

New Homoptera from the Early Cretaceous of Buryatia with notes on the insect fauna of Khasurty

Новые Homoptera из раннего мела Бурятии с замечаниями по энтомофауне Хасурты

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КЛЮЧЕВЫЕ СЛОВА: Hemiptera, Auchenorrhyncha, Cicadomorpha, Hylicellidae, Sternorrhyncha, Psyllomorpha, Liadopsyllidae, переднее крыло, птеростигма, нодальная линия, филогения, ископаемые, водные насекомые, наземные насекомые, тли, реликты, древнее озеро, дождевой лес умеренного климата.

ABSTRACT. *Reticycla drosopoulovi* **gen. et sp.n.** from the Early Cretaceous of Khasurty, Buryatia is described in Hylicellidae Vietocyclinae (Cicadomorpha). The genus *Jiphara* Ren, 1995 from the Early Cretaceous of China is transferred from Pereboriidae to Vietocyclinae. *Stigmapsylla klimaszewskii* **gen. et sp.n.**, *Liadopsylla (Basicella) lautereri* **subgen. et sp.n.** and *L. (B.) loginovae* **sp.n.** from Khasurty are described in Liadopsyllidae s. str. (Psyllomorpha). Free CuA base and nodal line are first reported in forewings of Mesozoic Psylloidea. Two species from Cretaceous ambers are transferred from *Liadopsylla* to *Cretapsylla* **gen.n.**: *C. apedetica* (Ouvrard, Burckhardt et Azar, 2010) **comb.n.**, *C. hesperia* (Ouvrard et Burckhardt, 2010) **comb. n.** Семейство Malmopsyllidae восстановлено из синонимии с Liadopsyllidae и разделено на Malmopsyllinae, **stat.n.** и Miralinae **subfam.n.** (для рода *Mirala* Burckhardt et Poinar, 2020 из бирманского янтаря). Кратко обсуждаются комплекс насекомых и другие ископаемые находки из Хасурты, а также возраст и среда обитания этой фауны.

передних крыльях мезозойских Psylloidea. Два вида из меловых янтарей перенесены из *Liadopsylla* в *Cretapsylla* **gen.n.**: *C. apedetica* (Ouvrard, Burckhardt et Azar, 2010) **comb.n.**, *C. hesperia* (Ouvrard et Burckhardt, 2010) **comb. n.** Семейство Malmopsyllidae восстановлено из синонимии с Liadopsyllidae и разделено на Malmopsyllinae, **stat.n.** и Miralinae **subfam.n.** (для рода *Mirala* Burckhardt et Poinar, 2020 из бирманского янтаря). Кратко обсуждаются комплекс насекомых и другие ископаемые находки из Хасурты, а также возраст и среда обитания этой фауны.

In 2003, Olga Minina and Andrey Filimonov (Geological Institute, Siberian Branch, RAS) discovered a new Late Mesozoic locality of insects and other fossils near the Khasurty (Hasurtyi) River, SW Buryatia and donated the insect fossils to the Paleontological Institute RAS (PIN). Field parties of the Arthropoda Lab (PIN) visited this site in 2004, 2009, 2014 and 2019 and collected about 7000 total insects along with other plant and animal fossils. Several taxa from Khasurty were described in Bryophyta [Ignatov, Shcherbakov, 2011; Mamontov, Ignatov, 2019], Cladocera [Kotov, 2009], Coleoptera [Legalov, 2010; Gratshev, Legalov, 2014; Strelnikova, 2019], Plecoptera [Sinitshenkova, 2011], Hymenoptera [Kopylov, 2011; Kopylov, Rasnitsyn, 2014; etc.], Diptera [Blagoderov, Lukashevich, 2013; Lukashevich et al., 2020; etc.], Ephemeroptera [Sinitshenkova, 2017], Neuroptera [Khranov, 2018], and Trichoptera [Ponomarenko et al., 2009; Sukatsheva, Vasilenko, 2019]. However, the

РЕЗЮМЕ. *Reticycla drosopoulovi* **gen. et sp.n.** из раннего мела местонахождения Хасурты, Бурятия, описан в Hylicellidae Vietocyclinae (Cicadomorpha). Род *Jiphara* Ren, 1995 из раннего мела Китая перенесён из Pereboriidae в Vietocyclinae. *Stigmapsylla klimaszewskii* **gen. et sp.n.**, *Liadopsylla (Basicella) lautereri* **subgen. et sp.n.** и *L. (B.) loginovae* **sp.n.** из Хасурты описаны в Liadopsyllidae s. str. (Psyllomorpha). Свободное основание CuA и нодальная линия впервые отмечены в

rich and peculiar biota of Khasurty is still insufficiently studied. The entomofauna of Khasurty and its age are discussed below.

The Khasurty insect assemblage is numerically co-dominated by phantom midges (Chaoboridae) and their aquatic immatures, as well as winged adult aphids. Homoptera other than aphids are rather rare and moderately diverse. The more numerous of them are primitive Peloridioidea (Karabasiidae), primitive Cicadomorpha (Hylcellidae), and Psyllomorpha, whereas other Auchenorrhyncha families are less common. A new genus of Hylcellidae, belonging to the Jurassic–Early Cretaceous subfamily Vietocyclinae, and a new genus and a new subgenus of the psyllomorph Jurassic–Cretaceous family Liadopsyllidae are described below from Khasurty.

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 micrographs of uncoated specimens were obtained with TESCAN VEGA microscope using backscattered electron detector.

Infraorder Cicadomorpha Evans, 1946

Family Hylcellidae Evans, 1956

Subfamily Vietocyclinae Shcherbakov, 1988

REVISED DIAGNOSIS. Tegmen: several postnodal R branches arising from RA and sometimes from dSc; at least 2 *r-m* crossveins; at least 4 terminations of M; M fused with CuA beyond basal cell in one point or for a short distance. Hind wing: *ir* crossvein absent; RP and M usually fused for a distance in place of *r-m* crossvein (rarely *r-m* developed); at least 3 terminations of M; CuA2 proximally arched posteriad, distally converging with CuA1. Postclypeus large, swollen, with transverse muscle impressions. Antennal flagellum thick,

segmented. Pronotum covering entire mesonotum except for scutellum, transversely striate.

COMPOSITION. *Cycloscytina* Martynov, 1927, *Vietocycla* Shcherbakov, 1988, *Jiphara* Ren, 1995, *Reticycla* **gen.n.**

DISTRIBUTION. Jurassic and Early Cretaceous of Asia.

Reticycla Shcherbakov, **gen.n.**

TYPE SPECIES: *Reticycla drosopoulovi* Shcherbakov, **sp.n.**

DIAGNOSIS. Distinct from the other genera in the M in tegmen fused with CuA for a short distance beyond the basal cell (in one point in other genera), basal cell strongly tapered towards apex, and 2–3 (or 1 forked) postnodal R branches arising from dSc (0 or rarely 1 branch on dSc in *Vietocycla* and *Cycloscytina*, 4 or more in *Jiphara*). Similar to *Cycloscytina* and distinct from *Vietocycla* in the fore legs not modified, and the ovipositor almost not extending beyond the tip of abdomen and no longer than the width of tegmen (the body structure is unknown in *Jiphara*).

COMPOSITION. Type species.

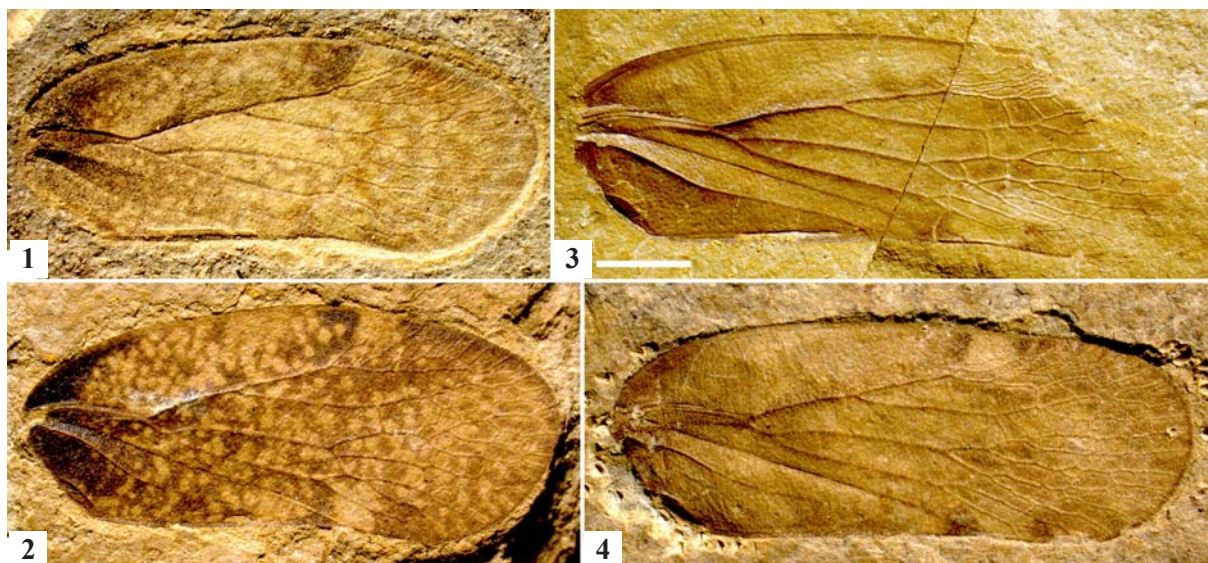
ETYMOLOGY. From Latin *retia* (net) and *cyclus* (ring); gender feminine.

Reticycla drosopoulovi Shcherbakov, **sp.n.**

Figs 1–12.

MATERIAL. Holotype tegmen PIN 5026/2134±; paratypes: tegmina PIN 5026/2133±, 5340/516±, 1356±; hind wing PIN 5340/1349; females PIN 5340/521, 1355; Khasurty, 10 km S of Tsakir, Zakamensk district, SW Buryatia, Russia; Lower Cretaceous.

DESCRIPTION. Tegmina 10.8–12.5 mm long, more or less elongate (2.4–2.9:1). Costal margin arched evenly or more so near base. Basal cell strongly tapered distally and deflected posteriad from longitudinal axis of tegmen (CuA base arched). Prenodal R branches faint. Branches of RA with 9–10, RP with 4–5, M with 4–8, CuA with 3–4 terminations, all these together with 22–26 terminations and about twenty or more crossveins. Tegmina with distinct colour pattern: pale, dark-margined markings at anterior and posterior nodus, and either small pale spots on dark background or darkened main vein stems on pale background; base of tegmen darkened. Hind wing about 10 mm



Figs 1–4. *Reticycla drosopoulovi* **gen. et sp.n.**, tegmina; Khasurty, Lower Cretaceous: 1 — holotype; 2–4 — paratypes PIN (photographs mirrored): 2 — 5340/1356; 3 — 5026/2133; 4 — 5340/516. Scale bar 2 mm for all figures.

Рис. 1–4. *Reticycla drosopoulovi* **gen. et sp.n.**, передние крылья; Хасурты, нижний мел: 1 — голотип; 2–4 — паратипы ПИН (фото перевернуты зеркально): 2 — 5340/1356; 3 — 5026/2133; 4 — 5340/516. Длина масштабной линейки 2 мм для всех рис.

long, *r-m* developed, M with 3 terminations, CuA2 characteristically bent. Female body 11.3–13.0 mm long. Postclypeus large, much inflated, with transverse muscle impressions. Antenna length subequal to head height; flagellum of about ten elongate segments, proximal 4 times, distal 3 times as long as wide. Pronotum with anterolateral depressions, in posterior zone with rough transverse striae. Fore legs apparently not modified. Hind tibiae slender, with minute widely spaced lateral teeth and apical pecten. Ovipositor almost not extending beyond tip of abdomen, no longer than tegmen width; inner valvulae with serrate section near apex.

VARIATION. Of the four isolated tegmina, two are slightly shorter, less elongate, darker and pale-speckled (holotype and PIN 5340/1356), and two others are a bit longer, more elongate and paler with reduced speckled pattern (PIN 5026/2133, 5340/516). The degree of the costal margin convexity, number of postnodal R branches on dSc, position of M fork, relative length of the postnodal part and development of pale areas are also somewhat variable. By analogy with *Vietocyclus peregrina* Shcherbakov, 1988, showing sexual dimorphism in size and colour pattern of tegmina, I tentatively consider all the specimens as representing the two sexes of *R. drosopoulovi*. Another possibility is colour polymorphism, as in some spittlebugs and leafhoppers [Drosopoulos et al., 2010; Tishechkin, 2012].

ETYMOLOGY. To the memory of a Greek expert in Auchenorrhyncha, Sakis Drosopoulos (1944–2014).

Infraorder Psyllomorpha Becker-Migdisova, 1962

Superfamily Psylloidea Latreille, 1807

Family Liadopsyllidae Martynov, 1927, s.str.

REVISED DIAGNOSIS. Forewing: Costal space elongate, usually ribbon-like. M forked; CuA fork triangular, CuA2 not recurrent or very short. R bifurcation at $<1/3$, R+M+CuA bifurcation at $<1/5$ wing length. Pterostigma usually present, but often poorly developed.

COMPOSITION. *Liadopsylla* Handlirsch, 1921, *Stigmapsylla* Shcherbakov, **gen.n.**, *Cretapsylla* Shcherbakov, **gen.n.**

DISTRIBUTION. Jurassic and Cretaceous of Eurasia and North America.

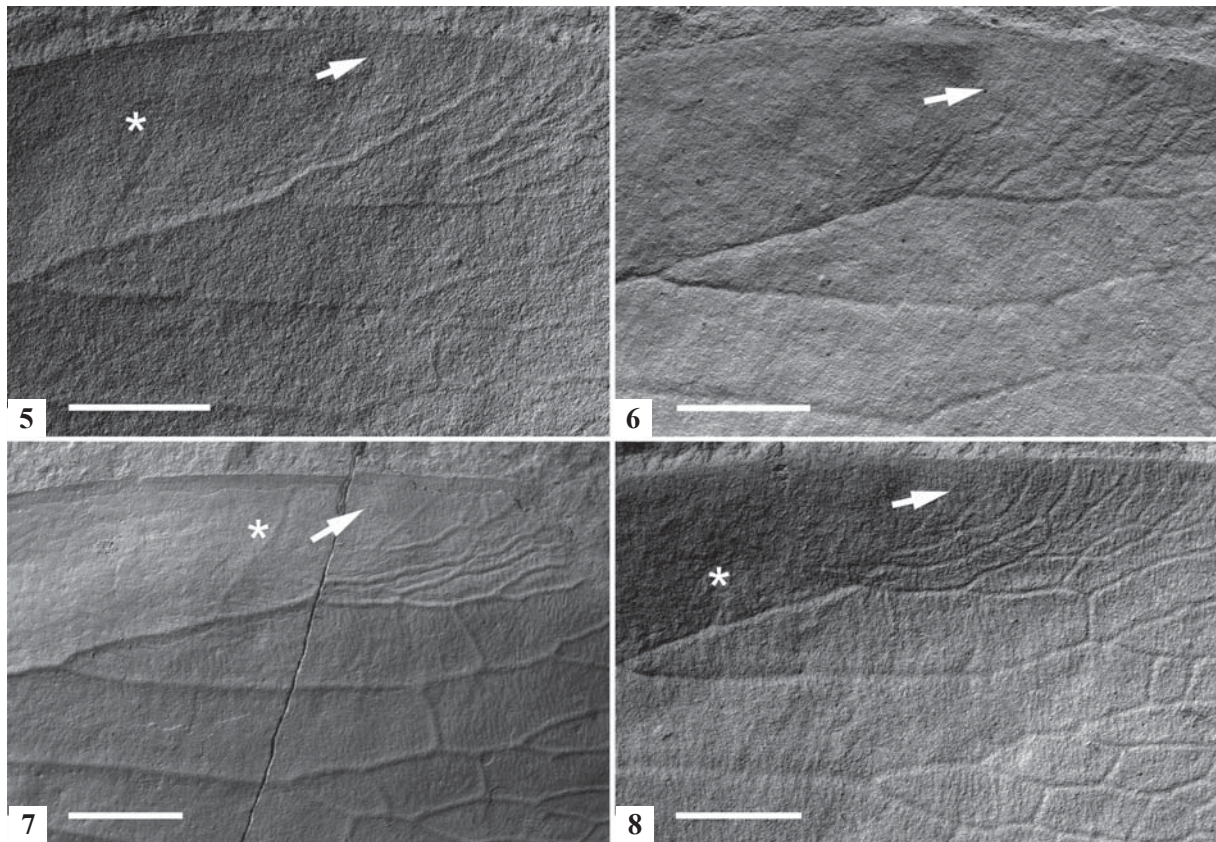
Stigmapsylla Shcherbakov, **gen.n.**

TYPE SPECIES: *Stigmapsylla klimaszewskii* Shcherbakov, **sp.n.**

DIAGNOSIS. Distinct from the other genera in the combination of well-developed, dark pterostigma, markedly arched costal margin, and basally narrow R fork in the forewing.

COMPOSITION. Type species.

ETYMOLOGY. From Greek *stigma* (mark, spot) and the generic name *Psylla*; gender feminine.



Figs 5–8. *Reticycla drosopoulovi* **gen. et sp.n.**, nodal area of tegmen, SEM; Khasurty, Lower Cretaceous: 5 — holotype; 6–8 — paratypes PIN (images mirrored): 6 — 5340/1356; 7 — 5026/2133; 8 — 5340/516; arrow — dSc; asterisk — prenodal R branch. Scale bars 1 mm in all figures.

Рис. 5–8. *Reticycla drosopoulovi* **gen. et sp.n.**, нодальная область переднего крыла, СЭМ; Хасурты, нижний мел: 5 — голотип; 6–8 — паратипы ПИН (изображения перевёрнуты зеркально): 6 — 5340/1356; 7 — 5026/2133; 8 — 5340/516; стрелка — dSc; звёздочка — пренодальная ветвь R. Длина масштабной линейки 1 мм на всех рис.

Stigmopsylla klimaszewskii Shcherbakov, **sp.n.**

Fig. 13.

MATERIAL. Holotype forewing (incomplete at RP apex) and underlying hind wing PIN 5340/1378±; Khasurty, 10 km S of Tsakir, Zakamensk district, SW Buryatia, Russia; Lower Cretaceous.

DESCRIPTION. Forewing 2.8 mm long, rather elongate (2.3:1), widened up to before nodus, narrowly rounded apically. Nodal line absent. Costal margin arched, more deeply in the middle; costal space moderately wide (4.8:1). Pterostigma distinct, subtriangular, with sharp, anteriorly recurrent basal boundary. R+M+CuA dividing before 1/5, R stem before 1/4, and M+CuA about 1/3 wing length. R fork basally narrow, with nearly straight RA and proximal RP. M+CuA stem thrice longer than R stem and slightly longer than R+M+CuA. M stem equal to M2 and x1.6 as long as CuA stem, M fork wide (2.4:1). CuA1 x1.6 as long as CuA stem and x4 as CuA2. Clavus rather wide, with arched posterior margin; Pcu+1A distally not running along the margin and joining it near clavus apex. Veins and pterostigma dark, membrane pale. Hind wing delicate, much shorter and narrower than forewing, R–RA and CuA are visible.

ETYMOLOGY. To the memory of a Polish expert in psyllids, Sędzimir Maciej Klimaszewski (1937–2001).

Liadopsylla Handlirsch, 1921

TYPE SPECIES: *Liadopsylla geinitzi* Handlirsch, 1921

REVISED DIAGNOSIS. Forewing: Costal margin feebly and/or evenly convex; costal space elongate, more or less ribbon-like. R fork not very narrow basally. M stem nearly straight or feebly curved; CuA stem at most twice shorter than

M+CuA stem. Pterostigma usually present, but poorly developed, slightly darkened, sometimes its base marked with slight bend of RA and its posterior margin with groove.

COMPOSITION. Two subgenera, nominate and *Basicella* **subgen.n.**

REMARKS. The publication date for the genus is 1921, not 1920 or 1925 as stated in some papers, because the part 3 of Band 3 of Handlirsch [1920–1921] containing p. 213 with the genus and type species name and illustration was printed in 1921. The detailed description appeared in Handlirsch [1939].

Basicella Shcherbakov, **subgen.n.**

TYPE SPECIES: *Liadopsylla (Basicella) lautereri* Shcherbakov, **sp.n.**

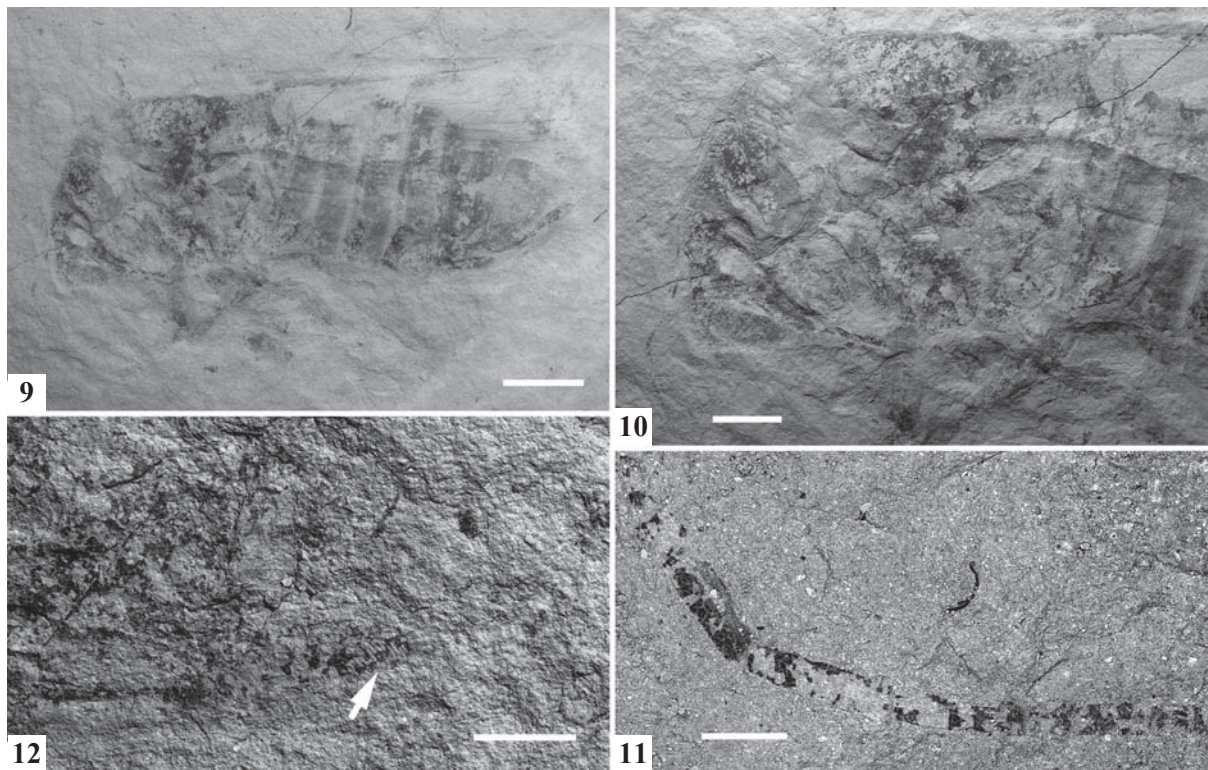
DIAGNOSIS. Distinct from the other liadopsyllids in the well-developed free CuA base joining R+M at a distance from its apex and separating a small triangular basal cell in the forewing; in one of two described species a nodal line is present (free CuA base, basal cell and nodal line were not previously reported in Liadopsyllidae).

COMPOSITION. Type species and *L. (B.) loginovae* Shcherbakov, **sp.n.**

ETYMOLOGY. From Latin *basis* (foundation, pedestal) and *cella* (chamber); gender feminine.

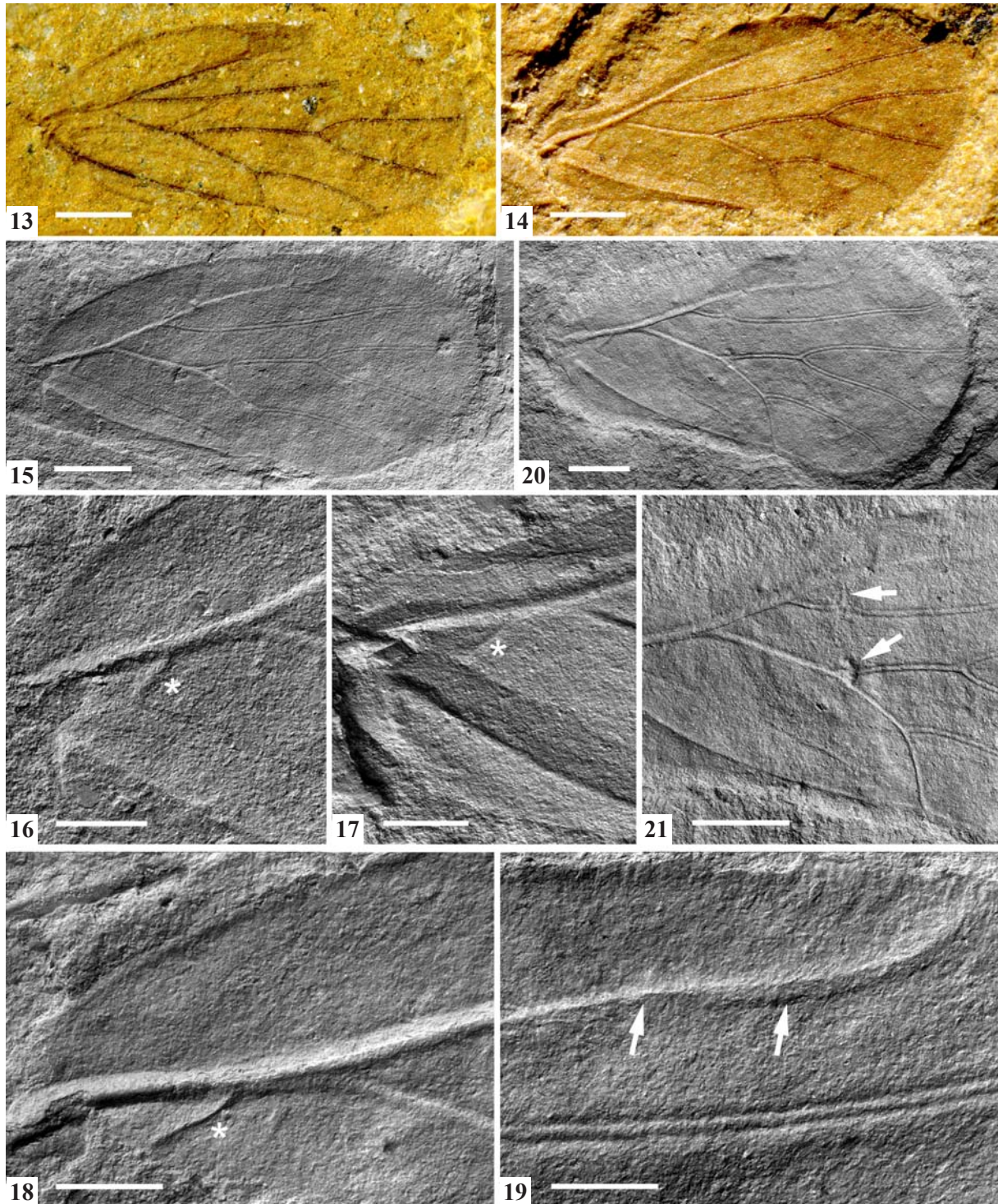
Liadopsylla (Basicella) lautereri Shcherbakov, **sp.n.**
Figs 14–19.

MATERIAL. Holotype forewing PIN 5340/1371±; paratype forewings PIN 5340/520, 1377±; paratype (sex unknown) PIN 5340/1498; Khasurty, 10 km S of Tsakir, Zakamensk district, SW Buryatia, Russia; Lower Cretaceous.



Figs 9–12. *Reticycla drosopouloshi* **gen. et sp.n.**, paratypes PIN, females, lateral view, SEM (images mirrored); Khasurty, Lower Cretaceous: 9–11 — 5340/521: 9 — body; 10 — head and thorax; 11 — antenna (apex not shown); 12 — 5340/1355, ovipositor (arrow — serrate section of inner valvulae). Scale bar: 9 — 2 mm, 10 — 1 mm, 11 — 0.2 mm, 12 — 0.5 mm.

Рис. 9–12. *Reticycla drosopouloshi* **gen. et sp.n.**, паратипы ПИН, самки, сбоку, СЭМ (изображения перевёрнуты зеркально); Хасурты, нижний мел: 9–11 — 5340/521: 9 — тело; 10 — голова и грудь; 11 — усик (вершина не показана); 12 — 5340/1355, яйцеклад (стрелка — пильчатый участок внутренних створок). Длина масштабной линейки: 9 — 2 мм, 10 — 1 мм, 11 — 0,2 мм, 12 — 0,5 мм.



Figs 13–21. Liadopsyllidae, forewings; Khasurty, Lower Cretaceous: 13 — *Stigmapsylla klimaszewskii* gen. et sp.n., holotype (photograph mirrored); 14–19 — *Liadopsylla (Basicella) lautereri* subgen. et sp.n.: 14, 17 — paratype PIN 5340/1377 (costal margin tucked under); 15–16 — holotype; 18–19 — paratype PIN 5340/520; 20–21 — *L. (B.) loginovae* sp.n., holotype (costal margin tucked under; images mirrored; arrows — *ir* crossvein and M break at nodal line); 15–21 — SEM; 16–18 — forewing base (asterisk — free CuA base); 19 — area of pterostigma (arrows — posterior boundary of pterostigma and RA bend at its base). Scale bar: 13–15, 20, 21 — 0.5 mm, 16–19 — 0.2 mm.

Рис. 13–21. Liadopsyllidae, передние крылья; Хасурты, нижний мел: 13 — *Stigmapsylla klimaszewskii* gen. et sp.n., голотип (фото перевёрнуто зеркально); 14–19 — *Liadopsylla (Basicella) lautereri* subgen. et sp.n.: 14, 17 — паратип ПИН 5340/1377 (костальный край подогнут); 15–16 — голотип; 18–19 — паратип ПИН 5340/520; 20–21 — *L. (B.) loginovae* sp.n., голотип (костальный край подогнут; изображения перевёрнуты зеркально; стрелки — поперечная жилка *ir* и разрыв М на нодальной линии); 15–21 — СЭМ; 16–18 — основание переднего крыла (звёздочка — свободное основание CuA); 19 — область птеростигмы (стрелки — задний край птеростигмы и изгиб RA в её основании). Длина масштабной линейки: 13–15, 20, 21 — 0,5 мм, 16–19 — 0,2 мм.

DESCRIPTION. Forewing 2.8–3.3 mm long, moderately elongate (2.0–2.1:1), widened up to apex of pterostigma, obliquely rounded apically, tornus inconspicuous. Nodal line absent. Costal margin evenly arched; costal space moderately wide. Pterostigma barely noticeable by darker, raised membrane and wider distal RA. R+M+CuA dividing before or at 1/5, R stem before 1/3, and M+CuA before 0.4 wing length. R fork moderately wide basally, acute with gently curved RA and proximal RP. RA x1.5 shorter than RP, curved forwards before apex; RP slightly sigmoidal distally. M+CuA stem x1.5–2.0 as long as R stem and slightly longer than R+M(+CuA). M stem somewhat shorter than (or equal to) M2 and x1.6–2.0 as long as CuA stem, M fork relatively short and wide (2.2–2.5:1). CuA1 x2.2–2.3 as long as CuA stem and x2.7–3.4 as CuA2. Clavus narrow, with concave posterior margin; Pcu+1A distally running along the margin and joining it near clavus apex. Veins dark, especially RP, M and CuA, membrane slightly darkened, more so around apex.

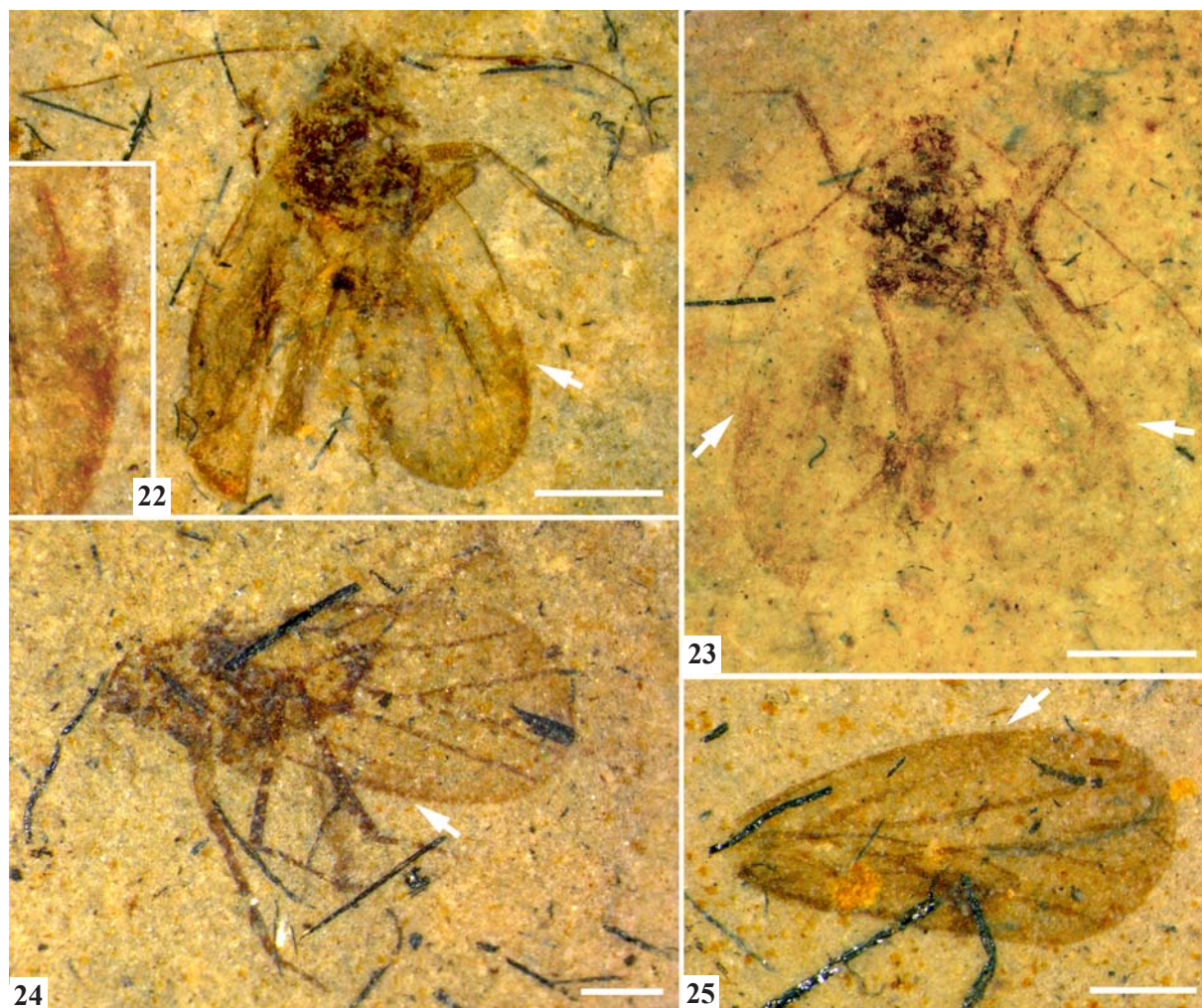
VARIATION. The largest forewing PIN 5340/520 with the base of pterostigma marked with a slight RA bend and its boundary with a groove posterior to RA (Fig. 19), and the M and CuA veins darker than in other specimens, may represent the female sex or another, closely similar species. In two other paratypes, the R stem is relatively shorter (about 1/2 of M+CuA stem) than in the holotype, and in one of them, M2 is equal to M stem and CuA2 short.

ETYMOLOGY. To the memory of a Czech expert in psyllids, Pavel Lauterer (1933–2016).

Liadopsylla (Basicella) loginovae Shcherbakov, **sp.n.**
Figs 20–21.

MATERIAL. Holotype forewing PIN 5340/2645±; Khasurti, 10 km S of Tsakir, Zakamensk district, SW Buryatia, Russia; Lower Cretaceous.

DESCRIPTION. Forewing 3.4 mm long, moderately elongate (2.0:1), widened up to apex of pterostigma, bluntly rounded apically, tornus well developed. Nodal line present,



Figs 22–25. *Liadopsylla* s. str.; Karatau, Middle-Upper Jurassic: 22 — *L. turkestanica* Becker-Migdisova, 1949, holotype (inset — area of pterostigma); 23 — *L. grandis* Becker-Migdisova, 1985, paratype PIN 2384/328; 24 — *L. asiatica* Becker-Migdisova, 1985, holotype (photograph mirrored); 25 — *L. brevifurcata* Becker-Migdisova, 1985, holotype forewing; arrow — pterostigma. Scale bar: 22–23 — 1 mm, 24–25 — 0.5 mm.

Figs 22–25. *Liadopsylla* s. str.; Карауай, средняя-верхняя юра: 22 — *L. turkestanica* Becker-Migdisova, 1949, голотип (врезка — область птеростигмы); 23 — *L. grandis* Becker-Migdisova, 1985, паратип ПИН 2384/328; 24 — *L. asiatica* Becker-Migdisova, 1985, голотип (фото перевёрнуто зеркально); 25 — *L. brevifurcata* Becker-Migdisova, 1985, голотип, переднее крыло; стрелка — птеростигма. Длина масштабной линейки: 22–23 — 1 мм, 24–25 — 0,5 мм.

with *ir* crossvein and RP bend not far from R fork, and break at base of M stem. Costal margin evenly arched; costal space moderately wide. Base of pterostigma marked with slight RA bend, and its boundary with groove posterior to RA. R+M+CuA dividing at 1/5, R stem at 1/3, and M+CuA at 0.4 wing length. R fork moderately wide basally, acute with gently curved RA. RA x1.5 shorter than RP, curved forwards before apex; RP slightly sigmoidal distally. M+CuA stem x1.7 as long as R stem and subequal to R+M(+CuA). M stem half as long as M2 and x1.5 as CuA stem, M fork long and wide (2.2:1). CuA1 nearly thrice longer than CuA stem or CuA2. Clavus relatively wide, with concave posterior margin; Pcu+1A distally running along the margin and joining it near clavus apex. Veins and membrane slightly darkened.

REMARKS. Distinct from the type species in the presence of nodal line with a supernumerary *ir* crossvein, longer M fork and blunt wing apex.

ETYMOLOGY. To the memory of a Russian expert in psyllids, Marianna M. Loginova.

Cretapsylla Shcherbakov, **gen.n.**

TYPE SPECIES: *Liadopsylla apedetica* Ouvrard, Burckhardt et Azar, 2010.

DIAGNOSIS. Distinct from the other genera in the CuA stem very short, 4–7 times shorter than M+CuA stem (at most twice shorter in other genera) and markedly curved M stem (feebly curved or nearly straight in other genera) in the

forewing. Similar to *Stigmopsylla* **gen.n.** in the very short R stem and basally narrow R fork, but differs from it in the more curved proximal RP and CuA1.

COMPOSITION. *C. apedetica* (Ouvrard, Burckhardt et Azar, 2010) **comb.n.**, *C. hesperia* (Ouvrard et Burckhardt, 2010) **comb.n.**

DISTRIBUTION. Early Cretaceous (Barremian) amber of Lebanon and Late Cretaceous (Turonian) amber of New Jersey.

ETYMOLOGY. From Cretaceous and the generic name *Psylla*; gender feminine.

Family Malmopsyllidae Becker-Migdisova, 1985

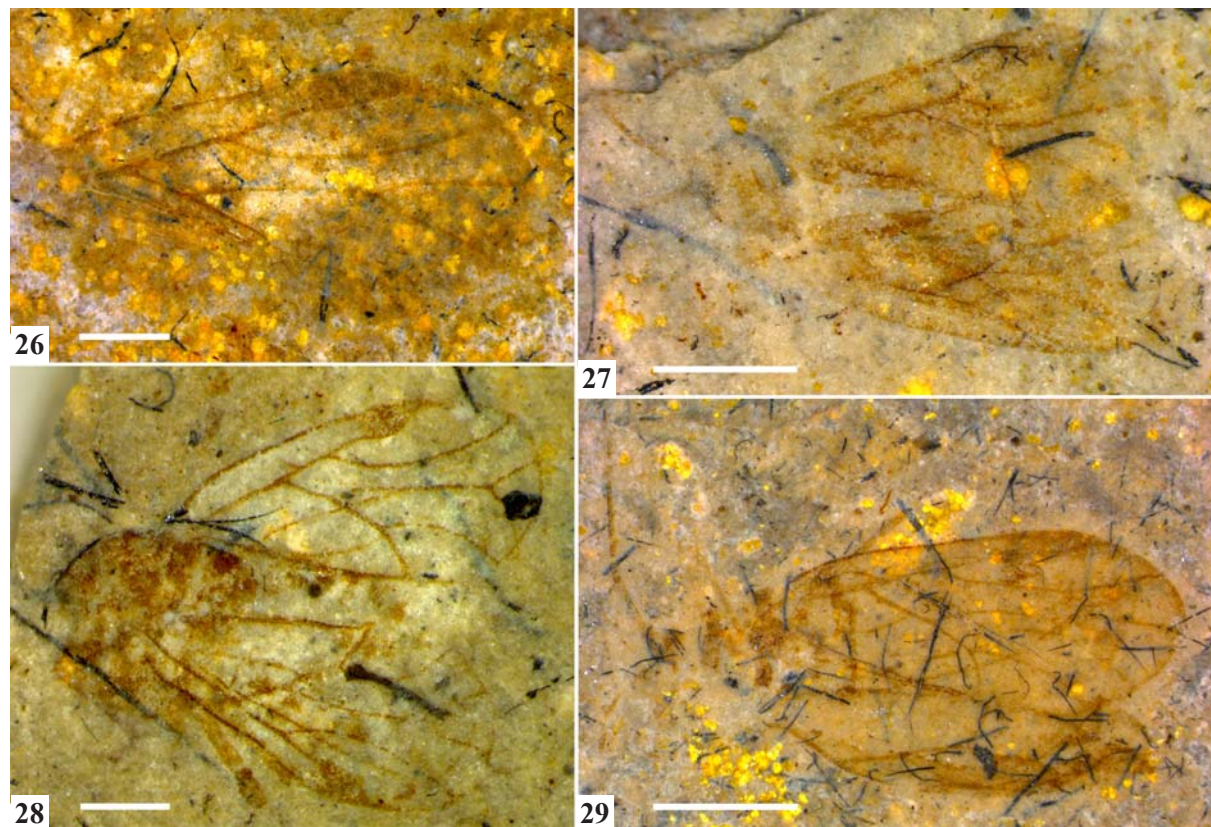
REVISED DIAGNOSIS. Forewing: Pterostigma distinct, dark; costal space widened proximally or distally. CuA2 rather long, sometimes recurrent. R bifurcation at >0.4, R+M+CuA bifurcation at >1/4 wing length.

COMPOSITION. Two subfamilies.

Subfamily Malmopsyllinae Becker-Migdisova, 1985, **stat.n.**

DIAGNOSIS. Forewing: Costal space not widened distally; M forked; CuA fork triangular, CuA2 long, not recurrent. R+M+CuA bifurcation at 1/4–1/3, R bifurcation at 0.4–0.5, M+CuA bifurcation at 0.35–0.5 wing length.

COMPOSITION. *Malmopsylla* Becker-Migdisova, 1985, *Neopsylloides* Becker-Migdisova, 1985, *Pauropsylloides*



Figs 26–29. Malmopsyllidae, holotypes; Karatau, Middle-Upper Jurassic: 26 — *Malmopsylla karatavica* Becker-Migdisova, 1985, forewing; 27 — *Neopsylloides turutanovae* Becker-Migdisova, 1985; 28 — *Pauropsylloides jurassica* Becker-Migdisova, 1985 (photograph mirrored); 29 — *Gracilinervia mastigmatoides* Becker-Migdisova, 1985. Scale bar: 26–27 — 1 mm, 28 — 0.5 mm, 29 — 2 mm.

Figs 26–29. Malmopsyllidae, голотипы; Каратау, средняя-верхняя юра: 26 — *Malmopsylla karatavica* Becker-Migdisova, 1985, переднее крыло; 27 — *Neopsylloides turutanovae* Becker-Migdisova, 1985; 28 — *Pauropsylloides jurassica* Becker-Migdisova, 1985 (фото перевернуто зеркально); 29 — *Gracilinervia mastigmatoides* Becker-Migdisova, 1985. Длина масштабной линейки: 26–27 — 1 мм, 28 — 0,5 мм, 29 — 2 мм.

Becker-Migdisova, 1985, *Gracilinervia* Becker-Migdisova, 1985 (Figs 26–29).

DISTRIBUTION. Middle-Late Jurassic of Kazakhstan.

Subfamily Miralinae Shcherbakov, **subfam.n.**

TYPE GENUS: *Mirala* Burckhardt et Poinar, 2020.

DIAGNOSIS. Distinct from the nominate subfamily in the apparently unforked M (M and CuA together with 3 branches), broad subquadragular CuA fork with long recurrent CuA₂, costal space widened distally, and further distal shift of main forks (R+M+CuA bifurcation just before, R and M+CuA bifurcations beyond wing midlength) in the forewing.

COMPOSITION. Monotypic.

DISTRIBUTION. Mid-Cretaceous amber of Myanmar.

Discussion

A new genus of Hylicellidae from Khasurty. The family Hylicellidae was described from the Triassic [Evans, 1956], and its second subfamily Vietocyclinae from the Jurassic and Cretaceous [Shcherbakov, 1988b]. Hylicellidae and Triassic Chiliocyclidae were separated into the superfamily Hylicelloidea, considered ancestral to all three extant superfamilies of Cicadomorpha (Membracoidea, Cercopoidea, and Cicadoidea) [Shcherbakov, 1996]. The family Ligavenidae (Cretaceous) and the superfamily Ligavenoidea [Hamilton, 1992] were synonymized under Hylicellidae and Hylicelloidea, respectively [Shcherbakov, 1996]. The family Archijassidae, once considered a subfamily of Hylicellidae [Shcherbakov, 1992], was moved to Membracoidea [Ansorge, 1996; Shcherbakov, 2012a]. The Triassic family Mesojabloniidae was transferred to Hylicelloidea by Shcherbakov [2011], and the third subfamily Coniucellinae was added to Hylicellidae [Shcherbakov, 2012b]. The family Minlagerrontidae from mid-Cretaceous Burmese amber is tentatively attributed to Hylicelloidea [Chen et al., 2019, 2020].

In addition to two genera and seven species originally assigned to Vietocyclinae by Shcherbakov [1988b], the second species of the genus *Vietocycla*, *V. katyae* Fu et Huang, 2019 was recently described from the Aptian of NE China and diagnosed from the type species *V. peregrina* Shcherbakov, 1988 by the number of cross-veins and vein terminations [Fu, Huang, 2019]. These characters are quite variable in the type series of *V. peregrina* (holotype and 28 paratypes) [Shcherbakov, 1988b] and are not diagnostic at the species level. However, *V. katyae* seems to be distinct in the absence of dark colour pattern on tegmen, so characteristic of *V. peregrina* from the Aptian of Transbaikalia.

Several other specimens identified as *Vietocycla* sp. were reported from three other Early Cretaceous localities in Transbaikalia (Shiviya, Tsagan-Nur, Borzya) [Shcherbakov, 1988b]. The record of *Vietocycla* sp. from the Late Jurassic Glushkovo Formation of Glinyanka, Transbaikalia in the Paleobiology Database [2020] is erroneous — there are no Hemiptera in the material from Glinyanka [Zherikhin, 1990: 8]. Therefore the genus *Vietocycla* is restricted to the Early Cretaceous.

The genus *Reticycla* **gen.n.** from Khasurty with a few strongly oblique postnodal R branches bridges the gap between the Early Cretaceous genera *Vietocycla* and *Jiphara*. Based on several postnodal R branches arising from dSc, the latter genus was originally ascribed to the family Pereboriidae [Ren, 1995] otherwise recorded only from the Permian, but in fact this genus agrees with Hylicellidae Vietocyclinae in the configuration of basal cell, vein polymerization and other characters.

New taxa of Mesozoic Psylloidea. *Liadopsylla geinitzii* was described from Early Jurassic of Germany [Handlirsch, 1920–1921, 1939]. Martynov [1927] described another species from the Middle-Late Jurassic of Karatau, Kazakhstan and created the family Liadopsyllidae. Several Jurassic species were added by Becker-Migdisova [1949, 1985] and Ansorge [1996]. The first Early Cretaceous *Liadopsylla* species was described by Shcherbakov [1988a]. Two *Liadopsylla* species were discovered in Cretaceous ambers by Ouvrard et al. [2010]. Becker-Migdisova [1985] revised all currently known fossil Psyllomorpha and described the families Malmopsyllidae (monotypic) and Neopsyllonidae (3 genera) from the Jurassic of Karatau. The latter family was synonymized under Malmopsyllidae by Klimaszewski and Wojciechowski [1992]. Burckhardt and Poinar [2020] described an extraordinary genus *Mirala* from mid-Cretaceous Burmese amber, synonymized Malmopsyllidae under Liadopsyllidae and assigned the new genus to the latter family in the broad sense.

Pterostigma is pigmented, clearly delimited from the costal space and marked at base with a distinct bend of RA in many extant psyllids, as well as in Jurassic Malmopsyllidae and Cretaceous *Mirala* and *Stigmopsylla* **gen.n.** Becker-Migdisova [1985: 60] characterized the pterostigma of *Liadopsylla* s.str. as “wide, open, forming a continuation of the costal space.” Seven available *Liadopsylla* species were re-examined for the development of pterostigma. Slightly darkened pterostigma is found in *Liadopsylla turkestanica* Becker-Migdisova, 1949, *L. grandis* Becker-Migdisova, 1985, *L. asiatica* Becker-Migdisova, 1985 and *L. brevifurcata* Becker-Migdisova, 1985 (Figs 22–25). Such underdeveloped, ‘imperfect’ pterostigma is marked at base with at most slight bend of RA. In *Basicella* **subgen.n.** the pterostigma is likewise present, though little conspicuous: it lacks distinct dark pigmentation, but its limits are often marked with a slight RA bend and then a groove posterior to RA (Figs 19–20).

The free CuA base is clearly visible in the forewings of *Basicella* **subgen.n.** finely preserved in the Cretaceous Khasurty fossil beds (Figs 16–18, 20). Such a CuA base was not found in the well-preserved isolated forewing of *L. mongolica* Shcherbakov, 1988 from the Aptian of Bon Tsagaan, as well as in six species of *Liadopsylla* described from the Jurassic of Karatau, in these latter perhaps because the relief is not preserved and most specimens are complete insects with wing bases superimposed on the body. The free CuA base is an important character: it is usually present in Protopsyllidiidae and more primitive groups and has not

been previously reported in Mesozoic Psylloidea. This character is of generic value, but it is the only known difference between *Liadopsylla* s. str. and *Basicella*, which cannot be checked in many fossils, so for practical purposes we rank the latter taxon as a subgenus. The free CuA base in *Basicella* can be a reversal rather than primitive character, i.e. restored, and not inherited directly from protopsyllidiid ancestors. Such a CuA base may be overlooked or not visible in many fossils, so special attention should be paid to this character in liadopsyllids.

Nodal line developed in some extant and Cenozoic Psylloidea [Heslop-Harrison, 1951; Ouvrard et al., 2013] was not previously reported in Liadopsyllidae. In *Liadopsylla* (*Basicella*) *loginovae* sp.n. (Figs 20–21), a nodal line is present, and in contrast to the condition found in recent psyllids (e.g. [Malenovsky et al., 2012]), it crosses not R bifurcation but RP slightly distad of its base, the point marked with a slight bend of RP and a supernumerary *ir* crossvein.

Two species of Liadopsyllidae known from Cretaceous ambers [Ouvrard et al., 2010] differ markedly from all others in the very short CuA stem and curved M stem, so they are separated into *Cretapsylla* gen.n.

Burckhardt and Poinar (2020) concluded that the family Malmopsyllidae is morphologically heterogeneous and polyphyletic, and synonymized it under Liadopsyllidae. However, all four genera assigned to Malmopsyllidae (Figs 26–29) differ from Liadopsyllidae s. str. at least in the more distal position of the R bifurcation (at >0.4 wing length,) and R+M+CuA bifurcation (at $>1/4$ wing length), compared to at $<1/3$ and $<1/5$ wing length, respectively, in Liadopsyllidae. Such a distal position of these bifurcations is characteristic of many extant Psylloidea, therefore Malmopsyllidae likely represent a group more derived than Liadopsyllidae, and synonymization of these two families is not justified. The Cretaceous genus *Mirala* agrees with malmopsyllids in the even more distal position of these bifurcations, but differs from them (as well as from all other Mesozoic Psylloidea) in the apparently unforked M and long recurrent CuA2, so it can be placed in Malmopsyllidae as a separate subfamily.

Psyllomorpha, so common in the Jurassic, were previously known from the Cretaceous for a few finds, some of which are still not described. Liadopsyllidae from Khasurty reveal unexpected taxonomic diversity and show some morphological characters formerly unknown in Mesozoic Psylloidea. In the Cretaceous, psyllomorphs were perhaps more locally distributed than in the Jurassic, and Khasurty likely belonged to one of their refugia. Some psyllomorph taxa from Khasurty may represent Jurassic relicts in the Early Cretaceous fauna.

The insects and other fossils of Khasurty. The fossil assemblage of this locality is rich and peculiar (numerical data are based mainly on specimen counts of the 2004 expedition headed by the author).

Aquatic insects are more numerically abundant than terrestrial. The commonest insect group is phantom midges (Chaoboridae) represented by innumerable pu-

pae and numerous adults and larvae. Only the well-preserved chaoborid specimens were collected, and most others discarded (the same was true about other super-plentiful groups such as aphids and tipuloid crane-flies). Much less abundant are other Diptera with aquatic larvae (Chironomidae, Simuliidae, Ptychopteridae, some Limoniidae s.l., some Empidoidea), Ephemeroptera (mainly nymphs), Plecoptera (mostly adults), larvae of the large beetle *Coptoclava longipoda* Ping, 1928 (Coptoclavidae; adults are exceptionally rare); Trichoptera (adults and rare larval cases, larvae and swimming pupae), and scorpionflies Nannochoristidae (adults). The finds of small water beetles (Hydrophilidae, Jurodidae, etc.), damselfly nymphs (Zygoptera), and adult water boatmen (Corixidae) are rare. Some of the minor aquatic groups likely inhabited small rivers and brooks rather than the Khasurty paleolake. Other aquatic arthropods are water fleas (Prochyridae) [Kotov, 2009] and clam shrimps (Conchostraca). Fish remains are exceptionally rare.

The terrestrial insect assemblage is dominated by super-plentiful winged aphids (Aphidomorpha). Only the better-preserved aphid specimens taken by collectors make up more than 30% of total terrestrial insects. It is higher share than in any other Mesozoic locality known to the author. Nematoceros Diptera are very diverse and abundant: common Trichoceridae and Limoniidae s.l, various Sciaroidea, uncommon Anisopodidae, Axymyiidae, and Perissommatidae. Hymenoptera are on the third place among terrestrial groups, or maybe on the second, if we consider that many groups of Diptera have aquatic larvae. Hymenopterans are more abundant than in other Mesozoic assemblages (more than 8% of total insects), very diverse (more than 25 families, half of the number of families of other terrestrial insects), and dominated by Xyelidae (about 30% of total hymenopterans). The less numerous are terrestrial bugs and beetles, brachycerous Diptera, and scorpionflies. Not rare are Neuroptera, small moths (Lepidoptera) and Lophioneuridae (ancestral to Thysanoptera). The rarest groups are Raphidioptera, Orthoptera, Grylloblattodea, and true Thysanoptera. Notable is the absence of Blattodea.

The non-aphid Homoptera are moderately diverse and comparatively rare (about twenty times less abundant than aphids). Coleorrhyncha are represented by numerous Karabasiidae and rare Progonocimicidae, and Auchenorrhyncha Cicadomorpha – with several Palaeontinidae and Hylcellidae and a few Proceropidae (Cercopoidea) and Archijassidae (Membracoidea). Notable is the extreme rarity of Fulgoroidea and the absence of Tettigarctidae (Cicadoidea). In contrast to all other known Cretaceous localities, jumping plant lice (Psyllomorpha) are common and diverse; both Protopsyllidiidae and Liadopsyllidae are found.

Besides insects, several small spiders and harvestmen were found, as well as small feathers of birds or dinosaurs. Bryophytes are quite common and represented by 4 genera and 6 species of mosses, all floating or growing on banks [Ignatov, Shcherbakov, 2011], and one species

of hepatics [Mamontov, Ignatov, 2019]. The finds of vascular plants are little diverse and fragmentary: fern pinnules, conifer needles and seeds (*Pityospermum*), hairy achenes of proangiosperms (*Baisia*), etc.

On the age of the Khasurty entomofauna. The Khasurty fossil beds belong to a very small, isolated block of the Mesozoic deposits surrounded by Paleozoic rocks [Gordienko et al., 2018]. These fossil beds were attributed to the Gusinoe Ozero (Gusinoozerskaya) Group, formerly dated as Middle Jurassic–Early Cretaceous, now as Early Cretaceous [Skoblo et al., 2001]. Several features of the Khasurty insect assemblage confirm the Early Cretaceous age of the strata.

1. Such a high numerical abundance of aphids is recorded only in several Early Cretaceous entomofaunas of Transbaikalia (Baissa, Turga) and Mongolia (Hotont, Hutel-Hara, Hutuliyn), all with aphids making up 16–24% (or even more) of terrestrial insects [Wegierek, 1990]. In many other Early Cretaceous insect faunas of Transbaikalia and Mongolia, the aphids make up from ~1 to 7%, and in some Jurassic faunas of Asia much less than 1% of terrestrial insects (ibid.); of course, in still many other Cretaceous insect faunas aphids are absent altogether (we have no numerical data on Chinese localities). Such localities as Hotont, Hutel-Hara, and Hutuliyn were formerly dated as belonging to the Late Jurassic–Early Cretaceous transitional interval, but a detailed analysis demonstrated that they are earliest Cretaceous (Turga Horizon, Berriasian–Valanginian) [Dmitriev, 2020].

Modern aphids are much more diverse in the northern temperate zone than in the tropics or southern temperate zone [Heie, 1994]. Such an unusual pattern of the geographical distribution, explained by the low thermal tolerance of bacterial symbiont of aphids, has existed since the Early Cretaceous [Perkovsky, Wegierek, 2017]. The five abovementioned aphid-rich localities and Khasurty are all confined to a comparatively small area (ca. 1000 x 1000 km; 45.8–56.0° paleoN, 101.4–111.4° paleoE) [Paleobiology Database, 2020] of the Cretaceous northern warm temperate zone close to the NE limit of boreotropical zone [Boucot et al., 2013]. In the latest Jurassic–earliest Cretaceous, this region underwent intense collisional orogeny west of the closing Mongol–Okhotsk Ocean and a cooling event [Yang et al., 2015]. Probably, the humid mountainous variant of temperate climate was characteristic of Khasurty in the Early Cretaceous, which favoured the high abundance and diversity of aphids.

2. The aquatic beetle *Coptoclava longipoda* (Coptoclavidae) common in the Khasurty assemblage is an index insect fossil confined to the Early Cretaceous of East Asia (Ponomarenko, 1961; Prokin et al., 2013; Zhao et al., 2018). However, the giant mayfly *Ephemeropsis* Eichwald, 1864 usually associated with *C. longipoda* in widespread faunas of the *Ephemeropsis*–*Coptoclava* type [Zherikhin, 1978; Zherikhin et al., 1999; Mostovski et al., 2000] is replaced in the Khasurty assemblage with smaller mayflies of several genera, including a related genus *Baikalogenites* Sinitshenkova, 2017 [Sinitshenkova, 2017].

3. The Khasurty fauna includes several families and genera recorded elsewhere only from the Early Cretaceous: hymenopterans Praeichneumonidae [Kopylov, 2012], Archaeocynipidae [Kopylov, 2014], *Trematothorax* Rasnitsyn, 1988 [Kopylov, Rasnitsyn, 2017], *Ampliplicella* Kopylov, 2010 and *Khasurtella* Kopylov, 2011 [Kopylov, 2011]; dipterans *Mangas* Kovalev, 1986 [Greenwalt, Blagoderov, 2019], *Zhiganka* Lukashevich, 1995 [Lukashevich, 2019], *Kaluginamyia* Lukashevich, Pepinelli et Currie, 2019 [Lukashevich et al., 2020], *Collessomma* Lukashevich et Blagoderov, 2020 [Lukashevich, Blagoderov, 2020], etc.

4. There are similarities at the species level between Khasurty and undoubtedly Cretaceous faunas. *Ampliplicella shcherbakovi* Kopylov, 2011 is recorded from Khasurty and Dabeigou Formation, Hauterivian of China [Kopylov, Zhang, 2015]. The Khasurty species of *Ghilarella* Rasnitsyn, 1988 is indistinguishable from *G. mercurialis* Rasnitsyn, 1988 from Bon-Tsagan, Aptian of Mongolia [Kopylov, Rasnitsyn, 2017]. Some other Khasurty species are closely similar to those from the Early Cretaceous, e.g. *Mesypochrysa cannabina* Khramov, 2018 to *M. cf. chrysopoides* Ponomarenko, 1992 from the Yixian Formation, Aptian of China [Khramov, 2018].

5. The Khasurty assemblage contains several insect families unknown from the pre-Cretaceous strata, such as Bolitophilidae, Braconidae, Proctotrupidae, and several others.

Therefore, there is little doubt about the Early Cretaceous age of the Khasurty entomofauna, in accordance with the opinion of regional stratigraphers.

However, there are some other features, which relate the Khasurty entomofauna to the Jurassic ones.

6. Comparative abundance of Lophioneuridae, Protopsyllidiidae, Liadopsyllidae, Karabasiidae, Megalyridae, Nemonychidae Brenthorhininae and several other taxa, which are usually rare in the Cretaceous.

7. Presence of some taxa unknown elsewhere after the Jurassic: beetles Jurodidae [Yan, Strelnikova, 2019] and *Gracilicupes* Tan, Ren et Shih, 2006 [Strelnikova, 2019] and stoneflies *Dimoula* Sinitshenkova, 2005 and *Rasnitsyrina* Sinitshenkova, 2011 [Sinitshenkova, 2011].

8. The species in common between Khasurty and Late Jurassic faunas — *Jurodes minor* Ponomarenko, 1990 (Coleoptera) [Yan, Strelnikova, 2019] known also from the Late Jurassic Glushkovo Formation of eastern Transbaikalia.

Concluding from the features 1–5 that Khasurty is of Early Cretaceous age, we could explain the features 6–8 through persistence of the Jurassic relicts in a favourable climate, perhaps not unlike the humid temperate climate of present-day extratropical rainforests of the Southern Hemisphere.

The Early Cretaceous Homoptera assemblage of Khasurty has a relict appearance: it is enriched with the families Protopsyllidiidae, Liadopsyllidae and Karabasiidae, which are widespread in the Jurassic and rare in the Cretaceous [Shcherbakov, 1988b; Popov, Shcherbakov, 1996]. Its fourth major component is an

endemic genus of the Jurassic–Early Cretaceous subfamily Vietocyclinae (Hylcellidae), intermediate between two other Early Cretaceous genera. Liadopsyllids from Khasurty belonging to an endemic genus and an endemic subgenus have derived traits as well as seemingly primitive features, and the genus shows some similarity to another Cretaceous genus.

On the paleoenvironment of Khasurty. Cockroaches, termites, earwigs, orthopterans, cicadas, and planthoppers are rather thermophilic. These groups are present and sometimes common in many Late Jurassic and Early Cretaceous faunas of Asia, but absent or (orthopterans, planthoppers) very rare in the Khasurty fauna. This fact, as well as the extraordinary abundance of aphids and relative abundance of xyelid sawflies, can be explained by the climate near Khasurty paleolake cooler and wetter than reconstructed for many other Late Mesozoic localities of Transbaikalia and Mongolia, probably due to some local geographic features.

High abundance of aphids (primitive groups of which live on trees and shrubs) and hymenopterans (including the groups with wood-boring larvae and their parasites), as well as finds of conifer seeds and needles, indicate the presence of various woody plants around the Khasurty paleolake. Living Coleorrhyncha feed on mosses, and the Mesozoic ones probably also fed on them, so plenty of mosses is a likely cause of the abundance of Karabasiidae in the Khasurty fauna. The low abundance and diversity of Auchenorrhyncha feeding on various vascular plants indicate that some plant groups were underrepresented or absent in the Khasurty paleoflora.

We can conclude that the Khasurty fossils were preserved in the deposits of a fish-deficient intermontane paleolake in a forested region with rather cool, humid temperate climate.

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