal 0.42 wing length. Costal margin slightly curved anteriorly. Vein ScA distinguishable, parallel to costal margin. Vein ScP arising basally, straight near wing base, slightly arched at basal 0.15 wing length, with 8 thin veinlets, and fused with vein RA at basal 0.3 wing length. Stem R + M branching into veins R and M at basal 0.15 wing length. Vein R parallel to vein ScP until its fork. Vein RA arising from stem R at about basal 0.3 wing length, free for a very short distance, and fused with vein ScP; it is slightly recurved at nodal line, tightly close to costal margin for distal half. Vein RP arched anteriorly, connected to vein M₁ by crossvein r-m distal of indentation, and ending in posterior margin near wing apex. Vein M distinctly geniculate at junction with crossvein m-cua at basal 0.16 wing length. Stem M bifurcating at basal 0.35 wing length. Branch M₁+₂ forking into veins M₁ and M₂ a little distal of the level of indentation. Branches M₁ and M₂ pointed posteriorly until wing margin in a subparallel state. Branch M₃+₄ forking into veins M₃ and M₄ at the same level of the bifurcation of stem M₁+₂. Branch M₄ slightly curved. Crossvein m₄-cua S-shaped, subparallel to stem M, connected with vein CuA almost at the same level of initial division of stem M. Stem Cu branching into veins CuA and CuP at about basal 0.1 wing length. Branch CuA curved anteriorly at junction with crossvein r + m-cua, branching into veins CuA₁ and CuA₂ after a short distance to the connection of crossvein m₄-cua with vein CuA. Discal cell large, length 13.9 mm, width 7.0 mm at nodal line; antenodal region length 7.1 mm; antenodal region and postnodal region about trapezoid, subequal in length. Nodal line traceable as a crease across veins ScP + RA and vein RA, and crossing vein M beyond its initial division. Marginal membrane present, thinner than vein width. Membrane with transverse wrinkles on both sides of veins.

*Martynovocossus bellus* (Wang and Ren, 2006) comb. nov.

Figure 1.

Holotype

CNU-H-NN2005002, deposited in the Capital Normal University; Middle Jurassic; Daohugou, China.

Other material

NIGP147862a, b, NIGP147863a, b, NIGP147864, NIGP147865, NIGP147866, NIGP147867; deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences; Middle Jurassic; Daohugou, China.

Diagnostic characters

Forewing large-sized (length 53–61 mm); indentation at about basal 0.42 wing length; vein ScP with about 5 veinlets, and subparallel to vein RP; vein RA dividing from vein R at about basal 0.3 wing length, and fused with
branch ScP at nodal line; vein RA arising at nodal line or very close to it; vein M straight basally; crossvein r + m-cua transverse; stem Cu longitudinal and straight; marginal membrane distinct and thicker than vein width; membrane infuscate with a transverse white fasciae at about distal 0.7 wing length.

Hindwing small; vein RP fused with vein M₁ for a short distance.

Description

Specimen NIGP147862a, b, part and counterpart. Forewing complete, part and counterpart, length 61.1 mm, width 29.2 mm. Forewing subtriangular, with nodal indentation at basal 0.42 wing length. Costal margin slightly curved anteriorly. Costal area slightly decreasing in width apically. Vein ScA distinguishable, parallel to costal margin. Vein ScP arising basally, straight near wing base, arched at basal 0.15 wing length, with 5 thin veinlets before its coalescence with vein RA (at basal 0.33 wing length). Stem R + M slightly curved, connected with vein CuA by crossvein r + m-cua at basal 0.15 wing base. Vein R departing from stem R + M slightly beyond crossvein r + m-cua, and parallel to vein ScP until its fork. Vein RA arising from stem R at nodal line, free for a very short distance, and fused with vein ScP; it is slightly recurved at nodal line, slightly arched anteriorly beyond nodal line. Vein RP arched anteriorly, connected to vein M₁ by crossvein r-m a little distal of indentation, and ending in posterior margin near wing apex. Stem M short, straight and bifurcating at basal 0.25 wing length. Branch M₁ +₂ forking into veins M₁ and M₂ a little basal of the level of indentation. Branches M₁ and M₂ pointed posteriorly until wing margin in a subparallel state. Branch M₃ +₄ forking into veins M₃ and M₄ at the same level of the bifurcation of stem M₁ +₂. Branch M₃ subparallel to branch M₂. Branch M₄ slightly curved. Crossvein m₄-cua S-shaped, subparallel to stem M, connected with vein CuA slightly distal of the level of initial division of stem M. Stem Cu short, branching into veins CuA and CuP at basal 0.09 wing length. Branch CuA curved anteriorly at junction with crossvein r + m-cua, branching into veins CuA₁ and CuA₂ after a very short distance to the connection of crossvein m₄-cua with vein CuA. Discal cell large, length 15.5 mm, width 6.5 mm at nodal line; antenodal region about trapezoid, length 5.5 mm along vein M; postnodal region rhomboid, much longer than antenodal region. Vein Pcu slightly sinuate. Branch A₁ nearly straight. Branch A₂ arising from vein A₁ +₂ basally, short. Nodal line traceable as a crease across vein ScP + RA, fused with vein RA, crossing stem M at its initial division, and then separating basal cell into two parts; it is continuously crossing vein CuA at its initial division, following the base of CuA₂ and the distal part of CuP, and then reaching the distal end of clavus. Marginal membrane distinct and thicker than vein width. Membrane infuscate with a transverse white fascia at about distal 0.7 wing length (completely separated spots convergent to form fascia).

Specimen NIGP147863a, b, part and counterpart. Forewing almost complete, part and counterpart, length 57.1 mm, width 32.5 mm. ScP veinlets indistinct. Branch M₁ +₂ forking into veins M₁ and M₂ a little basal of indentation. Branch M₃ +₄ forking into veins M₃ and M₄ at the same level of the bifurcation of stem M₁ +₂. Colour pattern distinct. Veneron and colour pattern in general as in holotype.

Specimen NIGP147864. Forewing with basal part and clavus destroyed, length as preserved 48.6 mm (estimated complete length about 53 mm), width 29.5 mm. Vein RA arising slightly basal of nodal line. Branch M₁ +₂ forking into veins M₁ and M₂ basal of indentation. Veneron in general as in holotype. Colour pattern unknown.

Specimen NIGP147865. Forewing with postero-apical part destroyed, length 53.0 mm, width about 24 mm. ScP veinlets indistinct. Vein RA arising slightly basal of nodal line. Branch M₁ +₂ forking into veins M₁ and M₂ basal of indentation. Veneron and colour pattern in general as in holotype.

Specimen NIGP147866. Body obscure, with a forewing and hindwing overlapped. Forewing with posterior portion missing and hindwing with basal part preserved. Forewing length 56.8 mm. Branch M₁ +₂ forking into veins M₁ and M₂ a little basal of the level of indentation. Branch M₃ +₄ forking into veins M₃ and M₄ at the same level of the bifurcation of stem M₁ +₂. Veneron in general as in holotype.

Specimen NIGP147867. Forewing with costal area and clavus missing, length as preserved 52.1 mm (estimated complete length about 57 mm). ScP veinlets indistinct. Vein RA arising slightly basal of nodal line. Branch M₁ +₂ forking into veins M₁ and M₂ a little basal of the level of indentation. Branch M₃ +₄ forking into veins M₃ and M₄ at the same level of the bifurcation of stem M₁ +₂. Veneron and colour pattern in general as in holotype.
Remarks

The variation is obviously present in the relative placement of ramifications of veins $M_{1+2}$ and $M_{3+4}$. Ramification of $M_{1+2}$ is at the same level of indentation in the holotype, but basal of the level of that in other specimens. Furthermore, vein $M_{1+2}$ bifurcates slightly distally of $M_{3+4}$ branching in both the holotype and specimen NIGP147864, while these two ramifications are at the same level in other specimens. Considering their almost identical wing venation and colour pattern, these slight differences are regarded as intraspecific variations.

*Martynovocossus bellus* is closely related to *M. punctulosus*, but differs in having a larger forewing with vein RA arising at nodal line or very close to it, vein RA fused with branch ScP at nodal line, postnodal region much longer than antenodal region, marginal membrane distinct and colour pattern different.

*Martynovocossus punctulosus* (Wang and Ren, 2006) comb. nov.

Figures 2, 3, 4.

2006 *Pseudocossus punctulosus* Wang and Ren, pp. 289–290, figures 1, 3.

Holotype

CNU-H-NN2005001, deposited in the Capital Normal University; Middle Jurassic; Daohugou, China.

Other material

Forewings and hindwings: NIGP147868, NIGP147869, NIGP147870a, b, NIGP147871, NIGP147872, NIGP147873, NIGP147874. Forewings: NIGP147875a, b, NIGP147876a, b, NIGP147877a, b, NIGP147878a, b, NIGP147879, NIGP147880a, b. Hindwings: NIGP147881a, b, NIGP147882, NIGP147883, NIGP147884,

Figure 2. *Martynovocossus punctulosus* (Wang and Ren, 2006) comb. nov. (A–D) photograph and illustrations of NIGP147872 (drawings with colour pattern omitted). Scale bar represents 10 mm. This figure is available in colour online at www.interscience.wiley.com/journal/gj

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DOI: 10.1002/gj
NIGP147885a, b, NIGP147886, NIGP147887a, b, NIGP147888, NIGP147889, NIGP147890, NIGP147891; deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences; Middle Jurassic; Daohugou, China.

**Diagnostic characters**

Forewing large-sized (length 42–52 mm); indentation at about basal 0.42 wing length; vein ScP with 5–6 veinlets, subparallel to vein RP; vein RA dividing from vein R at basal 0.3 wing length, and fused with branch Sc basal of nodal line; vein M straight basally; crossvein r + m-cua transverse; stem Cu longitudinal and straight; membrane infuscate with 2 transverse white fasciae at about middle portion and distal 0.75 wing length and about 8 separated white spots at anterior portion of costal area.

Hindwing small (length 24–35 mm), length/width ratio about 1.3–1.5; costal area wide, length/width ratio about 3.2, maximal width in basal 1/3; nodal indentation at basal 0.38 wing length; vein Sc terminating in costal margin slightly basal of nodal indentation; vein RA branching into veins RA1 and RA2 at the same level of nodal indentation; veins CuP and Pcu simple; vein A1 absent; marginal membrane present, thinner than vein width; membrane infuscate with 2 distinct transverse white fasciae at about middle portion and distal 0.75 wing length.

**Description**

Forewing subtriangular, length 42–51.0 mm (average 46.7 mm, n = 13), width 19.4–26.2 mm (average 23.4 mm, n = 13) (Table 1). Nodal indentation at basal 0.42 wing length. Costal margin slightly curved anteriorly. Vein ScA distinguishable, parallel to costal margin. Vein ScP arising basally, straight near wing base, arched at basal 0.13
wing length, with 5 thin veinlets before its coalescence with vein RA (at basal 0.3 wing length). Stem R + M slightly curved, connected with CuA by crossvein r + m-cua at basal 0.15 wing base. Vein R departing from stem R + M near crossvein r + m-cua, and parallel to ScP until its fork. Vein RA free for a very short distance after arising from stem R, and fused with ScP; it is slightly recurved at nodal line, slightly arched anteriorly beyond nodal

Figure 4. Martynovocossus punctulosus (Wang and Ren, 2006) comb. nov. (A–B) Photograph and illustration of NIGP147889; (C–D) photograph and illustration of NIGP147885a; (E–F) photograph and illustration of NIGP147887a. Scale bars represent 10 mm. This figure is available in colour online at www.interscience.wiley.com/journal/gj

line. Vein RP arched anteriorly, connected to vein M₁ by crossvein r-m a little distal of indentation, and ending in posterior margin near wing apex. Stem M short, straight and bifurcating at basal 0.25 wing length. Branch M₁₂ forking into veins M₁ and M₂ a little basal of indentation. Branches M₁ and M₂ pointed posteriorly until wing margin in a subparallel state. Branch M₃₄ forking into veins M₃ and M₄ almost at the same level of the bifurcation of stem M₁₂. Branch M₃ subparallel to vein M₂. Branch M₄ slightly curved. Crossvein m₄-cua oblique. Stem Cu short, branching into veins CuA and CuP at wing base. Branch CuA curved anteriorly at junction with crossvein rₗₘ-cua, branching into veins CuA₁ and CuA₂ after a very short distance to the connection of crossvein m₄-cua with vein CuA. Discal cell large, length about 0.25/C₂ wing length, width a little more than 0.25/C₂ wing length; antenodal region and postnodal region about trapezoid, subequal in length. Vein Pcu slightly sinuate. Branch A₁ simple. Branch A₂ arising from vein A₁₂ basally, short. Nodal line traceable as a crease across veins Scₚ + RA and RP, to stem M near its initial division, and then separating basal cell into two parts; it is continuously crossing vein CuA at its initial division, following the base of CuA₂ and the distal part of CuP, and then reaching the distal end of clavus. Marginal membrane present, thinner than vein width. Wing membrane infuscate; 2 transverse white fasciae at about middle portion and distal 0.75 wing length; about 8 separated white spots at anterior portion of costal area.

Hindwing length 24–35 mm (average 30.8 mm, n = 18), width 14–24 mm (average 20.2 mm, n = 18) (Table 1). Costal area wide, length/width ratio 3.2–3.3, maximal width in basal 1/3; nodal indentation at basal 0.38 wing length. Vein Sc lying alongside vein R, contact with vein R or RA at about basal 0.3 wing length, and then pointed anteriorly, terminating in costal margin slightly basal of nodal indentation. Vein R a little curved anteriorly, branching into veins RA and RP at basal 0.32 wing length. Branch RA₁ dividing from vein RA at the same level of indentation. Branch RA₂ slightly curved anteriorly, ending in costal margin. Vein RP inclined apically, fused with branch M₁ for a distance, and terminating in apex of wing. Stem M bifurcating into veins M₁ and M₂₃₄ at wing base. Branch M₁ almost straight. Vein M₂ simple. Vein M₃₄ dividing from vein M₂₃₄ at basal 0.1 wing length, connected with vein CuA by a very short crossvein m-cua at basal 0.2 wing base, and branching into veins M₃ and M₄ at about middle of wing. Vein CuA forking into veins CuA₁ and CuA₂ at basal 0.3 wing length. Veins CuA₁ and CuA₂ simple. Vein CuP curved anteriorly. Vein Pcu slightly curved posteriorly. Vein A₁ absent. Marginal membrane present, thinner than vein width. Wing membrane infuscate; with 3 transverse white fasciae, consisting

### Table 1. The measurements of specimens of Martynovocossus punctulosus

<table>
<thead>
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<th>Forewing</th>
<th>Length (mm)</th>
<th>Width (mm)</th>
<th>Hindwing</th>
<th>Length (mm)</th>
<th>Width (mm)</th>
<th>FL/HL</th>
<th>FW/HW</th>
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FL/HL: forewing length/hindwing length ratio; FW/HW: forewing width/hindwing width ratio.
of separated white spots, at about middle portion, distal 0.75 wing length and wing apex. The wide fascia at middle portion sometimes divided into two parts.

NIGP147885. Colour pattern a little different from others. White spots forming 2 transverse fasciae in middle portion, while 1 transverse fascia in other specimens.

NIGP147887. Vein RP fused with vein M₁ for a very short distance. Crossvein m-cua slightly longer.

**Remarks**

Vein RA is fused with vein ScP at the point of RA arising from vein R in the holotype and specimen NIGP147875 (Figure 3D), while it is free for a short distance before fused with vein ScP in the forewing of other specimens (Figure 3A–C). However, this difference is undoubtedly regarded as an intraspecific variation, judging by the
similarity of the venation and colour pattern. The venation and colour pattern of hindwings are more mutable than of forewings. Colour patterns show little variation in the relative distance between white fasciae among the hindwings (Figure 4). Additionally, the length of vein RP fused with vein M1 of the hindwing is also somewhat varied in some specimens (Figure 4). Considering the similarity of the wing venation and colour pattern, it is tentative to refer these hindwings to *M. punctulosus*. A possibility remains that these differences are due to sexual dimorphism. The similar differences in wing venation also occur between the sexes in extant *Tettigarcia* within Tettigarctidae of Cicadomorpha (Heads personal communication).

*Martynovocossus decorus* Wang and Zhang, sp. nov.

Figures 5, 6.

**Holotype**

NIGP147892; deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences; Middle Jurassic; Daohugou, China.

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Figure 6. *Martynovocossus decorus* Wang and Zhang, sp. nov., paratype. (A) Photograph of NIGP147893; (B) illustration of NIGP147893. Scale bar represents 10 mm. This figure is available in colour online at www.interscience.wiley.com/journal/gj

Paratype
NIGP147893, NIGP147894, NIGP147895a, b; deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences; Middle Jurassic; Daohugou, China.

Etymology
The specific name is from Latin decorus, in reference to the colourful wing membrane.

Diagnostic characters
Forewing with indentation at about basal 0.42 wing length; vein ScP with 5 veinlets, and subparallel to vein RP; vein RA dividing from vein R slightly basal of vein M initial division; Vein RP terminating in wing apex; crossvein r-m distal of indentation; vein M straight basally; crossvein r + m-cua long, a little curved; postnodal region and antenodal region trapezoidal, subequal in length; stem Cu longitudinal and straight; stem Cu bifurcating close to wing base; membrane with alternating black and white maculations. Hindwing unknown.

Description
Holotype, NIGP147892. Forewing with clavus missing, length 37.5 mm, width 17.1 mm. Forewing subtriangular, with nodal indentation at basal 0.42 wing length. Vein ScA distinguishable, parallel to costal margin. Vein ScP arising basally, straight near wing base, arched at basal 0.1 wing length, with 5 thin veinlets. Stem R + M slightly curved, connected with vein CuA by crossvein r + m-cua at basal 0.15 wing base. Vein R departing from stem R + M at crossvein r + m-cua, and subparallel to vein ScP until its fork. Vein RA arising from vein R at basal 0.27 wing length, free for a short distance, and fused with vein ScP; it is slightly recurved at nodal line and fused with it for a short distance, slightly arched anteriorly beyond nodal line, and terminating in the costal margin near wing apex. Vein RP connected with vein M1 by crossvein r-m distal of the level of indentation, and terminating in wing apex. Stem M short, straight and bifurcating at basal 0.27 wing length. Branch M1 + 2 forking into veins M1 and M2 a little basal of the level of indentation. Branch M1 + 4 forking into veins M3 and M4 at the same level of bifurcation of stem M1 + 2. Crossvein m4-cua connected with vein CuA at the same level of initial division of stem M. Stem Cu longitudinal, branching into veins CuA and CuP at wing base. Branch CuA curved anteriorly at junction with crossvein r + m-cua, branching into veins CuA1 and CuA2 after a very short distance to the connection of crossvein m4-cua with vein CuA. Discal cell large, length about 0.25 × wing length, width about 0.25 × wing length; antenodal region and postnodal region trapezoidal, subequal in length. Nodal line distinct. Marginal membrane thicker than vein width. Membrane with alternating black and white bands and patches.

Paratype NIGP147893. Forewing with clavus missing, length 34.7 mm, width 15.6 mm. Venation and colour pattern in general as in holotype.

Paratype NIGP147894. Body obscure, with a forewing and hindwing. Forewing deformed, with apex and clavus destroyed, length 33.2 mm, width 16.5 mm. Hindwing with only several veins preserved. Venation and colour pattern in general as in holotype.

Paratype NIGP147895a, b, part and counterpart. Forewing with clavus missing, length 32.7 mm, width 16.8 mm. Venation and colour pattern in general as in holotype.

Remarks
Martynovocossus decorus is similar to M. turgaiensis in the forewing by the following characters: wing small; colour pattern similar; vein R bifurcating slightly basal of vein M bifurcating. But it differs from the latter in stem Cu longitudinal and the location of Cu bifurcating closer to wing base. Furthermore, it differs from M. punctulosus, M. bellus and M. ancylivenius in having a smaller forewing with vein R bifurcating not distal of vein M bifurcating and colour pattern different; from M. zemcuznicovi in vein R bifurcating distinctly distal of crossvein r + m-cua and
crossvein r + m-cua long; and from *M. strenus* in possessing a smaller forewing with vein M straight, vein RA subparallel to costal margin and crossvein r + m-cua long.

*Martynovocossus cheni* Wang and Zhang, sp. nov.

*Figure 7.*

**Holotype**

NIGP147896; deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences; Middle Jurassic; Daohugou, China.

**Etymology**

The specific name is from Chen, the family name of Prof. Chen Peiji, a specialist on Mesozoic stratigraphy of China.

**Diagnostic characters**

Forewing with indentation at about basal 0.42 wing length; vein ScP with 7 veinlets, and subparallel to vein RP; vein RA dividing from vein R almost at the same level of vein M initial division; vein M straight basally; crossvein r - m basal of the level of indentation; crossvein r + m-cua long, a little curved; postnodal region and antenodal region trapezoid, subequal in length; stem Cu longitudinal and straight; stem Cu bifurcating close to wing base; membrane infuscate without distinct colour pattern.

Hindwing small; vein RP fused with vein M₁ for a short distance.

**Description**

Holotype. Body partly preserved, lacking the abdomen, with a forewing and hindwing completely overlapped. Forewing length 36.7 mm, width 20.1 mm. Forewing subtriangular, with nodal indentation at basal 0.42 wing.
length. Vein ScA distinguishable, parallel to costal margin. Vein ScP arising basally, straight near wing base, arched at basal 0.1 wing length, with 7 veinlets. Stem R + M slightly curved, connected with vein CuA by crossvein r + m-cua at basal 0.15 wing base. Vein R departing from stem R + M near crossvein r + m-cua, and parallel to vein ScP until its fork. Vein RA arising from vein R at basal 0.24 wing length, free for a short distance, and fused with vein ScP; it is slightly recurved at nodal line, slightly arched anteriorly beyond nodal line. Vein RP connected with vein M1 by crossvein r-m slightly basal of the level of indentation. Stem M short, straight and bifurcating at basal 0.25 wing length. Branch M1 + 2 forking into veins M1 and M2 a little basal of the level of indentation. Branch M3 + 4 forking into veins M3 and M4 slightly basal of the level of the bifurcation of stem M1 + 2. Crossvein m4-cua connected with vein CuA at the same level of initial division of stem M. Stem Cu longitudinal, branching into veins CuA and CuP at wing base. Branch CuA curved anteriorly at junction with crossvein r + m-cua, branching into veins CuA1 and CuA2 after a very short distance to the connection of crossvein m4-cua with vein CuA. Discal cell large, length about 0.25 × wing length, width a little more than 0.25 × wing width; antenodal region and postnodal region trapezoid, subequal in length. Branch A2 arising from vein A1 + 2 basally. Nodal line distinct. Marginal membrane thicker than vein width. Membrane infuscate without distinct colour pattern.

Hindwing small, length about 22 mm, width about 15 mm. Vein R a little curved anteriorly, branching into veins RA and RP. Branch RA1 dividing from vein RA at about the same level of indentation. Branch RA2 slightly curved anteriorly, ending in costal margin. Vein RP inclined apically, fused with branch M1 for a distance. Branch M1 almost straight. Branch M2 simple. Vein M3 + 4 branching into veins M3 and M4 at about middle of wing. Vein CuA forking into veins CuA1 and CuA2 basal of the level of M3 + 4 bifurcating. Veins CuA1 and CuA2 simple. Membrane infuscate without distinct colour pattern.

Remarks

Martynovocossus cheni differs from all other congeneric species in having a forewing with crossvein r-m basal of indentation and membrane infuscate without distinct colour pattern. Furthermore, it differs from M. punctulosus, M. bellus and M. ancylichenius in having a smaller forewing with vein ScP 7-branched, and vein R bifurcating not distinctly distal of vein M bifurcating.

4. DISCUSSION

As a result of the large number of exceptionally preserved specimens available, Martynovocossus now constitutes one of the best-known palaeontinid genera. Study of the numerous specimens described herein has allowed the identification of considerable variation between individuals within the same species. This intraspecific variation is most apparent in wing size, nature of the ScP veinlets and colour patterns. It is likely that such variation is also present in other, less well-known Palaeontinididae and should be taken into account in future revisions of such taxa.

4.1. ScP veinlets

Vein ScP has some veinlets in the costal area, which is an important diagnostic character for a genus or species. However, the number and location of veinlets are slightly variable among specimens within a species (e.g. M. bellus, see Figure 1). Furthermore, these weak veinlets are sometimes obscure or even invisible in the impression fossil because of poor preservation (e.g. Figure 1; Wang et al. 2006c, figure 2).

4.2. Length/width ratio

Generally, both the wing size and length/width ratio are useful characteristics to differentiate between species within a genus. However, they, especially the latter, is sometimes varied within a species (Table 1), because some impression fossils are liable to be distorted by the deformation of sedimentary rocks (e.g. some specimens from
4.3. Wing colour pattern

Palaeontinids have an inflated frons and long rostrum (Ren et al. 1998; Wang et al. 2007b), as in extant singing cicadas, suggesting that they fed on xylem fluids. Large numbers of complete palaeontinid adults from the Mesozoic of China and Brazil are preserved in dorsal or ventral aspect with four large wings spreading on each side of the body (Ren et al. 1998; Menon and Heads 2005; Menon et al. 2005; Wang et al. 2006b). When palaeontinids stay on the branch for a long time to pierce the xylem and suck the fluids, their large wings cover bodies, and so the wing colour pattern is essential for palaeontinids to hide themselves or frighten predators. Additionally, the wing colour pattern is probably also used to attract the opposite sex (Wang et al. 2006d).

Wing colour pattern occurs in most species of Palaeontinidae (e.g. Ren et al. 1998; Menon et al. 2005). Especially, a great complexity of colouration is present in *Martynovocossus punctulosus*. There is apparently a general colour pattern in all specimens of this species, but some fine-scaled differences among specimens can be observed and regarded as intraspecific variations (Figures 2–4). Furthermore, the contrast of colouration has probably been weakened or even erased by the diagenetic processes (e.g. Figure 1 shows two different contrasts of colouration in specimens of *M. bellus*). Given these conditions, the presence of slight colour pattern differences is not enough for the erection of a new species.

ACKNOWLEDGEMENTS

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Research Projects (2006CB806400) of MST of China and the National Natural Science Foundation of China (40472001, 40523004, 40632010).

REFERENCES


Key to species of the genus *Martynovocossus*

1. Forewing: large (52 mm–61 mm); vein RA arising at nodal line or very close to it; postnodal region much longer than antenodal region ........................................... *Martynovocossus punctulosus* (Wang and Ren, 2006)
   - Forewing: small or medium; vein RA arising not very close to nodal line; postnodal region subequal to antenodal region in length

2. Forewing: stem R bifurcating basal of stem M bifurcating ........................................... 4
   - Forewing: stem R bifurcating not basal of stem M bifurcating

3. Forewing: vein M₁₊₂ bifurcating basal of stem M₃₊₄ bifurcating; M₄ base transverse ............................................................... *M. ancylivenius* (Wang and Ren, 2006)
   - Forewing: not as above .............................................................. *M. bellus* (Wang and Ren, 2006)

4. Forewing: stem R bifurcating slightly distal of crossvein r + m-cua; crossvein r + m-cua very short ............................................................... *M. zemcuznicovi* (Martynov, 1931)
   - Forewing: stem R bifurcating distinctly distal of crossvein r + m-cua; crossvein r + m-cua long

5. Forewing: vein M base strongly curved; vein RA tightly close to costal margin for distal half .................................................. *M. strenus* (Zhang, 1997)
   - Forewing: vein M straight; vein RA subparallel to costal margin

6. Forewing: stem Cu oblique; stem Cu bifurcating near crossvein r + m-cua .......................... *M. turgaiensis* (Becker-Migdisova and Wootton, 1965)
   - Forewing: stem Cu longitudinal; stem Cu bifurcating close to wing base

7. Forewing: vein ScP 5-branched; crossvein r-m distal of indentation; membrane infuscate with distinct colour pattern ............................................................... *M. decorus* sp. nov.
   - Forewing: vein ScP 7-branched; crossvein r-m basal of indentation; membrane infuscate without distinct colour pattern ............................................................... *M. cheni* sp. nov.