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More on Mesozoic Membracoidea (Homoptera)

Снова о мезозойских мембракоидах (Homoptera)

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КЛЮЧЕВЫЕ СЛОВА: Homoptera, Cicadomorpha, Membracoidea, Hylicellidae, Archijassidae, Karajassinae, ископаемые, филогения, жилкование, прыжок, брохосомы, мезозой, триас, юра, мел.

ABSTRACT. New monobasic genera from the Middle Jurassic of South Siberia (*Kisa fasciata* **gen.** et **sp.n.,** *Kubecola guttatus* **gen.** et **sp.n.,** *Kemobius lux* **gen.** et **sp.n.**) and *Cicadellium* Westwood, 1854 are placed in the subfamily Karajassinae **stat.n.** *Cicadellium psocus* Westwood, 1854 (= *Cercopidium telesphorus* Westwood, 1854, **syn.n.**) is designated as the type species of the genus *Cicadellium* (the second species, *C. dipsas* Westwood, 1854 is transferred to Psocoptera). A new monobasic genus from the Upper Jurassic of South Mongolia (*Dellashara tega* **gen.** et **sp.n.**) and four Early Cretaceous genera are assigned to the subfamily Dellasharinae **subfam.n.** Both subfamilies are included into the family Archijassidae placed in the superfamily Membracoidea. *Mesojassus* Tillyard, 1916 and *Triassojassus* Tillyard, 1919 from the Upper Triassic of Australia belong in Archijassinae and represent the earliest records of the superfamily. The sequence of acquisition of membracoid features is outlined. The early evolution of Membracoidea is discussed. Karajassinae probably coated their integuments with brochosomes or related particles produced in the Malpighian tubules, because these insects already acquired the leafhopper characters associated with brochosome transport: long hind legs with rows of tibial macrosetae, narrow tegmina with MP+CuA1 anastomosis, and reduced surface sculpture.

РЕЗЮМЕ. Новые монотипные роды из средней юры Южной Сибири (*Kisa fasciata* **gen.** et **sp.n.,** *Kubecola guttatus* **gen.** et **sp.n.,** *Kemobius lux* **gen.** et **sp.n.**) и *Cicadellium* Westwood, 1854 помещены в подсемейство Karajassinae **stat.n.** *Cicadellium psocus* Westwood, 1854 (= *Cercopidium telesphorus* Westwood, 1854, **syn.n.**) обозначен как типовой вид рода *Cicadellium* (второй вид, *C. dipsas* Westwood, 1854 перенесен в Psocoptera). Новый монотипный род из верхней юры Южной Монголии (*Dellashara tega* **gen.** et **sp.n.**) и четыре нижнемеловых рода отнесены к подсемейству Dellasharinae **subfam.n.** Оба подсемейства включены в семейство Archijassidae, помещаемое в надсемейство Membracoidea. *Mesojassus* Tillyard, 1916 и *Triassojassus* Tillyard, 1919 из верхнего триаса Австралии принадлежат к Archijassinae и представляют собой древнейшие находки этого надсемейства. Прослежена последовательность приобретения мембракоидных признаков. Обсуждается ранняя эволюция мембракоидов. Вероятно, Karajassinae наносили на свое тело брохосомы или подобные им продукты секреции мальпигиевых сосудов, поскольку уже приобрели признаки цикаделлид, связанные с переносом брохосом: длинные задние ноги с рядами макрохет на голенях, узкие передние крылья со слиянием MP+CuA1, ослабленную скульптуру.

Introduction

The superfamily Membracoidea, which comprises two extant hemipteran groups, megadiverse leafhoppers and treehoppers, is traced back in the fossil record to the Triassic. However, the classification of Mesozoic membracoids remains controversial.

Westwood [1854] described various Mesozoic insects collected by Rev. Peter Brodie in the Purbeck Beds of England (now dated Early Cretaceous), including homopteran tegmina, named *Cercopidium signoretii* and *C. telesphorus,* and one hindwing, named *Cicadellium psocus.* Westwood interpreted *Cercopidium* as belonging to Cercopidae *sensu* Latreille, who united in this family frog-, leaf-, and treehoppers, and *Cicadellium* as belonging to Cercopidae Cicadellinae. Handlirsch [1906–1908] separated *Cercopidium signoretii* and *C. telesphorus* into the genus *Homopterulum,* left unplaced between Jassidae, Fulgoridae, and Cercopidae or Procercopidae.

Handlirsch [1906–1908, 1939] created *Archijassus* and several related genera in Jassidae from the Liassic of Dobbertin. Tillyard [1916, 1919] described Upper Triassic *Mesojassus* and *Triassojassus* in the same family. For these and several other Triassic genera, Evans

[1956] established the family Chiliocyclidae, placed near Cicadellidae. Becker-Migdisova [1962] transferred most of these genera into the family Archijassidae, left unplaced (along with Hylicellidae) between Cicadellidea and Cercopidea.

Martynov [1927] described from the Upper Jurassic of Kazakhstan the genus *Karajassus* in Jassidae. Later the family Karajassidae was erected and interpreted as the most basal group of Membracoidea, whereas Archijassinae were included into Hylicellidae, and this latter and Chiliocyclidae were separated into the superfamily Hylicelloidea, considered ancestral to all three extant superfamilies of Cicadomorpha [Shcherbakov, 1992, 1996]. However, Ansorge [1996] retained Archijassidae (including *Karajassus*) in the Membracoidea.

Hamilton [1971] created the family Jascopidae for a peculiar nymph found in Canadian Upper Cretaceous amber and combining cercopid and cicadellid characters. The genus *Myangadina* from the Lower Cretaceous of Asia was described in Cicadellidae [Shcherbakov, 1986, 1988]; later this genus, *Homopterulum* and some others were united into an unnamed group nearly filling the gap between Karajassidae and typical Cicadellidae and deserving at least subfamily rank [Shcherbakov, 1992]. However, Hamilton [1990, 1992] assigned *Homopterulum, Myangadina,* and two Early Cretaceous genera from Brazil (all four based on adults) to Jascopidae.

Additional fossils and new data on living leafhoppers allow reconsideration of the systematic position of some Mesozoic membracoids. The vein nomenclature used herein is after Shcherbakov [1984, 1996, 2011]. The specimens having both part and counterpart are indicated with "±". The material on the new taxa described below is deposited at the Borissiak Paleontological Institute, Russian Academy of Sciences (PIN). Photographs of these specimens were taken using a Leica M165C stereomicroscope and Leica DFC425 camera. *Kubecola guttatus* **sp.n.** was imaged without coating with a Tescan Vega XMU scanning electron microscope. The photograph of *C. psocus* was taken in the Sackler Biological Imaging Lab at the Natural History Museum, London (NHM) using a Leica M125 stereomicroscope, 1.6x adapter, and Canon EOS 550D camera.

Taxonomy

Superfamily Membracoidea Rafinesque, 1815

Family Archijassidae Becker-Migdisova, 1962

DIAGNOSIS. Tegmen: CP present; bSc reduced; 6–8 full-sized apical cells; 1–3 subapical cells (one or two *rm,* sometimes *ir* absent). Hindwing: 5–6 full-sized apical cells (RA long; MP connected or completely fused to CuA1); Pcu and 1A close but not connected proximally.

COMPOSITION. Archijassinae Becker-Migdisova, 1962, Karajassinae Shcherbakov, 1992, **stat.n.,** and Dellasharinae Shcherbakov, **subfam.n.** (keyed below).

COMPARISON. Other membracoids have tegmina with the maximum of 5 full-sized apical cells (or reticulate venation) and hindwings with the maximum of 4 full-sized apical cells (RA short; MP completely fused to CuA1).

KEY TO SUBFAMILIES OF ARCHIJASSIDAE (WINGS)

1 Tegmen: costal space broad (especially proximally); CP rather long, nearly longitudinal; MP and CuA1 connected by crossvein *mcu* or X-junction. Hindwing: MP and CuA1 connected by crossvein *mcu* or fused for some distance ..... Archijassinae
— Tegmen: costal space narrow (sometimes widened distally); CP shorter, oblique 2
2 Tegmen: MP and CuA1 connected by crossvein or fused for some (usually short) distance. Hindwing: MP and CuA1 connected by crossvein ..... Karajassinae
— Tegmen: MP and CuA1 fused for some (usually long) distance. Hindwing: MP and CuA1 completely fused .. .. Dellasharinae

Subfamily Archijassinae Becker-Migdisova, 1962

DIAGNOSIS. Tegmen: costal space broad; CP rather long; R and M leaving basal cell at one point; crossvein *mcu* (sometimes short) present or replaced with X-junction (not anastomosis)*;* 7–8 full-sized apical cells; 1–3 subapical cells (radiomedial one either open or closed with additional crossvein *rm;* occasionally *ir* absent and radial cell merged with next apical cell). Hindwing: 6 full-sized apical cells (RA long; MP and CuA1 connected with crossvein *mcu* or fused for some distance); posterior apical cell sublanceolate (CuA1 and CuA2 more or less converging distally).

COMPOSITION. *Archijassus* Handlirsch, 1906 (= *Atitizon* Handlirsch, 1939 = *Eojassus* Handlirsch, 1939 = *Liojassus* Handlirsch, 1939 = *Parajassus* Bode, 1953 = *Mesocicada* Becker-Migdisova, 1962 = *Cixiella* Becker-Migdisova, 1962) [see Ansorge, 1996], *Mesoledra* Evans, 1956 (= *Handlirschiana* Metcalf et Wade, 1966, nomina nova pro *Mesojassus* Handlirsch, 1939 non Tillyard, 1916), and *Ardela* Ansorge, 1996 from Lower and Middle Jurassic of Eurasia, and *Mesojassus* Tillyard, 1916 and *Triassojassus* Tillyard, 1919 from Upper Triassic of Australia.

REMARKS. Based on the photographs published by Jell [2004], *Mesojassus* and *Triassojassus* are assigned herein to Archijassinae. The tegmina of *T. proavitus* and *M. ipsviciensis* are very similar in their size and structure, except for the latter being narrower apically, with crossvein *mcu* replaced by X-junction. These conclusions have to be verified by re-examination of the holotypes.

KEY TO GENERA OF ARCHIJASSINAE (TEGMEN)

1 dSc more proximal (pterostigmal cell long). M 3-branched 2
— dSc more distal, about level of claval apex (pterostigmal cell short) 3
2 Short crossvein *mcu* present. Tegmen broadly rounded apically ..... *Triassojassus*
— Crossvein *mcu* replaced with X-junction. Tegmen narrowly rounded apically ..... *Mesojassus*
3 Single *rm* distal to M fork. M usually 4-branched .... *Archijassus*
— Two *rm* (additional *rm* at M fork) 4
4 R fork much before additional *rm*. *ir* basal to *im.* M usually 4-branched ..... *Ardela*
— R fork just additional *rm*. *ir* about level of *im.* M 3-branched ..... *Mesoledra*

Subfamily Karajassinae Shcherbakov, 1992, **stat.n.**

DIAGNOSIS. Tegmen: costal space narrow (at least basally); CP short; R and M leaving basal cell separately, at one point, or forming stalk beyond it; MP and CuA1 connected by crossvein *mcu* or fused for some distance*;* 7 full-sized apical

cells; 2 (occasionally 3) subapical cells (if radiomedial one closed with additional crossvein *rm,* then *ir* usually absent and radial cell merged with next apical cell). Hindwing: 6 full-sized apical cells (RA long; free MP and CuA1 connected with crossvein *mcu*); posterior apical cell lanceolate (CuA1 and CuA2 converging distally). Postclypeus large, inflated. Three close-set ocelli on crown. Antennal flagellum retaining primary segmentation. Hind coxae transverse, together occupying entire width of metathorax. Hind tibia with strong pecten at flared apex, macrosetae of outer row on prominent bases.

COMPOSITION. Type genus, *Cicadellium* Westwood, 1854, and three new genera (all keyed below) from Jurassic and Lower Cretaceous of Eurasia.

REMARKS. *Sinojassus* Zhang, 1985 and *Gurvanina* Shcherbakov, 1986 from the Lower Cretaceous of Asia, originally assigned to Karajassidae, belong outside Archijassidae as understood here.

KEY TO GENERA OF KARAJASSINAE (TEGMEN)

1 Two *rm* (additional *rm* at M fork). R fork just before additional *rm* and M fork. Crossvein *mcu* very short or replaced with short anastomosis. Clavus punctate, remaining tegmen (remigium) feebly punctate in costal space and along veins. Usually R and M forming stalk beyond basal cell, and *ir* absent ..... *Kisa* **gen.n.**
— Single *rm* distal to M fork. R fork much before M fork 2
2 R and M forming stalk beyond basal cell; arculus long. Crossvein *ir* present; *mcu* not replaced with anastomosis. Remigium feebly punctate in costal space and along veins ..... *Kubecola* **gen.n.**
— R and M not forming such stalk. Remigium distinctly punctate at least in costal space and along veins 3
3 Crossvein *mcu* developed. Medial cell shorter than M branches beyond it. Costal space as wide as radial and medial spaces combined. Remigium punctate only in costal space and along veins. Crossvein *ir* present. R and M leaving basal cell at same point; arculus long ..... *Kemobius* **gen.n.**
— Crossvein *mcu* replaced with anastomosis. Medial cell long and wide, larger than CuA fork, longer than M branches beyond it. Costal space narrower, as wide as radial space. Remigium more extensively punctate 4
4 Crossvein *ir* present. MP+CuA1 about as long as CuA1 beyond it. CuA beyond arculus arched to CuP and then diverging from it. Tegmen very elongate (ca 3.7:1) .... *Cicadellium* Westwood, 1854
— Crossvein *ir* absent. MP+CuA1 shorter than CuA1 beyond it. CuA beyond arculus nearly parallel to CuP. Tegmen less elongate (2.6–3.0:1) . *Karajassus* Martynov, 1927

Kisa Shcherbakov, **gen.n.**

TYPE SPECIES. *Kisa fasciata* **sp.n.**

DIAGNOSIS. Tegmen: moderately elongate; costal space feebly punctate; two *rm*; R fork just before M fork; R+M stalk usually present; arculus long; *ir* usually absent; medial cell large; *mcu* very short or replaced with short anastomosis; claval veins arched towards each other.

COMPOSITION. Monobasic.

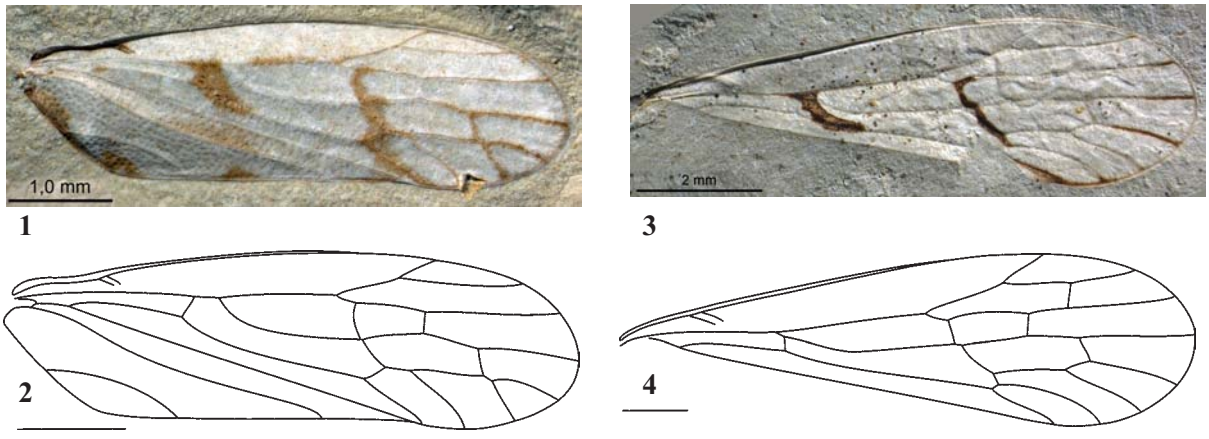
REMARKS. The largest tegmen assigned to the type species (1.7 times longer than the smallest one) lacks the R+M stalk and retains a weak crossvein *ir,* but in the other venation features and distinctive dark pattern agrees with the remaining specimens. Presumably this species had a pronounced sexual dimorphism in size.

ETYMOLOGY. From acronym “Kubekovo, Itat Suite”; gender feminine.

Kisa fasciata Shcherbakov, **sp.n.**

MATERIAL. Holotype male(?) left tegmen PIN 1255/1562±; paratype tegmina 1255/429± (female?), 1563, 1564±, 1565± (male?), 1567 and clavus 1255/1566±; Kubekovo NE of Krasnoyarsk, left bank of Yenisei River; Itat Formation, Middle Jurassic.

DESCRIPTION (Figs 1–4). Tegmen 5.5–9.1 mm long and 1.6–2.7 mm wide, elongate (about 3.4:1), broadest beyond or at midlength, rounded at apex. Hypocostal carina narrow, precostal one even narrower; costal margin nearly straight proximally. Basal cell about 0.3 of tegmen length. Radial space at R fork narrower than costal space and about as wide as medial one. Normally R+M stalk present and *ir* absent, but in largest specimen (PIN 1255/429) R+M stalk absent and weak *ir* present beyond midlength of pterostigmal cell. *rm* about midlength of medial cell. M stem continued with MA, medial cell more or less elongate. M branches beyond *im* shorter than medial cell, MP forked before or beyond *im* (sometimes MP2 with additional fork). *mcu* usually developed and very short, as well as 1st section of CuA1 (then two posterior apical cells very elongate and curved), but in smaller specimens often replaced with X-



Figs 1–4. *Kisa fasciata* **sp.n.,** Kubekovo, Middle Jurassic: 1–2 — holotype PIN 1255/1562, tegmen (1 — mirror image); 3–4 — paratype PIN 1255/429, tegmen.

Рис. 1–4. *Kisa fasciata* **sp.n.,** Кубеково, средняя юра: 1–2 — голотип ПИН 1255/1562, переднее крыло (1 — перевёрнуто зеркально); 3–4 — паратип ПИН 1255/429, переднее крыло.

junction (PIN 1255/1564) or short anastomosis (holotype), then 1st section of CuA1 longer. CuA stem not close to CuP. Clavus rather densely, evenly, shallowly punctate, costal space sparsely and faintly so, the rest of remigium punctate only along veins. Tegmen pale with three transverse dark bands interrupted at least in costal space (at base along scutellar margin; at level of arculus; at nodal level), dark marking at CP, and M and CuA branches darkened distally; clavus slightly suffused.

ETYMOLOGY. Latin *fasciatus* (banded).

Kubecola Shcherbakov, **gen.n.**

TYPE SPECIES. *Kubecola guttatus* **sp.n.**

DIAGNOSIS. Tegmen: moderately elongate; costal space feebly punctate; single *rm;* R fork much before M fork; R+M stalk present; arculus long; *ir* present; medial cell large; *mcu* short, not replaced with anastomosis; claval veins arched towards each other. Hindwing: rather broad; *mcu* at 1/3 of CuA1; *rm* more distal; CuA stem moderately curved; Pcu proximally well separated from 1A.

COMPOSITION. Monobasic.

REMARKS. All tegmina of *Kubecola guttatus* **sp.n.** are of similar size, suggesting that this species was less sexually dimorphic then *Kisa fasciata* **sp.n.**

COMPARISON. In the hindwing of *Karajassus crassinervis* Martynov, 1927*,* the crossvein *mcu* is about the same level as *rm*, and Pcu proximally very close to 1A.

ETYMOLOGY. From Kubekovo and Latin -*cola* (dweller); gender masculine.

Kubecola guttatus Shcherbakov, **sp.n.**

MATERIAL. Holotype right tegmen and incomplete hindwing PIN 1255/1570±; paratypes PIN 1255/1571± male? with detached tegmen and hindwing, 1255/1572± female with detached tegmen, and tegmina 1255/148±, 1568±, 1569±, 1573; Kubekovo NE of Krasnoyarsk, left bank of Yenisei River; Itat Formation, Middle Jurassic.

DESCRIPTION (Figs 5–9). Tegmen 6.4–7.5 mm long and 2.0–2.2 mm wide, elongate (ca 3.3:1), broadest beyond midlength, rounded at apex. Hypocostal carina narrow, precostal one even narrower; costal margin nearly straight proximally. Basal cell about 0.3 of tegmen length. R fork nearer to M fork than to arculus, radial space at R fork narrower than costal space and wider than medial one. *ir* beyond midlength of pterostigmal cell; *rm* at or beyond midlength of medial cell. M stem more or less continued with MA, medial cell more or less elongate. M branches beyond *im* shorter than medial cell, MP forked before or beyond *im* (sometimes MP2 with additional fork). *mcu* short (usually as long as 1st section of CuA1), sometimes very short. CuA stem not close to CuP. Clavus rather densely punctate, more deeply towards base, costal space sparsely and faintly punctate, the rest of remigium punctate and transversely wrinkled only along veins. Tegmen pale; clavus suffused; veins dark with regular pale patches (much more extensive towards base); dark markings on vein tips near apical margin. Hindwing (PIN 1255/1571 with tegmen 7.5 mm long) 6.0 mm long, 3.2 mm wide, rather broad (1.9:1), apical cells moderately long. Costal margin with low triangular projection in basal 1/3. Apical margin sinuate at CuA2. Basal cell wide, closed with arculus. R forked just before 1/2 wing length; RA not much shorter than RP. M and CuA forked about 3/5 wing length, M slightly later; 1st section of MA sigmoidal, 1st section of MP straight. Crossvein *mcu* at about 1/3 CuA1 length, *rm* more distal. RA and RP distally subparallel, MA and MP nearly so. CuA1 diverging from MP and converging to CuA2 from *mcu* up to marginal sinus (apices of CuA1 and CuA2 close together); CuA2 arched against *mcu*. M stem gradually diverging from R up to fork. CuA stem nearly straight; CuP and Pcu moderately sigmoidal; Pcu proximally well sepa-

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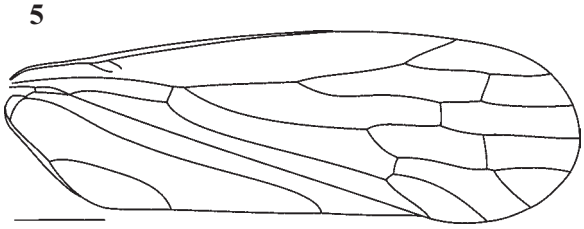

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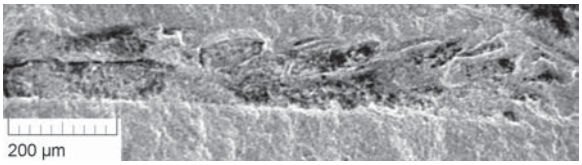

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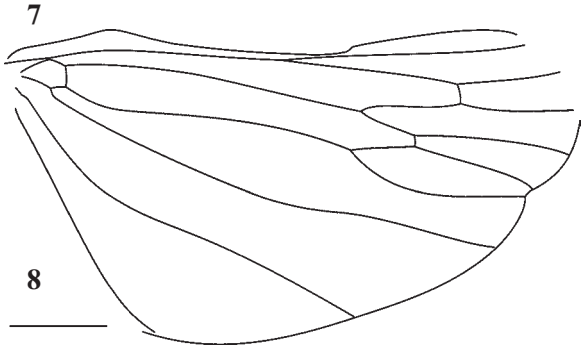

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Figs 5–9. *Kubecola guttatus* **sp.n.,** Kubekovo, Middle Jurassic: 5–6 — holotype PIN 1255/1570, tegmen (5 — mirror image of negative impression); 7–8 — paratype PIN 1255/1571, hindwing; 9 — paratype PIN 1255/1572, hind tibia, SEM micrograph.

Рис. 5–9. *Kubecola guttatus* **sp.n.,** Кубеково, средняя юра: 5–6 — голотип ПИН 1255/1570, переднее крыло (5 — обратный отпечаток, перевёрнуто зеркально); 7–8 — паратип ПИН 1255/1571, заднее крыло; 9 — паратип ПИН 1255/1572, задняя голень, СЭМ микрофотография.

rated from 1A. Body remains fragmentarily preserved. Hind tibia (PIN 1255/1571) with at least three longitudinal ribs; macrosetae of outer row relatively slender, nearly straight, about as long as tibia width, on prominent spine-like bases; these spines slightly inflated, bluntly pointed, set at about 30° to tibia axis. Ovipositor (PIN 1255/1572) projecting beyond 9th abdominal segment.

ETYMOLOGY. Latin *guttatus* (speckled).

Kemobius Shcherbakov, **gen.n.**

TYPE SPECIES. *Kemobius lux* **sp.n.**

DIAGNOSIS. Tegmen: rather broad; costal space wide, punctate; single *rm*; R fork much before M fork; R and M leaving basal cell at one point; arculus long; *ir* present; medial cell short; *mcu* not replaced with anastomosis.

COMPOSITION. Monobasic.

ETYMOLOGY. From *Kem* (Khakas name for upper reaches of the Yenisei River) and Greek *bios* (life); gender masculine.

Kemobius lux Shcherbakov, **sp.n.**

MATERIAL. Holotype left tegmen PIN 1255/1561± (without clavus); Kubekovo NE of Krasnoyarsk, left bank of Yenisei River; Itat Formation, Middle Jurassic.

DESCRIPTION (Figs 10–11). Tegmen 5.9 mm long and 2.0 mm wide, moderately elongate (ca 3.0:1), broadest beyond midlength, rounded at apex. Hypocostal carina rather wide; costal margin nearly straight proximally. Basal cell about 0.3 of tegmen length. R fork nearer to M fork than to arculus, radial space at R fork much narrower than costal space and as wide as medial one. *ir* about midlength of pterostigmal cell; *rm* beyond midlength of medial cell. M stem continued rather with MA, medial cell rather short. M branches beyond *im* longer than medial cell, MP forked just before *im* (MP1 with small additional fork). *mcu* short, as long as 1st section of CuA1. CuA stem not close to CuP. Costal space sparsely, deeply punctate, the rest of remigium punctate only along veins. Tegmen suffused, more so on hypocostal carina and in middle of spaces and cells in posterior half of remigium; veins dark (especially proximally) with regular pale patches.

ETYMOLOGY. Latin *lux* (light).

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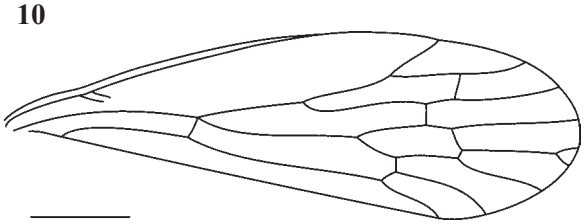

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Figs 10–11. *Kemobius lux* **sp.n.,** Kubekovo, Middle Jurassic, holotype PIN 1255/1561, tegmen.

Рис. 10–11. *Kemobius lux* **sp.n.,** Кубеково, средняя юра, голотип ПИН 1255/1561, переднее крыло.

Cicadellium Westwood, 1854

Cicadellium: Westwood 1854: 393.

TYPE SPECIES. *Cicadellium psocus* Westwood, 1854

DIAGNOSIS. Tegmen: very elongate; proximal part punctate; single *rm*; R fork much before M fork; R and M leaving basal cell separately; arculus short; *ir* present; radial and medial cells long; *mcu* replaced with rather long anastomosis; CuA beyond arculus arched and running close to CuP; nodal line present. Hindwing: elongate; *mcu* at 1/5 of CuA1; *rm* more distal; M and CuA stems, CuP and Pcu markedly curved; Pcu proximally well separated from 1A.

COMPOSITION. Monobasic: *Cicadellium psocus* Westwood, 1854 = *Cercopidium telesphorus* Westwood, 1854, **syn.n.**

COMPARISON. In the less elongated hindwings of *Kubecola* **gen.n.** and *Karajassus* the M and CuA stems, CuP, and Pcu are less curved, and *mcu* is at 1/3 CuA1 length; in *Karajassus* also the crossvein *mcu* is about the same level as *rm,* and Pcu proximally very close to 1A.

REMARKS. We designate here *Cicadellium psocus* Westwood, 1854 (based on the hindwing) as the type species of this genus. The second species originally assigned to the genus, *C. dipsas* Westwood, 1854 (based on the forewing), actually belongs in Psocoptera. There are diverse Karajassinae in the Purbeck Beds, but the *C. psocus* hindwing may be reliably associated with the *Cercopidium telesphorus* tegmen: both are collected by Rev. Peter Brodie from the same site and strata and agree in the size, the shape more elongated than in other genera, and some venation features (long distal forks, MP and CuA both arched backwards basally).

Cicadellium psocus Westwood, 1854

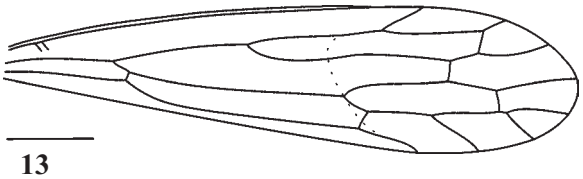
Cicadellium psocus: Westwood 1854: 394.
Cercopidium telesphorus: Westwood 1854: 394, **syn.n.**
Homopterulum telesphorus: Handlirsch 1906–8: 642.

MATERIAL. Holotype hindwing NHM I.11957 (nearly complete, costal margin poorly preserved); right tegmen (lacking base and clavus; holotype of *Cercopidium telesphorus*) on the slab NHM I.3968± (containing also holotypes of *Pterinoblattina pluma* (Giebel, 1856) and *Pteromixanum purbeckianum* (Handlirsch, 1906)); Brodie coll.; Durlston Bay, Swanage, Dorset, England; Middle Purbeck, Durlston Formation, Lowermost Cretaceous (Upper Berriasian).

DESCRIPTION (Figs 12–15). Tegmen 6.7 mm long and 1.8 mm wide (as preserved), very elongate (ca 3.7:1), broadest about midlength, acutely rounded at apex. Precostal carina very narrow (hypocostal one concealed in rock matrix); costal margin nearly straight proximally. Basal cell shorter than 1/3 of tegmen. R fork about halfway between arculus and M fork, radial space at R fork wider than either costal or medial one. M stem subparallel to RA and RP. *ir* near apex of pterostigmal cell; *rm* beyond midlength of medial cell. M fork rather symmetrical, medial cell elongate. M branches beyond *im* short, MP forked beyond *im*. MP+CuA1 about as long as CuA1 beyond it. CuA stem close to CuP. Surface proximally rather deeply and densely punctate, especially in radial space, distally only along veins. Tegmen proximally darkened, with pale regular patches along costal margin, few spots on veins, and two large rounded spots at M stem (beyond arculus and before fork), distally slightly infuscate, veins near margin (especially dSc and CuA branches) and crossveins dark.

Hindwing 6.5 mm long, rather elongate (ca 2.3:1), apical cells very long. Apical margin sinuate at CuA2. Basal cell wide, closed with arculus. R forked just before 1/2 wing length; RA not much shorter than RP. M and CuA forked about 5/8 wing length, M somewhat earlier; 1st section of MA straight, 1st section of MP arched backwards. Crossvein *mcu* at about 1/5 CuA1 length, *rm* more distal. MA and MP distally subparallel, RA and RP nearly so, all curved forwards. CuA1 diverging from MP and converging to CuA2

12



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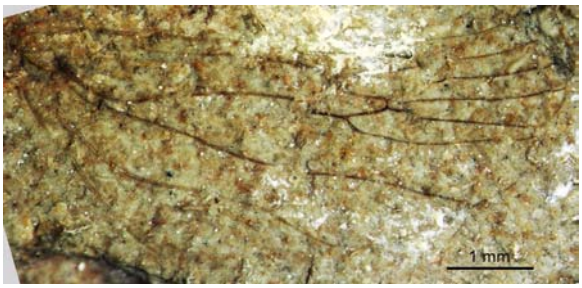

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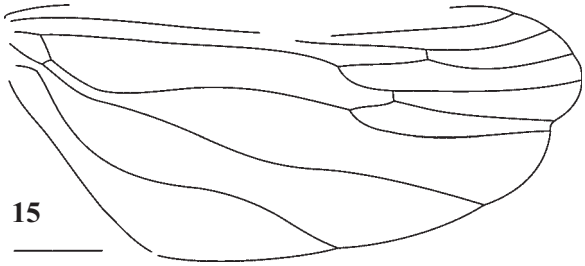

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Figs 12–15. *Cicadellium psocus* Westwood, 1854, Durlston Bay, Lowermost Cretaceous: 12–13 — specimen NHM I.3968 (holotype of *Cercopidium telesphorus* Westwood, 1854), tegmen; 14–15 — holotype NHM I.11957, hindwing (14 — mirror image); 12, 14 — © The Natural History Museum, London.

Рис. 12–15. *Cicadellium psocus* Westwood, 1854, Durlston Bay, базальный мел: 12–13 — экз. NHM I.3968 (голотип *Cercopidium telesphorus* Westwood, 1854), переднее крыло; 14–15 — голотип NHM I.11957, заднее крыло (14 — перевёрнуто зеркально); 12, 14 — © Музей естественной истории, Лондон.

from *mcu* up to marginal sinus (apices of CuA1 and CuA2 nearly meet); CuA2 arched proximally, straight distally. M stem arched forwards distally, running close to R proximally. CuA stem deeply sigmoidal, arched close to CuP basally; CuP slightly wavy; Pcu moderately sigmoidal, proximally widely separated from 1A.

Dellasharinae Shcherbakov, **subfam.n.**

TYPE GENUS. *Dellashara* **gen.n.**

DIAGNOSIS. Tegmen: costal space narrow; CP short; R and M leaving basal cell separately; crossvein *mcu* replaced with anastomosis; 6–8 full-sized apical cells (MP+CuA1 with 2–4 branches); 1–3 subapical cells (sometimes radiomedial one open and radial one merged with next apical cell). Hindwing: 5 full-sized apical cells (RA long; MP completely fused to CuA1). Large inflated postclypeus extends onto crown. Three close-set ocelli on crown. Antennal flagellum setiform. Hind coxae transverse, together occupying entire width of metathorax. Hind tibia not flared at apex, with well-developed macrosetae lacking prominent bases.

COMPOSITION. Type genus from Upper Jurassic of Asia, and 4 genera from Lower Cretaceous of Eurasia: *Acocephalites* Meunier, 1904, *Homopterulum* Handlirsch, 1907, *Mesoccus* Zhang, 1985, and *Myangadina* Shcherbakov, 1986.

Dellashara Shcherbakov, **gen.n.**

TYPE SPECIES. *Dellashara tega* **sp.n.**

DIAGNOSIS. Tegmen: R fork distal; dSc moderately oblique; *ir* absent and *rm* single (one subapical cell); arculus short; MP+CuA1 short; 6–7 apical cells. Hindwing: posterior apical cell (CuA fork) narrowed apically.

COMPARISON. In the other genera assigned, R fork more proximal (R stem subequal to 1st section of RA), dSc long and slanting, *ir* and at least weak additional *rm* at M fork present (three subapical cells), and MP+CuA1 longer in tegmen, and posterior apical cell not narrowed apically in hindwing.

COMPOSITION. Monobasic.

ETYMOLOGY. The genus and species are named from the genus *Cicadella* and Shar Teg; gender feminine.

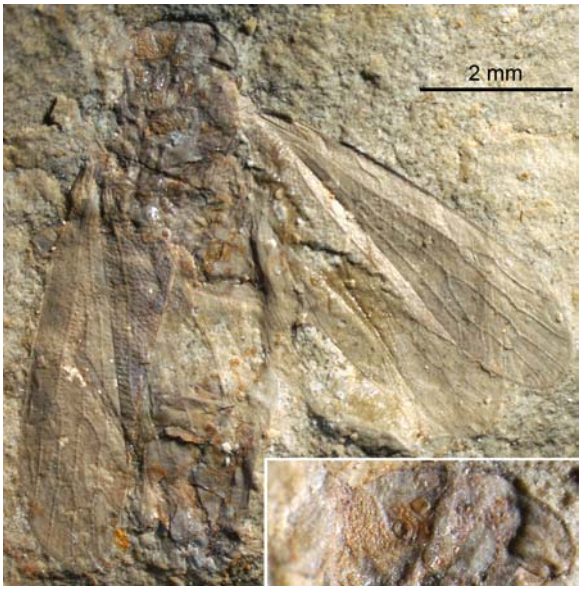
Dellashara tega **sp.n.**

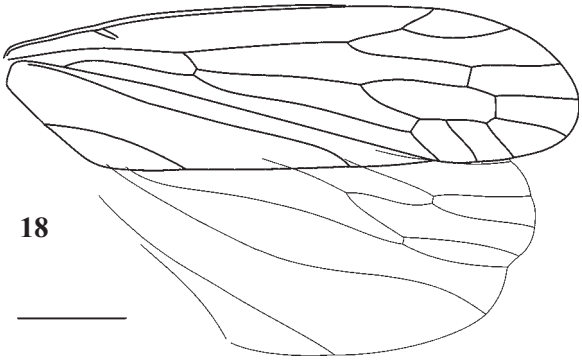
MATERIAL. Holotype male PIN 4270/811±; S of Shar Teg mt, SW of Aj Bogd Uul range, SW Mongolia; Shar Teg Sequence, Upper Jurassic.

DESCRIPTION (Figs 16–18). Tegmen 5.3 mm long and 1.5 mm wide, quite elongate (ca 3.5:1), broadest about midlength, acutely rounded at apex. Precostal and hypocostal carinae very narrow; costal margin nearly straight proximally. Basal cell as long as 1/3 of tegmen. Arculus shorter than 1st section of M stem. R fork just before M fork, so that R stem ca. 4 times as long as 1st section of RA (before dSc); radial space at R fork about as wide as costal space and wider than medial one. *rm* beyond midlength of medial cell. M fork rather symmetrical, medial cell elongate. M branches beyond *im* short, MP forked before *im*. 6–7 apical cells (MP+CuA1 with 2 branches in left tegmen and 3 branches in right tegmen). CuA stem not close to CuP. Clavus densely, shallowly punctate; remigium punctate mainly along veins and at base of costal space. Tegmen darkened, more so in costal space and especially in clavus. Hindwing 4.4 mm long and ca 2.0 mm wide, rather elongate (ca 2.2:1). Apical margin sinuate at CuA2. RA not much shorter than RP. M forked about 3/5 wing length, CuA about 3/4 wing length (just before *rm*). 1st section of MA sigmoidal, 1st section of MP straight. RA and RP distally subparallel, MA and MP+CuA1 nearly so; MP+CuA1 and CuA2 diverging and then slightly converging. Posterior apical cell widest about midlength. M stem distally curved; CuA stem, CuP and Pcu moderately sigmoidal. Pcu proximally separated from 1A. Hindwing suffused. Body 7.4 mm long, dark (especially head, pronotum, and genitalia). Head ca 1.7 mm wide, in dorsal aspect with prominent eyes; crown transverse (ca 2.2:1) with anterior margin truncate, rounded towards eyes. Ocelli close-set, lateral ocelli separated by distance slightly greater than their diameter; median ocellus smaller than lateral ones. Pronotum ca 1.9 mm wide, 1.3 mm long, weakly transverse (ca 1.5:1), rounded hexagonal, covering mesonotum except for small apical portion (0.3 mm long). Head and pronotum densely punctate. Hind legs slender, not much elongated, tibia (1.8 mm long) 1.2 times as long as femur (1.5 mm long); tibia with at least three longitudinal ribs; macrosetae of outer row relatively strong, about as long as tibia width, without prominent spine-like bases; macrosetae of inner and ventral rows much shorter, dark.

Discussion

The family Karajassidae was characterized [Shcherbakov, 1992] as the most primitive membracoids, retaining





Figs 16–18. *Dellashara tega* **sp.n.,** Shar Teg, Upper Jurassic, holotype PIN 4270/811, male: 16 — habitus, 17 — head in dorsal aspect; 18 — venation of right tegmen and hindwing.

Рис. 16–18. *Dellashara tega* **sp.n.,** Шар Тэг, верхняя юра, голотип ПИН 4270/811, самец: 16 — общий вид, 17 — голова сверху; 18 — жилкование правого переднего и заднего крыльев.

the median ocellus, primary segmentation of the antennal flagellum, the CP in the tegmen, and the hindwing with six full-sized apical cells and Pcu not joined to 1A. The karajassid characters shared with leafhoppers were all interpreted as correlated to improvement of jumping abilities and constituting the key apomorphy of Membracoidea ("leafhopper syndrome"): (i) hind coxae transversely enlarged, together occupying entire width of metathorax; (ii) hind femora and tibiae long (knees not concealed by tegmina, gliding over their costal margins); (iii) macrosetal rows on tibiae; (iv) tibial and tarsal apical pectens narrow; (v) costal margin of tegmen straightened; (vi) tegmen and remigial part of hindwing narrowed, with MP+CuA1 anastomosis. It was tacitly assumed that short-legged leafhoppers and treehoppers are not as good at jumping, and their hopping abilities have somewhat decreased secondarily.

Some facts on living membracoids cast doubt on this hypothesis. First, the long hind legs of leafhoppers with rows of tibial macrosetae are designed not only for jumping, but also (and perhaps more importantly) for distributing brochosomes over the body and tegmina through anointing and grooming behaviours. Brochosomes (microgranules produced in the Malpighian tubules) are found only in Cicadellidae; anointing behaviour is also observed in Membracidae [Rakitov, 1996, 1998, 2009, 2011].

Second, leafhoppers with shorter hind legs, like *Ulopa,* achieve similar take-off velocities and accelerate their bodies even more quickly than long-legged leafhoppers, such as *Cicadella,* but these latter have lower ground reaction forces and may jump better from less stiff substrates, such as leaves [Burrows & Sutton, 2008]. Both long- and short-legged ones are proficient hoppers, but the former are better in leaf-hopping, and the latter in stem- and tree-hopping (most treehoppers are short-legged).

Therefore, most if not all characters of the leafhopper syndrome (including (vii) surface sculpture of the body and tegmina reduced, and possibly (i) hind coxae differently shaped for more elaborate hind leg movements), can be interpreted as adaptations to manipulating brochosomes rather than to jumping, suggesting that Karajassinae already coated their integuments with these or related secretory particles.

Archijassinae, formerly placed in Cicadellidae or in or near Hylicellidae, remain insufficiently known; there are no data on their head and leg structure. They are undoubtedly ancestral to karajassines, being very similar in the fore and hind wing venation but showing none of the leafhopper syndrome characters, and therefore they were placed in Hylicelloidea as a subfamily of Hylicellidae [Shcherbakov, 1992]. The oldest, Middle Jurassic genera of Karajassinae described above nearly fill the gap between this group and Archijassinae, and this latter may be diagnosed only by the broader costal space with deeply arched costal margin in the tegmen. It seems reasonable to include both groups as subfamilies of the family Archijassidae within Membracoidea.

The Early Cretaceous genera assigned herein to Dellasharinae **subfam.n.** were previously mentioned as forming an unnamed group of at least subfamily rank, intermediate between karajassids and cicadellids. They were provisionally placed in Cicadellidae on account of the setiform antennal flagellum, three subapical cells in the tegmen, MP completely fused to CuA1 in the hindwing, and the long and stout tibial macrosetae. At the same time, these genera are more primitive than all living membracoids as indicated by the presence of five apical cells (due to long RA) and free Pcu and 1A in the hindwing [Shcherbakov, 1992]. The number of ocelli in these genera is still unknown.

The discovery of three close-set ocelli in Late Jurassic *Dellashara* **gen.n.** (the structure of the antennal flagellum in this genus is unknown) confirms that the Late Mesozoic membracoids with five apical cells in the hindwing were much more primitive than Cicadellidae and should be placed closer to Karajassinae. *Dellashara* **gen.n.** differs from the four Early Cretaceous genera (that resemble each other so closely that a revision is needed to confirm that some of them are not synonyms) in many tegminal characters, and no intermediates have been discovered so far. Despite this, we unite all five genera

under one subfamily and imply that it is homogeneous in the head structure, because the difference between tegmina of the type genus and other dellasharines is of the same nature and magnitude as between e.g. *Kisa* **gen.n.** and *Cicadellium,* this latter gap bridged by other genera of Karajassinae. (If no such intermediates are eventually found for Dellasharinae, it may mean that this group is diphyletic and that *Dellashara* and the Early Cretaceous genera had acquired the hindwing MP fused to CuA1 independently.)

At present we include Archijassinae, Karajassinae, and Dellasharinae **subfam.n.,** representing three successive stages of the early membracoid evolution, into one family Archijassidae. To elucidate the systematic position of Late Cretaceous *Jascopus* (based on a nymph) and Early Cretaceous Paracarsonini assigned to Jascopidae, further studies of Cretaceous Membracoidea are needed.

"Leafhopperization", i.e. successive acquisition of membracoid characters in the Archijassinae → Karajassinae → Dellasharinae → Cicadellidae lineage, was a long process spanning about a hundred million years. In the following list, these characters are arranged by the time of their first appearance in the fossil record:

– M with 3 branches (7 apical cells) in tegmen: *Triassojassus* — T3;
– arculus rather long in tegmen: *Triassojassus* — T3;
– Pcu and 1A proximally very close in hindwing: *Archijassus* etc. — J1;
– additional *rm* (3 subapical cells) in tegmen: *Ardela, Mesoledra* — J1;
– short MP+CuA1 anastomosis in hindwing: *Archijassus* — J1;
– narrow costal space and straight costal margin in tegmen: *Kubecola, Kisa* — J2;
– reduced surface sculpture of tegmen: *Kubecola, Kisa* — J2;
– hind tibiae with rows of macrosetae, in outer row on spine-like bases: *Kubecola* — J2;
– hind coxae transversely enlarged: *Karajassus* — J3, presumably J2, possibly earlier;
– MP2 completely fused to CuA1 (6 apical cells) in tegmen: *Dellashara* — J3;
– MP completely fused to CuA1 (5 apical cells) in hindwing: *Dellashara* — J3;
– hind tibiae with rows of long and stout macrosetae: *Dellashara* — J3;
– antennal flagellum setiform: *Myangadina, Mesoccus* — K1, presumably J3;
– RA short (4 full-sized apical cells) in hindwing: *Hallex* etc. — K1;
– MP completely fused to CuA1 (5 apical cells) in tegmen: *Hallex* etc. — K1;
– Pcu and 1A fused for some distance in hindwing — K1;
– two ocelli: *Hallex* etc. — K1.

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