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Permian insects from the Russky Island, South Primorye

Пермские насекомые с острова Русский в Южном Приморье

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КЛЮЧЕВЫЕ СЛОВА: ископаемые насекомые, Megasecoptera, Titanoptera, Grylloblattida, Homoptera, Neuroptera, Coleoptera, Mecoptera, энтомофауна, Южное Приморье, пермский период, кунгурский век.

ABSTRACT. The first Permian insect assemblage from the Russian Far East, collected in the lower Pospelovo Formation (Kungurian, Lower Permian) of the Russky Island near Vladivostok, is described. It is dominated by Grylloblattida (Ideliidae and Liomopteridae: *Liomopterites svetlanae* Aristov, **sp.n.**) and includes Megasecoptera (Scytohymenidae: *Oceanoptera elenae* Shcherbakov, **gen. et sp.n.**), Homoptera Auchenorrhyncha (Prosbolopseidae Ivaiinae: *?Cicadopsis* sp.), Plecoptera, Neuroptera (Permithonidae: *Okolpania eugeniae* Makarkin et Shcherbakov, **sp.n.**), Coleoptera Archostemata (Permocupedidae: *Maricoleus valentinae* Shcherbakov, **gen. et sp.n.**), Mecoptera (Permochoristidae: *Protopanorpa* sp., *?Petromantis* sp.), and presumed Titanoptera s.l. (Gerarina), but no Blattida or Orthoptera. Traces of insect-plant interactions include cordaite seeds with punctures made by Palaeodictyopteroidea and clutches of relatively large, lense-shaped eggs attached to leaves and stems (possibly produced by megasecopterans; the earliest record of exophytic oviposition). In the regular occurrence of palaeodictyopteroids and their feeding traces the Russky Island assemblage is similar to the Vorkuta Group (Pechora Basin) entomofauna, while in the absence of cockroaches it is closer to the Siberian Middle Permian assemblages. The systematic position of *Nemuropsis* Martynov, 1925 is discussed. The new insect species are named after the paleobotanists from Vladivostok, Elena B. Volynets, Valentina I. Burago, Svetlana A. Shorokhova and Eugenia V. Bugdaeva, who greatly facilitated our fieldwork.

РЕЗЮМЕ. Впервые с Дальнего Востока описан пермский комплекс насекомых — из нижней части поспеловской свиты (кунгурский ярус, нижняя пермь) острова Русский близ Владивостока. В нём доминируют Grylloblattida (Ideliidae и Liomopteridae: *Liomopterites svetlanae* Aristov, **sp.n.**), присутствуют Megasecoptera (Scytohymenidae: *Oceanoptera elenae* Shcherbakov, **gen. et sp.n.**), Homoptera Auchenorrhyncha (Prosbolopseidae Ivaiinae: *?Cicadopsis* sp.), Plecoptera, Neuroptera (Permithonidae: *Okolpania eugeniae* Makarkin et Shcherbakov, **sp.n.**), Coleoptera Archostemata (Permocupedidae: *Maricoleus valentinae* Shcherbakov, **gen. et sp.n.**), Mecoptera (Permochoristidae: *Protopanorpa* sp., *?Petromantis* sp.), и, возможно, Titanoptera s.l. (Gerarina), но не обнаружены Blattida и Orthoptera. Найдены следы взаимодействия насекомых и растений — проколотые палеодиктиоптероидами семена кордаитов и довольно крупные линзовидные яйца, отложенные на листья и стебли (самые древние экзофитные кладки, возможно, принадлежащие мегасекоптерам). По регулярным находкам палеодиктиоптероидов и следов их питания комплекс острова Русский сходен с энтомофауной воркутской серии Печорского бассейна, а по отсутствию тараканов — с комплексами из средней перми Сибири. Обсуждается систематическое положение *Nemuropsis* Martynov, 1925. Новые виды насекомых названы в честь Е.Б. Волынец, В.И. Бураго, С.А. Шороховой и Е.В. Бугдаевой — палеоботаников из Владивостока, оказавших нам неоценимую помощь в организации полевых работ.

The first Permian insect from Primorye was collected in 1923 near Vladivostok (the valley of Ob'yasnenie River, southern slope of Komarov Mt. — now within the city boundaries) by Pavel V. Vittenburg, an eminent Russian geologist, from the *Taonurus* horizon. These beds are now assigned to the upper subformation of the Pospelovo Formation (V.I. Burago, pers.comm.), dated Late Kungurian according to the International Stratigraphic Scale [Zakharov et al., 2009] (Ufimian of the East European Stratigraphic Scale). The fossil was described by Andrey V. Martynov [1925] as *Nemuropsis tenuis* Martynov, 1925, constituting a new family Nemuropsidae, which he placed, along with three other, Carboniferous families, in a new suborder (or even order) Paraplecoptera within Protorthoptera, on account of several similarities to Plecoptera.

The classification of Paleozoic orthopteroids is still disputable; most protorthopterans are now assigned to the orders Grylloblattida and Eoblattida. *Nemuropsis* is a poorly preserved, large insect (forewing length ca. 60 mm) possessing a nearly quadrate pronotum without paranota, and wings completely overlapping in repose. Although the two latter features are characteristic of stoneflies, the largest Permian Plecoptera are only half as large as *Nemuropsis*. The grylloblattids lacking pronotal paranota (part of suborder Protoperlina) are also smaller (forewing length less than 25 mm), and their wings only partly overlap in repose. So far as known, large eoblattids did not survive to the mid-Permian, but such a possibility cannot be excluded. Before re-examination of the holotype (the location of which is unknown) it is not possible to place *Nemuropsis* in one of these orders.

In the 1970s, four insect specimens were collected by V.I. Burago (Primorye Prospecting and Mapping Geological Expedition, Vladivostok) from three different Permian outcrops in Primorye (two of them from the lower Pospelovo Formation of Russky Island, outcrop 429), and one additional specimen by a field party of the Arthropoda Lab, Paleontological Institute (PIN), but these finds remain undescribed. In 2008, our field party of the Arthropoda Lab, PIN, joined by Elena B. Volynets and Valentina I. Burago, visited this outcrop on the Russky Island for several days and collected some seventy insects. The first Permian insect assemblage recorded from the Russian Far East is of high interest.

All the specimens mentioned below are deposited at PIN. They were collected from black coaly shales (containing abundant plant fossils, Bivalvia and few Conchostraca) of the lower sub-formation of Pospelovo Formation, cropping out in the coastal cliff 0.3 km SSW of the Cape Novosilsky, Russky Island near Vladivostok. This subformation is dated Middle Kungurian according to the International Stratigraphic Scale [Zakharov et al., 2009] (ca. 273 Ma; Late Kungurian of the East European Stratigraphic Scale; the Kungurian of the EESS is referred to as the Kungurian below).

The diverse vascular flora of the lower Pospelovo Formation is of the Siberian type, consists of sphenopsids, ferns, and Angaran cordaites and lacks undoubted pteridosperms and Cathaysian elements [Tashchi & Burago, 1974; Zimina, 1977, 1997; Zakharov et al., 2009]. This plant assemblage is similar to those from the Rudnik Subformation (Lek-Vorkuta Formation, Vorkuta Group, Kungurian or Ufimian) of the Pechora Basin and from the Usa and Starokuznetsk Formations (Kuznetsk Subgroup) of the Kuznetsk Basin [Kotlyar et al., 2006]. Abundant mosses (*Intia* sp. and *Uskatia* sp.: [Burago in Meyen, 1982]) and liverworts are recorded.

The insect remains are usually wing fragments or isolated body parts (nymphal wing pads, body segments, legs). The insect assemblage is quite diverse: 8 orders per 42 identifiable specimens. It is dominated by Grylloblattida (24 specimens, or more than half of all the identified insects). The palaeodictyopteroid Megasecoptera are represented with two wings, about 40 mm long, and probably also with several nymphal fragments. Homoptera (suborder Auchenorrhyncha) and Mecoptera are each known from two small wings. The remaining orders are represented each with a single specimen: one nymphal exuvium of Plecoptera, an incomplete forewing of Neuroptera, an elytron of Coleoptera (suborder Archostemata), and a large femur with two spine rows along the ventral surface, possibly belonging to a primitive Titanoptera s.l. (suborder Gerarina). More than thirty insect fragments were impossible to identify to order.

The insect groups recorded in this assemblage display a variety of diets: specialized sucking herbivory on vascular plants (Megasecoptera and Auchenorrhyncha), xylomycetophagy (i.e., feeding on rotting wood: larvae of Archostemata), saprophagy (most probable for Grylloblattida, larvae of Mecoptera, and nymphs of Plecoptera), and zoophagy (Gerarina, larvae of Neuroptera). The only doubtless aquatic insect is the nymph of Plecoptera.

The most significant traces of insect feeding are cordaite seeds with punctures made by beaks of Megasecoptera (represented in this assemblage by isolated wings) or some other palaeodictyopteroids (Figs 1–2), indicating that these insects were more abundant in the lower Pospelovo Formation than one may assume based only on their body fossils. Such feeding damage of cordaite seeds was first described from the Late Carboniferous of Tunguska Basin and attributed to Palaeodictyoptera by Sharov [1973]. Recently, it was reported also from the Early Permian Vorkuta Group (Kozhimrudnik Formation, correlated to the Lek-Vorkuta Formation, Kungurian or Ufimian) of the Pechora Basin [Shcherbakov, 2008]. Relatively large eggs, attached to fern-like leaves and other plants, provide the earliest record of the insect exophytic oviposition and may belong to megasecopterans (see below).

Several insect genera identified from the lower Pospelovo Formation of the Russky Island are most closely similar to those known from the Kungurian of the Urals (the megasecopteran *Oceanoptera* **gen.n.** and the lacewing *Okolpania eugeniae* **sp.n.**), the Mitino Formation, Kuznetsk Subgroup of the Kuznetsk Basin (formerly dated Ufimian, but now considered Kazanian

1 **2**

Figs 1–2. Cordaite seeds with punctures made by palaeodictyopteroids (possibly Megasecoptera): 1 — *Samaropsis* ex gr. *danilovii* Suchov, specimen PIN 5306/79; 2 — *S. postfrigida* Dombrovskaya, specimen PIN 5306/80 (identified by V.I. Burago). Scale bar 2 mm.

Рис. 1–2. Семена кордаитов, проколотые палеодиктиоптероидами (возможно, Megasecoptera): 1 — *Samaropsis* ex gr. *danilovii* Suchov, экз. ПИН 5306/79; 2 — *S. postfrigida* Dombrovskaya, экз. ПИН 5306/80 (определения В.И. Бураго). Длина масштабной линейки 2 мм.

[Shcherbakov, 2000; Ponomarenko, 2004]: the homopteran *?Cicadopsis* sp., the beetle *Maricoleus* **gen.n.**), and the Early Kazanian of the Arkhangelsk Region (the grylloblattid *Liomopterites svetlanae* **sp.n.**). The new beetle appears more primitive, and the new megasecopteran and lacewing more derived, than their western relatives.

The Russky Island belongs to the Bureya-Jiamusi-Khanka block at the east of Amuria microcontinent. In the Permian it was situated at the eastern margin of Asia. According to paleomagnetic data, Amuria had accreted to the North China block by the Late Carboniferous, but was not sutured to Siberia until the Late Jurassic [see Hankard et al., 2007]. Based on the wide occurrence of the Siberian-type flora and the high boreal marine fauna in Amuria, some authors suggested that, in the Permian, the latter block was situated closer to Siberia [Rees et al., 1999; Chumakov & Zharkov, 2002]. Other researchers explain these facts by global climatic oscillations rather than significant drift of the terranes, and consider the lower Pospelovo time belonging to one of the coolest intervals [Markevich & Zakharov, 2008; Zakharov et al., 2009].

The lower Pospelovo insect assemblage contains neither cockroaches (Blattida), nor Orthoptera. In the Middle and Late Permian these thermophilic groups disappeared from the record throughout Siberia, Mongolia and temperate Gondwana (except for orthopterans in South Africa), but remained present in warmer (frost-free?) climates; in particular, cockroaches are abundant in many Permian faunas of semiarid and arid zones [Shcherbakov, 2008]. In this respect the Russky Island assemblage resembles the roach-free Siberian and Mongolian faunas of the Middle and Late Permian, rather than the roach-rich faunas of the lower latitudes, including those from the Early Permian (Sakmarian–Artinskian) of North China, which contain abundant Blattida together with Orthoptera, Grylloblattida, and palaeodictyopteroids [Hong, 1998].

In the dominance of Grylloblattida, regular occurrence of palaeodictyopteroids (confirmed by finds of punctured seeds), and the record of a presumed titanopteran, the Vorkuta Group fauna of Pechora Basin [Rasnitsyn et al., 2005] is similar to the Russky Island assemblage, but in the former cockroaches co-dominate, Orthoptera are present, Homoptera and Oligoneoptera are very rare, and Neuroptera and Coleoptera are absent. These differences may be due to the maritime climate of the western periphery of Pangea having been milder than the monsoonal climate at its eastern periphery [Shcherbakov, 2008].

Order Megasecoptera

Two large incomplete wings represent two species of the family Scytohymenidae. Two nymphal exuvia (specimens PIN 5306/29–30) and several fragments probably belong to this order or to Palaeodictyoptera.

Family Scytohymenidae Martynov, 1937

REVISED DIAGNOSIS. RP once forked, other main stems simple. R–RA thickened, close to costal margin; weak

Sc along R–RA. MA anastomosed for short distance with RP, and CuA anastomosed with MP. Basal RP continued by distal MA, and basal M continued by distal CuA strong, convex; remaining veins weak. Crossveins few, most if not all in one gradate series.

COMPOSITION. *Scytohymen* Martynov, 1937 and *Tshekardohymen* Rohdendorf, 1940 from the Kungurian of the Urals; *Oceanoptera* **gen.n.** from the Kungurian of South Primorye.

REMARKS. The two monotypic genera from the Urals (the holotypes of their type species were re-examined) are more similar to each other than outlined by Rohdendorf [1940]. In *T. martynovi* Rohdendorf, 1940, the crossvein series is complete (including *mp-cua* and *cua-cup*), the second (submarginal) *ma-mp* seems present, and RA is slightly converging with RP1 distally. In *S. extremus* Martynov, 1937, preserved with less detail (crossveins poorly visible), the crossveins *ma-mp, mp-cua, cua-cup* and probably others in the series are present, whereas the double *ra-rp* may be an aberration or artifact. In both of these genera Sc seems traceable as a weak vein along R, in *Tshekardohymen* apparently terminating on RA slightly distad of RP+MA anastomosis. The genus *Karoohymen* Riek, 1976 from the Late Permian of South Africa, described in Scytohymenidae, was synonymized under *Asthenohymen* Tillyard, 1924 (Asthenohymenidae, Diaphanopterodea) by Carpenter [1992].

Oceanoptera Shcherbakov, **gen.n.**

TYPE SPECIES. *Oceanoptera elenae* Shcherbakov, **sp.n.**

DIAGNOSIS. RA with two anterior branches, distally parallel to costal margin and not converging with RP1. RP+MA anastomosis as long as free base of RP. RP arched anteriad beyond anastomosis. Free base of MA converging with R. MP+CuA anastomosis apparently rather long. Wing apex at RP1.

COMPOSITION. Type species.

COMPARISON. In *Scytohymen* and *Tshekardohymen,* RA distally diverges from the costal margin and at least slightly converges with RP1, the RP+MA anastomosis is extremely short (cross-junction), RP beyond it is straight, the free MA base is parallel to R, and the MP+CuA anastomosis is short. In the longer RP+MA and probably MP+CuA anastomosis the new genus is more advanced than two others.

ETYMOLOGY. From Greek *okeanos* (sea) and *pteron* (wing); gender feminine.

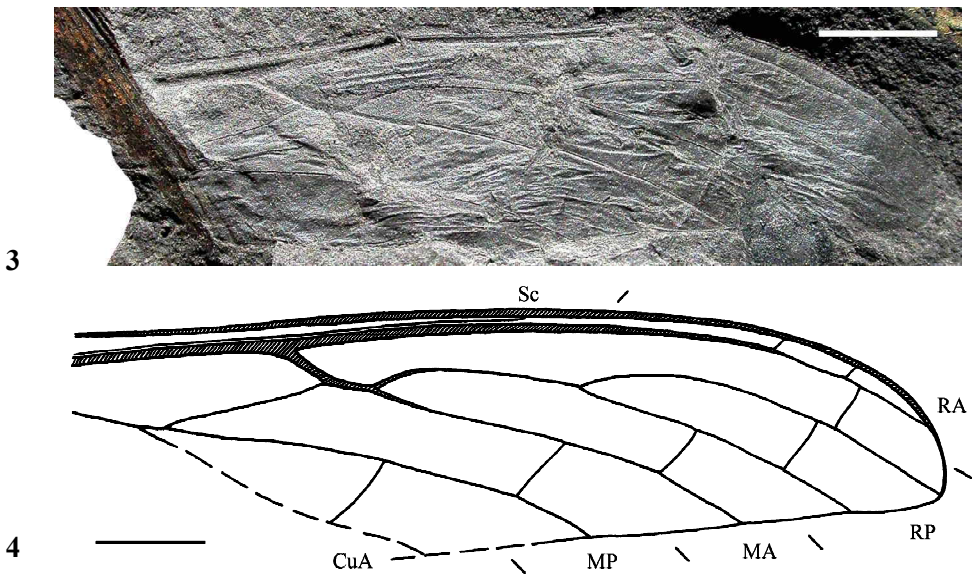
Oceanoptera elenae Shcherbakov, **sp.n.**

MATERIAL. Holotype PIN 5306/27, somewhat deformed wing (part and counterpart), basal part missing, cubital area bent under — Russky Island; lower Pospelovo Formation, Kungurian.

DESCRIPTION (Figs 3–4). Large, elongate wing, acutely rounded at apex; preserved length 40 mm (estimated complete length ca. 50 mm). C wide up to wing apex, with bases of spine-like setae. Sc probably terminates on C. R–R1, basal RP and RP+MA anastomosis are thickened, RP and MA shortly beyond anastomosis only slightly so, other preserved veins thin, crossveins faint. Distal portion of RP stem (beyond RP+MA anastomosis) 1/2 as long as RP1. MP+CuA anastomosis apparently longer than 1/2 of free base of MA; CuA leaving M just before separation of MA and MP. Crossveins *ra-rp, rp1-rp2, rp-ma, ma-mp* and *mp-cua* are present. Wing membrane and veins uniformly dark.

REMARKS. Another Megasecoptera specimen, PIN 5306/28, distal wing fragment (preserved length 25 mm, estimated complete length about 50 mm) belongs to the same family, but to a different species and probably to another genus. Unlike in *O. elenae* **sp.n.**, RA is more diverging from costal margin, RP is conspicuously thickened beyond the anastomosis, and the wing is dark in the stigmal space (between C and RA) and along longitudinal veins (broadly) and crossveins (narrowly), while the remaining membrane is colorless (transparent?); granulate microsculpture seems developed in dark areas. The costal vein is dilated up to wing apex, on lower surface with two rows of tubercles (bases of spine-like setae).

ETYMOLOGY. After Elena B. Volynets, a paleobotanist (Institute of Biology and Soil Sciences, Vladivostok).



Figs 3–4. *Oceanoptera elenae* Shcherbakov, **sp.n.** (Megasecoptera), holotype PIN 5306/27, wing: 3 — negative impression; 4 — venation. Scale bar 5 mm.

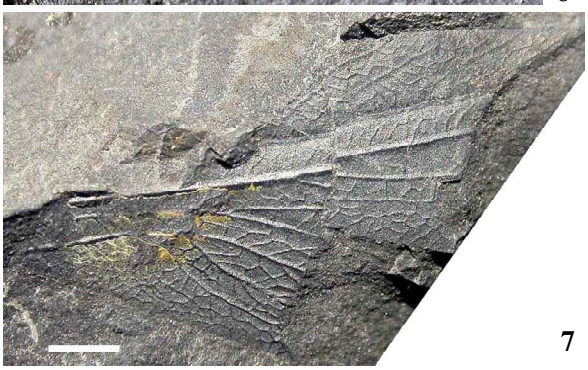
Рис. 3–4. *Oceanoptera elenae* Shcherbakov, **sp.n.** (Megasecoptera), голотип ПИН 5306/27, крыло: 3 — обратный отпечаток; 4 — жилкование. Длина масштабной линейки 5 мм.

Order Titanoptera s.l.?

A large femur with two spine rows along ventral surface (specimen PIN 5306/43; 11 mm long; Fig. 5) may belong to a primitive titanopteran (in this case reconstructed forewing length is about 50 mm). Paleozoic Geraridae were transferred to this order as the suborder Gerarina, and *Permotitan* Gorochov, 2004 (reconstructed forewing length about 140 mm) from the Early Permian Vorkuta Group of Pechora Basin was tentatively assigned to this suborder [Gorochov, 2004]. The earliest record of the second suborder, Mesotitanina is from the Late Permian of European Russia [Gorochov, 2007]. Titanoptera were ambush predators like praying mantises.

Fig. 5. ?Gerarina (Titanoptera s.l.), specimen PIN 5306/43, femur. Scale bar 2 mm.

Рис. 5. ?Gerarina (Titanoptera s.l.), экз. ПИН 5306/43, бедро. Длина масштабной линейки 2 мм.



Figs 6–7. 6 — Grylloblattida *incertae sedis,* specimen PIN 5306/12, pronotum; 7 — Ideliidae gen. sp., specimen PIN 5306/3, forewing fragment. Scale bar 2 mm.

Рис. 6–7. 6 — Grylloblattida *incertae sedis,* экз. ПИН 5306/12, пронотум; 7 — Ideliidae gen. sp., экз. ПИН 5306/3, фрагмент переднего крыла. Длина масштабной линейки 2 мм.

Order Grylloblattida

Suborder Grylloblattina

Among 24 specimens collected on the Russky Island (incomplete wings and pronotal shields: Fig. 6), only eight are identifiable to the family, and only two families are recorded: Liomopteridae (5 specimens, or more than 60% of identifiable grylloblattids) and Ideliidae (3 specimens: Fig. 7). Only one specimen can be identified to the species level (*Liomopterites svetlanae* Aristov, **sp.n.**).

This grylloblattid assemblage differs in its numerical composition from the Kungurian Chekarda assemblage, the Urals, where Liomopteridae account for some 10% and Ideliidae only 2% of all grylloblattid specimens), being more similar to that from the Early Kazanian of Soyana, Arkhangelsk Region (ca. 30% of each Liomopteridae and Ideliidae). Prevalence of Liomopteridae is characteristic of some Ufimian and Kazanian rather than Artinskian and Kungurian assemblages. However, this feature, as well as the low diversity (at Chekarda and Soyana there are 5 and 4 families per 10 grylloblattid specimens, respectively) may reflect some peculiarities of the paleoenvironment or taphonomic biases rather than the age of this fauna.

Family Liomopteridae Sellards, 1909

About 30 genera from the Permian of Europe, Asia, Africa and North America.

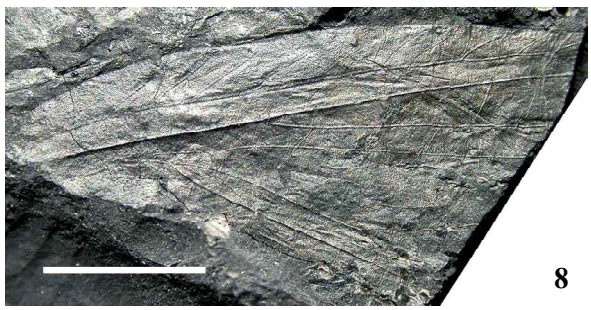
Liomopterites Sharov, 1961

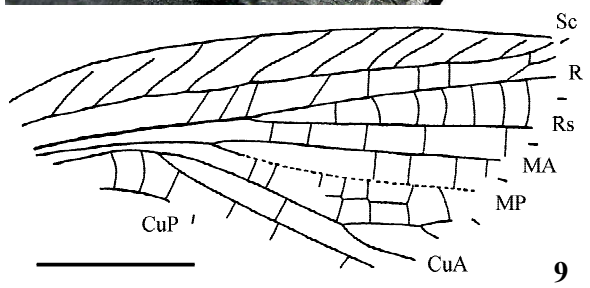
Thirteen species from the Early to Late Permian of Germany, European Russia, Kuznetsk Basin, and South Mongolia.

Liomopterites svetlanae Aristov, **sp.n.**

MATERIAL. Holotype PIN 5306/4, incomplete forewing (part and counterpart) — Russky Island; lower Pospelovo Formation, Kungurian.

DESCRIPTION (Figs 8–9). Medium-sized insects (reconstructed forewing length about 27 mm). Forewing with





Figs 8–9. *Liomopterites svetlanae* Aristov, **sp.n.** (Liomopteridae), holotype PIN 5306/4, incomplete forewing: 8 — positive impression; 9 — venation. Scale bar 5 mm.

Рис. 8–9. *Liomopterites svetlanae* Aristov, **sp.n.** (Liomopteridae), голотип ПИН 5306/4, фрагмент переднего крыла: 8 — прямой отпечаток; 9 — жилкование. Длина масштабной линейки 5 мм.

costal margin feebly convex. Costal area basally about as wide as, and at Rs origin nearly 1.5 times as wide as subcostal one. Sc with straight or slightly sigmoidal anterior branches, ending before distal 1/3 of wing. Rs originating 1/3 of wing length from base; Rs, MA and MP simple up to distal 1/3 of wing. CuA running close to M basally; CuA1 first forked in its distal third, with no less than 3 branches. CuP basally curved subparallel to CuA base. Crossveins simple, in median area forming double row of cells.

COMPARISON. Most similar to *L. pomorus* Storozhenko, 1992 from the Early Kazanian of Soyana, Arkhangelsk Region, but differs by the MA and MP not forked up to distal 1/3 of wing. In *L. pomorus* MA and MP are first forked about wing midlength [Storozhenko, 1992].

ETYMOLOGY. After Svetlana A. Shorokhova, a paleobotanist (Far Eastern State Technical University, Vladivostok).

Order Homoptera

Suborder Auchenorrhyncha

Infraorder Cicadomorpha

Family Prosbolopseidae Becker-Midgisova, 1946

Subfamily Ivaiinae Becker-Midgisova, 1960

The subfamily includes some ten genera from the Early to Late Permian of Europe and Asia.

An incomplete tegmen and isolated clavus (specimens PIN 5306/38–39), collected on the Russky Island, are similar to those of the monotypic genus *Cicadopsis* Becker-Migdisova, 1961, known from the Mitino Formation, Kuznetsk Subgroup of Kuznetsk Basin.

Order Neuroptera

Family Permithonidae Tillyard, 1922

The family comprises about 20 described Permian genera and includes nearly all the neuropterans known from that period [Novokshonov, 1996]. One species, tentatively assigned to Permithonidae, *Permantispa emelyanovi,* was described from the intertrappean deposits of the Tunguska Basin [Ponomarenko & Shcherbakov 2004], which are probably earliest Triassic. The only other neuropteran family recorded from the Permian is Archeosmylidae (one species in the terminal Permian of Australia, other species in the Triassic) [Ponomarenko & Shcherbakov 2004].

Only two, probably closely related genera of Permithonidae, are known to possess several crossveins in the distal portion of the subcostal space: *Okolpania* Vilesov, 1995 and *Kunguromaritus* Vilesov, 1995, both from the Kungurian of Chekarda, in the Urals. The new species from the Russky Island has a similar venation and therefore presumably belongs to the same generic group. It differs from both of these genera in having a narrower costal space and by the distinct posterior deflection of R1 at the junction with Sc, and, therefore, it may represent a new genus. However, because the specimen is too incomplete, the new species is tentatively assigned to *Okolpania,* based on its medium size (both species of *Kunguromaritus* are smaller), closely spaced crossveins between R1 and Rs, and the presence of costal crossveins. Until now, three species of *Okolpania* have been described by Vilesov [1995] and Novokshonov & Novokshonova [1997].

The holotype and paratype of the type species, *O. observabilis* Vilesov, 1995, turned out to be a part and a counterpart of the same specimen, PIN no. 1700/1674(1675).

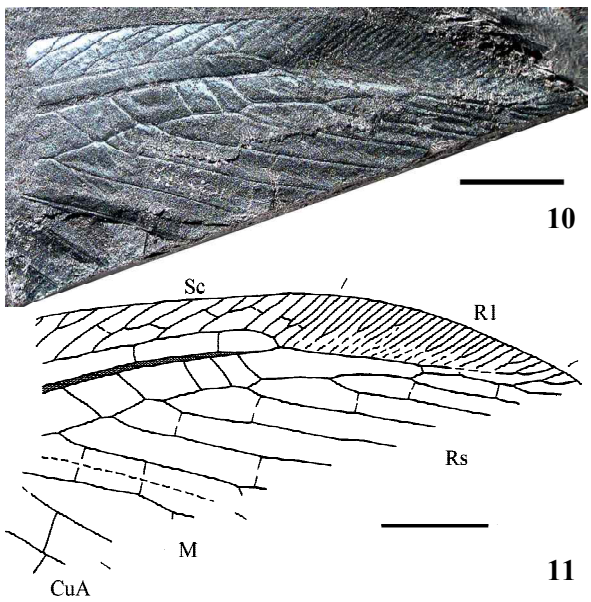
Okolpania Vilesov, 1995

Okolpania eugeniae Makarkin et Shcherbakov, **sp.n.**

MATERIAL. Holotype: PIN 5306/40 (part and counterpart), rather well-preserved distal portion of forewing — Russky Island; lower Pospelovo Formation, Kungurian.

DESCRIPTION (Figs 10–11). Medium-sized species. Forewing preserved length 10.8 mm (estimated complete length about 16–19 mm). Costal space relatively narrow (before junction of Sc with R1 less than twice width of subcostal space), somewhat dilated towards base. Trichosors not detected along preserved part of costal margin. Preserved subcostal veinlets rather strongly inclined to wing apex, widely spaced, simple or with one rather deep fork; connected by one crossvein (six weak crossveins detected). Sc short, terminating on R1 far distant from wing apex, sharply curved posteriad before junction. Veinlets of Sc+R1 mainly simple, some deeply forked, nearly straight, closely spaced, moderately inclined to wing apex. Subcostal space comparatively broad, with two crossveins preserved in distal portion. R1 thickened proximally, gradually narrowed towards apex; distinctly deflected posteriad at junction with Sc. Space between R1 and Rs moderately wide, narrowed distal to junction of Sc and R1, and very narrow apically (distal to origin of distalmost branch of Rs); five irregularly and closely spaced, oblique crossveins proximal to junction of Sc and R1, and one short crossvein distal to origin of most distal branch of Rs; Rs bent at these crossveins, somewhat zigzagged. Rs giving off six branches, most proximal one forked approximately at half length. Six weak crossveins between branches of Rs preserved. Distinct fold between Rs and M present. Only fragments of M and CuA preserved.

COMPARISON. The new species differs from the other three species by the narrower costal space and the distinct posterior deflection of R1 at its junction with Sc. It is most similar to *O. favorabilis* Novokshonov & Novokshonova, 1997



Figs 10–11. *Okolpania eugeniae* Makarkin et Shcherbakov, **sp.n.** (Permithonidae), holotype PIN 5306/40, incomplete forewing: 10 — negative impression (mirrored); 11 — venation. Scale bar 2 mm.

Рис. 10–11. *Okolpania eugeniae* Makarkin et Shcherbakov, **sp.n.** (Permithonidae), голотип ПИН 5306/40, неполное переднее крыло: 10 — обратный отпечаток (отражён зеркально); 11 — жилкование. Длина масштабной линейки 2 мм.

by its size, width of the costal space, and number of Rs branches, differing from it in the number and arrangement of crossveins between R1 and Rs and by a wider space between R1 and Rs.

REMARKS. The wing fragment is interpreted as a forewing, because the costal space is dilated towards wing base and the subcostal veinlets are forked. According to some authors, in all Neuroptera MA had shifted onto Rs (e.g. [Novokshonov, 1996]), but we follow here the traditional view that all branches of the sector belong to the radius [Comstock, 1918].

ETYMOLOGY. After Eugenia V. Bugdaeva, a paleobotanist (Institute of Biology and Soil Science, Vladivostok).

Order Coleoptera

Suborder Archostemata

Family Permocupedidae Martynov, 1933

The only beetle elytron from the Russky Island represents a new genus, which agrees in most characters with other permocupedids, but appears more primitive and similar to some Tshekardocoleidae in having four rows of cells in the subcostal space proximally. It is the earliest record of Permocupedidae, the other 9 genera being known from the Middle and Late Permian of Europe, Asia, Africa, and South America [Ponomarenko, 2004]. The vein nomenclature after Ponomarenko [1969].

Maricoleus Shcherbakov, **gen.n.**

Type species. *Maricoleus valentinae* Shcherbakov, **sp.n.**

DIAGNOSIS. Medium-sized beetles. Elytra elongate, widest before midlength, almost acuminate and less sclerotized apically. Costal margin evenly convex, epipleuron narrow, clearly deflected dorsad, with one row of small cells. Subcostal space with 4 rows of cells proximally and 3 rows distally, widened before 1/3 and beyond 2/3 elytron length (beyond R+M junction), narrower in between. R arched posteriad basally. M rather weak, forming common stalk with CuA basally, merging (or nearly so) into R far from elytral apex (R and M distinctly curved towards each other at junction). Radial and medial spaces each with 2 rows of cells. Cubital space at base with 4 rows of cells. 2A reaching 1/2 elytron length. Cells small, closely spaced, polygonal.

COMPOSITION. Type species.

COMPARISON. Distinguishable from all Permocupedidae by 4 rows of cells in the proximal part of the subcostal space (maximum 3 rows in other genera). Similar to *Uralocupes* Ponomarenko, 1969 in the elytron shape, but in this genus the medial space with 3 rows of cells. Similar to *Kaltanicupes* Rohdendorf, 1961, *Cytocupes* Rohdendorf, 1961 and *Eocupes* Rohdendorf, 1961 (at least to their type species, all from the Mitino Formation, Kuznetsk Subgroup, of the Kuznetsk Basin) by the M merging (or nearly so) into R far from the elytral apex (R and M distinctly curved towards each other at junction), but in these genera the subcostal space is not widened proximally, and the elytron is widest about midlength. Similar to *Kaltanicupes* (more exactly, to its type species *K. richteri* Rohdendorf, 1961) by the subcostal space conspicuously widened beyond the R+M junction, M weak, and cells small, closely spaced, and polygonal, but in the latter genus the subcostal space is proximally narrowed, with only 2 rows of cells. In other species assigned to *Kaltanicupes*, the R+M junction is absent or not evident, and the subcostal space is not widened distally; therefore *Kaltanicupes* is probably a heterogeneous taxon.

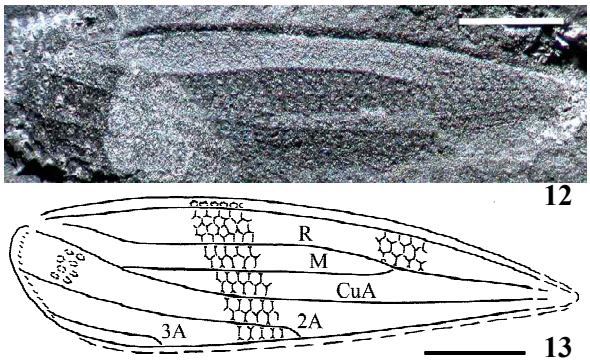
REMARKS. The M+CuA stalk, previously not reported in the family, is developed also in some other permocupedids, e.g. *Kaltanicupes acutus* Ponomarenko, 1963 (pers. obs.).

ETYMOLOGY. From Latin *mare* (sea) and *coleus* (sheath); gender masculine.

Maricoleus valentinae Shcherbakov, **sp.n.**

MATERIAL. Holotype PIN 5306/41, elytron (part and counterpart), cracked across at 2/3 length and along medial space — Russky Island; lower Pospelovo Formation, Kungurian.

DESCRIPTION (Figs 12–13). Elongate elytron (L/W ca. 3.8), widest about 1/4 its length; preserved length 5.3 mm (tip appears damaged; estimated complete length 5.7 mm). Subcostal space proximally with at least 8 cells in fourth row. M merging into R at 2/3 elytron length. R and CuA raised up to level of R+M junction, weak more distally, directed towards elytral apex; subcostal and medial spaces in distal 1/3 equally wide, cubital one narrower. 3A reaching about 1/4 elytron length.



Figs 12–13. *Maricoleus valentinae* Shcherbakov, **sp.n.** (Permocupedidae), holotype PIN 5306/41, elytron: 12 –combined photographs of negative (base) and positive impression (distal part, mirrored); 13 — venation. Scale bar 1 mm.

Рис. 12–13. *Maricoleus valentinae* Shcherbakov, **sp.n.** (Permocupedidae), голотип ПИН 5306/41, надкрылье: 12 — комбинация из фотографий обратного (основание) и прямого отпечатков (дистальная часть, отражена зеркально); 13 — жилкование. Длина масштабной линейки 1 мм.

ETYMOLOGY. After Valentina I. Burago, a paleobotanist (Primorye Prospecting and Mapping Geological Expedition, Vladivostok).

Order Mecoptera

Family Permochoristidae

The family includes numerous genera from the Permian, Triassic, and Jurassic. Two wings from the Russky Island are

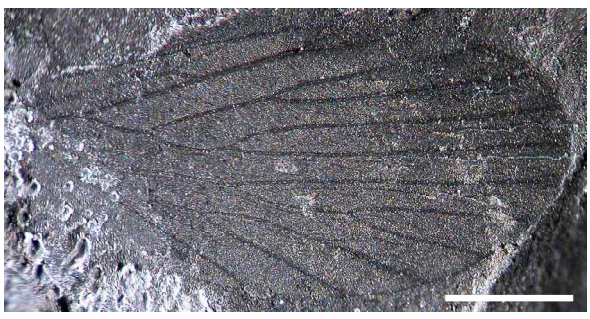


Fig. 14. *?Petromantis* sp. (Permochoristidae), specimen PIN 5306/44, hindwing (mirrored). Scale bar 1 mm.

Рис. 14. *?Petromantis* sp. (Permochoristidae), экз. ПИН 5306/44, заднее крыло (отражено зеркально). Длина масштабной линейки 1 мм.

identified as *Protopanorpa* sp. (by V.G. Novokshonov) and *?Petromantis* sp. (by A.S. Bashkuev; specimen PIN 5306/44; Fig. 14). The genus *Protopanorpa* Tillyard, 1926 comprises 4 species from the Early and Middle Permian of Europe and North America, and the genus *Petromantis* Handlirsch, 1904, some 20 species from the Early to Late Permian of Europe, Asia, and South America; both genera are quite common in the Kungurian of the Urals.

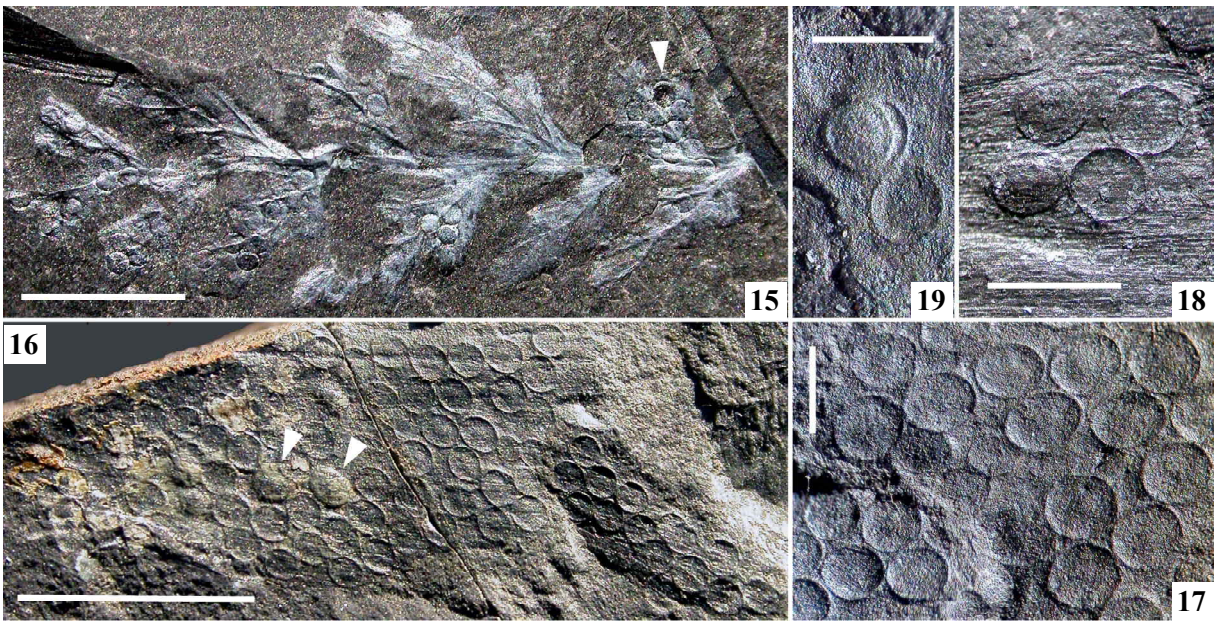
Traces of insect feeding

Two seeds of Angaran cordaites (*Samaropsis* spp.) each bear an oval hole (0.6×0.4 mm on one seed and 0.8×0.65 mm on another; Figs 1–2) in the centre of the nucleus, the greater diameter being oriented lengthwise. The hole penetrates through the integument on one side, leaving the opposite side intact. Such a damage type is attributed to Palaeodictyoptera and palaeodictyopteroids in general [Labandeira, 1998]. Two additional round perforations of a slightly greater diameter (ca. 1 mm), found on a third seed and an unidentified plant fragment, also belong to this category of feeding traces.

Insect eggs

The lense-shaped, usually oval structures of a uniform morphology and similar size (0.6–0.9 mm long, 0.5–0.7 mm wide), found on various plants, are interpreted here as insect eggs. Groups of 3–10 irregularly arranged eggs often occur on the small, narrow pinnules and sometimes on the midrib of pinnae of *Sphenopteris septentrionalis* Tschirkova and *Sphenopteris* sp. (identified by V.I. Burago; Fig. 15); *Sphenopteris* is a form genus for fern-like leaves, which includes both seed ferns and true ferns. The eggs are found also on plant fragments with parallel venation (some of them possibly cordaite leaves), sometimes in large clutches of up to some 70 eggs, closely spaced, arranged in rows, and in places almost hexagonally packed (Figs 16–17). The outlines of the eggs only occasionally overlap with one another. A few eggs are preserved isolated from plants. The salient feature of these eggs is a very distinct, narrow marginal rim, which is raised above the concave central area on the part and depressed below the convex central area on the counterpart. Most if not all eggs preserved on the same plant fragment are of the same convexity, sometimes with several eggs of the opposite convexity interspersed (Figs 15–16, 18). In a few cases, two eggs of the opposite convexity appear more or less superimposed (Fig. 19). We suggest that the eggshell consisted of the bottom and the top halves, which separated along the peripheral rim at eclosion. Assuming that the females oviposited onto only one side of the plant leaf or stem, we suggest that the most numerous objects are empty bottom halves of the eggshells, among which several intact eggs and a few eggs with a displaced top half are preserved. On fern-like leaves, the eggs were laid onto either the upper (Fig. 15) or the lower surfaces. The absence of any deformed eggs indicates that the eggshells were quite rigid and suggests the lenticular rather than spherical shape. Apparently, the bottom halves were shaped like a frying pan, with a somewhat flattened central area, and the top halves were rather cup-shaped, with the rim less distinct. The chorion seems to bear some surface sculpture, probably tuberculate.

These eggs were found mostly on *Sphenopteris* pinnae and sometimes on parallel-veined plant fragments, but not on



Figs 15–19. Exophytic insect eggs (?Megasecoptera) on plants: 15 — a pinna of *Sphenopteris* sp. with groups of empty eggshells on the upper surface of pinnules, specimen PIN 5306/84 (arrow — egg with displaced top); 16–17 — a large clutch of empty eggshells on a ?cordaite leaf fragment, specimen PIN 5306/86: 16 — entire impression (arrows: intact eggs), 17 — same, detail; 18 — two intact eggs (on the left) and two empty eggshells on a plant fragment with parallel venation, specimen PIN 5306/87; 19 — an egg with a displaced top (upper) and an empty eggshell on a pinnule of *Sphenopteris* sp., specimen PIN 5306/85. Scale bar 5 mm (Figs 15–16) and 1 mm (Figs 17–19).

Рис. 15–19. Экзофитные яйца насекомых (?Megasecoptera) на растениях: 15 — перо *Sphenopteris* sp. с группами пустых оболочек яиц на верхней стороне пёрышек, экз. ПИН 5306/84 (стрелка — яйцо со сдвинутой крышечкой); 16–17 — большая кладка из пустых оболочек яиц на фрагменте ?листа кордаита, экз. ПИН 5306/86: 16 — весь отпечаток (стрелки — невскрывшиеся яйца), 17 — часть кладки (увеличено); 18 — два невскрывшихся яйца (слева) и две пустые оболочки яиц на фрагменте растения с параллельным жилкованием, экз. ПИН 5306/87; 19 — яйцо со сдвинутой крышечкой (сверху) и пустая оболочка яйца на пёрышке *Sphenopteris* sp., экз. ПИН 5306/85. Длина масштабной линейки 5 мм (рис. 15–16) и 1 мм (рис. 17–19).

any other plants occurring in the fossil bed. Therefore, we can exclude the possibility that they were laid onto fallen leaves by some soil or freshwater invertebrates and reconstruct the egg producers as large, plant dwelling insects, apparently herbivores (large predators are never so abundant), demonstrating some degree of habitat specificity. The eggs were laid onto the surface of the plants instead of being inserted into plant tissues with an ovipositor. So far as we know, these Early Permian fossils represent the earliest record of the insect exophytic oviposition, previously known since the Middle Triassic (clusters of numerous small eggs surrounded by a mucous sheath, laid by aquatic insects in the Anisian of Vosges [Grauvogel-Stamm & Kelber, 1996]). Exophytic eggs with dorsal operculum, sometimes closely spaced in large clutches, are now met with e.g. in Lepidoptera and Heteroptera Pentatomomorpha. The rather large exophytic eggs from the Russky Island presumably belong to Palaeodictyopteroidea, more likely to Megasecoptera (the only large phytophagous insects in the assemblage) than to Palaeodictyoptera (not found there as body fossils), because the egg producers must have had their ovipositors greatly reduced, which is more probable in the former, less generalized order. Such attribution of these eggs means that Scytohymenidae and possibly some other advanced Megasecoptera may have lost their ovipositors. Because the two megasecopteran wings from the Russky Island represent two species of similar size, it is possible that, despite their similarity, different groups of eggs, particularly those preserved on different plants, may have belonged to multiple megasecopteran species.

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