

Jurassic Progonocimicidae (Hemiptera) from China and phylogenetic evolution of Coleorrhyncha

WANG Bo^{1,3†}, SZWEDO Jacek² & ZHANG HaiChun¹

¹ LPS, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China;

² Museum and Institute of Zoology, Polish Academy of Sciences, 64, Wilcza Street, PL00-679 Warsaw, Poland;

³ Graduate University of the Chinese Academy of Sciences, Beijing 100049, China

The fossil record of Progonocimicidae of Hemiptera suborder Coleorrhyncha from China is reviewed. *Ovicimex laiyangensis* Hong et Wang, 1990, from the Lower Cretaceous of Laiyang, is excluded from Coleorrhyncha. The available generic name *Mesocimex* Hong, 1983 is resurrected from synonymy and proposed for replacement of the preoccupied name and junior homonym *Mesoscytina* Hong, 1983, non *Mesoscytina* Tillyard, 1919. It resulted in following new combinations: *Mesocimex abditus* (Yu. Popov, 1982) comb. n., *Mesocimex ambiguus* (Yu. Popov, 1985) comb. n., *Mesocimex brunneus* (Hong, 1983), comb. n., *Mesocimex fidus* (Yu. Popov, 1982) comb. n., *Mesocimex intermedius* (Yu. Popov, 1985) comb. n., *Mesocimex kuzbasicus* (Yu. Popov, 1985) comb. n., *Mesocimex liliputus* (Yu. Popov, 1988) comb. n., *Mesocimex minutus* (Yu. Popov, 1982) comb. n., *Mesocimex modestus* (Yu. Popov, 1985) comb. n., *Mesocimex paulinus* (Yu. Popov, 1982) comb. n., *Mesocimex cognatus* (Yu. Popov, 1982) comb. n. An annotated list of species of *Mesocimex* is given. In addition, a new species, *Mesocimex lini* sp. nov., is described based on well-preserved specimens with wings and bodies from the Middle Jurassic of Daohugou, China. This discovery supports the Middle Jurassic age of Daohugou Lagerstätte, since all species of *Mesocimex* are confined to the Lower–Middle Jurassic. The phylogenetic evolution of Coleorrhyncha is discussed: Cicadocorinae, Karabasiinae, Hoploridiinae, and Peloridiidae are monophyletic clades whereas Progonocimicinae and Karabasidae are clearly paraphyletic groups.

Coleorrhyncha, Peloridioidea, Jurassic, new species, new combinations, evolution, China

The hemipterous suborder Coleorrhyncha Myers et China, 1929 is an interesting insect group, with long evolutionary history, peculiar morphological features and limited distribution of its recent representatives^[1–4]. The Coleorrhyncha contains three families: Peloridiidae Breddin, 1897 and Karabasiidae Yu. Popov, 1985 within Peloridioidea Breddin, 1897, and Progonocimicoidea Handlirsch, 1906 within Progonocimicoidea Handlirsch, 1906. The sole extant family of Coleorrhyncha, Peloridiidae, has been found only from the Southern Hemisphere^[4]. Because of retaining some primitive characters, this group offers some important clues about the evolutionary process of Coleorrhyncha, even Hemiptera. Peloridiidae was previously referred to the Heteroptera^[5], and lately transferred to the Homoptera^[6]. China sug-

gested that the family was closely related to the Triassic Ipsviciidae and should be transferred to the Auchenorrhyncha^[7]. Evans thought it had no close affinity with Ipsviciidae^[8]. Schlee outlined some evidence to support the Peloridiidae as a sister group of the Heteroptera^[9]. Schlee's conclusion was disputed by Cobben^[10] and by Popov and Shcherbakov^[11], but it has been proved by

Received February 16, 2009; accepted August 3, 2009

doi: 10.1007/s11430-009-0160-6

†Corresponding author (email: savantwang@gmail.com)

Supported by Knowledge Innovation Program of the Chinese Academy of Sciences (Grant No. KZCX2-YW-154), National Natural Science Foundation of China (Grant Nos. 40872015, J0630967), National Basic Research Program of China (Grant No. 2006CB806400), Scientific Exchange Project of Chinese Academy of Sciences and Polish Academy of Sciences "Palaeobiodiversity of Fulgoromorpha and Cicadomorpha (Insecta: Hemiptera) of Daohugou Biota", and the Chinese-Polish Scientific and Technological Cooperation Project "Fulgoromorpha and Cicadomorpha (Insecta: Hemiptera) of the Daohugou Biota: Morphology, Classification, Evolution"

some molecular phylogenetic studies and morphological evidence^[12–20]. Furthermore, the close relationship of Cicadomorpha, Coleorrhyncha and Heteroptera is also confirmed by recently described vibrational signalling and jumping mechanisms of peloridiids^[21–23].

So far, only three species from China have been placed in Progonocimicidae of Coleorrhyncha. Two species, *Mesocimex sinensis* and *Mesocimex brunneus*, reported by Hong from the Middle Jurassic of Liaoning, have been discussed and attributed to Progonocimicidae^[11,24]. *Ovicimex laiyangensis* Hong et Wang, 1990, originally placed in Progonocimicidae, was described from the Lower Cretaceous of Laiyang, Shandong Province, China. However, the original photograph and illustration (text-figs. 6-5-66, 6-5-67; pl. 14, fig. 1)^[25] show that the pronotum lacks paranotal expansions and veins R and M bear much more branches, which exclude *O. laiyangensis* from the Coleorrhyncha. Its systematic position requires re-examination. Herein, two new Progonocimicidae from the Middle Jurassic of Daohugou are described based on well-preserved specimens with wings and body.

1 Geological settings

The new specimens described here were collected from the Middle Jurassic Daohugou deposits (41°18'38"N, 119°13'20"E) near Daohugou Village, Ningcheng County, Chifeng City, Inner Mongolia of China. The Daohugou deposits, consisting of grey tuff, tuffaceous siltstones and mudstones, yielded abundant well-preserved plant and animal fossils^[26–28]. Especially, it is now considered to be one of the most important insect

Lagerstätte. Most of fossil insects from Daohugou are preserved in organic remains on the surface of grey tuffaceous siltstones^[29]. The stratigraphy of this locality has been discussed in detail^[30,31]. The age of the fossil-bearing strata is still debatable. The radiometric dating of the overlying ignimbrite yielded a date of 164 Ma^[30] or 159.8 Ma^[32], a Middle Jurassic or early Late Jurassic age. However, the stratigraphy at the Daohugou fossil site was considered to be either a normal sequence^[30,31] or an overturned one^[32,33]. Apparently, a further geological survey is required to clarify matters. Judging from the Daohugou insect fauna, the age is Middle Jurassic^[34], early Middle Jurassic^[35] or late Middle Jurassic to early Late Jurassic^[26]. Herein, we adopt the Middle Jurassic from the analysis of the hymenopteran fossil assemblage^[34] and other invertebrate fossils^[36–38].

2 Material and methods

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 digital camera (DXM1200) connected to the above stereomicroscope, and the line drawings were readjusted on photographs using image-editing software (CorelDraw 13.0 and Adobe Photoshop CS). All specimens, described herein, are deposited in the Nanjing Institute of Geology and Palaeontology (NIGP), Chinese Academy of Sciences.

To date, there is no consensus on the interpretation of vein nomenclature in Coleorrhyncha^[11,39,40] (Table 1). We follow the wing venation nomenclature amended by Popov and Shcherbakov^[11].

Table 1 Correspondences between vein nomenclatures in Coleorrhyncha

Popov ^[39]	Wootton and Betts ^[40]	Kukalová-Peck ^[41]	Popov and Shcherbakov ^[11]
R ₁	R ₁	RA ₁₊₂	dSc
R ₂	R ₂	RA ₃₊₄	R ₁
R _s	R _s	RP+MA	R _s
M	M	MP	M
CuA	CuA	CuA	CuA
	CuA ₁		CuA ₁
	CuA ₂		CuA ₂ (av)
	(Pcu+A ₁)		
CuP	CuP	CuP	CuP
Pcu	1A	AA ₃₊₄	Pcu
A ₁	2A	AP ₁₊₂	1A

3 Systematics

Order Hemiptera Linnaeus, 1758

Suborder Coleorrhyncha Myers et China, 1929

Superfamily Progonocimicoidea Handlirsch, 1906

Family Progonocimicidae Handlirsch, 1906

= Eocimicidae Handlirsch, 1906

= Actinoscytinidae Evans, 1956

= Cicadocoridae Becker-Migdisova, 1958

Subfamily Cicadocorinae Becker-Migdisova, 1958

Mesocimex Hong, 1983

1958 *Olgamartynovia* Becker-Migdisova, p. 62; pro parte

1982 *Olgamartynovia* Becker-Migdisova; Popov, p. 83

1983 *Mesoscytina* Hong, p. 66

[non] 1919 *Mesoscytina* Tillyard, p. 871 (type species: *Mesoscytina australis* Tillyard, 1919)

1985 *Asianisca* Popov, p. 32

1991 *Mesoscytina* Hong, 1983; Popov and Shcherbakov, p. 222

Type species: *Mesocimex sinensis* Hong, 1983: 65.

Type horizon and locality: Haifanggou Formation, Middle Jurassic; Beipiao City, Liaoning Province, China.

Included species: 13 species (see an annotated list below).

Diagnostic characters: Tegmen narrow in basal portion, usually narrower than 1/3 of full length at claval apex; costal margin slightly arcuate; precostal carina very narrow; costal area narrow; stem R beyond dSc parallel to costal margin; stem M_{1+2} fork basad of r-m veinlet; branch M_1 longer than Rs; branch M_{3+4} usually longer than stem M. Tegmina more overlapping than in *Cicadocoris* and *Eocercopis* Handlirsch, 1939.

Remarks: Hong erected the genus *Mesoscytina* on the basis of one specimen from the Middle Jurassic of China^[24]. However, the generic name *Mesoscytina* had already been used for a genus of Scytinoptera of Hemiptera^[42], so it must be replaced by the next oldest available name from among its synonyms^[43]. Popov and Shcherbakov^[11] and Becker-Migdisova^[44] revised generic diagnosis of *Mesoscytina* Hong, 1983, and transferred some species of the genus *Olgamartynovia* Becker-Migdisova, 1958 to this genus. Furthermore, Popov and Shcherbakov^[11] suggested that *Mesocimex* Hong, 1983 and *Asianisca* Popov, 1985 are junior syno-

nyms of *Mesoscytina*. According to Popov and Shcherbakov, the type species of *Olgamartynovia* (*O. turanica* Becker-Migdisova, 1958) and *Cicadocoris* (*C. kuliki* Becker-Migdisova, 1958) show no essential differences and are congeneric^[11]. In addition, some of the species placed in *Olgamartynovia* are synonymised, and placed in *Cicadocoris*^[11]. The other species originally described in *Olgamartynovia*, merit generic separation: '*Olgamartynovia*' *rigida* Yu. Popov, 1982 = '*Olgamartynovia*' *paula* Yu. Popov, 1982; '*Olgamartynovia*' *beckermigdisovae* Yu. Popov, 1982, '*Olgamartynovia*' *nana* Yu. Popov, 1982; '*Olgamartynovia*' *transbaikalica* Yu. Popov, 1985; '*Olgamartynovia*' *distincta* Yu. Popov, 1982^[11,45]. Thus, the oldest name proposed is *Olgamartynovia* Becker-Migdisova, 1958, but it is not available to replace homonymic name *Mesoscytina* Hong, 1983. Then, the next available name to replace a homonym is *Mesocimex* Hong, 1983, which is here resurrected from synonymy. An annotated list of species within this genus is given below.

Judging from the original drawings, descriptions and plates, the numbers of original plates shown by Hong in his 1983 paper^[24] are evidently fallacious. *Mesocimex sinensis* should be shown in figure 3 of Plate 11 while *Mesocimex brunneus* (under name *Mesoscytina brunnea*) in figures 1 and 2 of Plate 11. Hong^[24] wrote that the lengths of forewings of *Mesocimex sinensis* and *M. brunneus* were 3.4 mm and 4.5 mm respectively. However, based on the original photos and captions, both forewings are clearly longer than 5 mm. Therefore, both specimens need re-examination.

So far, all *Mesocimex* fossils are recorded from the Lower-Middle Jurassic of Central and East Asia (Appendix I). Therefore, the discovery of *Mesocimex* from Daohugou supports the Middle Jurassic age of Daohugou Lagerstätte.

Mesocimex lini sp. nov. (Figures 1–3)

Etymology: Specific epithet is after Lin Qibin, one of pioneers in study of Chinese fossil insects.

Holotype: NIGP150276a, b; part and counterpart. Deposited in the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Horizon and locality: Middle Jurassic; Daohugou Village, Chifeng City, Inner Mongolia, China.

Diagnosis: Similar in venation pattern to other spe-

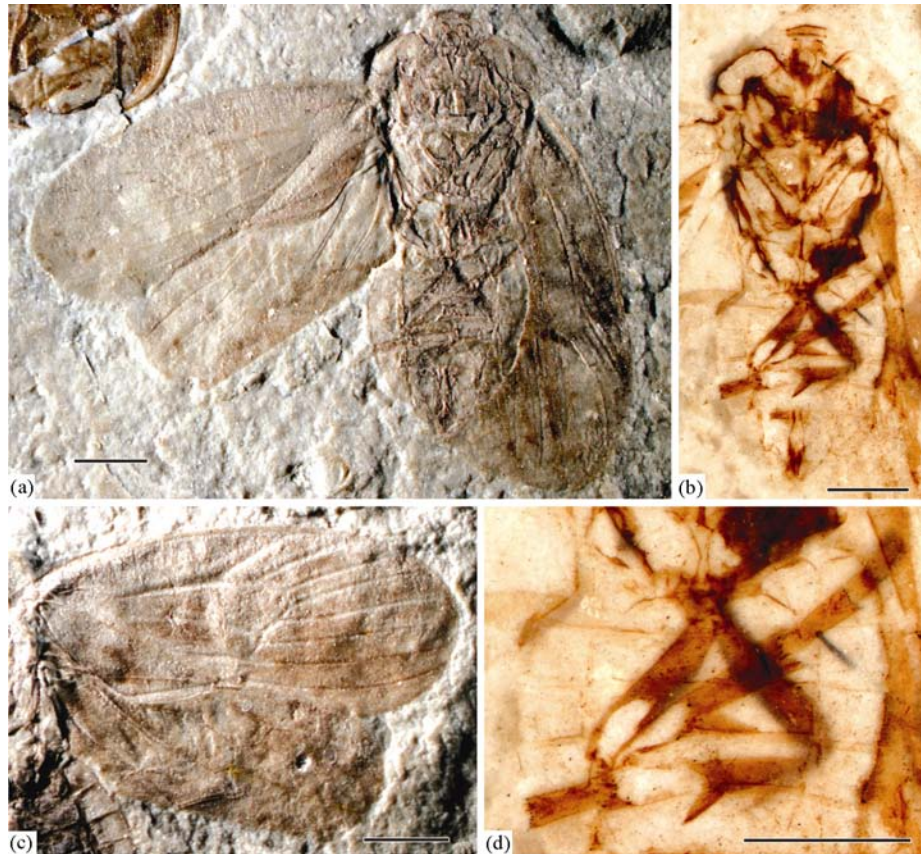


Figure 1 *Mesocimex lini* sp. nov., holotype. (a) Photograph of NIGP150276a; (b) photograph of the body in NIGP150276a; (c) photograph of right tegmen and hindwing in NIGP150276b; (d) photograph of hind legs. Scale bars = 1 mm.

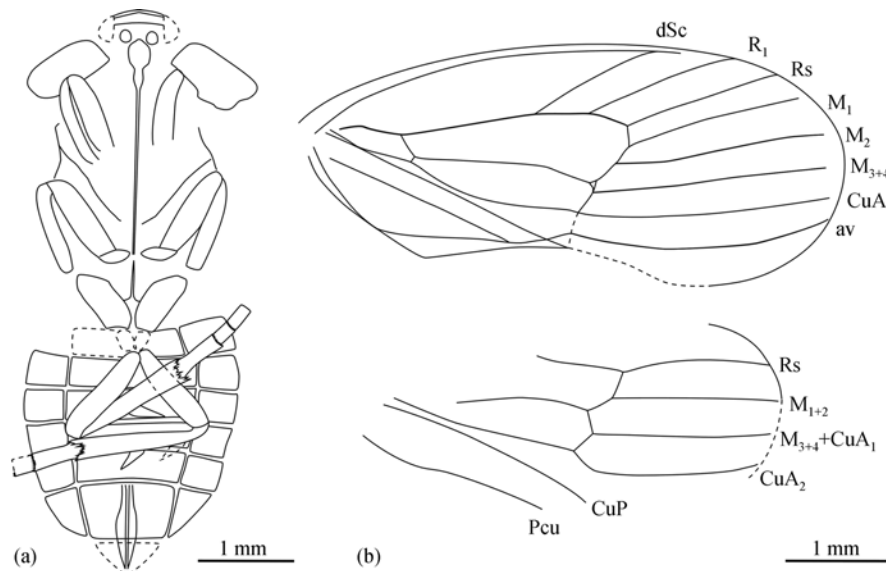


Figure 2 *Mesocimex lini* sp. nov., holotype. (a) Illustration of the body in NIGP150276a; (b) illustration of right tegmen and hindwing in NIGP150276b.

cies placed in the genus. It differs from them in having the larger tegmen (tegmina in other species varies between 2.0–4.7 mm). It is characterized by the following

combination of characters: head small, 0.4 times as wide as pronotum; hind tibia with 2 large movable conical spurs; hind tibia with apex swallow-tailed; basitar-



Figure 3 Reconstruction of *Mesocimex lini* sp. nov.

somere 2.5 times as long as mid tarsomere; abdomen with 4–6 laterotergites about 0.33 times as wide as sternites; ovipositor almost reaching apices of 9th segment; tegmen length 5.3 mm, width at claval apex 1.8 mm; branches dSc, R₁ and R_s evenly spaced and parallel; dSc forking 2.5 times closer to R_s than to wing base.

Description: Body impunctate and dark; tegmen membrane uniformly grey; hindwing membrane uniformly grey.

Total length 5.8 mm. Head length 0.4 times as wide as pronotum. Rostrum slender, extending to mid coxae. Pronotum trapezoidal, transverse, angles rounded, sides slightly arcuate and strongly diverging caudad. Fore coxae elongated. Fore femur length 0.8 mm, slightly thicker than fore tibia. Mid coxae unclear, probably transverse. Mid femur length 1.0 mm, slightly thicker than fore femur. Hind coxae enlarged and transverse. Hind femur length 1.1 mm, slightly thinner than mid femur. Hind tibia length 1.3 mm, slightly thinner than hind femur, with 2 large movable conical spurs, longer than diameter of tibia, one near its base, the other at about its midlength; hind tibia apex swallow-tailed and bearing pecten of 10–11 apical teeth. Hind tarsus length 1.0 mm; length of tarsal segments 1–3: 0.52 mm, 0.20 mm, 0.25 mm, respectively. Apices of first two tarsomeres bearing pecten of apical teeth in formula 10–11: 9–11. Abdomen slightly longer than wide, laterotergites 4–6 about 0.33 times as wide as sterna. Ovipositor ta-

pering to acute apex, almost reaching apex of 9th segment.

Right tegmen length 5.3 mm, width at claval apex 1.8 mm. Tegmen rounded apically, with apex at M₃₊₄. Anterior margin weakly arcuate, precostal carina narrow and nearly horizontal. Costal area narrow, not widening toward dSc; bSc obsolete, dSc slightly convex. Stem R slightly convex at the point of dSc origin, and then parallel to costal margin, dividing into R₁ and R_s slightly basal of M forking, and halfway between M forking and costal margin. Branches dSc, R₁ and R_s evenly spaced and parallel. Arculus short and subtransverse. Stem M₁₊₂ dividing basad of r-m veinlet. Branch M₁ close to R_s, and branch M₂ nearly straight. Branch M₃₊₄ longer than stem M. Stem CuA beyond arculus slightly curved posteriorly. Branch CuA₂ transverse. Right hindwing partly preserved, length 4.6 mm. Hindwing rounded apically, with apex at M₁₊₂. Branch R_s connected with M₁₊₂ by a subtransverse crossvein r-m a little distal of M₁₊₂ origin. Stem M forked into M₁₊₂ and M₃₊₄ a little beyond middle of wing (at basal 0.56 wing length). Branch M₃₊₄ fused with branch CuA₁. Stem CuA bifurcating into veins CuA₁ and CuA₂ at the same level as stem M branching.

Remarks: This species can be assigned to *Mesocimex* by the following characters: tegmen narrower in basal half and rounded apically; its apex at branch M₃₊₄; branch R forking not closer to M forking than to costal margin; M₁₊₂ forking before veinlet r-m; branch M₃₊₄ longer than stem M. It is most similar to *Mesocimex brunneus* in the tegmina with branches dSc, R₁ and R_s evenly spaced and sub-parallel, but differs from the latter in the larger tegmina with fork of dSc 2.5 times closer to R_s than to wing base. Furthermore, it differs from other species of the genus in having the larger tegmina (tegmen in other species varies between 2.0–4.7 mm), and branches dSc, R₁ and R_s evenly spaced and parallel. So far, only one specimen presenting the complete body has been described in detail, and was assigned to ?*Mesocimex* sp. because of its lack of wings^[11].

4 The evolution of Coleorrhyncha

The Coleorrhyncha, traceable back via Progonocimiciidae to the latest Permian (255 Ma), are derivable from Cicadomorpha: Prosboloidea: Ingrididae. This lineage evolved in parallel to true bugs, Heteroptera, acquiring

some superficial similarities but retaining basic differences^[2,11]. As a coleorrhychan stem-group, Progonocimicidae was widely spread in Eurasia, Australia, and South America from the Upper Permian to Lower Cretaceous^[46-50]. Both nymphs and imagines of Progonocimicidae were probable phloem-feeders^[2]. They have the tegmen with 8 apical cells and head without areolae^[11]. Their hind tibiae (at least in Cicadocorinae) generally have two lateral movable spurs, and their hind tarsi are three-segmented, with basitarsomere the largest, and basitarsomere and midtarsomere have apical pectens of macrosetae bearing teeth^[2]. Progonocimicidae consists of two subfamilies: Progonocimicinae Handlirsch, 1906 and Cicadocorinae Becker-Migdisova, 1958. Early Progonocimicinae was still similar to Ingridae by the head structure and tegminal venation^[2] (Figure 4). En-

tering into Triassic, Progonocimicinae shows a high diversity of tegminal venation, and consists of ancestors of Cicadocorinae and Karabasiinae. Therefore, this subfamily is clearly a paraphyletic group and required extensive revision. Cicadocorinae was originated from some early Progonocimicinae in the Late Triassic, and diversified markedly in the Jurassic and distributed worldwide in the Early Cretaceous (Figure 4). Cicadocorinae is a monophyletic unit defined by following characters of tegmina: branch A_1 shorter than half of claval fracture; vein Pcu diverging from the fracture before joining A_1 and vein dSc convex.

The second superfamily, Peloridioidea, is of strict monophyly limited by following autapomorphies: tegmen with huge basal cell longer than one enclosed by Y-vein, arculus very long and longitudinal, vein Sc

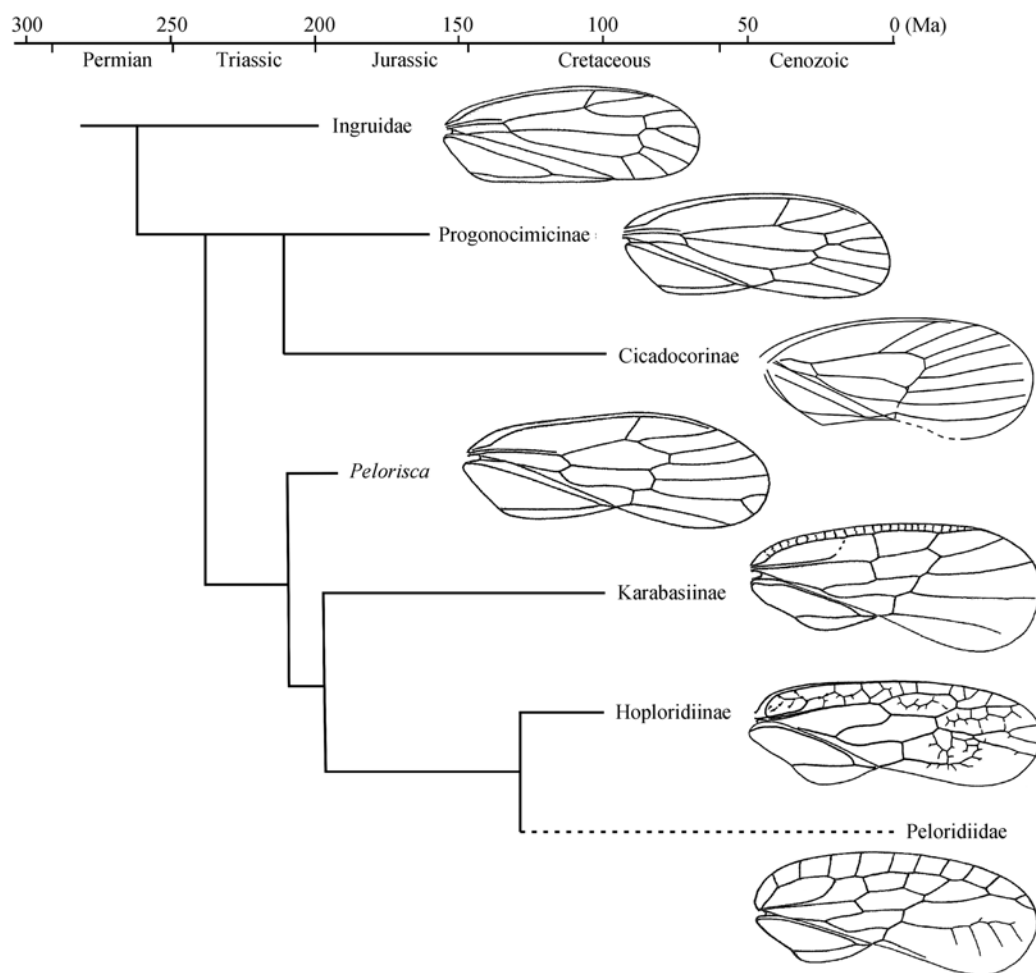


Figure 4 Phylogram of Coleorrhyncha (modified after refs. [2, 50]). Cicadomorpha: Ingridae (*Kaltanospes kuznetskiensis* Becker-Migdisova, 1961), Progonocimicinae (*Actinoscytina belmontensis* Tillyard, 1926), Cicadocorinae (*Mesocimex lini* sp. nov.), *Pelorisca* (*Pelorisca connectens* Yu. Popov and Shcherbakov, 1991), Karabasiinae (*Karabasia evansi* Yu. Popov and Shcherbakov, 1991), Hoploridiinae (*Hoploridium dollingi* Yu. Popov and Shcherbakov, 1991), Peloridiidae (*Peloridium hammoniorum* Breddin, 1897).

short and entirely free; hindwing without closed cells or reduced; head with a pair of translucent areolae at anterior margin; antennae 3-segmented, incrassate; anteclypeus and lora marginally concealed by prothoracal preepisterna. Peloridioidea contains two families: Karabasiidae and extant Peloridiidae. Popov and Shcherbakov^[11] indicated that Karabasiidae consisted of two subfamilies: Karabasiinae Yu. Popov, 1985 and Hoploridiinae Yu. Popov and Shcherbakov, 1991. The earliest Peloridioidea were Karabasiidae: Karabasiinae — the genera *Minuta* from Lower Jurassic of Kazakhstan and *Karabasia* known from Middle-Upper Jurassic of Central and East Asia. Karabasiinae was probably originated from *Pelorisca*-like progonocimicids in the Late Triassic (Figure 4). The second subfamily of Karabasiidae, Hoploridiinae, were only discovered from the Lower Cretaceous of Transbaikalia^[11]. They probably also were corticolous, with cryptic habitus and long rostrum, being bark-dwellers and associated with thick plant stems^[2]. The anteclypeus is separated from the postclypeus in *Hoploridium* and is distinctly different from that of extant Peloridiidae, in which the anteclypeus is fused with postclypeus. This character of *Hoploridium* is resulted from the retention of the nymphal condition^[2]. Popov and Shcherbakov^[2] showed that Hoploridiinae is a blind offshoot. However, Heads^[50] considered it as a sister-

group to Peloridiidae. Hoploridiinae and Peloridiidae are similar by the following characters: wide paranotal lobes without areolation, tegminal venation reticulate, metepisterna entirely sclerotized and hind legs unarmed, with two tarsomeres and the first tarsomere small. Although the first two characters are considered as the result of convergent evolution by Popov and Shcherbakov^[2], other characters support that Hoploridiinae is more close to extant Peloridiidae than to Karabasiinae. Therefore, Hoploridiinae are probably the sister group of Peloridiidae (Figure 4).

The extinction of Cicadocorinae, Karabasiinae, Hoploridiinae, occurring at the beginning of Late Cretaceous, was possibly caused by the Middle Cretaceous phyto-coenotic changes^[2,51] (Figure 4). During the drastic Middle Cretaceous vegetation changes, ancient host-plant associations were largely destroyed. Many plant taxa disappeared completely, and the descendants of their consumers were forced to shift to other hosts^[52]. Most of Early Cretaceous coleorrhynchans, as other Hemiptera lineages, probably failed to shift from original hosts to flowering plants (or other hosts) at this period.

The authors are grateful to Mr. Yang Dinghua (Nanjing Arts Institute) for drawing Figure 3, and two anonymous referees for reviewing the manuscript.

Appendix I: An annotated list of species of the genus *Mesocimex* Hong, 1983

- Mesocimex sinensis* Hong, 1983 – type species
Middle Jurassic Haifanggou Formation; Beipiao City, western Liaoning, China.
- Mesocimex abditus* (Yu. Popov, 1982) comb. nov.
Olgamartynovia abditus Yu. Popov, 1982: 87. Shurab III
Mesocymetina abditus (Yu. Popov, 1982): Popov and Shcherbakov 1991: 222
Olgamartynovia distans Yu. Popov, 1982: 88. Sagul
Mesocymetina distans (Yu. Popov, 1982): Popov and Shcherbakov 1991: 222
Olgamartynovia admota Yu. Popov, 1982: 91. Sagul
Mesocymetina admota (Yu. Popov, 1982): Popov and Shcherbakov 1991: 222
Lower–Middle Jurassic (Lower Liassic) Sogul Formation; Sagul locality (Shurab III), Osh Region, Kyrgyzstan.
- Mesocimex ambiguus* (Yu. Popov, 1985) comb.

nov.

- Asianisca ambigua* Yu. Popov, 1985: 33.
Mesocymetina ambigua (Yu. Popov, 1985)
Lower–Middle Jurassic (Lower Liassic) Sogul Formation; Sagul locality, Osh Region, Kyrgyzstan.
- Mesocimex brunneus* (Hong, 1983), comb. nov.
Mesocymetina brunnea Hong, 1983: 66.
Middle Jurassic Haifanggou Formation; Beipiao City, Western Liaoning, China.
 - Mesocimex fidus* (Yu. Popov, 1982) comb. nov.
Olgamartynovia fida (Yu. Popov, 1982): 86.
Mesocymetina fida (Yu. Popov, 1985): Popov and Shcherbakov 1991: 222.
Lower–Middle Jurassic (Lower Liassic) Sogul Formation; Sagul locality, Osh Region, Kyrgyzstan.
 - Mesocimex intermedius* (Yu. Popov, 1985) comb. nov.
Olgamartynovia intermedia Yu. Popov, 1985: 32.
Mesocymetina intermedia (Yu. Popov, 1985): Popov and Shcherbakov 1991: 222.

Lower Jurassic Abashevo Formation; Kuznetsk County, Kemerovo Region, Western Siberia, Russia.

7. *Mesocimex kuzbasicus* (Yu. Popov, 1985) comb. nov.

Olgamartynovia kuzbasica Yu. Popov, 1985: 31.

Mesoscytina kuzbasica (Yu. Popov, 1985): Popov and Shcherbakov 1991: 222.

Lower Jurassic Abashevo Formation; Kemerovo Region, Western Siberia, Russia.

8. *Mesocimex liliputus* (Yu. Popov, 1988) comb. nov.

Olgamartynovia liliputa Yu. Popov, 1988: 70.

Mesoscytina liliputa (Yu. Popov, 1988): Popov and Shcherbakov 1991: 222.

Lower–Middle Jurassic Kalgansk Formation; Chita Region, Eastern Siberia, Transbaikalia, Russia.

9. *Mesocimex lini* sp. nov.

Middle Jurassic; Daohugou Village, Inner Mongolia, China.

10. *Mesocimex minutus* (Yu. Popov, 1982) comb. nov.

Olgamartynovia minuta Yu. Popov, 1982: 85.

Mesoscytina minuta (Yu. Popov, 1982): Popov and Shcherbakov 1991: 222.

Lower Jurassic (Sinemurian) Dzhil Formation;

Sogyuty, Tonsk Region, Kyrgyzstan.

11. *Mesocimex modestus* (Yu. Popov, 1985) comb. nov.

Asianisca modesta Yu. Popov, 1985: 33.

Mesoscytina modesta (Yu. Popov, 1985): Popov and Shcherbakov 1991: 222

Lower–Middle Jurassic Sogul Formation; Sagul locality, Osh Region, Kyrgyzstan.

12. *Mesocimex paulinus* (Yu. Popov, 1982) comb. nov.

Olgamartynovia paulina Yu. Popov, 1982: 93.

Mesoscytina paulina (Yu. Popov, 1982): Popov and Shcherbakov 1991: 222

Lower–Middle Jurassic (Lower Liassic) Sogul Formation; Sagul locality, Osh Region, Kyrgyzstan.

13. *Mesocimex cognatus* (Yu. Popov, 1982) comb. nov.

Olgamartynovia cognata Yu. Popov, 1982: 94.

Mesoscytina cognata (Yu. Popov, 1982)

Lower–Middle Jurassic (Lower Liassic) Sogul Formation; Sagul locality, Osh Region, Kyrgyzstan.

Note: The species probably included in this genus (Popov and Shcherbakov, 1991: 222).

- 1 Evans J W. A review of present knowledge of the family Peloridiidae and new genera and new species from New Zealand and New Caledonia (Hemiptera: Insecta). *Rec Aust Mus*, 1981, 34: 381–406
- 2 Popov Yu A, Shcherbakov D E. Origin and evolution of the Coleorrhyncha as shown by the fossil record. In: Schaefer C W, ed. *Studies on Hemipteran Phylogeny*. Lanham: Thomas Say Publications in Entomology, Entomological Society of America, 1996. 9–30
- 3 Grimaldi D, Engel M S. *Evolution of the Insects*. Cambridge: Cambridge University Press, 2005. 312–314
- 4 Bechly G, Szewo J. Coleorrhyncha: Moss bugs. In: Martill D M, Bechly G, Loveridge R F, eds. *The Crato Fossil Beds of Brazil: Window into an Ancient World*. Cambridge: Cambridge University Press, 2007. 313–317
- 5 Breddin G. Hemipteren. *Ergebnisse der Hamburger Magalhaensischen Sammlerreise, Herausgegeben vom naturhistorischen Museum zu Hamburg*. Hamburg: L. Friederichsen and Co., 1897. 10–13
- 6 Myers J G, China W E. The systematic position of the Peloridiidae as elucidated by a further study of the external anatomy of *Hemiodocus leai* China. *Ann Mag Nat Hist*, 1929, 3: 282–294
- 7 China W E. South American Peloridiidae (Hemiptera-Homoptera: Coleorrhyncha). *T Roy Entomol Soc London*, 1962, 114: 131–161
- 8 Evans J W. The systematic position of the Ipsviciidae (Upper Triassic Hemiptera) and some new Upper Permian and Middle Triassic Hemiptera from Australia (Insecta). *Aust J Entomol*, 1963, 2: 17–23
- 9 Schlee D. Morphologie und symbiose, ihre bewertkraft für die verwandtschaftsbeziehungen der Coleorrhyncha. *Phylogenetische Studien an Hemiptera IV: Heteropteroidea (Heteroptera + Coleorrhyncha) als monophyletische Gruppe*. *Stuttg Beitr Naturk Nr*, 1969, 210: 1–27
- 10 Cobben R H. Evolutionary trends in Heteroptera. Pt. II. Mouthpart-structures and Feeding Strategies. Wageningen: Agricultural University, 1978. 1–407
- 11 Popov Yu A, Shcherbakov D E. Mesozoic Peloridioidea and their ancestors (Insecta: Hemiptera, Coleorrhyncha). *Geol Palaeont*, 1991, 25: 215–235
- 12 Wheeler W, Schuh R T, Bang R. Cladistic relationships among higher groups of Heteroptera: Congruence between morphological and molecular data sets. *Entomol Scand*, 1993, 24: 121–137
- 13 Campbell B C, Steffen-Campbell J D, Sorensen J T, et al. Paraphyly of Homoptera and Auchenorrhyncha inferred from 18S rDNA nucleotide sequences. *Syst Entomol*, 1995, 20: 175–194
- 14 Sorensen J T, Campbell B C, Gill R J, et al. Non-monophyly of Auchenorrhyncha (“Homoptera”), based upon 18S rDNA phylogeny: Ecoevolutionary and cladistic implications within pre-Heteropteroidea Hemiptera (s.l.) and a proposal for new monophyletic suborders. *Pan-Pac Entomol*, 1995, 71: 31–60
- 15 Ouvrard D, Campbell B C, Bourgoin T, et al. 18S rRNA secondary structure and phylogenetic position of Peloridiidae (Insecta, Hemiptera). *Mol Phylogenet Evol*, 2000, 16: 403–417
- 16 Bourgoin T, Campbell B C. Inferring a phylogeny for Hemiptera: Falling into the ‘Autapomorphic Trap’. *Denisia*, 2002, 4: 67–82
- 17 Schaefer C W. Prosorrhyncha (Coleorrhyncha + Heteroptera). In: Resh V H, Cardé R T, eds. *Encyclopedia of Insects*. San Diego:

- Academic Press, 2003. 947–965
- 18 Brožek J. Labial sensillae and the internal structure of the mouthparts of *Xenophyes cascus* Bergroth, 1924 (Peloridiidae: Coleorrhyncha: Hemiptera) and their significance in evolutionary studies on the Hemiptera. Aphids and Other Hemipterous Insects, Monograph, 2007, 13: 35–42
 - 19 Wappler T, Wedmann S, Rust J. Die Fossilgeschichte der Wanzen ein Überblick. Mainzer Naturwiss Archiv-Beiheft, 2007, 31: 47–61
 - 20 Xie Q, Tian Y, Zheng L, et al. 18S rRNA hyper-elongation and the phylogeny of Euhemiptera (Insecta: Hemiptera). Mol Phylogenet Evol, 2008, 47: 463–471
 - 21 Sweet M H. Comparative external morphology of the pregenital abdomen of the Hemiptera. In: Schaefer C W, ed. Studies on Hemipteran Phylogeny. Lanham: Thomas Say Publications in Entomology, Entomological Society of America, 1996. 119–158
 - 22 Hoch H, Deckert J, Wessel A. Vibrational signalling in a Gondwanan relict insect (Hemiptera: Coleorrhyncha: Peloridiidae). Biol Lett, 2006, 2: 222–224
 - 23 Burrows M, Hartung V, Hoch H. Jumping behaviour in a Gondwanan relict insect (Hemiptera: Coleorrhyncha: Peloridiidae). J Exp Biol, 2007, 210: 3311–3318
 - 24 Hong Y C. Middle Jurassic Fossil Insects in North China (in Chinese with English summary). Beijing: Geological Publishing House, 1983. 65–66
 - 25 Hong Y C, Wang W L. Insect fossils of Laiyang Formation. In: the Regional Geological Surveying Team, Shandong Bureau of Geology and Mineral Resources, ed. The Stratigraphy and Palaeontology of Laiyang Basin, Shandong Province (in Chinese). Beijing: Geological Publishing House, 1990. 44–189
 - 26 Zhang J F. New winter crane flies (Insecta: Diptera: Trichoceridae) from the Jurassic Daohugou Formation (Inner Mongolia, China) and their associated biota. Can J Earth Sci, 2006, 43: 9–22
 - 27 Zhou Z Y, Zheng S L, Zhang L J. Morphology and age of *Yimaia* (Ginkgoales) from Daohugou Village, Ningcheng, Inner Mongolia, China. Cretaceous Res, 2007, 28: 348–362
 - 28 Zhang F C, Zhou Z H, Xu X, et al. A bizarre Jurassic maniraptoran from China with elongate ribbon-like feathers. Nature, 2008, 455: 1105–1108
 - 29 Wang B, Li J F, Zhang H C, et al. Preliminary elemental analysis of fossil insects from the Middle Jurassic of Daohugou, Inner Mongolia and its taphonomical implications. Chin Sci Bull, 2009, 54(5): 783–787
 - 30 Chen W, Ji Q, Liu D Y, et al. Isotope geochronology of the fossil-bearing beds in the Daohugou area, Ningcheng, Inner Mongolia (in Chinese with English abstract). Geol Bull China, 2004, 23: 1165–1169
 - 31 Gao K Q, Ren D. Radiometric dating of ignimbrite from Inner Mongolia provides no indication of a post-Middle Jurassic age for the Daohugou beds. Acta Geol Sin, 2006, 80: 42–45
 - 32 He H Y, Wang X L, Zhou Z H, et al. $^{40}\text{Ar}/^{39}\text{Ar}$ dating of ignimbrite from Inner Mongolia, northeastern China, indicates a post-Middle Jurassic age for the overlying Daohugou Bed. Geophys Res Lett, 2004, 31: L20609, doi: 10.1029/2004GL020792
 - 33 Wang X L, Zhou Z H, He H Y, et al. Stratigraphy and age of the Daohugou Bed in Ningcheng, Inner Mongolia. Chin Sci Bull, 2005, 50(19): 2369–2376
 - 34 Rasnitsyn A P, Zhang H C. Composition and age of the Daohugou hymenopteran assemblage from Inner Mongolia, China. Palaeontology, 2004, 47: 1507–1517
 - 35 Ren D, Gao K Q, Guo Z G, et al. On the biostratigraphy of the Jurassic fossil beds at Daohugou near Ningcheng, Inner Mongolia (in Chinese with English abstract). Geol Bull Chin, 2002, 21: 584–591
 - 36 Shen Y B, Chen P J, Huang D Y. Age of the fossil conchostracans from Daohugou of Ningcheng, Inner Mongolia (in Chinese with English abstract). J Strati, 2003, 27: 311–313
 - 37 Huang D Y, Nel A, Shen Y B, et al. Discussions on the age of the Daohugou fauna — Evidence from invertebrates. Prog Nat Sci, 2006, 16(Spec Iss): 308–312
 - 38 Wang B, Zhang H C, Fang Y. Middle Jurassic Palaeontinidae (Insecta, Hemiptera) from Daohugou of China. Alavesia, 2007, 1: 89–104
 - 39 Popov Yu A. Upper Jurassic hemipterans, genus *Olgamartynovia* (Hemiptera, Progonocimicidae) from Central Asia. Paleontol J, 1982, 2: 78–94
 - 40 Wootton R J, Betts C R. Homology and function in the wings of Heteroptera. Syst Entomol, 1986, 11: 389–400
 - 41 Kukulová-Peck J. Fossil history and the evolution of hexapod structures. In: Naumann I D, Crane P B, Lawrence J F, et al, eds. The insects of Australia. A Textbook for Students and Research Workers. 2nd ed. Carlton: Melbourne University Press, 1991. 141–179
 - 42 Tillyard R J. Mesozoic insects of Queensland. No. 7. Hemiptera Homoptera with a note on the phylogeny of the suborder. P Linn Soc N S W, 1919, 44 (4): 857–895
 - 43 ICZN. International Code of Zoological Nomenclature. 4th ed. London: International Trust for Zoological Nomenclature, 1999
 - 44 Becker-Migdisova E E. New fossil Homoptera. Pt. 1 (in Russian). Mater Fundam Paleontol, 1958, 2: 57–67
 - 45 Popov Yu A. Jurassic bugs and Coleorrhyncha of southern Siberia and western Mongolia (in Russian). Trudy Paleontol Inst AN SSSR, 1985, 211: 28–47
 - 46 Wootton R J. Actinoscytinidae (Hemiptera: Heteroptera) from the Upper Triassic of Queensland. Ann Mag Nat Hist, 1963, 6: 249–255
 - 47 Popov Yu A, Wootton R J. The Upper Liassic Heteroptera of Mecklenburg and Saxony. Syst Entomol, 1977, 2: 333–351
 - 48 Jarzembowski E A. New insects from the Weald Clay of the Weald. P Geologist Assoc, 1991, 102: 93–108
 - 49 Klimaszewski S M, Popov Yu A. New fossil hemipteran insects from southern England (Hemiptera: Psylliina + Coleorrhyncha). Ann Upper Silesian Mus Entomol, 1993, (Suppl 1): 13–36
 - 50 Heads S W. A new species of *Yuripopovia* from the Early Cretaceous of the Isle of Wight (Coleorrhyncha: Progonocimicidae). Br J Entomol Nat Hist, 2008, 21: 247–253
 - 51 Rasnitsyn A P. Problem of the global crisis of the non-marine biocoenoses in the mid-Cretaceous. In: Ponomarenko A G, ed. Cretaceous Biocoenotic Crisis and Evolution of Insects (in Russian). Moscow: Nauka, 1988. 191–207
 - 52 Zherikhin V V. Ecological history of the terrestrial insects. In: Rasnitsyn A P, Quicke D L J, eds. History of Insects. Dordrecht-Boston-London: Kluwer Academic Publishers, 2002. 331–388