

Middle Jurassic Palaeontinidae (Insecta, Hemiptera) from Daohugou of China

Bo WANG, Hai-Chun ZHANG & Yan FANG

State Key Laboratory of Palaeobiology and Stratigraphy and Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, 39 East Beijing Rd., Nanjing 210008, China. E-mail: bowang@nigpas.ac.cn

ABSTRACT

Two new genera and six new species within the Mesozoic family Palaeontinidae are described from the Middle Jurassic of Daohugou, China, including *Abrocossus longus* n. gen., n. sp., *Neimengguocossus normalis* n. gen., n. sp., *Palaeontinodes daohugouensis* n. sp., *P. locellus* n. sp., *P. separatus* n. sp. and *Suljuktocossus chifengensis* n. sp. The discovery of *S. chifengensis* n. sp. supports that the “*Ilerdocossus*-complex” and Brazilian palaeontinids originated from Central or East Asia in the Middle Jurassic. The holotype of *P. separatus* n. sp. exceptionally possesses one additional crossvein respectively between veins RP and M₁ and between M₃ and M₄ in the right forewing. The Jurassic palaeontinids could be divided into two groups mainly on the basis of hindwings, which implies an early evolutionary event probably occurring in the Late Triassic or Early Jurassic. The palaeontinids from Daohugou are closely related to those from the Middle Jurassic of northern China and Lower-Middle Jurassic of Central Asia. So far, eleven recognized genera within Palaeontinidae have been reported from Daohugou. The key to these genera is presented and all the species of Palaeontinidae are tabled. The Middle Jurassic palaeontinid diversity is greater than those in any other epoch, suggesting that the family probably went into its most prosperous stage in the Middle Jurassic.

KEY WORDS: Palaeontinidae. Hemiptera. Middle Jurassic. Daohugou. China.

INTRODUCTION

The Middle Jurassic Daohugou Lagerstätte yields abundant well-preserved fossils including macroplants, bivalves, conchostracans, insects, spiders, salamanders, pterosaurs, dinosaurs and mammaliaforms (Ren & Krzeminski 2002, Gao & Shubin 2003, Wang 2004, Xu & Zhang 2005, Ji *et al.* 2006, Jiang 2006). Of these fossils, insects are particularly diverse and plenty of specimens within at least 18 orders have been collected and await description. To date, only the hymenopteran assemblage has been described (Rasnitsyn & Zhang 2004, Rasnitsyn *et al.* 2006), whereas others are sparsely documented. Very recently, some well-preserved palaeontinid specimens from Daohugou have been reported (Tan & Ren 2002, Wang & Ren 2006, Wang *et al.* 2006a-d). The Jurassic palaeontinids have been mainly reported from Central Asia (see Carpenter 1992), so the recent discovery at Daohugou undoubtedly adds significant distributional and stratigraphic extensions to the Palaeontinidae. On the other hand, the newly discovered Jurassic palaeontinids, together with Cretaceous records from Brazil (Menon & Heads 2005), provide an adequate basis for discussing some general trends in the palaeontinid evolution.

Six new species within four genera collected from Daohugou are described herein, with two genera new to science. The described palaeontinids from Daohugou are tabled at the specific level and presented as a key at the generic level.

MATERIAL AND METHODS

Six new specimens were collected from the Daohugou deposits (41°18' N, 119°13' E) near Daohugou Village, Chifeng City, China. The Daohugou deposits, consisting of grey tuff, tuffaceous siltstones and mudstones, become one of the most important insect Lagerstätte (Rasnitsyn *et al.* 2006). The taphonomy of vertebrate assemblages of the Early Cretaceous Yixian Fm shows that the sudden death resulting from the poisonous gas of the abrupt volcanic eruption and quick burial process make the animals and plants excellently preserved (Guo *et al.* 2003, Zhang & Gong 2003, Zheng & Zheng 2004). The insect fossils from Daohugou, similar to those from western Liaoning, are preserved as impressions on the surface of grey tuffaceous siltstones and accompanied with some well-preserved vertebrate fossils such as salamanders and primitive mammals (Gao & Shubin 2003, Ji *et al.* 2006), implying an analogical death reason and taphonomic process.

The composition and age of the biota have been discussed in detail by Huang *et al.* (2006) and Zhang (2006), so herein they will not be repeated again. There are three opinions regarding the age of the Daohugou insect fauna: Middle Jurassic (Rasnitsyn *et al.* 2006); early Middle Jurassic (Ren & Krzeminski 2002); or late Middle Jurassic – early Late Jurassic (Zhang 2006). We adopt the Middle Jurassic from the analysis of the hymenopteran fossil assemblage (Rasnitsyn & Zhang 2004) and stratigraphic evidence (Chen *et al.* 2004, Chen *et al.* 2005, Gao & Ren 2006).

There is no consensus on the interpretation of vein nomenclature of Palaeontinidae between Becker-Migdisova (1949), Emeljanov (1977) and Dworakowska (1988). Therefore, we tentatively followed the traditional terminologies with slight modifications (Wang *et al.* 2006a). Menon *et al.* (2005) delineate the two separate regions of discal cell divided by nodal line as antenodal region (basal of nodal line) and postnodal region (distal of nodal line).

The venation patterns and vein widths were drawn with a stereomicroscope (Nikon SMZ1000) and camera lucida at the State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing. In order to reach the best resolution, some specimens being taken photographs are under alcohol. The line drawings were readjusted on photographs using image-editing software (CorelDraw 13.0 and Adobe Photoshop CS). These new specimens are deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences.

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.

SYSTEMATIC PALAEONTOLOGY

Order: Hemiptera Linnaeus, 1758

Superfamily: Palaeontinoidea Handlirsch, 1906

Family: Palaeontinidae Handlirsch, 1906

GENUS: *Palaeontinodes* Martynov 1937

Type species: *Palaeontinodes shabarovi* Martynov (1937); by original designation.

Type horizon and locality. Lower Jurassic; Shurab 2, Kyrgyzstan.

Revised diagnosis. Forewing triangular, length 22–58 mm, length/width ratio 2.1–3.2; anterior margin fringed with a thick border; nodal indentation weak; apex pointed; branch ScA distinguishable and ends at the bottom of indentation; branch ScP unbranched and fused with vein RA at about basal 0.3 wing length; crossvein r+m-cua long and subvertical; discal cell divided by a long crossvein m-cua; vein Pcu simple; branch A2 short and fused with A1 basally; clavus about 0.3 times as long as wing length; nodal line distinct.

Hindwing oval, length 21–23 mm, length/width ratio 1.3–1.6, anterior margin straight for distal part; costal area wide; nodal indentation at basal 0.3–0.4 wing length; stem M with 4 branches; branch M3+4 branched from branch M2+3+4; branch M3+4 connected to CuA by crossvein m-cua; veins CuP and Pcu simple.

Included species. Seven species, the type species *P. shabarovi*, *P. angarensis* Becker-Migdisova & Woot-

ton (1965) (Lower-Middle Jurassic Cheremkhovo Fm of Ust-Baley, Irkutsk), *P. minor* Becker-Migdisova & Wootton (1965) (Lower-Middle Jurassic of Shurab 3, southern Fergana, Kyrgyzstan), *P. haifanggouensis* Hong (1983) (Middle Jurassic Haifanggou Fm of Beipiao, China), and *P. daohugouensis* n. sp., *P. locellus* n. sp. and *P. separatus* n. sp. described below.

Remarks. *Palaeontinodes* differs distinctively from *Ijacossus* in the forewing with only one crossvein in the discal cell and absence of branches of ScP, and a little from *Cicadomorpha* in losing branches of vein ScP in the forewing and having a comparatively wide hindwing (hindwing length/width ratio less than 1.6 for *Palaeontinodes*, while about 2.0 for *Cicadomorpha*). *Palaeontinodes* differs from *Gansucossus* Wang *et al.* (2006b) and *Daohugoucossus* Wang *et al.* (2006b) in the hindwing with the distal part of anterior margin straight; from *Suljuktaja* Becker-Migdisova (1949) and *Shurabocossus* Becker-Migdisova (1949) in the hindwing possessing the distal part of anterior margin straight and vein Pcu ending in the anal margin; distinctly from *Plachutella* Becker-Migdisova (1949) in the hindwing with vein M3+4 branching from vein M2+3+4 and vein Pcu ending in the anal margin; and markedly from *Sinopalaeocossus* Hong (1983) (Wang *et al.* 2006c) in the hindwing with stem M 4-branched, vein M3+4 branching from vein M2+3+4 and vein Pcu present.

Palaeontinodes daohugouensis n. sp. Wang & Zhang
Figure 1

Etymology. The specific name is after Daohugou, the type locality.

Holotype. NND04021 a, b, part and counterpart. Deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences.

Type locality. Daohugou Village, Ningcheng County, Chifeng City, Inner Mongolia, China.

Occurrence. Middle Jurassic.

Diagnosis. Forewing very small; nodal indentation clear; costal area wide; membrane with four pale vertical strips in costal area and a wide pale vertical strip in the center. Hindwing unknown.

Description. Forewing triangular, length 22.1 mm, width 10.4 mm, length/width ratio 2.1. Costal margin slightly curved anteriorly. Outer margin inclined with a narrow border. Costal area wide. Branch ScA distinguishable, slightly arched, ending at the bottom of indentation (basal 0.40 wing length). Branch ScP straight near wing base, and then arched and fused with branch RA at basal 0.27 wing length. Stem R+M close to but not coalesced with ScP. Discal cell long, length 6.8 mm, width 2.7 mm at nodal line, ratio of length to width about 2.5. Vein R departing from stem R+M a little distal of the initial curve of vein ScP and running close to

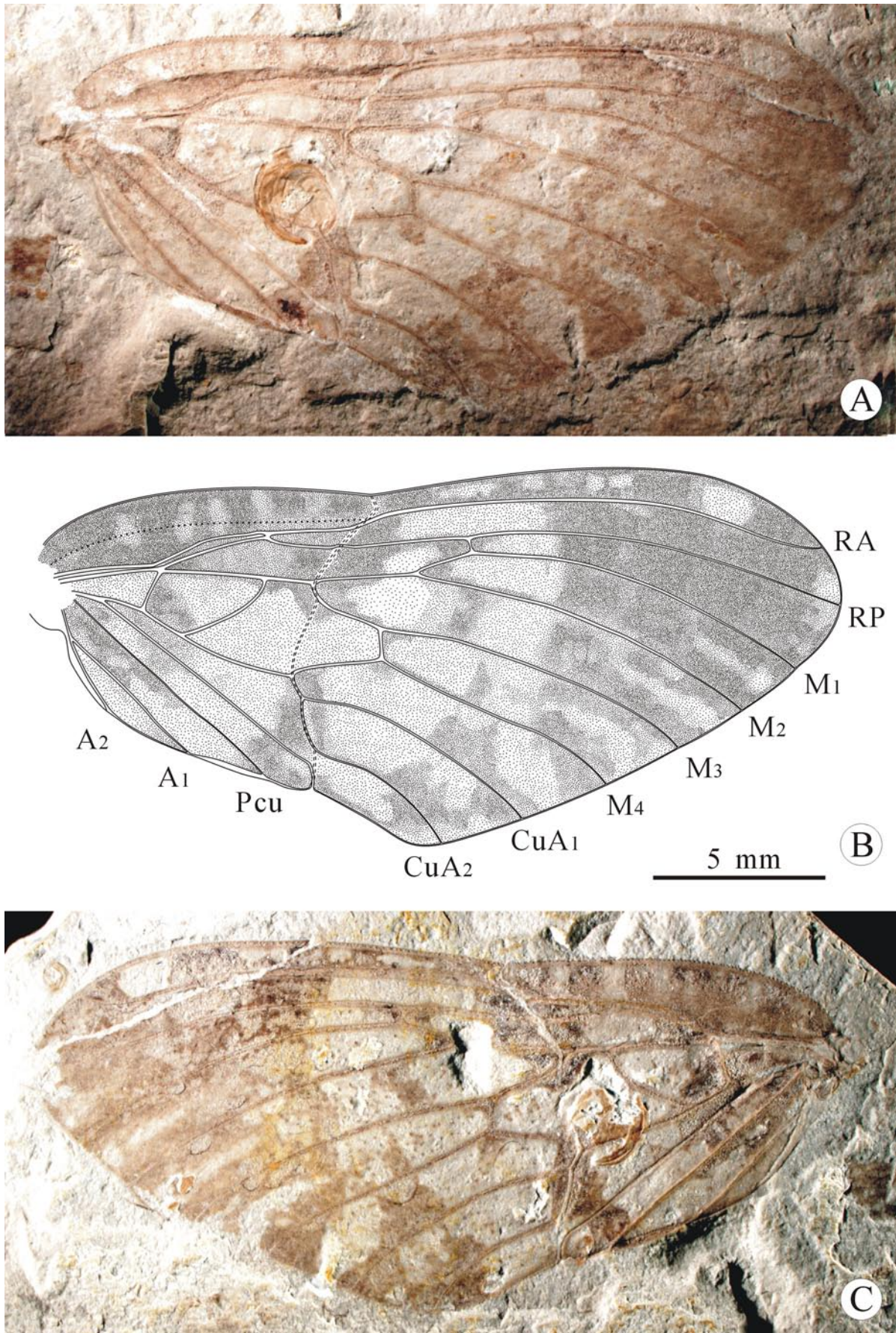


Figure 1. *Palaeontinodes daohugouensis* n. sp., holotype, forewing. A, photograph of part, NND04021a; B, illustration based on part; C, photograph of counterpart, NND04021b. All to scale.

vein ScP. Branch RA free for a very short distance after its departure from stem R, and then fused with vein ScP. Branch RP connected to vein M1 by crossvein r-m at basal 0.54 wing length. Stem M straight, branching into veins M1+2 and M3+4 at basal 0.33 wing length. Branch M1+2 forking into veins M1 and M2 a little distal of the level of indentation. Branch M3+4 dividing into veins M3 and M4 at the same level of indentation. Crossvein r+m-cua long and nearly vertical. Crossvein m-cua long and curved. Crossvein m4-cua long, connected to vein CuA at about the same level of the initial division of vein M. Stem Cu dividing into veins CuA and CuP near base. Branch CuA distinctly angled at junction with crossveins m4-cua, branching into veins CuA1 and CuA2 after a short distance to crossvein m4-cua. Vein CuP vertical. Vein Pcu very slightly sinuate. Branch A1 simple. Branch A2 short and fused with vein A1 basally. Nodal line

distinct. Membrane infusate, with four pale vertical strips in costal area and a wide pale vertical strip in the center. Hindwing unknown.

Palaeontinodes locellus n. sp. Wang & Zhang
Figure 2

Etymology. Specific epithet is from Latin *locellus*, in reference to the small discal cell in the forewing.

Holotype. NND04033. Deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences.

Type locality. Daohugou Village, Ningcheng County, Chifeng City, Inner Mongolia, China.

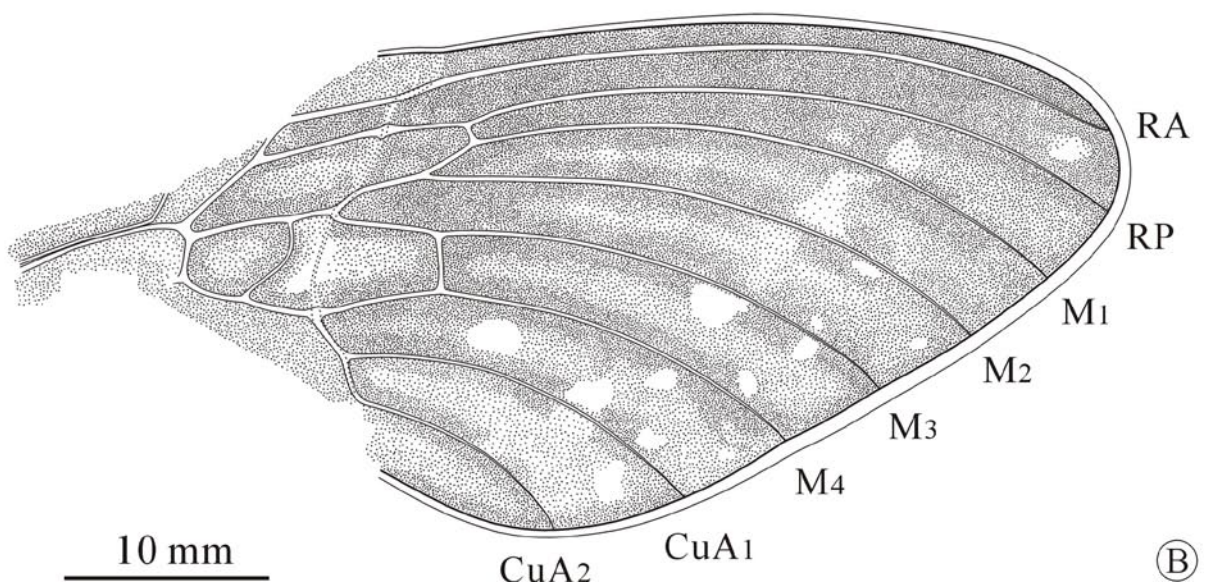


Figure 2. *Palaeontinodes locellus* n. sp., holotype, forewing. A, photograph of NND04033; B, illustration based on NND04033. Both to scale.

Occurrence. Middle Jurassic.

Diagnosis. Forewing with discal cell far smaller (about 1/5 of wing length); branch ScP fused with vein RA at basal 0.2 wing length; branch M4 arising at right angle; crossvein m4-cua subparallel to costal margin; marginal membrane much wider than vein width. Hindwing unknown.

Description. Forewing with costal area and clavus destroyed. Hindwing unknown. Forewing triangular, length 51.2 mm, width as preserved 23.8 mm. Indentation at basal 0.4 wing length. Branch ScP very slightly arched near wing base, strongly bent anteriorly at basal 0.1 wing length. Stem R+M pressed close to but not coalesced with vein ScP. Discal cell long, length 11.2 mm, width 4.5 mm at nodal line, ratio of length to width about 2.5. Vein R departing from stem R+M slightly beyond the initial curve of vein ScP. Branch RA free for a short distance after arising from stem R, and fused with vein ScP. Branch RP parallel to vein ScP+RA until nodal line, connected with M1 by crossvein r-m just distal of the level of indentation, and arched anteriorly beyond crossvein r-m. Stem M straight, branching into veins M1+2 and M3+4 at basal 0.33 wing length. Branch M1+2 forking into veins M1 and M2 at the same level of indentation. Branch M3+4 dividing into veins M3 and M4 at the same level of vein M1+2 fork. Branch M4 arising at right angle, connected to vein CuA by crossvein m4-cua, and then parallel to vein M3. Crossvein r+m-cua long and nearly vertical. Crossvein m-cua long and curved. Crossvein m4-cua subparallel to stem M, connected to vein M4 at the same level of indentation. Branch CuA curved anteriorly at junction with crossvein r+m-cua, nearly straight and subparallel to stem M3+4 until meeting crossvein m4-cua, branching into veins CuA1 and CuA2 after a distance to the connection of crossvein m4-cua with vein CuA. Nodal line distinct. Membrane grey with narrow brown bands alongside veins and several white speckles in distal-posterior part of forewing. Marginal membrane much wider than vein width.

Palaeontinodes separatus n. sp. Wang & Zhang

Figure 3

Etymology. Specific epithet is from Latin *separatus*, separate, in reference to veins RP and M1 are separate in the hindwing.

Holotype. NND04135a, b, part and counterpart. Deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences.

Type locality. Daohugou Village, Ningcheng County, Chifeng City, Inner Mongolia, China.

Occurrence. Middle Jurassic.

Diagnosis. The diagnosis is based on the left forewing and hindwing with no aberrance. Forewing triangular, length

34 mm, length/width ratio 2.4; crossvein m-cua curved; postnodal region long trapezoid; crossvein m4-cua long, vertical and coalesced with nodal line for a considerable interval, and then subparallel to vein M3+4; outer margin inclined with a narrow border. Hindwing small; costal area wide, length/width ratio about 4, maximal width in basal 3/5; nodal indentation at about basal 0.3 wing length; branch RP connected to vein M1 by crossvein r-m; branch M2+3+4 branching into veins M2 and M3+4 just basal of R initial division.

Description. Holotype. Adult in dorsal aspect with four articulated wings. Body stout and obscure, length about 21 mm. Hindwings are overlapped under the corresponding forewings. The good preservation of the holotype allows the examination of main features of all four wings.

Left forewing triangular, length 33.8 mm, width 14.3 mm, length/width ratio 2.4. Indentation at basal 0.40 wing length. Branch ScA obsolete. Branch ScP fused with RA at basal 0.26 wing length. Discal cell long, length 10.8 mm, length/width ratio about 3; postnodal region long trapezoid. Vein R departing from stem R+M slightly beyond the initial curve of vein ScP. Branch RA free for a short distance after arising from stem R, and fused with vein ScP; it nearly parallel to anterior margin beyond nodal line, ending in anterior margin. Branch RP running subparallel to vein RA, connected to vein M1 by crossvein r-m and ending in the wing apex. Stem M branching into veins M1+2 and M3+4 at basal 0.28 wing length. Branch M1+2 forking into veins M1 and M2 at the same level of indentation. Branch M3+4 dividing into veins M3 and M4 at about the same level of vein M1+2 fork. Crossvein m-cua long and curved. Crossvein m4-cua long, vertical and coalesced with nodal line for a considerable interval, and then subparallel to vein M3+4. Branch CuA branching into veins CuA1 and CuA2 after a short distance to the connection of crossvein m4-cua with vein CuA. Outer margin inclined with a very narrow border.

Right forewing with middle portion preserved. Vein RA connected to vein M1 by two short crossveins at middle of wing. Vein M3 connected with vein M4 by crossvein m3-m4 at the same level of crossvein r-m. Almost the same as the right forewing in respect to venation pattern.

Left hindwing small, length about 21 mm, width about 13 mm. Costal area wide, length/width ratio about 4, maximal width in basal 3/5. Nodal indentation at about basal 0.3 wing length. Branch RP connected to vein M1 by crossvein r-m at the same level of indentation. Branch M2+3+4 branching into veins M2 and M3+4 at basal 0.15 wing length. Branch M3+4 bifurcating at the same level of indentation. Branch CuA bifurcating at basal 0.20 wing length. Outer margin inclined with a very narrow border. In left hindwing, veins M1 and M2 ending in the same point.

Right hindwing small, with basal part and apex destroyed. Vein M1 curved posteriorly, and fused with vein M2 terminally. Almost the same as the right hindwing in respect to venation pattern.

Remarks. This species is remarkably different from others in the following characters: forewing with postnodal region long trapezoid and crossvein m-cua vertical for basal part; and hindwing with costal area wide and crossvein r-m present. Crossvein r-m of the hindwing, which was regarded as a primitive character (Wootton 1971), is present not only in primitive Palaeontinoidea, such as *Fletcheriana* Evans (1956), but also in some derived Palaeontinidae, such as *Palaeontinodes* and *Miracossus* Ren, Yin & Dou (1998).

In some insects (e.g. cicadas and stoneflies), the wing venation is often slightly variable in different individuals belonging to the same species, and it can differ between the right and left wings in the same individual. In the holotype of *P. separatus* n.sp., there is one more crossvein respectively between veins RP and M1 and between M3 and M4 in the right forewing as compared with the venationally

normal left forewing. Such a phenomenon is very rare in the record of fossil insects. Occasionally, such forewings, if disarticulated, are probably misattributed to two different species. Therefore, study of the venational variability is particularly important for fossil insects, since they are often represented by isolated wings that can only be identified with great difficulty (Sinitshenkova 2005). The discovery of such a bizarre example has provided new insights into the intraspecific variation, particularly individual aberration, of Cicadomorpha. A similar venational aberrance, in which one more crossvein is present between veins M3 and M4 in the right forewing (Becker-Migdisova & Wootton 1965: pl. 8, figs. 1-2, text-fig. 4) is also found in the holotype of *Pseudocossus turgaiensis* Becker-Migdisova & Wootton (1965). Such aberrance is also sometimes present in singing cicadas (Chou & Lei 1997). Judging from palaeontinids and sing-

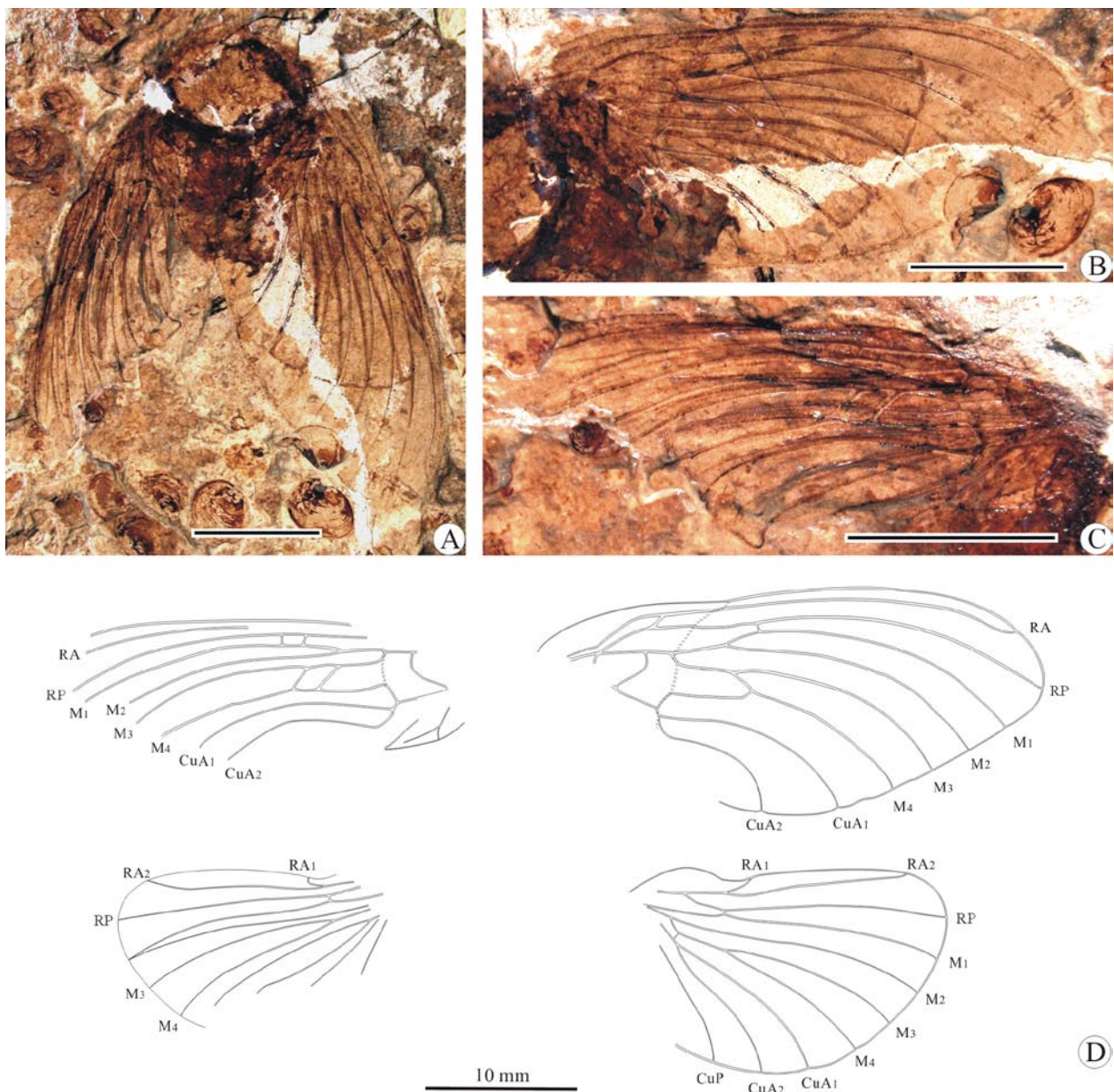


Figure 3. *Palaeontinodes separatus* n. sp., holotype. A, photograph of part, NND04135a; B, photograph of right forewings and hindwings from part; C, photograph of left forewings and hindwings from part; D, reconstruction of forewings and hindwings based on the holotype. Scale bars represent 10 mm.

ing cicadas, the number and location of crossveins are more variable than those of longitudinal veins, and probably less important for the diagnosis. The above two fossil examples suggest that the individual aberration may be extensively present in the Mesozoic Palaeontinidae.

GENUS: *Suljuktocossus* Becker-Migdisova 1949

Type species: *S. prosboloides* Becker-Migdisova (1949); by original designation.

Type horizon and locality. Early Jurassic; Sulyucta, Kirghiz.

Revised diagnosis. Forewing medium-sized (length 35–45 mm), nearly triangular and with pointed apex; nodal inden-

tation just basal of middle of wing; vein ScA obscure; vein ScP arising basally, unbranched and coalesced with branch RA; crossvein r+m-cua short and oblique; crossvein m4-cua long, subparallel to costal margin; stem Cu short, bifurcating near base; discal cell a little less than 1/3 of wing length, almost equally bisected by nodal line; antenodal and postnodal regions trapezoid; branch CuA bifurcating just beyond junction with crossvein m4-cua; clavus about 1/3 of wing length; branch CuP curved anteriorly, terminating in the distal end of clavus; vein Pcu thick; branch A1 curved posteriorly; branch A2 short. Hindwing unknown. Included species. Two species, the type species and *S. chifengensis* n. sp. described below.

Remarks. *Suljuktocossus* differs distinctively from *Palaeocossus* Oppenheim (1885) in having a forewing of different

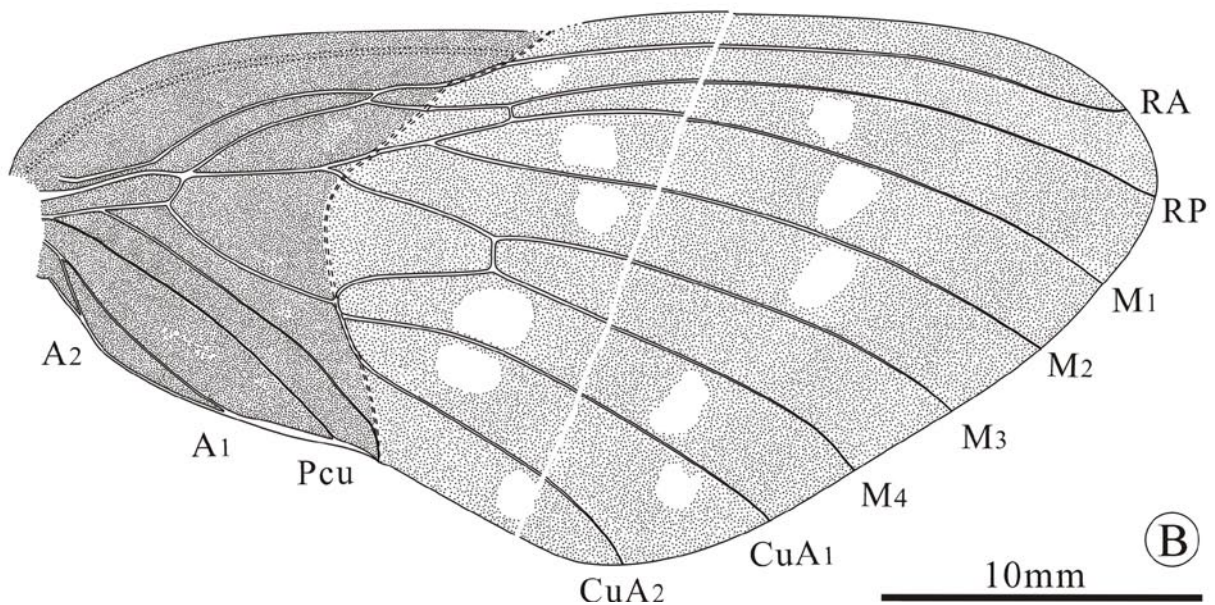


Figure 4. *Suljuktocossus chifengensis* n. sp., holotype, forewing. A, photograph of NND04116; B, illustration based on NND040116. Both to scale.

shape with unbranched vein Sc; from *Pseudocossus* Martynov (1931) (Becker-Migdisova & Wootton 1965) in unbranched vein Sc; from *Palaeontinodes* Martynov (1937) in the absence of a crossvein in the discal cell; and from *Phragmatoecites* Oppenheim (1885) and *Turgaiella* Becker-Migdisova & Wootton (1965) in the forewing possessing a different shape and long crossvein r+m-cua.

***Suljuktocossus chifengensis* n. sp.** Wang & Zhang

Figure 4

Etymology. Specific epithet is from Chifeng, to which the type locality is subject regionally.

Holotype. NND04116. Deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences.

Type locality. Daohugou Village, Ningcheng County, Chifeng City, Inner Mongolia, China.

Occurrence. Middle Jurassic.

Diagnosis. Forewing small; stem R bifurcating at about 0.3 wing length; branch M3+4 bifurcating basal of branch M1+2 fork; stem Cu straight basally; colour pattern distinct.

Description. Right forewing preserved; nearly triangular, length 34.5 mm, width 16.1 mm. Costal margin slightly curved anteriorly. Vein ScA obscure, slightly curved and ending at the bottom of indentation (basal 0.48 wing length). Vein ScP arising basally, fused with branch RA at basal 0.32 wing length. Stem R+M a little curved anteriorly. Vein R departing from stem R+M at basal 0.14 wing length and running close to vein ScP. Branch RA free for a short distance after its departure from stem R, and then fused with vein ScP; its remaining part after nodal line subparallel to anterior margin, ending in anterior margin near apex of wing. Branch RP subparallel to costal margin, connected to branch M1 by short crossvein r-m just distal of indentation. Stem M straight, dividing into veins M1+2 and M3+4 at basal 0.28 wing length. Branch M1+2 branching into veins M1 and M2 at basal 0.37 wing length. Branch M3+4 branching into veins M3 and M4 a little basal of indentation. Branch M4 directed posteriorly basally, geniculate at junction with crossvein m4-cua, and then subparallel to branch M3. Crossvein m4-cua long and longitudinal. Stem Cu branching into veins CuA and CuP near wing base. Branch CuA distinctly angled at junction with crossveins r+m-cua and m4-cua, a little curved between crossveins r+m-cua and m4-cua, branching into veins CuA1 and CuA2 slightly beyond crossvein m4-cua. Discal cell length 9.6 mm, width 3.2 mm at nodal line; antenodal region trapezoid, length 4.7 mm; postnodal region rhomboid. Branches CuP and Pcu slightly curved anteriorly. Branch A1 slightly curved posteriorly. Branch A2 fused with vein A1 basally. Nodal line traceable as a crease

across ScP+RA and RP to M a little beyond its initial division, and then almost equally separating discal cell into two parts; it continuously crossing m4-cua, following the base of CuA2, and reaching the distal end of clavus. Membrane infusate basal of nodal line, distal part with two vertical rows of white speckles at about midwing and distal 0.75 wing length. Hindwing unknown.

Remarks. The new species is distinguished from the type in having forewing a smaller with clavus smaller, location of stem R bifurcating more distal, branch M3+4 bifurcating basal of branch M1+2 fork, stem Cu straight basally and colour pattern distinct.

Suljuktocossus is considered to have a sister group relationship with some Cretaceous palaeontinids and they share some venation characters including a reduced costal area, short rs-m1 crossvein and subtriangular antenodal region of discal cell (Menon *et al.* 2005). However, the latter two character states are also present in some other Jurassic palaeontinids, such as *Turgaiella pomerantsevae* Becker-Migdisova & Wootton (1965), can not be treated as their synapomorphies. Compared to *S. prosboloides* from the Lower Jurassic of Kirghiz, *S. chifengensis* n. sp. has a comparatively smaller clavus and a narrower forewing, much closer to Cretaceous palaeontinids. The discovery of *S. chifengensis* n. sp. supports the previous view that the “*Ilerdocossus*-complex” and Brazilian palaeontinids probably originated from Central or East Asia in the Middle Jurassic and subsequently spread into Western Europe and South America during the Late Jurassic (Menon *et al.* 2005).

GENUS: ***Abrocossus* n. gen.** Wang & Zhang

Type species: *Abrocossus longus* n. gen., n. sp.; by present designation and monotypy.

Type horizon and locality. Middle Jurassic; Daohugou Village, Ningcheng County, Chifeng City, Inner Mongolia, China.

Etymology. The generic name is from Greek *abro*, graceful.

Diagnosis. Forewing large (length 60 mm) and nearly triangular, with pointed apex; nodal indentation clear and at middle of wing; branch ScA obscure; branch ScP arising basally, unbranched, coalesced with vein R for a very short distance, and terminating in costal margin, a little beyond indentation; crossvein r+m-cua vertical and very short; crossvein m4-cua long, subparallel to costal margin and coalesced with nodal line for a considerable interval, and then subparallel to branch M3; stem Cu short, bifurcating near wing base; discal cell about 1/3 of wing length; antenodal region hemicycle; postnodal region nearly trapezoid; Clavus a little less than 1/3 of wing length; branch CuP straight and thick; vein Pcu curved anteriorly; branches A1 and A2 short. Membrane infusate with some pale speckles. Hindwing unknown.

Remarks. The new genus differs distinctively from *Palaeocossus* in the large forewing possessing a different shape, a long discal cell and unbranched vein ScP; from *Pseudocossus* (Becker-Migdisova & Wootton 1965) in having a large forewing with unbranched vein ScP and long discal cell; from *Phragmatoecites* in the large forewing possessing a different shape, clear nodal indentation and long discal cell; and from *Palaeontinodes* and *Ijacossus* Becker-Migdisova (1950) in the absence of the crossvein dividing the discal cell.

Although similar to *Suljuktocossus* in the forewing having a subtriangular shape and pointed apex, *Abrocossus* n. gen. differs in having veins ScP and R fused for a distance, crossvein r+m-cua short and nodal line strongly curved, antenodal region semicircular and postnodal region trapezoid.

Abrocossus n. gen. is also similar to *Eoiocossus* Wang & Zhang (2006) in the large-sized forewing with nodal indentation clear, vein ScP ending just basally of nodal indentation, the nodal line strongly curved distally in the discal cell and crossvein m4-cua long and coalesced with nodal line for a considerable distance. The latter is different from *Abrocossus* n. gen. in possessing a wide forewing with a very small clavus, branched vein ScP, 2-branched vein CuA and a different colour pattern.

The forewing of *Abrocossus* n. gen. most closely resembles that of *Turgaiella* in the following characteristics: costal area long; branch ScA obscure; nodal indentation clear and at middle of wing; branch ScP ending just basal of nodal indentation; crossvein r-m very short; and discal cell long. The latter, however, differs in the forewing with vein ScP not coalesced with stem R, vein RP fused with branch M1, crossvein m4-cua slightly curved and branch CuA2 very short. Furthermore, judging from the preserved outer margin, the forewing of *Turgaiella* is not so pointed apically as that of *Abrocossus* n. gen., suggesting that *Turgaiella* has a different shape of the forewing.

***Abrocossus longus* n. sp.** Wang & Zhang
Figure 5

Etymology. Specific epithet is from Latin *longus*, long, with reference to the elongate forewing.

Holotype. NND04052a, b, part and counterpart. Deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences.

Type locality. Daohugou Village, Ningcheng County, Chifeng City, Inner Mongolia, China.

Occurrence. Middle Jurassic.

Diagnosis. As for genus.

Description. Right forewing preserved, nearly triangular, length 60.1 mm, width 23.5 mm. Costal margin long and slightly curved anteriorly. Outer margin inclined with a

narrow border. Branch ScP arising basally, fused with vein R at basal 0.29 wing length, and then branching from stem ScP+RA slightly basal of indentation, terminating in costal margin a little beyond indentation. Stem R+M long, connected with vein CuA by crossvein r+m-cua at basal 0.15 wing base. Vein R departing from stem R+M just beyond crossvein r+m-cua, and running close to branch ScP. Vein RA fused with branch ScP after its departure from stem R; its remaining part after nodal line subparallel to anterior margin, ending in anterior margin. Branch RP subparallel to costal margin, connected to vein M1 by short crossvein r-m at the same level of indentation, and ending in outer margin slightly posterior to wing apex. Stem M straight, bifurcating into veins M1+2 and M3+4 at basal 0.38 wing length. Vein M1+2 branching into veins M1 and M2 a little basal of indentation. Vein M3+4 bifurcating into veins M3 and M4 just basal of vein M1+2 fork. Crossvein r+m-cua vertical and very short. Crossvein m4-cua subparallel to stem M basal of nodal line, and then parallel to vein M3 and meeting vein M4 at the same level of indentation. Stem Cu bifurcating into veins CuA and CuP near base. Vein CuA distinctly angled at junction with crossvein r+m-cua, curved between crossveins r+m-cua and m4-cua, branching into veins CuA1 and CuA2 at junction with crossvein m4-cua. Discal cell length 20.5 mm, width 6.0 mm at nodal line; antenodal region hemicycle, length 13.1 mm; postnodal region nearly trapezoid. Branch CuP straight. Vein Pcu slightly curved anteriorly. Branches A1 and A2 short. Nodal line traceable as a crease across veins ScP, RA and RP to M a little beyond its initial division, and then separating discal cell into two parts; it continuously crossing m4-cua, following the base of CuA2, and reaching the distal end of clavus. Membrane infusate with a large white speckle at distal half of antenodal region, and distal part with one row of small white speckles at about distal 0.75 wing length.

Remarks. In some insect fossils, the matrix does not separate from white regions cleanly when splitting, leaving a coating of rock over the white portion (Archibald 2005). Therefore, these regions where the matrix has similarly adhered to the wing of the type are precisely white regions, which were figured in the drawing (Fig. 5B).

GENUS: *Neimengguocossus* n. gen. Wang & Zhang

Type species: *Neimengguocossus normalis* n. gen., n. sp.; by present designation and monotypy.

Type horizon and locality. Middle Jurassic; Daohugou Village, Ningcheng County, Chifeng City, Inner Mongolia, China.

Etymology. The generic name is after Neimenggu (Inner Mongolia) Autonomous Region, where the type quarry is located.

Diagnosis. Hindwing oval, anterior margin straight for distal part, length/width ratio about 1.40; costal area wide,

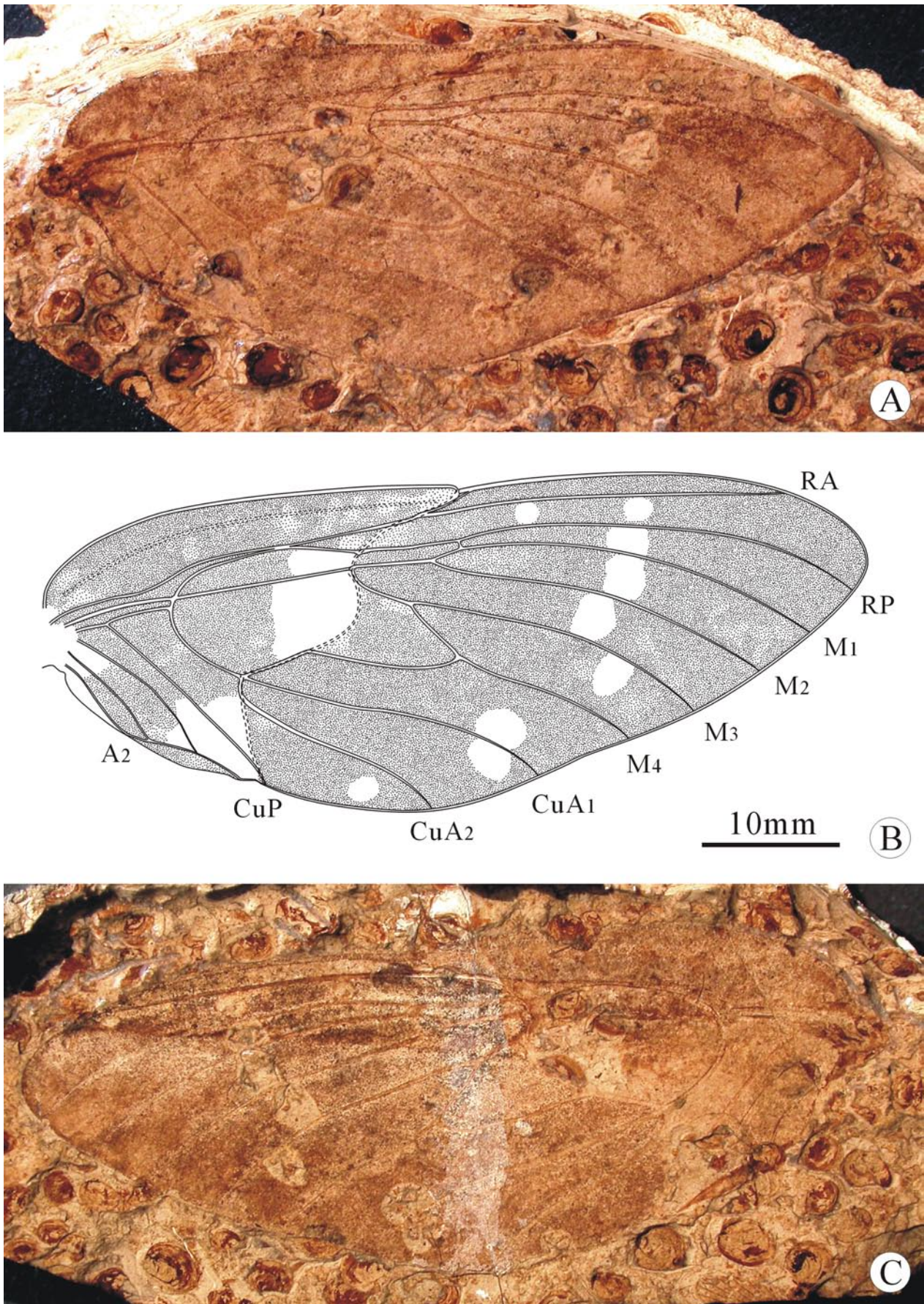


Figure 5. *Abrocossus longus* n. gen., n. sp., holotype, forewing. A, photograph of part, NND04052a; B, illustration based on part; C, photograph of counterpart, NND04052b. All to scale.

length/width ratio 3.8, maximal width at middle of wing; nodal indentation at basal 0.38 wing length; branch RP fused with vein M1 for a considerable interval, and terminating near apex; stem M bifurcating into veins M1+2 and M3+4 at wing base; branches M1 and M2 straight for distal half; branch M3+4 divided from stem M basally, close to vein CuA at one point, and then bifurcating at the same level of vein RP fused with vein M1; veins CuP and Pcu simple; vein A1 absent.

Remarks. *Neimengguocossus* n. gen. greatly resembles *Sinopalaeocossus* Hong 1983 (Wang *et al.* 2006c) in possessing a hindwing of similar shape with anterior margin straight for the distal part, stem M bifurcating into M1+2 and M3+4, branch M3+4 close to CuA at one point, and branch A1 absent. But the new genus has 4-branched vein M, while the latter 3-branched.

Neimengguocossus n. gen. differs distinctly from other genera with hindwings preserved in having vein M3+4 branching from stem M basally. Furthermore, differs from *Plachutella* Becker-Migdisova (1949) in having crossvein m-cua and vein A1 absent; from *Shurabocossus* Becker-Migdisova (1949) in the wing apex sharp, anterior margin

straight for the distal part and Pcu simple; from *Suljuktaja* Becker-Migdisova (1949) in having the wing apex sharp, anterior margin straight for distal part, vein RP coalesced with branch M1 for a long distance and vein Pcu simple; from *Cicadomorpha* Martynov (1926) (Shcherbakov 1988) in having a much wider hindwing with the costal area broadest at middle of wing; from *Gansucossus* Wang, Zhang & Fang (2006b) and *Daohugoucossus* Wang, Zhang & Fang (2006b) in the costal area comparatively wider.

Neimengguocossus normalis n. sp. Wang & Zhang
Figure 6

Etymology. Specific epithet is from Latin *normalis*, normal.

Holotype. NND04134a, b, part and counterpart. Deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences.

Type locality. Daohugou Village, Ningcheng County, Chifeng City, Inner Mongolia, China.

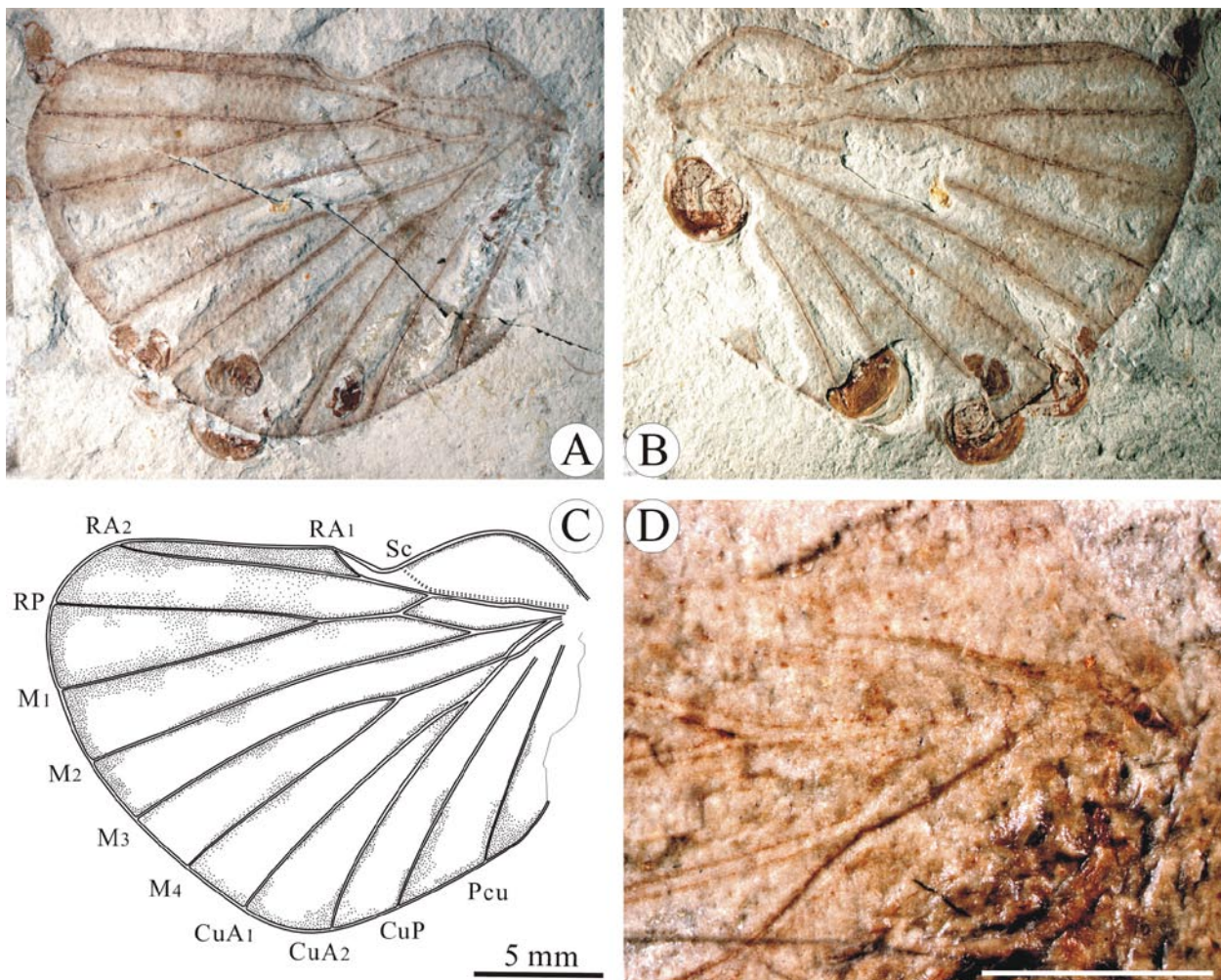


Figure 6. *Neimengguocossus normalis* n. gen., n. sp., holotype, hindwing. A, photograph of part, NND04134a; B, photograph of counterpart, NND04134b; C, illustration based on part. A, B and C to scale. D, photomicrograph of basal part of NND04134a. Scale bar represents 5 mm.

Occurrence. Middle Jurassic.

Diagnosis. As for genus.

Description. Hindwing, part and counterpart, almost complete with anal area a little destroyed. Length 21.2 mm, width 15.0 mm. Hindwing oval. Costal area wide, length/width ratio 3.8, maximal width midway. Nodal indentation at basal 0.38 wing length. Vein Sc obscure, arising basally, running close to stem R but not coalesced with it, and terminating in costal margin just basal of indentation. Stem R+M forking into veins R and M at wing base. Stem R branching into veins RA and RP at basal 0.38 wing length. Branch RA1 dividing from branch RA just distal of indentation, ending in costal margin distal of indentation. Branch RA2 slightly curved, ending in costal margin. Branch RP coalesced with M1 at basal 0.36 wing length, and terminating near wing apex; vein RP+M1 length 3.5 mm. Stem M bifurcating into veins M1+2 and M3+4 at wing base. Branch M1 departing from vein M1+2 at basal 0.19 wing length, subparallel to vein RA until fusing with vein RP, and straight for distal half; branch M2 a little curved. Stem M3+4 short (3/5 length of its branches), close to vein CuA at one point at about basal 0.13 wing length, and branching into veins M3 and M4 at the same level of vein RP fused with vein M1. Branch CuA arising basally, forking into veins CuA1 and CuA2 at about basal 0.20 wing length. Branches CuA1 and CuA2 a little curved. Branch CuP slightly curved anteriorly. Vein Pcu simple. Vein A1 absent. Marginal membrane clear and wider than vein width. Thin grey bands along veins.

DISCUSSION

Early evolutionary event. Within Palaeontinidae, three unquestionable genera, *Cicadomorpha* (Shcherbakov 1988), *Palaeontinodes* and *Ijacossus* possess a forewing with crossvein m-cua dividing the discal cell. *Palaeontinodes* forms a special group with *Cicadomorpha*, defined by the long forewing with a crossvein in the discal cell and the long hindwing with the distal part of anterior margin straight, branch M3+4 dividing from vein M2+3+4 and vein Pcu ending in the anal margin. If presence of crossvein m-cua dividing the forewing discal cell is an autapomorphy, *Ijacossus* is probably included in this group. An unambiguous conclusion, however, requires confirmation of the hindwing of *Ijacossus*. Becker-Migdisova & Wootton (1965) suggested it a diagnostic character shared by the above three genera that vein ScP is fused with stem R+M basally. This character, however, based on several basally obscure forewings, has been disproved by the subsequently discovered Palaeontinidae including *Cicadomorpha* (Shcherbakov 1988) and *Palaeontinodes* (Wang *et al.* 2006a), whose vein ScP is close to or meets but does not fuse with stem R+M.

In hindwings of the primitive Triassic Palaeontinoidea, such as *Fletcheriana* and *Dunstaniodes* Becker-Migdisova & Wootton (1965), veins M1, M2 and M3+4 are divided from stem M almost at the same point. In those of the

subsequent palaeontinids, the location where vein M3+4 branches from stem M has two evolutionary tendencies: shifting basally (vein M3+4 branches from stem M) or distally (vein M3+4 branches from stem M2+3+4). The former exists in the genera *Neimengguocossus* n. gen., *Plachutella*, and *Sinopalaeocossus*; the latter characterizes *Cicadomorpha*, *Daohugoucossus*, *Gansucossus*, *Palaeontinodes*, *Shurabocossus*, and *Suljuktaja*. Vein M3+4 specially fused with vein CuA basally in the hindwing of *Plachutella* is considered as an autapomorphy of this genus.

Of the above-mentioned genera, however, only three genera are represented by both forewings and hindwings, including *Cicadomorpha*, *Palaeontinodes*, and *Sinopalaeocossus*. *Cicadomorpha* and *Palaeontinodes* are undoubtedly included in a group, which possibly also comprises *Ijacossus*, *Daohugoucossus*, *Gansucossus*, *Shurabocossus*, and *Suljuktaja*. *Sinopalaeocossus* is a representative of the other group possibly including *Neimengguocossus* n. gen. and *Plachutella*. This implies an early evolutionary event present in the Palaeontinidae. These groups have been discovered extensively from the Lower-Middle Jurassic of Central Asia and northern China (Becker-Migdisova & Wootton 1965, Zhang 1997, Wang *et al.* 2006a, b), suggesting the evolutionary event probably occurring in the Late Triassic or Early Jurassic. Further discussions require more material, especially specimens with both forewings and hindwings articulated.

Comparisons with other assemblages. With the continuing fieldwork in the Daohugou area and accumulation of new material, the Palaeontinidae from Daohugou will undoubtedly increase at the specific level in the future, but tend to be constant at the generic level. So far, 18 species within 11 genera of the Palaeontinidae have been described from the Middle Jurassic of Daohugou (Table 1). Those by Tan & Ren (2002), lacking figures and descriptions, are not involved herein. Far more genera and species in the Middle Jurassic than those in any other epoch of the history of Palaeontinidae implies that the family probably arrived to the highest diversity in the Middle Jurassic.

The Daohugou palaeontinids are endemic on the whole although two species assigned cf. status (*Palaeontinodes* cf. *shabarovi* Martynov 1937 and *P.* cf. *angarensis* Becker-Migdisova & Wootton 1965) are almost the same as those from the Lower-Middle Jurassic of Central Asia (Wang *et al.* 2006a). Therefore, comparisons between the Daohugou palaeontinids and others are feasible merely at the generic level.

Four genera known from Daohugou, namely *Gansucossus*, *Palaeontinodes*, *Plachutella*, and *Sinopalaeocossus*, have been also reported from the Middle Jurassic of northern China including Gansu, northern Hebei and western Liaoning (Hong 1983, Zhang 1997, Wang *et al.* 2006b). No distinct difference can be detected among these assemblages. On the other hand, four genera known from Daohugou including *Palaeontinodes*, *Plachutella*, *Pseudocossus*, and *Suljuktocossus* have also been reported from the Lower-Middle Jurassic of Central Asia (Becker-

Migdisova 1949, Becker-Migdisova & Wootton 1965). Besides the common representatives from both Daohugou and Central Asia, a few derived elements such as *S. chifengensis* n. sp. are found from Daohugou, and further some hindwings from Daohugou, such as those of *Neimengguocossus* n. gen. and *Sinopalaeocossus*, are also very different from those from Central Asia in possessing a different hindwing shape without anal veins. Considering the presence of anal veins in hindwings of primitive Palaeontinoidea, the absence of anal veins is treated as a derived character. Two genera, *Pseudocossus* and *Palaeontinodes* from Daohugou, are very similar to those from Central Asia both in abundance and in wing venation. Therefore, the Daohugou palaeontinids are still closely related to those from Central Asia.

The typical Triassic genus *Fletcheriana*, reported from Australia and South Africa (Evans 1956, Riek 1976), however, is systematically debatable and its certain characters are mainly based on the forewing (Riek 1976, Shcherbakov 1984). Four hindwings from Xinjiang and Daohugou were attributed to three species within this genus based on two important characters of the hindwing: crossvein r-m present and veins M1, M2 and M3+4 branching at the same point (Zhang 1997, Wang *et al.* 2006a). However, recently these characters have also been found in some hindwings of other genera. Therefore, the systematic position of the above four specimens is probably problematic and the re-examination requires the corresponding forewings. Besides *Fletcheriana*, two endemic species, respectively belonging to genera *Pseudocossus* and *Plachutella*, have been described from the Lower Jurassic of Xinjiang (Zhang 1997). These two genera, present from the Lower Jurassic to Upper Jurassic, however, are less stratigraphically significant.

The disagreement on the age of the Daohugou insect fauna among some palaeontologists mainly resulted from comparisons of different kinds of insects between from Daohugou and from Karatau (Ren *et al.* 2002, Rasnitsyn & Zhang 2004, Zhang 2006), so the relationship between the two insect faunas is very important. However, it is difficult to get enough information from the Karatau palaeontinids. To date, only two specimens, respectively belonging to *Plachutella* and *Pseudocossus*, have been briefly reported from the Upper Jurassic of Karatau (Becker-Migdisova 1949, Shcherbakov & Popov 2002). Although identified as *Plachutella picta* Becker-Migdisova (1949), the specimen is unfortunately a fragmented hindwing with the important basal part missing. It is reasonable to believe that there would be more palaeontinids from Karatau speculated by plenty of insects of other kinds reported from this area (e.g. beetles and hymenopterans, see Rasnitsyn & Quicke 2002). Apparently, the Karatau palaeontinids have not yet been well known, and therefore it is impossible at present to give a detailed comparison between the palaeontinids respectively from Daohugou and from Karatau. However, the two assemblages are undoubtedly related, considering that both the two known genera from Karatau also have representatives in the Daohugou assemblage.

The Late Jurassic (Early Tithonian) palaeontinids from

the Solnhofen limestone are not preserved well, so some of them are systematically questionable at the generic level (Handlirsch 1906, Carpenter 1992). On the whole, the Solnhofen palaeontinids are closely related to the Cretaceous representatives by the triangular forewing with the reduced costal area and clavus (Wootton 2003), and are more derived than the Daohugou ones. The Cretaceous palaeontinids including *Ilerdocossus* Gómez 1984 (Martínez-Delclòs 1990) and *Miracossus* Ren *et al.* (1998), widespread in the nearby Cretaceous strata (Ren *et al.* 1998), have never been discovered from the Daohugou deposits, suggesting that the palaeontinids from Daohugou are little related to those from the Cretaceous, especially of the Jehol biota, and in other words, much earlier than the latter.

In conclusion, the Daohugou palaeontinids are similar to those from the Middle Jurassic (or Early-Middle Jurassic) and more primitive than those from the latest Jurassic and Early Cretaceous. At present, it is difficult to get more exact results on the age of Daohugou deposits based on the Palaeontinidae.

Appendix 1: Key to the recognized genera of Palaeontinidae from Daohugou

Forewing:

1. Forewing with a crossvein in discal cell.....
..... *Palaeontinodes* Martynov (1937)
– Forewing without crossvein in discal cell
2. Vein ScP unbranched 5
– Vein ScP branched
3. Forewing large (> 60 mm); clavus < 1/6 of wing length;
vein CuA2 2-branched
..... *Eoiocossus* Wang & Zhang (2007)
– Clavus > 1/6 of wing length; vein CuA2 unbranched
4. Forewing small (~ 25 mm); branches of Sc obscure;
antenodal region square; discal cell 1/5 of wing length
..... *Sinopalaeocossus* Hong (1983)
– Forewing medium-sized (38–52 mm); antenodal region
trapezoid; discal cell about 1/3 of wing length
..... *Pseudocossus* Martynov (1931)
5. Forewing large (~ 60 mm); vein ScP fused with R;
crossvein r+m-cua short; nodal line strongly curved;
antenodal region hemicycle; postnodal region trapezoid
..... *Abrocossus* n. gen.
– Forewing medium-sized (35–45 mm); crossvein r+m-cua
long; antenodal region trapezoid
..... *Suljuktocossus* Becker-Migdisova (1949)

Hindwing:

1. Veins M1, M2 and M3+4 branched from stem M almost
at the same point *Fletcheriana* Evans (1956)
– Veins M1, M2 and M3+4 branched from stem M not at
the same point

2. Vein M3+4 branched from stem M2+3+4; vein A1 terminating in the anal margin.....5
 - Vein M3+4 branched from stem M; anterior margin straight for distal part; vein M3+4 close to CuA at one point
3. Vein M3+4 fused with CuA basally; vein A1 present*Plachutella* Becker-Migdisova (1949)
 - Vein M3+4 not fused with CuA basally; vein A1 absent
4. Stem M 3-branched*Sinopalaeocossus* Hong (1983)
 - Stem M 4-branched.....*Neimengguocossus* n. gen.
5. Vein M3+4 connected to CuA by crossvein m-cua; medial area wide.....*Gansucossus* Wang, Zhang & Fang (2006b)
 - Vein M3+4 in contact with CuA; medial area very narrow *Daohugoucossus* Wang, Zhang & Fang (2006b)

ACKNOWLEDGEMENTS

We thank D.E. Shcherbakov (Moscow, Russia) for helpful discussions about the individual aberration of the Cicadomorpha and X. Delclòs (Barcelona, Spain) for providing his paper. We are also grateful to two reviewers for helpful comments that improved this paper. This research has been financially supported by the National Natural Science Foundation of China (40472001, 40523004), and the Major Basic Research Projects (2006CB806400) of MST of China.

REFERENCES

- ARCHIBALD, S.B. 2005. New Dinopanorpidae (Insecta: Mecoptera) from the Eocene Okanagan Highlands (British Columbia, Canada; Washington State, USA). *Canadian Journal of Earth Sciences*, 42: 119–136.
- BECKER-MIGDISOVA, E.E. 1949. Mesozoic Homoptera of Central Asia. *Trudy Paleontologicheskogo Instituta*, 22: 1–20 [In Russian].
- BECKER-MIGDISOVA, E.E. 1950. Jurassic Palaeontinidae from a new locality on the Ii River. *Doklady Akademii Nauk*, 71: 1105–1108 [In Russian].
- BECKER-MIGDISOVA, E.E. & WOOTTON, R.J. 1965. New palaeontinids of Asia. *Paleontologicheskii Zhurnal*, 2: 69–79 [In Russian].
- CARPENTER, F.M. 1992. *Treatise on invertebrate paleontology, Part R, Arthropoda 4(3)*. Geological Society of America and University of Kansas Press, Lawrence: 655 pp.
- CHEN, W., JI, Q., LIU, D.Y., ZHANG, Y., SONG, B. & LIU, X.Y. 2004. Isotope geochronology of the fossil-bearing beds in the Daohugou area, Ningcheng, Inner Mongolia. *Geological Bulletin of China*, 23: 1165–1169. [In Chinese, English abstract].
- CHEN, P.J., WANG, Q.F., ZHANG, H.C., CAO, M.Z., LI, W.B., WU, S.Q. & SHEN, Y.B. 2005. Jianshangou Bed of the Yixian Formation in West Liaoning, China. *Science in China Ser. D Earth Sciences*, 48(3): 298–312.
- CHOU, I. & LEI, Z.R. 1997. The Cicadidae of China (Homoptera: Cicadoidea). Tianze Eldoneio, Hong Kong: 380 pp. [In Chinese]
- DWORAKOWSKA, I. 1988. Main veins of the wings of Auchenorrhyncha (Insecta: Rhynchota: Hemelytrata). *Entomologische Abhandlungen Staatliches Museum für Tierkunde Dresden*, 52(3): 63–108.
- EMELJANOV, A.F. 1977. Homology of wing structures in Cicadina and primitive Polyneoptera. Terminology and homology of venation in insects. *Trudy Vsesouznogo Entomologicheskogo Obshchestva*, 58: 3–48. [In Russian]
- EVANS, J.W. 1956. Palaeozoic and Mesozoic Hemiptera (Insecta). *Australian Journal of Zoology*, 4: 223–227.
- GAO, K.Q. & REN, D. 2006. Radiometric dating of ignimbrite from Inner Mongolia provides no indication of a post-Middle Jurassic age for the Daohugou beds. *Acta Geologica Sinica*, 80(1): 42–45.
- GAO, K.Q. & SHUBIN, N.H. 2003. Earliest known crown-group salamanders. *Nature*, 422: 424–428.
- GÓMEZ, J.E. 1984. Nuevos Paleontínidos del yacimiento infracretácico de la Pedrera de Meíá (Lérida). *Boletín Geológico y Minero España*, 95: 301–309.
- GUO, Z.F., LIU, J.Q. & WANG, X.L. 2003. Effect of Mesozoic volcanic eruptions in the western Liaoning Province, China on paleoclimate and paleoenvironment. *Science in China (Series D)*, 46(12): 1261–1272.
- HANDLIRSCH, A. 1906–1908. Die fossilen Insekten und die Phylogenie der rezenten Formen. Ein Handbuch für Paläontologen und Zoologen. Engelmann, Leipzig: 1430 pp.
- HONG, Y.C. 1983. Middle Jurassic fossil insects in north China. Geological Publishing House, Beijing: 187 pp. [In Chinese, English summary]
- HUANG, D.Y., NEL, A., SHEN, Y.B., SELDEN, P.A. & LIN, Q.B. 2006. Discussions on the age of the Daohugou fauna evidence from invertebrates. *Progress in Natural Science*, 16 (Special Issue): 308–312.
- JI, Q., LUO, Z.X., YUAN, C.X. & TABRUM, A.R. 2006. A swimming mammaliaform from the Middle Jurassic and ecomorphological diversification of early mammals. *Science*, 311: 1123–1127.
- JIANG, B.Y. 2006. Non-marine Ferganoconcha (Bivalvia) from the Middle Jurassic in Daohugou area, Ningcheng County, Inner Mongolia, China. *Acta Palaeontologica Sinica*, 45: 252–257.
- LINNAEUS, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tomus I. Editio decima, reformata. L. Salvii, Holmiae (= Stockholm): 824 pp.
- MARTÍNEZ-DELCLÒS, X. 1990. Insectos del Cretácico inferior de Santa Maria de Meíá (Lleida): Colección Lluís Marià Vidal i Carreras. *Treballs del Museu de Geologia de Barcelona*, 1: 91–116.

- MARTYNOV, A.V. 1926. To the knowledge of fossil insects from the Jurassic beds in Turkestan. *Izvestiya Akademii Nauk SSSR*, 20, 1349–1366.
- MARTYNOV, A.V. 1931. To the morphology and systematical position of the fam. Palaeontinidae Handl., with a description of a new form from Ust-Baley, Siberia. *Annals Society Palaeontologica Russia*, 9: 93–122. [In Russian, English summary]
- MARTYNOV, A.V. 1937. Liassic insects from Shurab and Kizil-Kiya. *Trudy Paleontologicheskogo Instituta*, 7: 101–107. [In Russian]
- MENON, F. & HEADS, S.W. 2005. New Species of Palaeontinidae (Insecta: Cicadomorpha) from the Lower Cretaceous Crato Formation of Brazil. *Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie)*, 357: 1–11.
- MENON, F., HEADS, S.W. & MARTILL, D.M. 2005. New Palaeontinidae (Insecta: Cicadomorpha) from the Lower Cretaceous Crato Formation of Brazil. *Cretaceous Research*, 26: 837–844.
- OPPENHEIM, P. 1885. Die Ahnen unserer Schmetterlinge in der Sekundär- und Tertiärperiode. *Berliner Entomologische Zeitschrift*, 28: 331–347.
- RASNITSYN, A.P. & QUICKE, D.L.J. 2002. History of insects. Kluwer Academic Publisher, Dordrecht: 152–155.
- RASNITSYN, A.P. & ZHANG, H.C. 2004. Composition and age of the Daohugou Hymenopteran assemblage from Inner Mongolia, China. *Palaeontology*, 47: 1507–1517.
- RASNITSYN, A.P., ZHANG, H.C. & WANG, B. 2006. Bizarre fossil insects, the web-spinning sawflies of the genus *ferganolyda* (Vespida, Pamphilioidea) from the Middle Jurassic of Daohugou, Inner Mongolia, China. *Palaeontology*, 49: 907–916.
- REN, D. & KRZEMIŃSKI, W. 2002. Eoptychopteridae (Diptera) from the Middle Jurassic of China. *Annales Zoologici (Warszawa)*, 52(2): 207–210.
- REN, D., YIN, J.C. & DOU, W.X. 1998. Late Jurassic Palaeontinids (Homoptera: Auchenorrhyncha) from Hebei and Liaoning province in China. *Entomologia Sinica*, 5: 222–232.
- REN, D., GAO, K.Q., GUO, Z.G. & JI, S.A. 2002. On the biostratigraphy of the Jurassic fossil beds at Daohugou near Ningcheng, Inner Mongolia. *Geological Bulletin of China*, 21: 584–591. [In Chinese, English abstract]
- RIEK, E.F. 1976. A new collection of insects from the Upper Triassic of South Africa. *Annals of the Natal Museum*, 22: 791–820.
- SHCHERBAKOV, D.E. 1984. Systematics and phylogeny of Permian Cicadomorpha (Cimicida, Cicadina). *Paleontological Journal*, 2: 87–97.
- SHCHERBAKOV, D.E. 1988. New cicadas (Cicadina) from the later Mesozoic of Transbaikalia. *Paleontological Journal*, 4: 52–63.
- SHCHERBAKOV, D.E. & POPOV, Y.A. 2002. Superorder Cimicidea Laicharting, 1781 order Hemiptera Linné, 1758. The bugs, cicadas, plantlice, scale insects, etc. In: *History of insects*, RASNITSYN, A.P. & QUICKE, D.L.J. (Eds.) Kluwer Academic Publisher, Dordrecht: 152–155.
- SINITSHENKOVA, N.D. 2005. The oldest known record of an imago of Nemouridae (Insecta: Perlida=Plecoptera) in the late Mesozoic of eastern Transbaikalia. *Paleontological Journal*, 39(1): 38–40.
- TAN, J.J. & REN, D. 2002. Palaeoecology of insect community from Middle Jurassic Jiulongshan Formation in Ningcheng County, Inner Mongolia, China. *Acta Zootaxonomica Sinica*, 27(3): 428–434. [In Chinese, English abstract]
- WANG, B., ZHANG, H.C. & FANG, Y. 2006a. Some Jurassic Palaeontinidae (Insecta, Hemiptera) from Daohugou, Inner Mongolia, China. *Palaeoworld*, 15(1): 115–125.
- WANG, B., ZHANG, H.C. & FANG, Y. 2006b. *Gansucosus*, a replacement name for *Yumenia* Hong, 1982 (Insecta, Hemiptera, Palaeontinidae), with description of a new genus. *Zootaxa*, 1268: 59–68.
- WANG, B., ZHANG, H.C., FANG, Y. & DUAN, Y. 2006c. Revision of the genus *Sinopalaeocossus* Hong (Hemiptera, Palaeontinidae), with description of a new species from the Middle Jurassic of China. *Zootaxa*, 1349: 37–45.
- WANG, B., ZHANG, H.C., FANG, Y. & ZHANG, Z.L. 2006d. A new genus and species of Palaeontinidae (Insecta, Hemiptera) from the Middle Jurassic of Daohugou, China. *Annals Zoologici (Warszawa)*, 56(4): 757–762.
- WANG, Y. & REN, D. 2006. Middle Jurassic *Pseudocossus* fossils from Daohugou, Inner Mongolia in China (Homoptera, Palaeontinidae). *Acta Zootaxonomica Sinica*, 31(2): 289–293.
- WANG, Y. 2004. Taxonomy and stratigraphy of late Mesozoic anurans and urodeles from China. *Acta Geologica Sinica (English Edition)*, 78(6): 1169–1178.
- WHALLEY, P.E.S. & JARZEMBOWSKI, E.A. 1985. Fossil insects from the Lithographic Limestone of Montsech (late Jurassic-early Cretaceous), Lérida Province, Spain. *Bulletin of the British Museum (Natural History), Geology*, 38: 381–412.
- WOOTTON, R.J. 1971. The evolution of Cicadoidea (Homoptera). *Proceedings of 13th International Congress of Entomology*, 1: 318–319.
- WOOTTON, R.J. 2003. Reconstructing insect flight performance from fossil evidence. *Acta Zoologica Cracoviensia*, 46 (suppl. Fossil Insects): 89–99.
- ZHANG, H.C. 1997. Jurassic Palaeontinids from Karamai, Xinjiang, with a discussion of Palaeontinidae (Homoptera: Palaeontinidae) in China. *Entomologia Sinica*, 4: 312–323.
- ZHANG, J.F. 2006. New winter crane flies (Insecta: Diptera: Trichoceridae) from the Jurassic Daohugou For-

- mation (Inner Mongolia, China) and their associated biota. *Canadian Journal of Earth Sciences*, 43: 9–22.
- ZHANG, L.J. & GONG, E.P. 2003. Discussion and analysis on the cause of birds mass mortality in the Sihetun area of Beipiao, Liaoning, in the early Early Cretaceous. *Geological Review*, 49(4): 347–354. [In Chinese, English abstract]
- ZHENG, D.Z. & ZHENG, R.F. 2004. A new explanation to the reason for mass mortality of birds in Sihetun, Liaoning Province. *Geology and Resources*, 13(4): 251–252. [In Chinese, English abstract]
- XU, X. & ZHANG, F.C. 2005. A new maniraptoran dinosaur from China with long feathers on the metatarsus. *Naturwissenschaften*, 92(4): 173–177.

Table 1

<i>Daohugoucossus solutus</i> Wang, Zhang & Fang 2006 ⁽¹⁾
<i>Eoiocossus validus</i> Wang & Zhang 2006 ⁽²⁾
<i>Fletcheriana colorata</i> Wang, Zhang & Fang 2006 ⁽³⁾
<i>F. minuta</i> Wang, Zhang & Fang 2006 ⁽³⁾
<i>Gansucossus typicus</i> Wang, Zhang & Fang 2006 ⁽¹⁾
<i>Palaeontinodes</i> cf. <i>shabarovi</i> Martynov 1937 ⁽⁴⁾
<i>P.</i> cf. <i>angarensis</i> Becker-Migdisova & Wootton 1965 ⁽⁵⁾
<i>P. daohugouensis</i> n. sp. ⁽⁶⁾
<i>P. locellus</i> n. sp. ⁽⁶⁾
<i>P. separatus</i> n. sp. ⁽⁶⁾
<i>Plachutella magica</i> Wang, Zhang & Fang 2006 ⁽³⁾
<i>Pseudocossus ancylivenius</i> Wang & Ren 2006 ⁽⁷⁾
<i>P. bellus</i> Wang & Ren 2006 ⁽⁷⁾
<i>P. punctulosus</i> Wang & Ren 2006 ⁽⁷⁾
<i>Sinopalaeocossus trinervus</i> Wang, Zhang & Fang 2006 ⁽⁸⁾
<i>Suljuktocossus chifengensis</i> n. sp. ⁽⁶⁾
<i>Abrocossus longus</i> n. gen., n. sp. ⁽⁶⁾
<i>Neimengguocossus normalis</i> n. gen., n. sp. ⁽⁶⁾

Table 1. Reported taxa of Palaeontinidae from Daohugou, China. ⁽¹⁾ Wang *et al.* 2006b. ⁽²⁾ Wang *et al.* 2006d. ⁽³⁾ Wang *et al.* 2006a. ⁽⁴⁾ Martynov 1937, Becker-Migdisova & Wootton 1965, Wang *et al.* 2006a. ⁽⁵⁾ Becker-Migdisova & Wootton 1965, Wang *et al.* 2006a. ⁽⁶⁾ This study. ⁽⁷⁾ Wang & Ren 2006. ⁽⁸⁾ Wang *et al.* 2006c.

Received: 16th November 2006

Accepted: 1st March 2007