Russian Entomol. J. 30(2): 129–134

New Curvicubitidae and Paraknightiidae (Homoptera: Cicadomorpha) from the Triassic of Central Asia

Новые Curvicubitidae и Paraknightiidae (Homoptera: Cicadomorpha) из триаса Средней Азии

Dmitry E. Shcherbakov
Д.Е. Щербаков

Borissiak Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya St. 123, Moscow 117647, Russia. E-mail: dshh@narod.ru
Палеонтологический институт им. А.А. Борисяка РАН, ул. Профсоюзная 123, Москва 117647, Россия.

KEY WORDS: Hemiptera, Auchenorrhyncha, Pereborioidea, Palaeontinoidea, Scytinopteroidea, Heteroptera, true bugs, forewing, hemelytron, venation, nodal line, phylogeny, fossil, relict, Lagerstätte, Madygen.

КЛЮЧЕВЫЕ СЛОВА: Hemiptera, Auchenorrhyncha, Pereborioidea, Palaeontinoidea, Scytinopteroidea, Heteroptera, клопы, переднее крыло, гемиэлитра, жилкование, нодальная линия, филогения, ископаемые, реликт, лагерштетт, Мадыген.

ABSTRACT. Three new species and one new genus of Cicadomorpha are described from the Middle or Upper Triassic of Madygen, Kyrgyzstan. The family Curvicubitidae includes one genus, *Beaconiella* Evans, 1963 (= *Curvicubitus* Hong, 1984, **syn.n.**; *Beaconiella triassica* (Hong, 1984), **comb.n.**). The wing venation of *Beaconiella pulchra* **sp.n.** and closely related *B. cincta* **sp.n.** confirms that this family belongs to Pereborioidea, despite some similarities with Palaeontinoidea. *Triknightia mira* **gen.** et **sp.n.** (Scytinopteroidea: Paraknightiidae) combines the heteropterous forewing structure and folding with the homopterous head structure. This is the first Mesozoic find of Paraknightiidae, representing an early side branch near the root of true Heteroptera. The head structure is first described for paraknightiids, and the clavus and hindwing for curvicubitids — their hindwing bears a row of hooks instead of coupling lobe. Curvicubitidae and *Triknightia* **gen.n.** are the last relics of the Permian groups Pereborioidea and Paraknightiidae in the Triassic fauna, and both taxa are highly advanced compared to their Permian relatives.

РЕЗЮМЕ. Три новых вида и новый род Cicadomorpha описаны из среднего или верхнего триаса Мадыгена в Киргизии. Семейство Curvicubitidae включает единственный род *Beaconiella* Evans, 1963 (= *Curvicubitus* Hong, 1984, **syn.n.**; *Beaconiella triassica* (Hong, 1984), **comb.n.**). Жилкование *Beaconiella pulchra* **sp.n.** и близкого *B. cincta* **sp.n.** подтверждает принадлежность семейства к Pereborioidea, несмотря на отдельные признаки сходства с Palaeontinoidea. *Triknightia mira* **gen.** et **sp.n.** (Scytinopteroidea: Paraknightiidae) приобрёл характерное для клопов строение и складывание передних крыльев, но сохранил характерное для равнокрылых строение головы. Это первая мезозойская находка семейства, представляющего собой раннюю боковую ветвь у корня настоящих Heteroptera. Впервые описывается строение головы паранайтиид и клавуса и заднего крыла курвикубитид, последнее на месте сцепочной лопасти несёт ряд крючков. Curvicubitidae и *Triknightia* **gen.n.** — последние реликты пермских групп Pereborioidea и Paraknightiidae в триасовой фауне, и оба таксона сильно продвинуты по сравнению со своими пермскими родичами.

The famous fossil site near the village of Madygen in Kyrgyzstan has yielded the world's richest Triassic insect fauna, unusual tetrapods, fishes, crustaceans, bivalves, plants etc. [Voigt et al., 2016]. The Madygen Formation, dated to Ladinian–Carnian based on megaflora, crops out in five adjacent areas, and the outcrop richest in insects is Dzhailoucho in the northern area. Twenty insect orders and more than one hundred families (including twenty families of Homoptera) have been recorded, and more than half a thousand species described from these beds [Shcherbakov, 2008].

John W. Evans [1963] described the genus *Beaconiella* from the Middle Triassic (Anisian) Hawkesbury Sandstone of Beacon Hill, Australia in Fulgoroidea incertae familiae. Hong [1984] described the genus *Curvicubitus* and the family Curvicubitidae from the Middle Triassic (latest Ladinian) Tongchuan Forma-

How to cite this article: Shcherbakov D.E. 2021. New Curvicubitidae and Paraknightiidae (Homoptera: Cicadomorpha) from the Triassic of Central Asia // Russian Entomol. J. Vol.30. No.2. P.129–134. doi: 10.15298/rusentj.30.2.02

tion of Shaanxi, China and tentatively assigned it to Lepidoptera. Shcherbakov [1984, 1996] transferred *Beaconiella* first to Palaeontinoidea incertae familiae, and then to Curvicubitidae assigned to Pereborioidea. Two closely related new species of Curvicubitidae from the Triassic of Madygen are described below.

Evans [1943, 1950] described the genus *Paraknightia* from the uppermost Permian (Changhsingian) of Lake Macquarie, Australia in Ipsviciidae (Auchenorrhyncha), and later separated this genus into the family Paraknightiidae and transferred to Heteroptera. Shcherbakov [1984, 1996, 2000] moved this family back to Auchenorrhyncha, included the genus *Tychticola* Becker-Migdisova, 1952 from the Upper Permian (Wuchiapingian) of Kuznetsk Basin, Siberia, assigned the family to Scytinopteroidea (Cicadomorpha), and considered this superfamily ancestral to the true bugs. A peculiar new genus of Paraknightiidae from the Triassic of Madygen is described below.

The new Triassic genus of Paraknightiidae acquired the structure and folding of forewings similar to that of Heteroptera, but retained the head structure of primitive Cicadomorpha and was phytophagous and phytophilous, presumably cryptic on plants. On the contrary, the earliest heteropterans are thought to be zoophagous, living on the ground in the littoral zone [Shcherbakov, Popov, 2002]. Likewise the family Curvicubitidae acquired some similarities to the Mesozoic superfamily Palaeontinoidea (e.g. well-developed nodal line, proximal MP running along it, blind vein branches in M area), but demonstrates more important similarities to other (Permian) Pereborioidea (extremely prolific venation of tegmen and hindwing, including numerous, slanting to longitudinal branches of distal Sc, etc). Apparently, both the Triassic paraknightiid genus and curvicubitids are unsuccessful attempts to construct a true bug and a large, moth-like cicada, respectively, which were soon replaced by their better-adapted counterparts — Heteroptera and Palaeontinoidea (both known since the Middle Triassic).

The material is deposited at Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow (PIN). Photographs were taken using a Leica M165C stereomicroscope with a Leica DFC425 digital camera. Scanning electron images of uncoated specimens were obtained with TESCAN VEGA microscope using backscattered electron detector. The vein nomenclature is after Shcherbakov [1984, 1996, 2011]. The clayey rock matrix at Dzhailoucho is linearly distorted, so that some specimens are extended lengthwise and others crosswise. A more accurate size estimate for fossils thus deformed is the square root of length x width ($\sqrt{LW}$).

Infraorder Cicadomorpha Evans, 1946

Superfamily Pereborioidea M.Zalessky, 1930

Family Curvicubitidae Hong, 1984

REVISED DIAGNOSIS. Medium-sized polyneurous cicadas. Tegmina shallowly tectiform in repose, with distinct nodal line, fuscous with pale spots and sometimes subtransverse bands; distal vein branches very numerous and closely parallel, crossveins sparse. Tegmen: Costal margin deeply arched at base; precostal carina narrow. Sc fused with RA near base for short distance, then running not far from RA (rarely Sc completely free). Distal Sc and RA with many slanting branches. Basal cell narrow, tapered to apex, RP separating not far from it. RA and RP curved and M forked at nodal line, the line forming angle at M bifurcation; proximal MP section long, subtransverse, arched distad, running along nodal line nearly to sharp bend of CuA; branches of MP and CuA usually forming one bunch; medial and anterior cubital areas and discal cell broad. CuP arched forwards distally. Claval veins converging, distally forked and connected by crossveins, but not forming Y-vein. Narrow marginal membrane beyond apex of clavus. Blind veins running distally from proximal MP and scutellar margin of clavus, and backwards from CuA stem. Membrane finely punctate, more heavily near base; veins granulate, especially in pterostigmal area. Hindwing wide; anterior margin at base deeply arched, near midlength shallowly sinuate and with series of hooks in place of coupling lobe. Sc free, running close to RA, with faint slanting branches; RA with longitudinal posterior branches; R forked close to basal cell; RA, RP and M forked before nodal level, CuA concave, straight, with posterior branches; anal area rather narrow.

COMPOSITION. *Beaconiella* Evans, 1963 (= *Curvicubitus* Hong, 1984, **syn.n.**).

REMARKS. Evans [1963] described *Beaconiella* with two species, *B. multivenata* Evans, 1963 based on a complete insect with tegmina 21 mm long, and *B. fennahi* Evans, 1963 (type species) based on the wing 17 mm long interpreted as a hindwing. However, the photo of the latter specimen published by Jell [2004: 64] leaves no doubt that it is a tegmen quite similar to those of two new species described below.

Hong [1984] described *Curvicubitus* with one species, *C. triassicus* Hong, 1984 based on the distal two thirds of a tegmen, 15 mm long as preserved (implying the tegmen length ca. 23 mm). A part of pterostigmal area with one slanting Sc branch visible on the original photo was not figured by Hong [1984]. Based on venation of the preserved part, *Curvicubitus* is considered a synonym of *Beaconiella*. According to Article 40.1 of the 4th edition of ICZN [ICZN, 1999], when the type genus of a family is synonymized under another genus, the family name is not replaced on that account.

Beaconiella Evans, 1963

Beaconiella: Evans, 1963: 21.

Curvicubitus: Hong, 1984: 783, **syn.n.**

TYPE SPECIES. *Beaconiella fennahi* Evans, 1963.

DIAGNOSIS. As for family.

COMPOSITION. *Beaconiella fennahi* Evans, 1963, *B. multivenata* Evans, 1963, *B. triassica* (Hong, 1984), **comb.n.**, and two new species described below.

REMARKS. *B. multivenata* is possibly synonymous with *B. fennahi*, because their tegmina agree in many essential characters [see photograph of the latter in Jell, 2004], and their difference in size is only x1.24, so that they may represent two sexes of one species (see below).

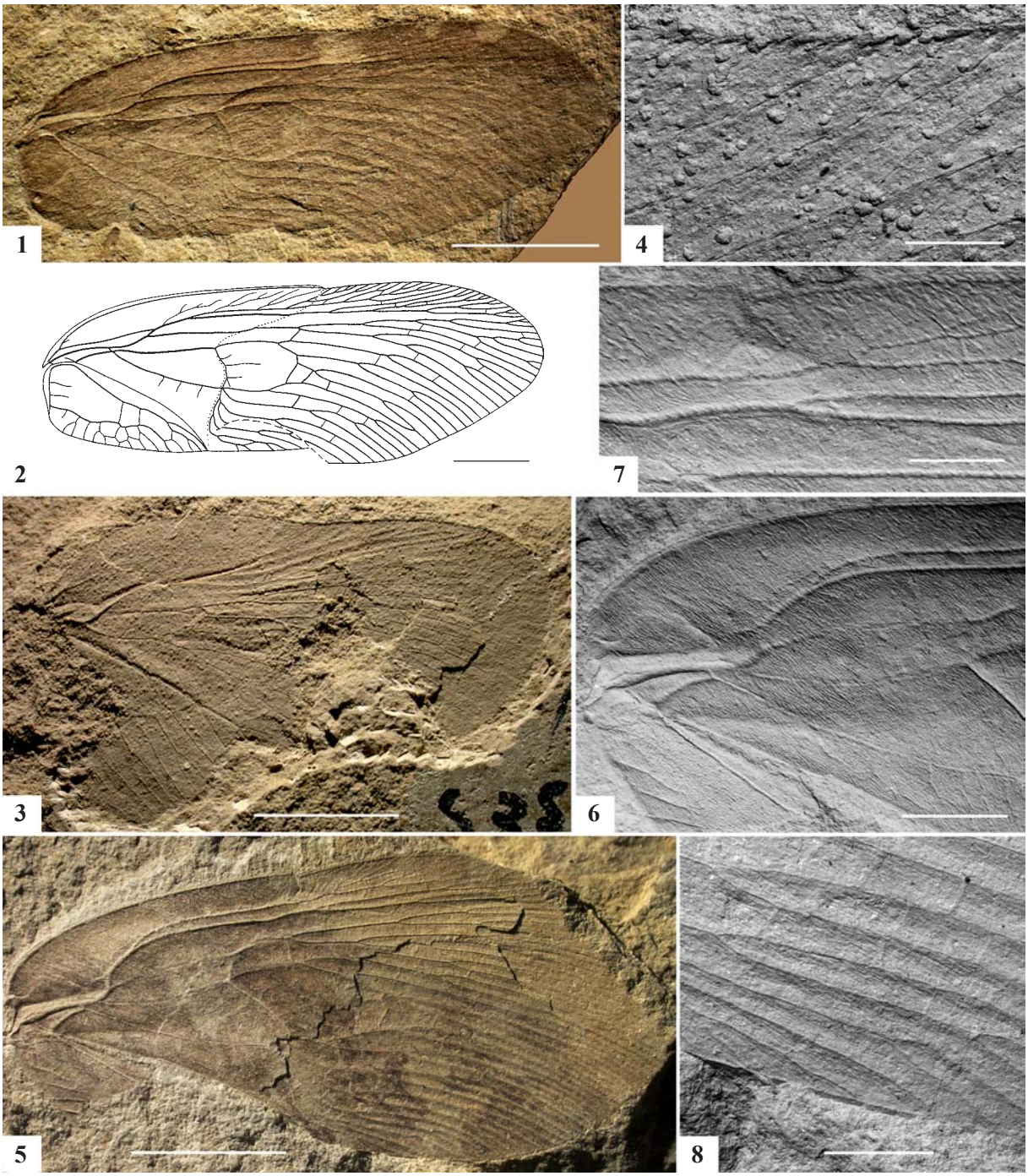
Beaconiella pulchra Shcherbakov, **sp.n.**

Figs 1–4.

MATERIAL. Holotype: tegmen PIN 2785/3022(3073)±. Paratypes: tegmina PIN 2240/4643(4679)±, 2555/2360, 2368(2386)±, 2429, 2908, 2785/3387(3893)±, 3405; hindwing PIN 2555/2320±;

Dzhailoucho (Madygen, northern area), Leilek District, Batken Region, SW Kyrgyzstan; Madygen Formation, Ladinian–Carnian.

DESCRIPTION. Tegmen 12.9–19.4 mm long, 6.7–9.1 mm wide (19.4 x 7.1 mm in holotype), variation exaggerated by rock distortion; √LW 9.3–11.8 mm (x1.27). Interradial area about as wide as radial area. RP and MA forks distant from nodal line. Proximal MP section (along nodal line) feebly arched, distal MP section (from nodal line to fork)



Figs 1–8. *Beaconiella* spp., Madygen, Triassic: 1–4 — *B. pulchra* **sp.n.**: 1–2 — holotype tegmen; 3–4 — paratype hindwing PIN 2555/2320 (images mirrored): 3 — hindwing; 4 — coupling hooks along costal margin, SEM; 5–8 — *B. cincta* **sp.n.**, holotype tegmen: 5 — tegmen; 6–8 — SEM: 6 — proximal part of tegmen; 7 — nodus (note granules on veins); 8 — CuA branches (note marginal membrane). Scale bars: 1, 3, 5 — 5 mm, 2 — 3 mm, 4 — 0.5 mm, 6 — 2 mm, 7–8 — 1 mm.

Рис. 1–8. *Beaconiella* spp., Мадыген, триас: 1–4 — *B. pulchra* **sp.n.**: 1–2 — переднее крыло, голотип; 3–4 — заднее крыло, паратип ПИН 2555/2320 (перевернуто зеркально): 3 — заднее крыло; 4 — сцепочные крючки по костальному краю, СЭМ; 5–8 — *B. cincta* **sp.n.**, переднее крыло, голотип: 5 — переднее крыло; 6–8 — СЭМ: 6 —проксимальная часть крыла; 7 — нодус (видны зёрна на жилках); 8 — ветви CuA (видна периферическая мембрана). Длина масштабных линеек: 1, 3, 5 — 5 мм, 2 — 3 мм, 4 — 0.5 мм, 6 — 2 мм, 7–8 — 1 мм.

rather long, sigmoidal, straight or arched backwards, MP1 arched forwards. CuA branches sigmoidal, in middle part subparallel to posterior wing margin. RP, M and CuA altogether with 30–35 terminations. Tegmen fuscous, especially at base and anteriorly, with small pale streaks along costal margin, 2–3 larger markings in pterostigmal area, and pale spots at nodus, on M stem, before crossvein *im*, and at base of CuA branches. Not only the sequence of distal branching and the number of terminations of all main veins are variable (as is usual in polyneurous wings), but also the degree of Sc+RA fusion (up to completely free Sc in paratypes 2555/2360, 2785/3405) and the structure of the apex of basal cell: M separating from R at or slightly beyond arculus (in smaller tegmina) or fused with CuA at a very short distance in place of arculus (in larger tegmina). Hindwing 17.4 mm long, 10.4 mm wide; RA, RP, M and CuA forked about same level.

COMPARISON. Similar to *Beaconiella fennahi* and *B. multivenata*, but in these latter the interradial area is much wider than the radial area, and the RP and MA forks are close to the nodal line. Distinct from incompletely known *B. triassica* in smaller size and structure of MP and CuA: in the latter species, the proximal MP section is deeper arched, the distal one is very short, and CuA branches converge with the posterior wing margin.

ETYMOLOGY. Latin *pulcher* (beautiful, lovely).

Beaconiella cincta Shcherbakov, **sp.n.**
Figs 5–8.

MATERIAL. Holotype tegmen PIN 2785/3107(3381)±. Paratypes: tegmina PIN 2555/2192(2866)±, 3514(3642)±; hindwing PIN 2240/2931; Dzhailoucho (Madygen, northern area), Leilek District, Batken Region, SW Kyrgyzstan; Madygen Formation, Ladinian–Carnian.

DESCRIPTION. Tegmen ~22–26 mm long, 9.9–11 mm wide (~22 x 9.9 mm in holotype), variation exaggerated by rock distortion; √LW 14.8–16.7 mm (x1.13). Tegmen fuscous with large pale streaks along anterior margin and two incomplete oblique pale bands — just before nodal line and from nodus towards tornus. Interradial area about as wide as radial area. MA fork and usually RP fork distant from nodal line. RP, M and CuA altogether with 45–50 terminations. Branches of MP and CuA sometimes not forming one bunch. Hindwing 23.1 mm long, 10.0 mm wide; RA, RP and M forked about same level, CuA more distally.

COMPARISON. Very similar to *B. pulchra*, but larger, with more prolific venation and well developed pale bands. Differences from the Australian species are the same as in *B. pulchra*. Distinct from *B. triassica* in the richer and denser distal venation and sigmoidal CuA branches in the tegmen: in the latter species, RP, M and CuA altogether have about 30 terminations, and CuA branches converge with the posterior wing margin.

REMARKS. The difference in size between *B. cincta* and *B. pulchra* seems too great to be explained only by sexual dimorphism in size within the same species. For example, in the modern archaic cicadoid *Tettigarcta tomentosa* White, 1845 the tegmen length in the largest females is only x1.28 greater than in the smallest males [Moulds, 1990]. Secular fluctuations in average size within one species also seem unlikely, because both the largest *B. cincta* tegmen and the smallest *B. pulchra* tegmen were collected by the same field party in 1965, presumably from the same layer.

ETYMOLOGY. Latin *cinctus* (girded).

Superfamily Scytinopteroidea Handlirsch, 1906

Family Paraknightiidae Evans, 1950

DIAGNOSIS. Rather small, dorsoventrally depressed hoppers with well-developed pronotal paranota. Tegmina heavily sclerotized, punctate, folded nearly flat in repose and at least slightly overlapping distally. Tegmen: Basal cell very long, tapered near apex, closed with long basal section of M and short arculus; subcostal arc reduced. RA either very long, longitudinal, with dSc separating far from its base, or subtransverse and parallel to dSc and RP branches; dSc weakly convex. More than one *r-m* crossvein. Transverse groove at nodal level rudimentary or absent, M straight there and connected with CuA (or CuA1) by crossvein. Clavus with convex stripe along commissural margin. Survace densely punctate, sometimes except smooth posterodistal part.

COMPOSITION. *Paraknightia* Evans, 1943, *Tychticola* Becker-Migdisova, 1952, *Triknightia* **gen.n.**

Triknightia Shcherbakov, **gen.n.**

TYPE SPECIES. *Triknightia mira* **sp.n.**

DIAGNOSIS. Strongly flattened, pronotal paranota and anterior part of head broadly foliaceous, eyes remote from anterior head margin. Head and mouthparts homopterous: rostrum adpressed to body venter, clypeus and lora situated posterior to eyes. Tegmina transformed into hemielytra: their distal parts (membrane) broadly overlapping in repose, wide, membranous, smooth, veinless, sharply separated from sclerotized, veined, punctate proximal parts (corium). Oblique costal fracture inserted between faint anterior branches of pectinate R distal to claval apex. More than two *r-m* crossveins.

COMPOSITION. Type species.

COMPARISON. In hypertrophied paranota and overlapping membranized posterodistal parts of tegmina, similar to *Paraknightia*, but in the latter tegmina are tapered beyond claval apex, their overlapping parts are narrow and not clearly separated, the transverse costal fracture is situated near the apex of basal cell before R branches, and there are two *r-m* crossveins.

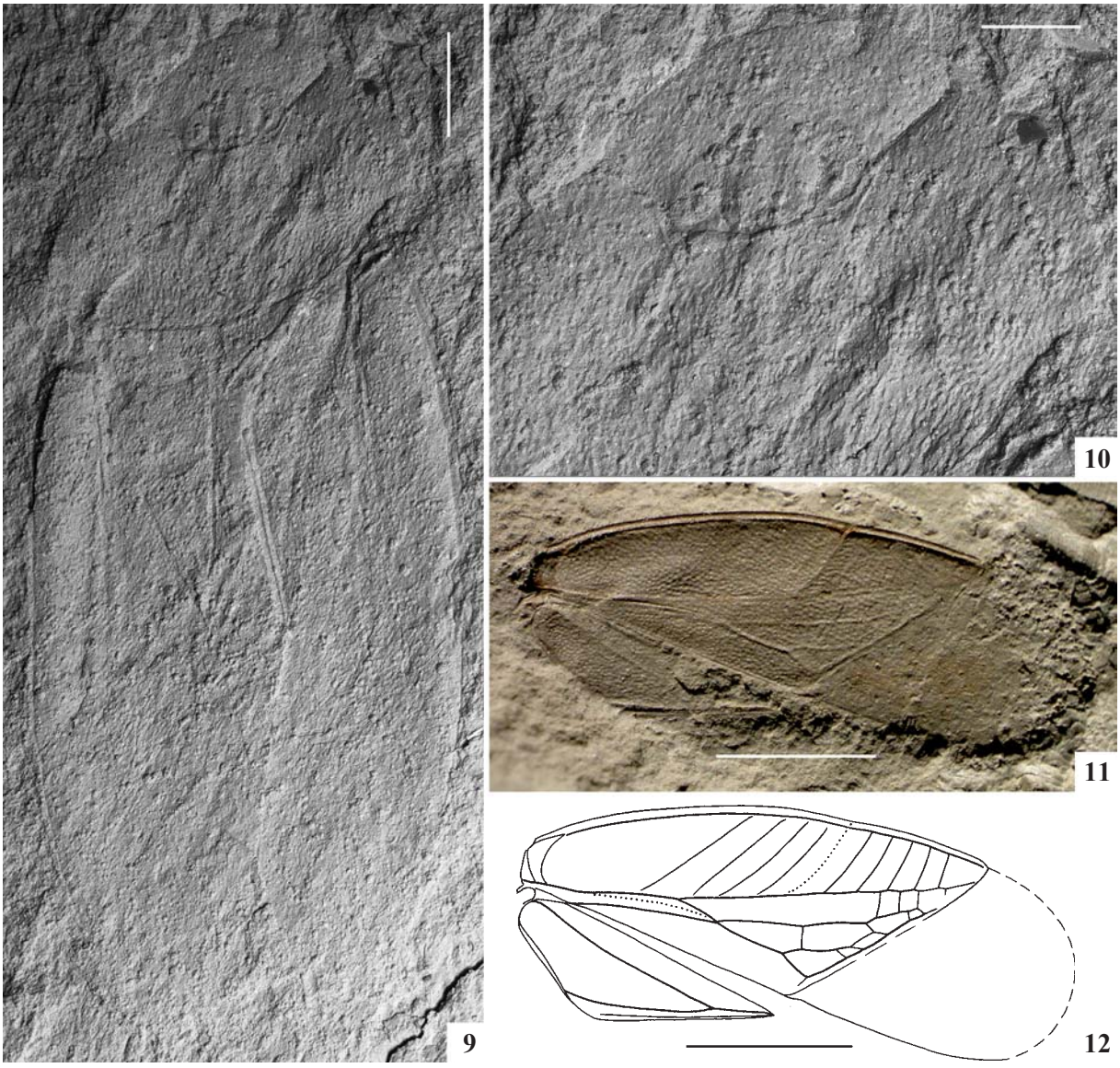
ETYMOLOGY. From Triassic and *Paraknightia*; gender feminine.

Triknightia mira Shcherbakov, **sp.n.**
Figs 9–12.

MATERIAL. Holotype PIN 2069/3278±, complete insect, Dzhailoucho (Madygen, northern area). Paratype PIN 2083/244±, tegmen, Madygen (western area); Leilek District, Batken Region, SW Kyrgyzstan; Madygen Formation, Ladinian–Carnian.

DESCRIPTION. Body with folded hemielytra 9.6 mm long, 3.8 mm wide, hemielytron 6.9 mm long (holotype); paratype hemielytron 7.1 mm long, 2.3 mm wide (3.1:1). Head quarter circle in plane, foliaceous in anterior 1/2 radius; eyes small, ovoid; clypeus plus lora twice wider than eye. Pronotum low U-shaped, posterior margin arched medially, truncate laterally; paranota wide with arched lateral margins. Mesonotum low triangular, rostrum traceable beyond it. Dorsum finely minutely punctate-areolate. Hemielytron: Costal margin truncate at base, shallowly arched beyond; basal extension of costal carina reaching R+M; costal area at level of claval apex nearly as wide as remaining corium. Basal cell 1/3 hemielytron length, or 3/4 clavus length, with long medial fracture; free M base very long. R stem running nearly to apex of corium. M and CuA with small triangular forks. Anterior cubital area wide. Clavus almost 1/2 hemielytron length, claval veins uniting at 3/4 clavus length.

ETYMOLOGY. Latin *mirus* (wonderful, strange).



Figs 9–12. *Triknightia mira* **gen.** et **sp.n.**, Madygen, Triassic: 9–10 — holotype, SEM: 9 — whole insect; 10 — head and pronotum; 11–12 — paratype hemielytron (mirrored); dotted line, costal and medial fractures. Scale bar: 9 — 1 mm, 10 — 0.5 mm, 11–12 — 2 mm.

Figs 9–12. *Triknightia mira* **gen.** et **sp.n.**, Мадыген, триас: 9–10 — голотип, СЭМ: 9 — насекомое целиком; 10 — голова и переднеспинка; 11–12 — паратип, гемиэлитра (перевернута зеркально); пунктиром — костальный и медиальный надломы. Длина масштабной линейки: 9 — 1 мм, 10 — 0.5 мм, 11–12 — 2 мм.

Acknowledgements. I am greatly indebted to Lian Xinneng (Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences) for his prompt assistance with the literature and to Roman Rakitov (PIN) for his generous help with SEM imaging. The study was supported by the Russian Science Foundation (project 21-14-00284).

References

Evans J.W. 1943. Upper Permian Homoptera from New South Wales // Rec. Aust. Mus. Vol.21. P.180–198.

Evans J.W. 1950. A re-examination of an Upper Permian insect, *Paraknightia magnifica* Ev. // Rec. Aust. Mus. Vol.22. P.246–250.

Evans J.W. 1963. The systematic position of the Ipsviciidae (Upper Triassic Hemiptera) and some new Upper Permian and Middle Triassic Hemiptera from Australia (Insecta) // Aust. J. Entomol. Vol.2. P.17–23.

Hong You-chong 1984. Curvicubitidae fam. nov. (Lepidoptera? Insecta) from Middle Triassic of Shaanxi // Acta Palaeontol. Sin. No.6. P.782–785, 815.

International Commission of Zoological Nomenclature, 1999. The International Code of Zoological Nomenclature. 4th Edition. London: The International Trust for Zoological Nomenclature. xxix+306 pp.

Jell P.A. 2004. The fossil insects of Australia // Mem. Qld Mus. Vol.50. P.1–124. https://doi.org/10.1082/j.2204-1478.50-1.2004.2004.01

Moulds M.S. 1990. Australian Cicadas. Kensington: N.S.W. University Press. x+217 pp.

Shcherbakov D.E. 1984. System and phylogeny of Permian Cicadomorpha (Cimicida, Cicadina) // Paleontological Journal. Vol.18. No.2. P.87–97.

Shcherbakov D.E. 1996. Origin and evolution of the Auchenorrhyncha as shown by the fossil record // C.W. Schaefer (ed.). Studies on Hemipteran Phylogeny. Lanham (Maryland): Entomological Society of America. P.31–45.

Shcherbakov D.E. 2000. Permian faunas of Homoptera (Hemiptera) in relation to phytogeography and the Permo-Triassic crisis // Paleontological Journal. Vol.34. Suppl.3. P.S251–S267.

Shcherbakov D.E. 2008. Madygen, Triassic Lagerstätte number one, before and after Sharov // Alavesia. No.2. P.113–124.

Shcherbakov D.E. 2011. New and little-known families of Hemiptera Cicadomorpha from the Triassic of Central Asia — early analogs of treehoppers and planthoppers // Zootaxa. Vol.2836. P.1–26 https://doi.org/10.11646/zootaxa.2836.1.1.

Shcherbakov D.E., Popov Yu.A. 2002. Order Hemiptera Linné, 1758. The bugs, cicadas, plantlice, scale insects, etc. // Rasnitsyn A.P., Quicke D.L.J. (eds.). History of Insects. Dordrecht: Kluwer. P.143–157.

Voigt S., Buchwitz M., Fischer J., Kogan I., Moisan P., Schneider J.W., Spindler F., Brosig A., Preusse M., Scholze F., Linnemann U. 2016. Triassic life in an inland lake basin of the warm-temperate biome — the Madygen Lagerstätte (southwest Kyrgyzstan, Central Asia) // Fraser N.C., Sues H.-D. (eds.). Terrestrial Conservation Lagerstätten — Windows into the Evolution of Life on Land. Edinburgh: Dunedin. P.65–104.