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New Permian and Triassic Scytinopteridae (Homoptera: Cicadomorpha) with elytrized tegmina, with notes on the origin of true bugs (Heteroptera)

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Abstract. New Scytinopteridae with elytrized tegmina are described: *Ooscyta chertoprudi* gen. et sp. n. from the Late Permian of Karaungir, East Kazakhstan and *Synelytra tverdokhlebovorum* gen. et sp. n. from the Early Triassic of Petropavlovka, Southern Cis-Urals, European Russia. The fossil insect assemblages of Karaungir and Petropavlovka are briefly characterized. In the Late Olenekian of Petropavlovka, the earliest Ipsviciidae and Curvicubitidae are recorded, as well as the genera and possibly species characteristic of Madygen, which indicates that the Middle Triassic entomofauna began to form towards the end of the Early Triassic. The evidence supporting the origin of true bugs from scytinopteroids is briefly discussed.

Key words: Hemiptera, Auchenorrhyncha, Ipsviciidae, Curvicubitidae, Madygen, Permian-Triassic crisis, paleoclimate, zoophagy.

Новые пермские и триасовые Scytinopteridae (Homoptera: Cicadomorpha) с элитризованными передними крыльями, с замечаниями о происхождении клопов (Heteroptera)

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Резюме. Описаны новые Scytinopteridae с элитризованными передними крыльями: *Ooscyta chertoprudi* gen. et sp. n. из поздней перми Караунгира, Восточный Казахстан и *Synelytra tverdokhlebovorum* gen. et sp. n. из раннего триаса Петропавловки, Южное Приуралье, Европейская Россия. Кратко охарактеризованы комплексы ископаемых насекомых Караунгира и Петропавловки. В позднем оленёке Петропавловки найдены древнейшие Ipsviciidae и Curvicubitidae, а также роды и, возможно, виды, характерные для Мадыгена, что свидетельствует о начале формирования среднетриасовой энтомофауны к концу раннего триаса. Кратко обсуждаются доказательства, подтверждающие происхождение клопов от сцитиноптероидов.

Key words: Hemiptera, Auchenorrhyncha, Ipsviciidae, Curvicubitidae, Мадыген, пермо-триасовый кризис, палеоклимат, зоофагия.

Introduction

Scytinopteridae is a diverse family of extinct Cicadomorpha known from both Laurasia and Gondwana in the Permian and the Triassic [Lambkin, 2016]. This group was understood broadly [Evans, 1956], but was later restricted to the genera with sclerotized punctate tegmina having a costal fracture and a hypocostal socket coupled to the thorax in repose, and was placed in the superfamily Scytinopteroidea [Shcherbakov, 1984]. Based on these features, it was hypothesized that scytinopteroids lived on waterside vegetation and gave rise to Heteroptera [Shcherbakov, 1996, 2000]. In the Permian-Triassic boundary beds of South Mongolia, a peculiar monotypic genus of Scytinopteridae was discovered with coleopterous tegmina lacking the costal fracture and the claval furrow [Shcherbakov, 2022a]. Below we describe two more genera with similar modifications of highly convex, strongly sclerotized tegmina, found in the Late Permian of Karaungir, East Kazakhstan and the Early Triassic of Petropavlovka, Southern Cis-Urals, European Russia.

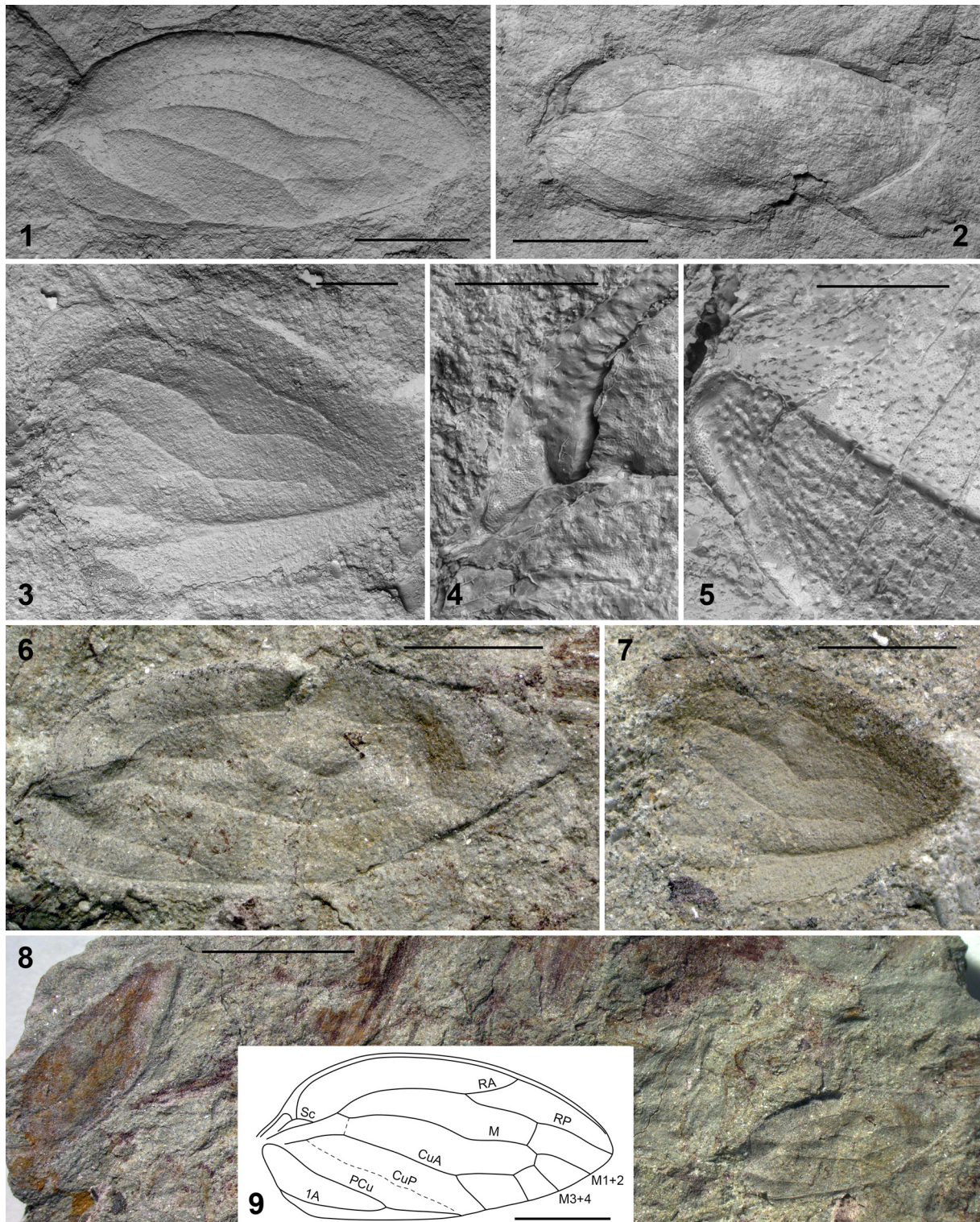
Material and methods

The material was collected by field parties of the Arthropoda Lab, and is deposited at Borissiak Paleontological Institute of the Russian Academy of Sciences (PIN, Moscow, Russia). Photographs were taken using a Leica M165C stereomicroscope with a Leica DFC425 digital camera. Scanning electron images of uncoated specimens were obtained with a TESCAN VEGA3 microscope using a backscattered electron detector.

Family Scytinopteridae Handlirsch, 1906 Genus *Synelytra* gen. n.

Type species *Synelytra tverdokhlebovorum* sp. n.

Diagnosis. Similar to *Beloscyta* Shcherbakov, 2022 in the veins carinate, basal cell wide open (CuA base not converging with R + M) and both costal fracture and claval furrow undeveloped, but differs in the broadly ovate tegmen acutely rounded at apex, short claval cell, M stem sigmoidal distally, M and CuA branches less numerous, and



Figs 1-9. *Synelytra tverdokhlebovorum* sp. n., tegmina (Early Triassic of Petropavlovka).
 1, 9 – holotype; 2-8 – paratypes: 2, 4 – 5640/34, 3, 7 – 5640/36, smallest specimen (male?), pair of coupled tegmina, 5 – 5640/277, 6, 8 – 5640/32, largest tegmen (of female?; 6 and 7 in one scale); 8 – tegmen (on the right) on the rock surface near a peltasperma seed (on the left). 4-5 – surface sculpture near base (5 – mirrored); 9 – venation. 1-3, 6, 7, 9 – 2 mm, 4-5 – 0.5 mm, 8 – 5 mm.

Рис. 1-9. *Synelytra tverdokhlebovorum* sp. n., передние крылья (ранний триас Петропавловки).
 1, 9 – голотип; 2-8 – паратипы: 2, 4 – 5640/34, 3, 7 – 5640/36, самый маленький экземпляр (самец?), пара сцепленных передних крыльев, 5 – 5640/277, 6, 8 – 5640/32, самое крупное переднее крыло (самки?; 6 и 7 в одном масштабе); 8 – переднее крыло (справа) на породе рядом с семенем пельтасперма (слева). 4-5 – скульптура поверхности около основания (5 – перевернуто зеркально); 9 – жилкование. 1-5 – СЭМ. Масштабные линейки: 1-3, 6, 7, 9 – 2 мм, 4-5 – 0.5 мм, 8 – 5 мм.

CuA cell elongated along the wing margin. Left and right tegmen tightly coupled at life and often preserved together.

Composition. Type species.

Notes. Assigned to Scytinopteridae because of the small, strongly convex, well sclerotized, punctate tegmen with very simple venation, Sc base arched forwards and meeting the basicostal projection, short basal cell, M stem arched backwards at the nodal level, one crossvein *r-m*, M with at most 3 branches, and the claval Y-vein entering the claval apex.

Etymology. From Greek *syn* (together, with) and *elytron* (cover, sheath, husk, shell); gender feminine.

Synelytra tverdokhlebovorum sp. n.
(Figs 1–9)

Material. Holotype tegmen 5640/278 and paratypes 5640/31, 32±, 33, 34, 35, 36±, 37±, 38±, 39, 231±, 233, 234, 235±, 236±, 277 (isolated tegmina, sometimes with attached part of opposite tegmen); Petropavlovka-3 near the village of Petropavlovka, Orenburg Region, Russia; Petropavlovka Formation, upper Olenekian, Lower Triassic.

Description. Tegmina 5.3–8 mm long, 2.7–3.7 mm wide, broadly ovate, widest before midlength, acutely rounded at apex, somewhat variable in shape. Among the nine complete tegmina, four (PIN 5640/31, 32, 34, 278) are more elongated (length to width ratio 2.1–2.3 : 1), less sharply narrowed distally, with a more developed postnodal part, on average larger (length 6.1–8 mm); these presumably belonged to females. The five other complete tegmina (PIN 5640/33, 35, 36, 39, 235) are less elongated (length to width ratio 1.8–1.9 : 1), more sharply narrowed distally, with a less developed postnodal part, on average smaller (length 5.3–6.9 mm); these presumably belonged to males. The left and right tegmina were tightly coupled along the claval commissure at life, so they were regularly buried in pairs and found with the clavus or a larger part of the opposite tegmen still attached (5640/35, 36±, 39, 277) (Figs 3, 7). Costal margin deeply arched near base and more or less evenly arched distally; precostal carina wide near base, deflected dorsad; hypocoastal carina narrow; basicostal projection large, reaching low arched base of Sc; costal fracture absent; costal area of equal width throughout. Basal cell wide open (arculus absent or very faint, long, transverse); R + M and CuA parallel near base and diverge more distally; M diverging from CuA level with or slightly distad of R–M divergence. R stem arched forwards, R forked at nodal level, RA oblique, RP without discernible branches. M stem arched forwards proximally and distally, and backwards at nodal level; M forked distal to *r-m* crossvein, usually with 2 discernible branches. CuA stem fairly straight, CuA cell oblique trapezoidal, elongated along tegmen margin (up to 2 : 1). Two crossveins (*r-m* and *m-cu*) about same level, *m-cu* distal to M bifurcation (sometimes replaced by short anastomosis). CuP obscure, faintly concave, slightly wavy. Clavus occupying about 0.55 tegmen length; claval veins (Pcu and 1A) united about 0.65 clavus length (about 0.35 tegmen length); commissural area not narrowed. Tegmen strongly convex, except for depressed area of basal cell; main veins carinate; upperside covered with rasp-like punctures (bases of setae, deepest near clavus base); underside densely covered with microscopic granules (stub-like microtrichia, 7–9 per 100 µm). Tegmen darkened, sometimes unevenly, in some specimens more so along veins.

Etymology. After Valentin P. Tverdokhlebov and Galina I. Tverdokhlebova, enthusiastic explorers of the Permian and Triassic of the East European Platform.

Genus *Ooscyta* gen. n.

Type species *Ooscyta chertoprudi* sp. n.

Diagnosis. Similar to *Synelytra* gen. n. in the ovate tegmen acutely rounded at apex, claval furrow undeveloped, and fairly short claval cell, but differs in R forked distally, M with 3 branches, basal cell closed, veins not raised, and costal fracture traceable.

Composition. Type species.

Notes. Assigned to Scytinopteridae because of the small, highly convex, well sclerotized, finely punctate tegmen with simple venation, developed costal fracture, Sc base arched forwards and meeting the basicostal projection, short subtriangular basal cell, M stem arched backwards distally, one crossvein *r-m*, M with 3 branches, and the claval Y-vein entering the claval apex.

Etymology. From Greek *oon* (egg) and *skytos* (hide, skin, leather); gender feminine.

Ooscyta chertoprudi sp. n.
(Figs 10–14)

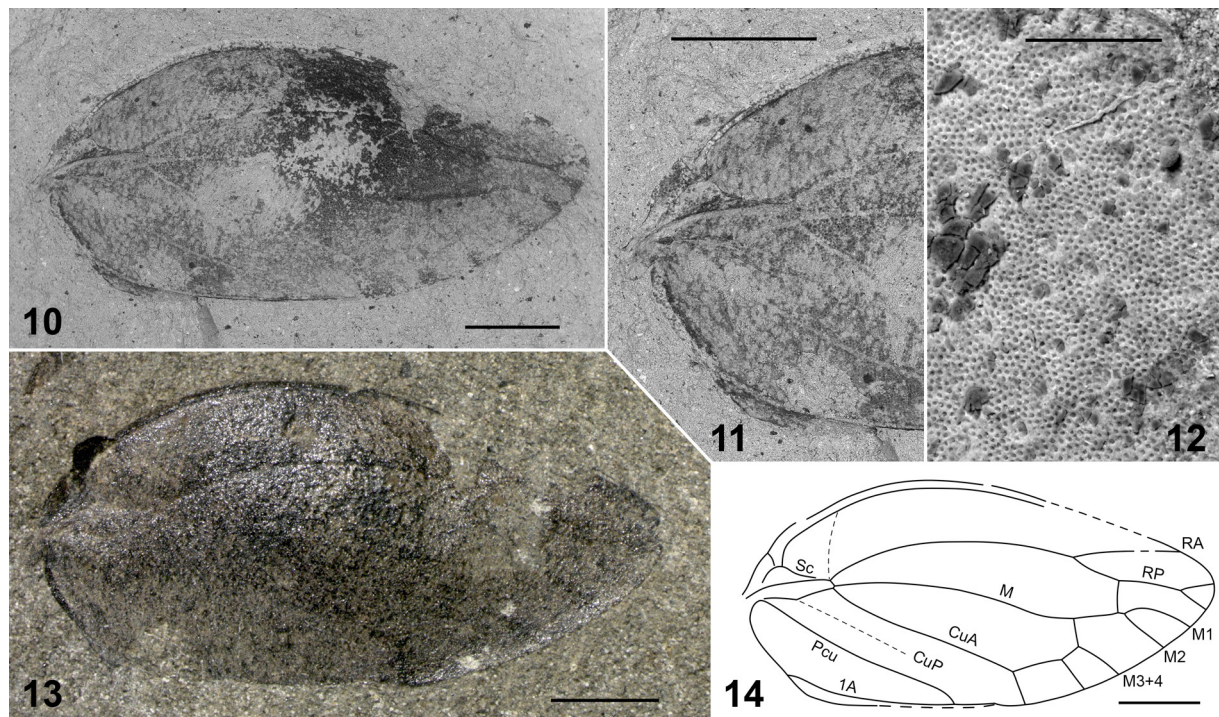
Material. Holotype tegmen 2781/142±; right bank of Karaungir River 400–500 m downstream of Maichat Creek (Karaungir-2 locality), 50 km ESE of Zaisan town, East Kazakhstan Region, Kazakhstan; Akkolka Formation (2–3 m above its base), Changhsingian, Upper Permian.

Description. Tegmen 5.7 mm long, 2.8 mm wide, broadly ovate (length to width ratio 2 : 1), widest before midlength, acutely rounded at apex. Costal margin fairly evenly arched; precostal carina wide near base, deflected dorsad; hypocoastal carina narrow proximally; basicostal projection large, reaching high arched base of Sc; costal fracture faint, arched basad, apparently non-functional; costal area widest at 1/3 tegmen length. Basal cell tapered to apex, closed by short oblique section of M and very short arculus. R stem arched forwards, R forked beyond 2/3 tegmen length, RA almost longitudinal, RP with small apical fork. M stem sigmoidal, arched forwards proximally and backwards distally; M forked level with R bifurcation, with three branches in posterior pecten. CuA stem slightly arched backwards proximally, CuA cell rectangular, elongated along tegmen margin (1.5 : 1). Two crossveins, *r-m* and *m-cu*, distal to M bifurcation, *r-m* more distal. CuP weak, straight, concave proximally, traceable up to 1/3 tegmen length. Clavus occupying 0.55 tegmen length; claval veins (Pcu and 1A) united about 0.8 clavus length (about 0.45 tegmen length); commissural area narrowed and depressed distally. Tegmen highly convex, especially about midlength, except for depressed area of basal cell; main veins not prominent; upperside covered with faint punctures (bases of setae); underside densely covered with microscopic granules (stub-like microtrichia, ca 9 per 100 µm). Tegmen dark, finely pale-speckled, except for large dark area anterodistally and dark markings at vein terminations and in distal part of claval cell.

Etymology. To the memory of Mikhail V. Chertoprud (1975–2023), hydrobiologist and entomologist.

Key to the genera of Scytinopteridae with elytrized tegmina

- Basal cell tapered to apex; costal fracture traceable; M stem distally arched backwards; veins not raised. Tegmen broadly ovate, acutely rounded at apex; R forked distally, RA almost longitudinal; M with 3 branches; claval cell shorter than 1/2 of tegmen
..... *Ooscyta* gen. n.
- Basal cell wide open (R + M not converging to CuA base); costal fracture absent; M stem distally not as above; veins carinate 2



Figs 10–14. *Ooscyta chertoprudi* sp. n., holotype tegmen (Late Permian of Karaungir).

10–11 – positive impression; 12–13 – negative impression (mirrored). 12 – surface sculpture; 14 – venation. 10–12 – SEM. Scale bars: 10–11, 13–14 – 1 mm, 12 – 0.2 mm.

Рис. 10–14. *Ooscyta chertoprudi* sp. n., переднее крыло, голотип (поздняя пермь Караунгира).

10–11 – прямой отпечаток; 12–13 – обратный отпечаток (перевернуто зеркально). 12 – скульптура поверхности; 14 – жилкование. 10–12 – СЭМ. Масштабные линейки: 10–11, 13–14 – 1 мм, 12 – 0.2 мм.

2. Tegmen elongate, pointed; RA reduced; M stem distally arched forwards; M with more than 3 branches; claval cell longer than 1/2 of tegmen *Beloscyta*
 – Tegmen broadly ovate, acutely rounded at apex; RA oblique; M stem distally sigmoidal; M with at most 3 branches; claval cell about 1/3 of tegmen. Left and right tegmen tightly coupled at life (and often preserved together) *Synelytra* gen. n.

Discussion

Karaungir. Along the Karaungir River 50 km ESE of Zaisan town, East Kazakhstan, in the Kenderlyk Trough, fossiliferous beds of the Karaungir (Karaungur) locality are exposed. Insects were found in the upper part of the Maichat (Maychat) Formation (Karaungir-1) and in the lower part of the overlying Akkolka (Ak-Kolka) Formation (Karaungir-2; these two insect beds are separated by only 20 m of the section). These coal-bearing formations were dated to the Late Permian (Lopingian) by the regional stratigraphy, plants, Conchostraca, and insects [Ponomarenko, 1969; Novojilov, 1970; Vakhrameev et al., 1970; Shcherbakov, 2000]. Despite this, the entomofauna of Karaungir was considered Middle Permian on account of relatively high percentage of ancient families [Rasnitsyn et al., 2013]. However, this argument is untenable, since primitive forms persist as relicts in refugia with milder climates, and this effect is especially noticeable in epochs of pronounced climatic zonation, such as the Permian or Recent [Shcherbakov, 2008a].

The warm temperate Late Permian climate of the Kenderlyk Trough, warmer than in the Kuznetsk Basin and more humid than on the East European Platform [Rees et al., 2002; Chumakov, Zharkov, 2003], supported coal-producing vegetation, although not as cordaite-rich as in Siberia, so this area could have served as a refugium during the progressive aridization in the Permian. Thermophilic groups such as Blattodea and Orthoptera were common in the Permian and Triassic East European faunas of arid and semiarid climates, rare in Karaungir, and are not found in numerous Middle and Late Permian Siberian faunas of temperate and cool temperate climates (Kuznetsk and Tunguska basins) [Shcherbakov, 2008a].

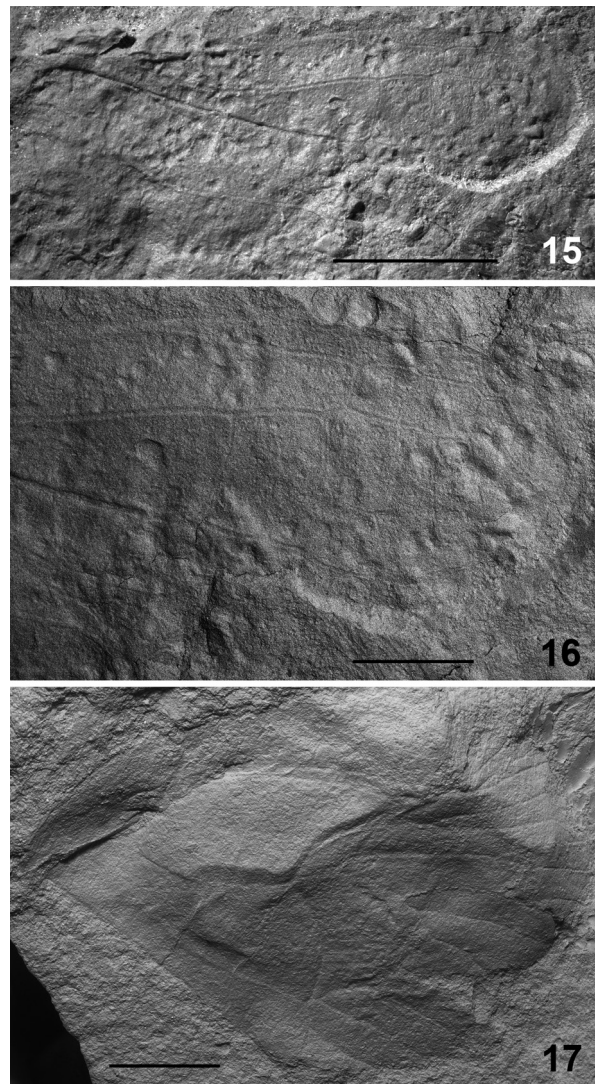
The less rich insect assemblage of Karaungir-1 (Maichat Formation), dominated by Coleoptera and Homoptera Auchenorrhyncha, represents the near-shore facies, whereas the much more diverse assemblage of Karaungir-2 (Akkolka Formation, ca 254 Ma) represents the off-shore facies [Shcherbakov, 2000]. The latter assemblage includes 14 insect orders and is similar to some Kuznetsk faunas in the dominance of Mecoptera (25% of ca 530 insect specimens identified to the order) [Novokshonov, 1995, 1997, etc.]. Other dominant groups are Plecoptera (19%) [Sinitshenkova, 1987], Auchenorrhyncha (17%) and Trichoptera (13%) [Sukatsheva, 1976, etc.]; protorthopterans (8%) [Storozhenko, 1991; Aristov, 2013, etc.], Permosialidae (Miomoptera; 6%) [Aristov, Rasnitsyn, 2023], Neuroptera (4%) [Vilesov, Novokshonov, 1994; Novokshonov, 1996] and Coleoptera (4%) [Ponomarenko, 1969] are less numerous,

and Lophoneuridae [Vishniakova, 1981], Ephemeroptera, Odonata, Glosselytroidea [Vilesov, Novokshonov, 1994], Dermaptera, and Orthoptera are rare.

Petropavlovka. Along the Sakmara River near the village of Petropavlovka 45 km NE of Orenburg, European Russia, in the Cis-Ural Trough, the Petropavlovka Formation is exposed, dated to the Late Olenekian (ca 248 Ma) by tetrapods, lungfishes, miospores and magnetostratigraphy [Tverdokhlebov et al., 2003]. It consists of red beds formed in an arid climate and containing a meter-thick grey lens of lacustrine sediments (Petropavlovka-3, bed 43). This lens yielded abundant and diverse plants and insects, tomiulid millipedes (8 specimens) [Hannibal, Shcherbakov, 2019] and freshwater dwellers, such as horseshoe crabs *Attenborolimus superspinosus* Bicknell et Shcherbakov, 2021 (Austrolimulidae; eight specimens) [Bicknell, Shcherbakov, 2021], infrequent Conchostraca, numerous microconchids (extinct minute lophophorates that lived in spiral tubes) [Shcherbakov et al., 2021], and the earliest microdrile oligochaete [Shcherbakov et al., 2020].

The insect assemblage of Petropavlovka is dominated by cockroaches (48% of ca 260 insect specimens identified to the order), Coleoptera and Homoptera Auchenorrhyncha (19% each); protorthopterans and Orthoptera (6% each) are less numerous; Odonata and possible Miomoptera and Neuroptera are rare. The insect remains are mostly isolated elytra and tegmina of beetles, cockroaches and Homoptera Auchenorrhyncha, while large wings, e.g. those of Orthoptera, are represented by fragments. The rare finds of Odonata belong to the family Triadophlebiidae and the genus *Cladophlebia* Pritykina, 1981 known from Madygen [Felker, Vasilenko, 2019]. Diverse and abundant Blattodea include (P. Vršanský, personal communication): *Subioblatta* sp. (Subioblattidae), barely distinguishable from *S. madygenica* Papier et Nel, 2001 sensu Hinkelman [2022] from Madygen, and a mixture of advanced Phylloblattidae [Vršanský, 2010], Caloblattinidae [Vršanský, 2000] and the *Voltziablatta*-group [Vršanský, 2008]. The protorthopterans belong to the common Chaulioditidae (*Chauliodites sakmaris* Aristov, 2020) and rare Blattogryllidae (*Baharellinus orenburgensis* Aristov, 2022) [Aristov, 2020, 2022]. The elytra of Coleoptera belong to numerous and diverse Schizocoleidae and to rare Permosynidae and Asiocoleidae (A.G. Ponomarenko, personal communication). Various Homoptera Auchenorrhyncha are represented mainly by numerous Surijokocixiidae and Scytinopteridae, including the very common *Synelytra tverdokhlebovorum* sp. n. known from 16 specimens. The families Dymorphoptilidae, Ipsviciidae (Figs 15, 16) and Curvicubitidae (*Beaconiella* sp. cf. *B. pulchra* Shcherbakov, 2021 known from Madygen (Fig. 17)) are rarer. The last two families were previously recorded only starting from the Middle Triassic (Lambkin, 2020; Shcherbakov, 2021), so the specimens from Petropavlovka are their earliest finds. The presence of taxa characteristic of Madygen indicates that the Middle Triassic entomofauna began to form towards the end of the Early Triassic.

Scytinopteridae. The body shape of scytinopterids with elytrized tegmina probably helped them mimic the seeds or buds of their host plants (plant-part mimicry).



Figs 15–17. The earliest finds of Cicadomorpha families in the Early Triassic of Petropavlovka.

15–16 – Ipsviciidae gen. sp., hind wing, specimen ПИН 5640/65±, positive impression (mirrored); 16 – distal part; 17 – Curvicubitidae, *Beaconiella* cf. *pulchra*, tegmen, specimen PIN 5640/16. 16–17 – SEM. Scale bars: 15 – 5 mm, 16–17 – 2 mm.

Рис. 15–17. Древнейшие находки семейств цикадоморф в раннем триасе Петропавловки.

15–16 – Ipsviciidae gen. sp., заднее крыло, экземпляр ПИН 5640/65±, прямой отпечаток (перевернуто зеркально); 16 – дистальная часть; 17 – Curvicubitidae, *Beaconiella* cf. *pulchra*, переднее крыло, экземпляр PIN 5640/16. 16–17 – СЭМ. Масштабные линейки: 15 – 5 мм, 16–17 – 2 мм.

This assumption is supported by the fact that the isolated *Synelytra* tegmina are so seed-like that they can fool even my lab colleagues, experienced insect fossil hunters. This similarity can be seen on a rock slab where one of these tegmina is preserved near a peltasperm seed (identified by E.V. Karasev) (Fig. 8).

In the Triassic of Petropavlovka, *Synelytra tverdokhlebovorum* sp. n. is very common, and the tegmina of this species are regularly found in pairs, the left and the right tegmina being still connected along the posterior margins. This fact, as well as the strong convexity of the

tegmina and reduction of the flexion lines controlling their deformation in flight, indicate that the flying ability was reduced in such scytinopterids with completely elytrized tegmina compared to their relatives that retained flexion lines.

In some modern Auchenorrhyncha, e.g. in subbrachypterous spittlebugs *Lepyronia* Amyot et Serville, 1843, the tegmina of males are less elongated, with a shorter postnodal part than in females. Similar dimorphism of isolated tegmina, by analogy interpreted as sexual dimorphism, is observed in *Synelytra* **gen. n.** (see Description).

Scytinopteroids and the origin of Heteroptera.

Six extinct families of the infraorder Cicadomorpha (Scytinopteridae, Ipsviciidae, Paraknightiidae, Stenoviciidae, Serpentinividae and Saaloscytinidae) were united in the superfamily Scytinopteroidea [Shcherbakov, 1984, 2011]. This grouping is based first of all on the specific structure of the proximal costal area of the tegmen, typically with a transverse costal fracture and with the Sc base arched forwards and meeting the basicostal projection (associated with the hypocostal socket coupled to the mesepimeral knob in repose). In some scytinopteroids, some of these characters may be modified or reduced, but other characteristics (simple venation; claval Y-vein entering the claval apex; tegmen well sclerotized, punctate or areolate) confirm the assignment of these taxa to the superfamily.

Among modern insects, the costal fracture is known only in true bugs. It is the groundplan feature of Heteroptera, found in all infraorders except Gerronomorpha (in Pentatomomorpha, it is retained only in the Mesozoic families Pachymeridiidae and Mesopentacoridae) [Shcherbakov, 2008b]. Therefore, it is not surprising that Evans [1950, 1956], having discovered a costal fracture in Paraknightiidae and Ipsviciidae, transferred these families to Heteroptera. It was subsequently shown that the costal fracture and associated structures are also developed in the other scytinopteroid families, and that this superfamily exhibits the head structure and other features characteristic of primitive Cicadomorpha [Shcherbakov, 1984]. On the other hand, the unique combination of the costal fracture, the arched base of Sc, and the basicostal projection (on the forewing underside with a hypocostal socket coupled to the mesepimeral knob in repose) is shared only by Scytinopteroidea and Heteroptera and leaves no doubt that true bugs are descendants of scytinopteroids [Shcherbakov, 1996, 2008b].

Among true bugs, water bugs (Hydrocorisae Latreille, 1802 = Cryptocerata Fieber, 1851 = Nepomorpha Popov, 1968) are most similar to their scytinopteroid ancestors. Water bugs constitute the most basal branch of Heteroptera in the phylogenies of Handlirsch [1906–1908], Reuter [1910] and Weirauch et al. [2019]. Heteroptera enter the fossil record at the beginning of the Middle Triassic (Anisian) [Shcherbakov, 2010] and until the end-Triassic (Rhaetian) are represented almost exclusively by nepomorphs [Shcherbakov, Popov, 2002].

Acceptance of cicadomorphs, namely scytinopteroids, as the ancestors of Heteroptera results in reconsidering the polarity of many crucial characters (compared to what was proposed e.g. by Cobben [1978, 1981]), and suggests that

neoteny and structural simplification played an important role in the origin of true bugs. The dorsoventrally depressed body and few-segmented antennae may be nymphal characters retained at the adult stage. The Nepomorpha as a whole retain a greater number of ancestral features than any other heteropteran infraorder: convex dorsum, short tapering antennae without intersegments, primitive structure of the rostrum base, hemelytron with a broad costal area coupled to the mesepimeral knob in repose, costal fracture in the proximal position, indistinct corium/membrane boundary, long clavus, hind legs with enlarged cardinate (pagiopodous) coxae and elongated basitarsi, tarsus 3-segmented in the adult and 2-segmented in the first instar, multifaceted eyes without trichobothria in the first instar, etc. [Schiödtte, 1870; Börner, 1934; Shcherbakov, Popov, 2002].

The transformation of the hopper-like scytinopteroid habit into the flattened heteropteran habit can be explained by migration from a three-dimensional habitat (vegetation) to a two-dimensional one (land or water surface). The first bugs are believed to have been scavengers and passive predators that used their long probing rostrum to feed on soil microfauna in the littoral zone, like Ochteridae and Saldidae [Rieger, 1976; Kerzhner, 1981], or inhabited floating plant carpets, like Mesoveliidae [Andersen, 1982].

The Triassic genus *Triknightia* Shcherbakov, 2021 (Paraknightiidae) resembled a true bug in the structure of the forewings and their flat folding with distal overlap, but retained the head structure of primitive Cicadomorpha and was phytophagous. Judging by its foliaceous pronotal paranota and the costal areas of tegmina, this bug-like paraknightiid was phytophilous and cryptic on host plants [Shcherbakov, 2021].

The association with water is widespread among primitive Heteroptera and may have been characteristic of ancestral bugs. As in Nepomorpha, the most primitive true bugs, the knob coupling of tegmina to the thorax in scytinopteroids can be interpreted as an adaptation to subelytral air storage. An analogous coupling of elytra to the thorax was developed in amphibiotic schizophoroid beetles [Ponomarenko, 1969]. In the genus *Unturella* Shcherbakov, 2022 (Dysmorphoptilidae, Prosboloidea), the underside of the strongly sclerotized and heavily punctate tegmina is densely covered with stub-like microtrichia trapping a thin layer of air (plastron) [Shcherbakov, 2022b]. A similar non-wettable covering of modified microtrichia, found in two new scytinopterid genera, apparently also served to keep the air store under the tegmina.

The coupling of tegmina to the thorax and their waterproof underside in scytinopteroids provide an evidence of a more amphibious lifestyle than in any other Homoptera. These hoppers probably lived on helophytes and other waterside vegetation and were capable of temporary submergence. Helophytes and flood-adapted plant communities were more common and diverse in the Late Paleozoic than they are today [Ponomarenko, 1996]. The Late Permian entomofaunas of Kerbo-1 and Neptenne-2 in the Tunguska Basin consist almost entirely of numerous nymphs and a few adults of a single species of Paraknightiidae (both the abundance and the instar ratio are unusual for truly terrestrial insects), whereas the

copious plant megafossils in the Kerbo-1 insect bed almost all belong to the equisetalean *Phyllothea turnaensis*. The co-occurrence of numerous flightless nymphs and well preserved horsetails testifies that both were buried autochthonously in a shore biotope and that these hoppers fed on the horsetails [Shcherbakov, 2000].

The combination of extreme heating and drought reduced the habitable land area during the Permian-Triassic crisis [Benton, 2018]. It is therefore not surprising that scytinopteroids, small hoppers that lived on riparian vegetation and could submerge, survived the end-Permian extinction better than other homopteran superfamilies: Scytinopteroidea lost none of their four families, and Scytinopteridae retained their dominance into the Triassic [Shcherbakov, 2000, 2008a]. This success of scytinopteroids was a prerequisite for the great Mesozoic expansion of their descendants, the Heteroptera, originally littoral zoophages that later occupied various other biotopes. Scytinopterids with elytrized tegmina are known only from the Permian-Triassic transition (latest Permian to early Triassic), indicating that the association of scytinopteroids with waterside habitats became especially intimate during the Permian-Triassic crisis. This was the time when scytinopteroids gave rise to Nepomorpha, the basal group of Heteroptera.

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