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An extraordinary new family of Cretaceous planthoppers (Homoptera: Fulgoroidea)

Новое необычайное семейство меловых носаток (Homoptera: Fulgoroidea)

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КЛЮЧЕВЫЕ СЛОВА: Fulgoroidea, Auchenorrhyncha, Caliscelidae, носатки, покрытосеменные, неотения, филогения, ископаемые, меловой период, бирманский янтарь, янтарь Нью-Джерси, таймырский янтарь, Монголия.

ABSTRACT. A new family of somewhat cicadellid-like Cretaceous planthoppers, Perforissidae **fam.n.** is described, comprising two subfamilies and five new genera: Perforissinae **subfam.n.** for *Perforissus muiri* **gen.** et **sp.n.** (Late Cretaceous New Jersey amber) and *Cretargus emeljanovi* **gen.** et **sp.n.** (Late Cretaceous Taimyr amber); Cixitettiginae **subfam.n.** for *Cixitettix yangi* **gen.** et **sp.n.** (Late Cretaceous Taimyr amber), *Foveopsis fennahi* **gen.** et **sp.n.** (Early Cretaceous Burmese amber), and *Tsaganema oshanini* **gen.** et **sp.n.** (Early Cretaceous of Mongolia). The new family is interpreted as neotenous offshoot of Mesozoic Fulgoridiidae and as an early attempt to construct leafhopper-like forms from planthoppers, associated with colonization of the earliest angiosperms (or proangiosperms) in coastal-littoral environments. Caliscelidae demonstrating analogous neotenic traits presumably stand closest to ancestors of the issoid and ricanioid family groups. Some variants of hind leg armature in Perforissidae anticipate those later acquired by ricanioid families.

РЕЗЮМЕ. Описано новое семейство «цикадкообразных» меловых носаток, Perforissidae **fam.n.,** включающее два подсемейства и пять новых родов: Perforissinae **subfam.n.** для *Perforissus muiri* **gen.** et **sp.n.** (позднемеловой янтарь Нью-Джерси) и *Cretargus emeljanovi* **gen.** et **sp.n.** (позднемеловой таймырский янтарь); Cixitettiginae **subfam.n.** для *Cixitettix yangi* **gen.** et **sp.n.** (позднемеловой таймырский янтарь), *Foveopsis fennahi* **gen.** et **sp.n.** (раннемеловой бирманский янтарь) и *Tsaganema oshanini* **gen.** et **sp.n.** (ранний мел Монголии). Новое семейство рассматривается как неотеническое производное мезозойских Fulgoridiidae и как ранняя попытка сконструировать «цикаделлид» на основе носаток в связи с колонизацией первых покрытосеменных (или проангиоспермов) в прибрежных местообитаниях. Caliscelidae, демонстрирующие аналогичные неотенические преобразования, вероятно, наиболее близки к предкам иссоидной и риканиоидной групп семейств. Некоторые варианты вооружения задних ног перфориссид предвосхищают те, что возникли позднее в риканиоидной группе.

In 1970–1971 unusual planthoppers were discovered in the Late Cretaceous Taimyr amber. Later similar insects were found in the Late Cretaceous New Jersey amber, Early Cretaceous Burmese amber (mentioned in Shcherbakov [2000: 36]), and as compression fossils in the Early Cretaceous of Mongolia. A new family for these peculiar Fulgoroidea is established below. The first preliminary account on this family was given at the 9th International Auchenorrhyncha Congress, Sydney, 1997.

The type specimens of the new taxa are deposited in the Paleontological Institute, Russian Academy of Sciences, Moscow (PIN), the American Museum of Natural History, New York (AMNH), and the Natural History Museum, London (NHM). The photographs were processed with Helicon Focus 4.16.

Perforissidae Shcherbakov, **fam.n.**

TYPE GENUS. *Perforissus* **gen.n.**

DIAGNOSIS. Small to minute (3–5 mm), compact, caliscelid- and even macropsine-like planthoppers. Tegmina narrow with four main stems and little distal branching (6–10 apical cells). Lateral ocelli present. Pronotum deeply cleft posteriorly and produced between eyes. Apical pecten of hind tibia setigerous, metatarsal armature variable. Head, thorax and abdomen with rounded sensory pits persisting in adult; mesonotum with pits mediad of lateral carinae. Nymphs adult-like, not depressed dorsoventrally, abdomen without carinae or wax plates.

DESCRIPTION. Head with basic set of carinae. Eyes large, ovoid. Lateral ocelli well developed, median one lacking. Antenna below eye, unmodified, scape ring-like. Ros-

trum reaching at least hind trochanters, with last segment short and dark. Anteclypeus elevated along midline, angulate in profile. Lora faced laterad, indistinctly separated from short ecarinate postclypeus. Eumetope ('frons') broad, tricarinate (without submedian carinae), with numerous sensory pits and nearly straight lateral and ventral margins (areas of planthopper cranium termed after Anufriev & Emeljanov [1988]). Acrometope as narrow stripe between eumetope and coryphe. Coryphe ('vertex') arcuately transverse, posteriorly more or less overhung by produced anterior margin of pronotum.

Pronotum narrower than head with eyes, inverted V-shaped; disc divided into two halves by angular posterior incision, with short median carina and numerous sensory pits not arranged in regular rows, laterally extremely short; rounded pectoral (= paranotal) lobe (overlapping costal margin of tegmen in repose) with rounded group of pits and (just beneath small tegula) with incomplete collateral carina (nomenclature of pronotum after Emeljanov [1993]). Mesonotum medially depressed, with few sensory pits at sides, weak lateral carinae and sometimes also submedian carinae.

Tegmen narrow, leathery, usually membranized about crossveins and beyond. Prenodal part with four unbranched stems: (Sc+)R, M, CuA1 and CuA2, the latter sometimes forked into longitudinal CuA2a and CuA2b. (An alternative interpretation, i.e. (Sc+)R1, RS, M and CuA, was rejected, because the simple hindwing radius implies distal rather than proximal RS origin in tegmen. The forking of CuA much more proximal than that of (Sc+)R or M, and early division of CuA2 into CuA2a & CuA2b are commonplace in Mesozoic fulgoroids.) CuA stem rather short; (Sc+)R and M usually forming even shorter common stalk beyond narrow basal cell. (Sc+)R and M with short distal forks. 3–4 crossveins in nodal series: *r-m, m-cu,* 1–2 *icu*, in addition to transverse veinlet from CuA2 (or CuA2b) to ambient vein. Costal margin arched and usually with narrow hypocostal carina at base, straight to sinuate and foliaceous beyond. CuP developed only as claval furrow, ending blind before cubital veinlet (clavus open). Pcu+1A stalk short (sometimes undeveloped); 1A, Pcu+1A and ambient vein in one line, so that narrow commissural area directly continued with marginal membrane, often extended around tip of tegmen. Posterior vein stems sometimes with small pustulae.

Hindwing subtriangular, simple R–RS (R1 reduced) distally arched backwards, entering margin far beyond coupling lobe; all stems simple; two crossveins (*r-m* and *m-cu*); Pcu diverging from 1A, and the latter from jugal fold; marginal membrane sometimes developed.

Legs rather short, tibiae (especially fore) more or less flattened. Hind tibia carinate, unarmed or with one small spine laterally; hind tibia and 1st(–2nd) tarsomere more or less widened apically, with setigerous apical pectens (including tibial) of variable structure: (a) tibia and 1–2nd tarsomere with uniserial pectens; (b) 2nd tarsomere narrow, toothless, with acute ventroapical projection: (b1) tibia with biserial, 1st tarsomere with uniserial pecten; (b2) tibia with triserial, 1st tarsomere with biserial pecten. Claws simple, arolium shorter than claws.

The base of abdomen with paired internal sound-producing apodemes. Sides of 4–9th abdominal tergites with several sensory pits. Ovipositor ensiform with cutting inner valvulae, of variable length, adpressed to convex pygophore or diverging from concave pygophore.

Nymph (only early instars known) similar to adult, short-legged, elongate, not depressed dorsoventrally. Eumetope without submedian carinae. Pro- and mesonotum with diagonally running jugal carinae (= anterodiscal + postocular + lateral carina after Emeljanov [2001]), mesonotum with homologue of pronotal subocular carina, metanotum without carinae. Hind tibia and 1st metatarsomere with rudimentary apical pectens. Abdomen in dorsal aspect subtriangular with tergites not V-shaped, without median and submedian carinae and wax plates; sides of 4–7th segments with grooves homologous to sublateral carinae; 3–8th segments short, 9th and 10th longer, subcylindrical; 10th segment (anal tube) not much smaller than 9th. Rounded sensory pits on eumetope, pronotum (on disc and pectoral lobe), mesonotum (at both sides of jugal carina), metanotum (centre of each half), sides of 3–7th and posterior margin of 9th abdominal tergites.

COMPOSITION. Two subfamilies and five monobasic genera from the Cretaceous of Asia and North America.

COMPARISON. Many distinctive characters combined in the new family coexist elsewhere only in the extant family Caliscelidae (see below), but the latter is easily distinguishable from Perforissidae in having: ocelli absent; coryphe longer; pronotum less modified; tegmen with 3 stems in prenodal part, and Pcu+1A joining CuP; hindwing with Pcu close to 1A running along jugal fold; hind tibial pecten of asetigerous teeth.

Key to genera of Perforissidae (see also Table)

1. Hind tibia with bi- or triserial pecten, 2nd hind tarsomere toothless, with acute ventroapical projection. Tegmen with costal margin gibbous about midlength .... Perforissinae **subfam.n.** ... 2
— Hind tibia, 1st and 2nd tarsomere with uniserial apical pectens ..... Cixitettiginae **subfam.n.** ... 3
2. 1st hind tarsomere with irregular biserial pecten. Tegmen dark with pale-margined veins, posterior vein stems pustulate, costal area narrow distally, CuA2 unforked, two *icua* crossveins ..... *Perforissus muiri* **gen.** et **sp.n.** Late Cretaceous of New Jersey
— 1st hind tarsomere with uniserial V-shaped pecten. Tegmen pale with dark markings, costal area wider distally ..... *Cretargus emeljanovi* **gen.** et **sp.n.** Late Cretaceous of Taimyr
3(1) Tegmen unicolorous, costal margin gibbous about midlength, CuA2 forked before crossveins, costal area very narrow distally, R and M forming short stalk beyond basal cell, M proximally nearer to CuA1. Hind tibia and 1–2nd tarsomere slender, weakly widened apically. Ovipositor shorter than hind tibia, adpressed to pygophore .... *Foveopsis fennahi* **gen.** et **sp.n.** Early Cretaceous of Myanmar
— Tegmen with contrasting pale and dark pattern, gradually widened up to beyond midlength or nearly parallel-sided, CuA2 normally unforked. Hind tibia and 1–2nd tarsomere conspicuously widened apically 4
4. Tegmen not much widened beyond basal cell, costal area very narrow distally, R and M forming short stalk beyond basal cell, M proximally close to R, Pcu+1A extremely short or undeveloped, CuA2 sometimes forked. Mesonotum with well developed submedian carinae and convex prescutum. Hind tibia and 1–2nd tarsomere stout, much widened apically, tibial pecten with more than 10 teeth. Ovipositor longer than hind tibia, robust, adpressed to pygophore ..... *Tsaganema oshanini* **gen.** et **sp.n.** Early Cretaceous of Mongolia
— Tegmen conspicuously widened beyond basal cell up to beyond midlength, costal area not so narrow, R and M leaving basal cell separately, M proximally nearer to CuA1, Pcu+1A longer, CuA2 unforked. Mesonotum flat-

Table. Selected characters of tegmen, thorax, hind legs and ovipositor in the genera of Perforissidae
Таблица. Некоторые признаки переднего крыла, груди, задних ног и яйцеклада родов Perforissidae

		Tsaganema	*Cixitettix*	*Foveopsis*	*Cretargus*	*Perforissus*
teeth (number) in hind leg pectens	metatibial	uniserial (~13)	uniserial (8)	uniserial (7)	**~biserial (~13)**	**~triserial (~15)**
	1st tarsal	uniserial (~10)	uniserial (6)	uniserial (7)	uniserial (9)	**~biserial (~10)**
	2nd tarsal	uniserial (~9)	uniserial (?4)	uniserial (5)	**no (0)**	
tegmen shape		***~parallel-sided***	widened to 2/3	**gibbous at 1/2**		
hind legs		stout	~slender	**slender**	stout	
CuA2		normally unforked	unforked	**forked**	unforked	
colour pattern		+		**no**	+	
Pcu+1A		very short	short	**longer**	?	short
costal area distally		very narrow	**wider**	very narrow	**wider**	narrow
ovipositor		long adpressed	**short diverging**	short adpressed	?	
R+M stalk		–	**no**	+		
proximal M nearer		**to R**	to CuA1			
mesonotal carinae		**four**	two rudimentary or absent			

tish, without distinct carinae. Hind tibia and 1–2nd tarsomere rather slender, less widened apically, tibial pecten with less than 10 teeth. Ovipositor much shorter than hind tibia, slender, diverging from pygophore .... *Cixitettix yangi* **gen.** et **sp.n.**
Late Cretaceous of Taimyr

Perforissinae Shcherbakov, **subfam.n.**

TYPE GENUS. *Perforissus* Shcherbakov, **gen.n.**

DIAGNOSIS. Hind tibia with bi- or triserial pecten; 2nd hind tarsomere toothless, with acute ventroapical projection. Tegmen with costal margin gibbous about midlength.

COMPOSITION. Two monobasic genera from the Late Cretaceous ambers of New Jersey (*Perforissus* **gen.n.**) and Taimyr (*Cretargus* **gen.n.**).

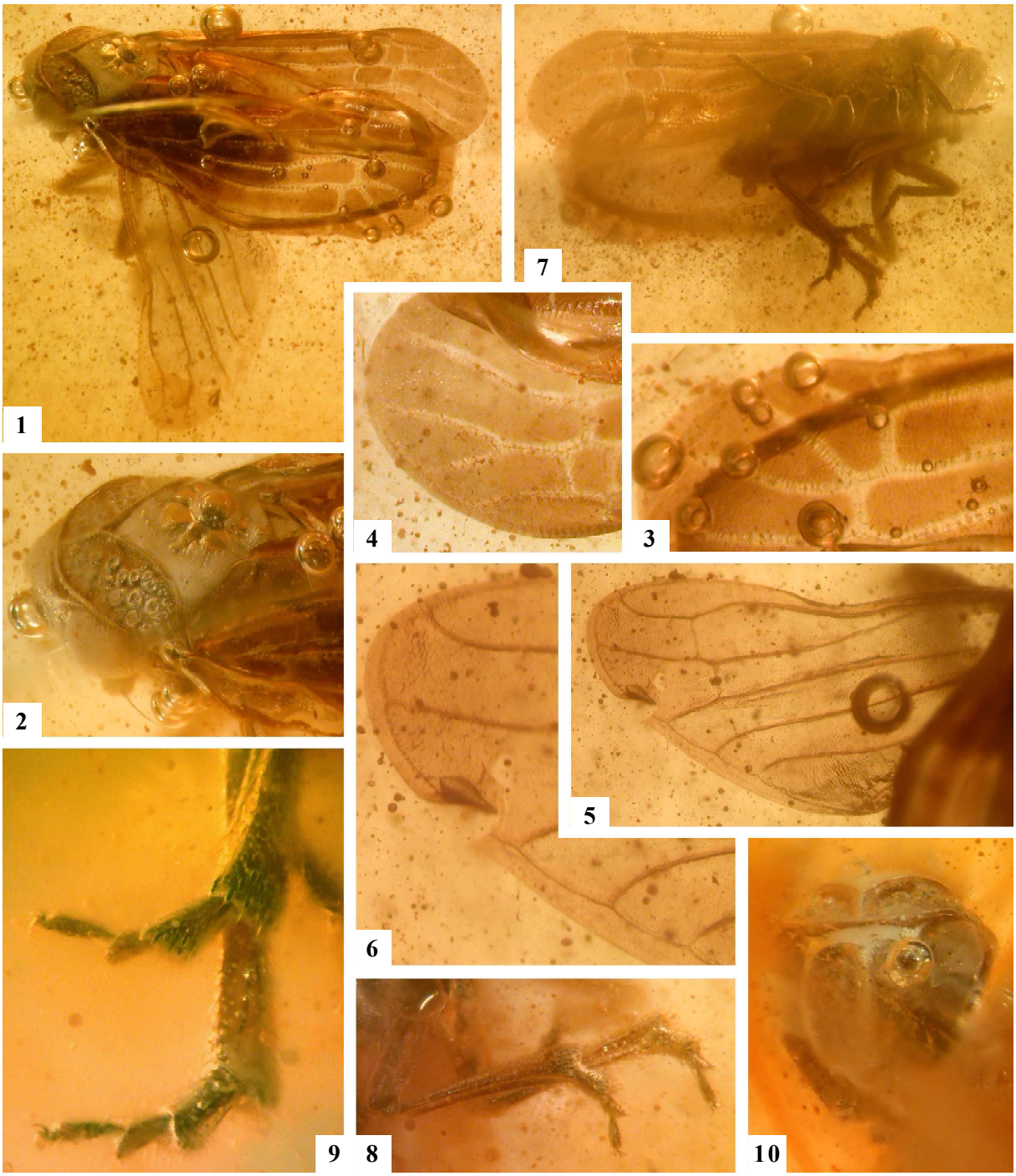
Perforissus muiri Shcherbakov, **gen.** et **sp.n.**
Figs 1–13, 47–50

MATERIAL. Holotype: male AMNH NJ-256 (in turbid amber, body mostly covered with thin milky layer); paratype: female(?) AMNH NJ-716 (in turbid amber, body covered with milky layer, ventral view partly blocked by large gas bubble); also isolated tegmen [Grimaldi et al., 2000: fig. 12 below] — New Jersey, Middlesex Co., Sayreville, White Oaks Pits, New Jersey amber, coll. Keith Luzzi; Late Cretaceous, Turonian, Raritan Formation (ca. 92 Ma = million years ago) [Grimaldi et al., 2000].

DIAGNOSIS. 1st metatarsomere with irregular biserial pecten. Tegmen dark with pale-margined veins, posterior vein stems pustulate, costal area narrow distally, R+M stalk short, CuA stem shorter than basal cell, CuA2 unforked, two *icua*. Mesonotum without distinct carinae.

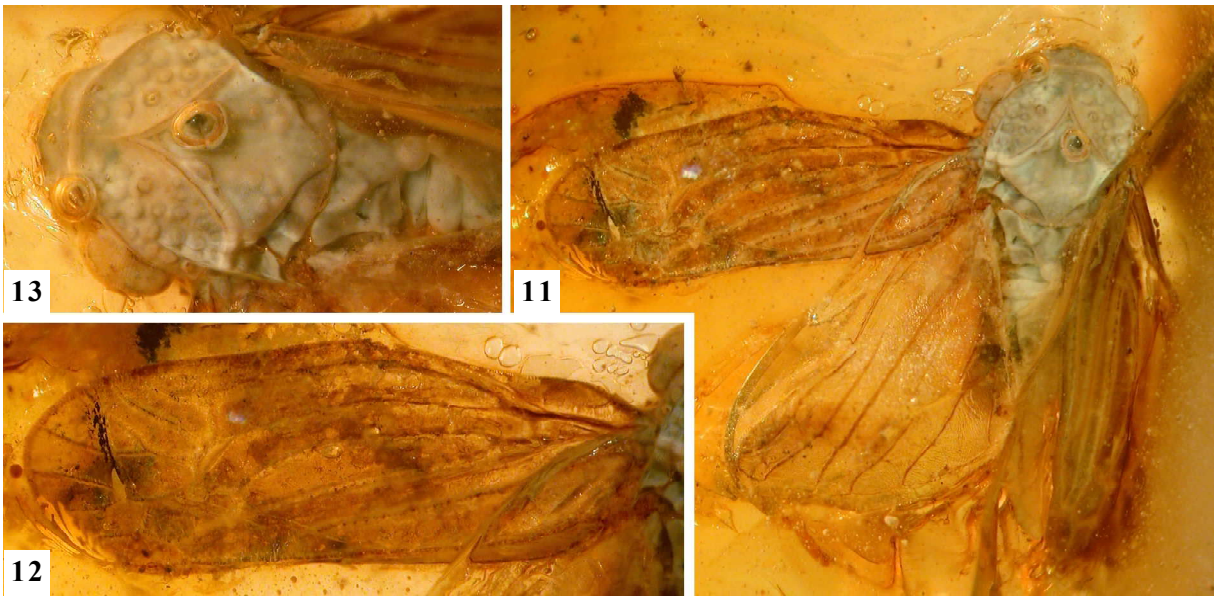
DESCRIPTION. Adult. Body with folded tegmina 3.1–4.0 mm long. Coryphe and acrometope very short (i.e. narrow), acrometope faced more or less upwards, its anterior margin angulate at junction with slightly arched median carina of eumetope (apparently shorter, less angulate and more horizontal in the paratype ?female, presumably due to sexual dimorphism); eumetope flattish, each half with no less than 12 sensory pits (5 pits ventrally, no pits along upper part of median carina); anteclypeus anteriorly produced. Rostrum reaching hind trochanters. Pronotum arcuately or somewhat trapezoidally produced between eyes over posterior head margin, overlapped by eyes laterally, with deep acutangular incision posteriorly, carinate medially and along anterior and posterior margins; each half of disc covered with no less than 25 sensory pits of different size (most of larger pits situated anterolaterally, no pits posteromedially); pectoral lobe posteriorly with at least 7 sensory pits. Mesonotum with narrow median depression widened towards flat, depressed, obtuse scutellum; sides of mesonotum evenly convex, each with no less than 5 sensory pits posteriorly (and possibly few smaller ones anteriorly). Tegmen 2.55–3.1 mm long, 0.95–1.1 mm wide, anterior areas not broadened (costal area distally narrow; CuA1 nearer to costal hump than to commissural margin), postnodal part more membranized; cells darkened, veins pale-margined (sometimes dark); costal margin convex and with hypocostal carina at base, shallowly sinuate and foliaceous beyond, gibbous about midlength; costal area deflected downwards; R+M stalk about as long as arculus, CuA stem at most twice longer than arculus and shorter than basal cell; M proximally diverging from R and running nearer to CuA1; 6–9 apical cells; R with at least 2 branches, M with 2–3, CuA1 with 1–2 branches; *m-cu* distal to *r-m* and between two *icua*; claval furrow ending blind at oblique or recurrent cubital veinlet; Pcu+1A very short (much shorter than clavus width at Pcu & 1A junction); 1A, Pcu+1A and ambient vein in straight line; commissural area continued into crimpled marginal membrane, widest between Pcu+1A and cubital veinlet, and traceable around tegminal tip up to nodus; prenodal veins raised; claval veins, CuA2, CuA1, and to a lesser degree M stems pustulate (with at most microscopic setae inserted in pustulae), veins in postnodal part crimpled; membrane finely granulate to transversely wrinkled. Hindwing 2.1–2.6 mm long; coupling lobe just beyond wing midlength; costal margin sinuate just before the lobe; R–RS up to *r-m* double-humped, closely parallel to margin proximally, diverging from it beyond coupling lobe, curved forwards apically; M proximally desclerotized and closely parallel to R; arculus long; R–RS, M, CuA and CuP simple; *r-m* distal to *m-cu;* claval fold straight from CuP to apex of CuA; CuP and Pcu curved backwards apically; Pcu apex twice nearer to CuP than to 1A; 1A distally diverging from jugal fold; marginal membrane well developed around wing tip up to jugal fold, not crimpled, widened along posterior margin (widest at Pcu); hindwing membrane finely wrinkled. Legs rather short, setose; tibia (especially fore) flattened. Hind tibia and tarsi beset with stiff setae on plantar surfaces; tibia

0.7–0.9 mm long, laterally unarmed, nearly twice longer than femur, twice widened to apex, with about 15 apical setigerous teeth in three irregular rows; 1st tarsomere with about 10 teeth in two irregular rows interspersed with dense hairs; apices of tibia and 1st tarsomere oblique, with teeth displaced towards acute outer angle, inner angle rounded; 2nd tarsomere shortest, with acute, setose ventroapical projection lacking teeth; 3rd tarsomere slender, less hairy. Male abdomen small, tapered, reaching slightly beyond midlength of tegmina; female abdomen longer, subtriangular in ventral aspect.



Figs 1–10. *Perforissus muiri* **gen.** et **sp.n.**: holotype male AMNH NJ-256: 1–6 — laterodorsal view: 1 — habitus; 2 — head and thorax; 3 — distal part of left tegmen; 4 — apex of right tegmen; 5 — hindwing; 6 — distal part of hindwing; 7–9 — lateroventral view: 7 — habitus; 8 — hind legs; 9 — distal parts of hind legs (note macrosetae of tibial pecten); 10 — head, anterior view.

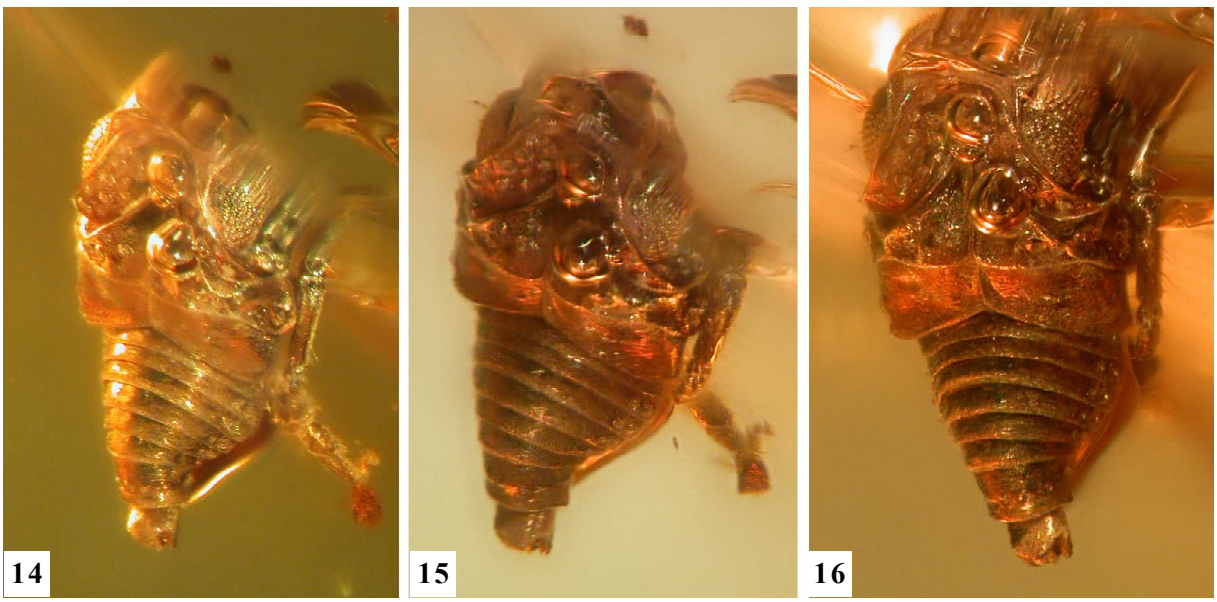
Рис. 1–10. *Perforissus muiri* **gen.** et **sp.n.**: самец, голотип AMNH NJ-256: 1–6 — сбоку-сверху: 1 — общий вид; 2 — голова и грудь; 3 — дистальная часть левого переднего крыла; 4 — вершина правого переднего крыла; 5 — заднее крыло; 6 — дистальная часть заднего крыла; 7–9 — сбоку-снизу: 7 — общий вид; 8 — задние ноги; 9 — дистальные части задних ног (видны макрохеты тибиального гребня); 10 — голова, спереди.



Figs 11–13. *Perforissus muiri* **gen.** et **sp.n.**: paratype female(?) AMNH NJ-716, dorsal view: 11 — habitus; 12 — left tegmen; 13 — head and thorax.

Рис. 11–13. *Perforissus muiri* **gen.** et **sp.n.**: самка(?), паратип AMNH NJ-716, сверху: 11 — общий вид; 12 — левое переднее крыло; 13 — голова и грудь.

REMARKS. An early (1st?) instar nymph from the same locality (Figs 14–16; AMNH NJ-230B, coll. G.R. Case; body somewhat shriveled, abdomen telescoped, ventral side obscured by gas bubble; photographed in Grimaldi et al. [2000: fig. 44f]) is tentatively assigned to the same species (yet more than one perforissid genus is known from some other localities, e.g. Yantardakh). Body 0.8 mm long, 0.4 mm wide, not depressed dorsoventrally; head and dorsum dark, venter and legs paler. Coryphe and acrometope short, anterior margin of acrometope angulate at junction with median carina of eumetope; prominent median carina of eumetope somewhat arched in profile; each half of eumetope with at least 4 sensory pits dorsolaterally (no pits along median carina). Eyes large, ovoid. Pronotum inverted V-shaped, trapezoidally produced between eyes, with deep acutangular posterior incision; each disc half with no less than 12 sensory pits; jugal carina arched; pectoral lobe with at least 4 pits. Mesonotum with small posterior incision; each half of mesonotum with a group of 4 sensory pits mediad of arched jugal carina, 5th pit at this carina (that kinked outwards there and giving off a rudimentary carina running anterolaterad and serially homologous to subocular carina of pronotum), 6th pit just laterad of jugal carina, and 2



Figs 14–16. *?Perforissus muiri* **gen.** et **sp.n.**, 1st(?) instar nymph AMNH NJ-230B, habitus, oblique anterodorsal views (in 16, face not visible beyond reflective fissure).

Рис. 14–16. *?Perforissus muiri* **gen.** et **sp.n.**, нимфа 1-го(?) возраста AMNH NJ-230B, общий вид спереди-сбоку-сверху (на 16, лицо скрыто за зеркальной трещиной).

pits on rudimentary forewing pad. Metanotum with posterior margin shallowly V-shaped, 2 small close-set sensory pits near the centre of each half, hindwing pads not developed. Legs short, tibiae and tarsi with sparse setae, tarsi two-segmented; hind tibia 0.25 mm long, widened towards apex in lateral aspect; hind tibia and 1st metatarsomere with uniserial apical pectens of pale macrosetae, at least some of which provided with dark, tooth-like bases. Abdomen short, subtriangular in dorsal view, 3–8th tergites (especially 3–4th) very short, 3rd at each side with one, 4–7th with two sensory pits (large outer and small inner ones) separated by a groove (homologue of sublateral carina), 9th tergite twice longer, its posterior third depressed, separated by a row of 6 sensory pits faced caudad. 10th segment (anal tube) cylindrical, about as long as wide, with three low rounded flaps (dorsal and paired lateral) at apical margin.

ETYMOLOGY. Latin *perforo* (perforate) and the genus *Issus;* gender masculine. The type species is named after Frederick Muir (1872–1931) who laid down the principles of planthopper classification.

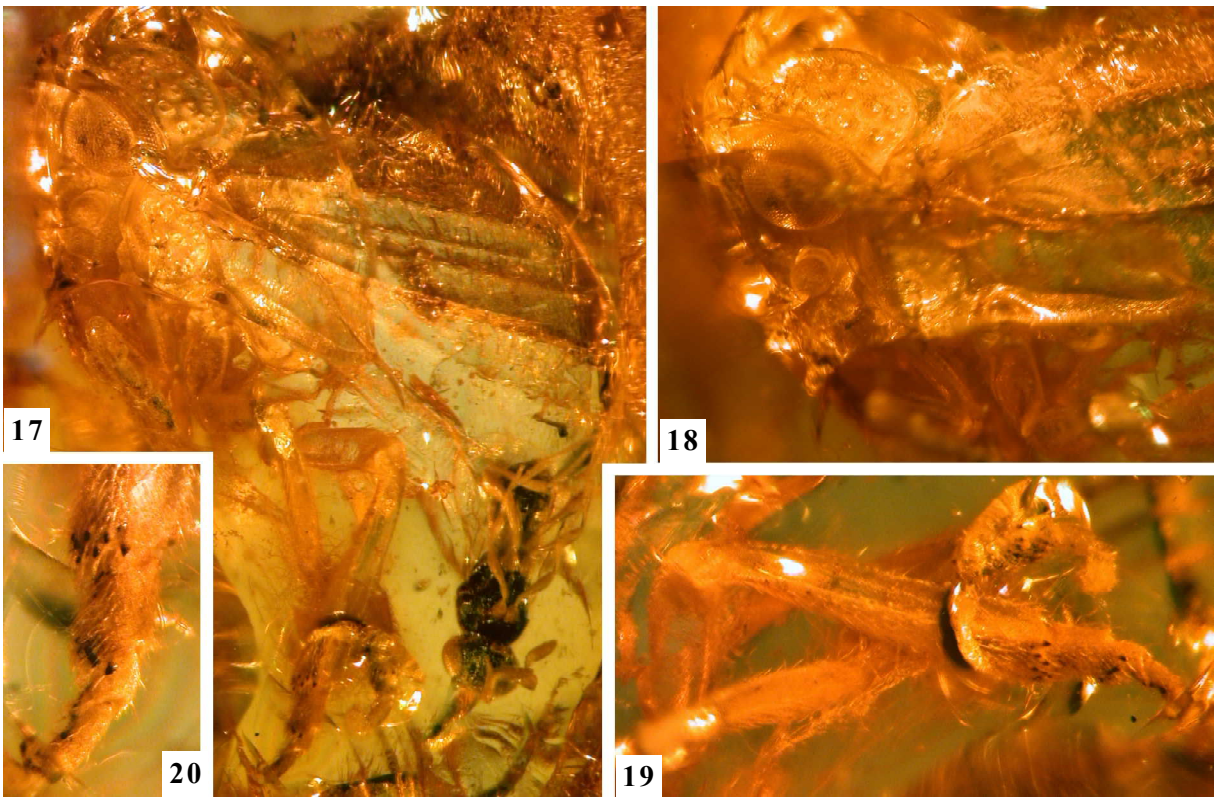
Cretargus emeljanovi Shcherbakov, **gen.** et **sp.n.**
Figs 17–20, 51

MATERIAL. Holotype: adult PIN 3311/562a (exposed to amber surface with right side, abdomen and distal part of left tegmen missing; this amber piece contains also a scelionid) — Yantardakh, Maimecha River, east of Taimyr Peninsula; Late Cretaceous, Santonian (ca. 85 Ma), Kheta Formation, retinite [Eskov, 2002]; coll. V.V. Zherikhin et al. 1971.

DIAGNOSIS. 1st metatarsomere with uniserial V-shaped pecten. Tegmen pale with dark markings, costal area distally not very narrow, R+M stalk short, CuA stem about as long as basal cell. Mesonotum with rudimentary lateral carinae.

DESCRIPTION. Adult. Body as preserved 3.0 mm long (reconstructed length with folded tegmina ca. 4.5 mm). Lateral ocelli well developed. Scape ring-like; pedicel subglobose, distally with small sensillar rosettes. Paranotum with deep acutangular incision posteriorly; each half of disc with about 25 sensory pits; pectoral lobe with no less than 12 pits, overlapping hypocostal carina in repose. Mesonotum (as observed from inside) with feeble, short lateral carinae and 3 sensory pits in each half (at and just mediad of lateral carina), broadly depressed and shortly carinate medially; scutellum depressed and transversely wrinkled, its tip raised. Tegmen 1.3 mm wide, 2.3 mm long as preserved (reconstructed ca. 3.5 mm long), pale with 1st cubital and anal areas darkened; anterior areas broadened (costal area distally not very narrow; CuA1 nearer to commissural margin than to costal hump); costal margin steeply convex and with hypocostal carina at base, shallowly sinuate and foliaceous beyond, gibbous about midlength; costal area deflected downwards; R carinate; R+M stalk about as long as arculus, CuA stem about as long as basal cell; M proximally diverging from R and running nearer to CuA1. Tibiae somewhat flattened; hind tibia 1.1 mm long, nearly twice widened towards apex in lateral aspect, unarmed laterally; hind tibia and 1st tarsomere with plantar surfaces densely setose and apical pectens setigerous; tibial pecten of about 13 teeth, biserial at outer side, zigzagged at inner side; 1st tarsal pecten V-shaped, uniserial of some 9 teeth; 2nd tarsomere toothless, with acute ventroapical projection.

ETYMOLOGY. Cretaceous, and Argus Panoptes (Argus "all eyes"), a giant with a hundred eyes in Greek mythology; gender masculine. The type species is named after Prof Alexander Fyodorovich Emeljanov, eminent Russian entomologist.



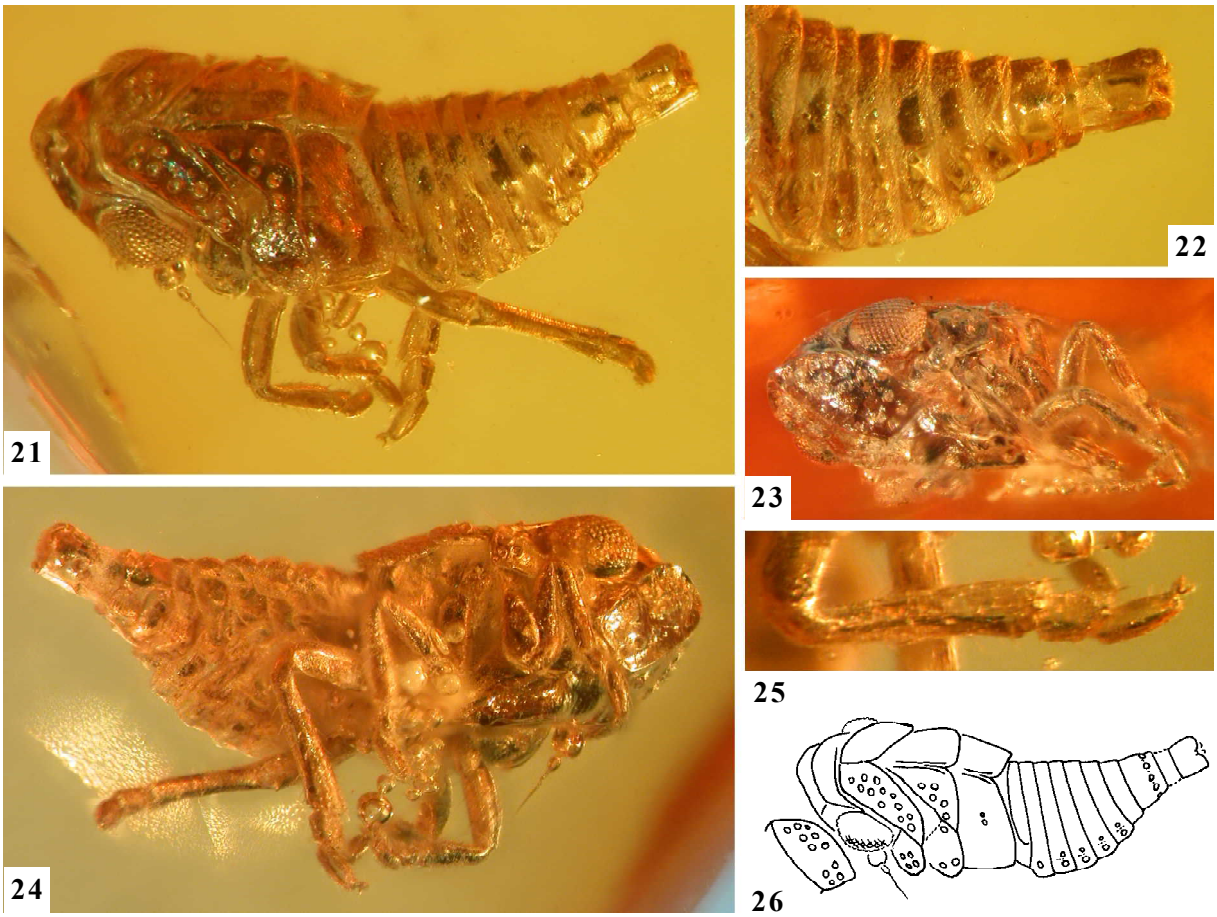
Figs 17–20. *Cretargus emeljanovi* **gen.** et **sp.n.**, holotype adult PIN 3311/562a, lateral view: 17 — habitus; 18 — head and thorax; 19 — mid and hind legs; 20 — distal part of left hind leg (note macrosetae on tibial and 1st tarsal pectens).

Рис. 17–20. *Cretargus emeljanovi* **gen.** et **sp.n.**, имаго, PIN 3311/562a, сбоку: 17 — общий вид; 18 — голова и грудь; 19 — средние и задние ноги; 20 — дистальная часть левой задней ноги (видны макрохеты тибиального и 1-го тарзального гребней).

?Cretargus emeljanovi Shcherbakov, **gen.** et **sp.n.**
Figs 21–26

MATERIAL. Early instar nymph PIN 3311/561 (body slightly inflated, abdomen extended) — Yantardakh, Maimecha River, east of Taimyr Peninsula; Late Cretaceous, Santonian (ca. 85 Ma), Kheta Formation, retinite [Eskov, 2002]; coll. V.V. Zherikhin et al. 1971.

DESCRIPTION. Nymph (1st instar?). Body 1.35 mm long, 0.5 mm wide, elongate, not depressed dorsoventrally; head and thorax darkened, abdomen and legs paler. Coryphe appearing not very short, trapezoidal with anterior margin arched; acrometope shorter, separated from eye by low vertical carina; anterior margin of acrometope slightly angulate at junction with median carina of eumetope; each half of eumetope with 11 sensory pits (7 dorsally and 4 ventrally, no pits along median carina); prominent median carina of eumetope arched in profile; ventral carinae of eumetope submarginal, cutting off a low triangular space adjacent to postclypeus. Eyes large, ovoid. Scape short, pedicel subglobose, base of flagellum elliptically swollen. Postclypeus convex, contiguous with lora dorsally; anteclypeus large, highly convex, raised along midline and subangulately produced in anterior third, apically narrowed, reaching beyond fore coxae. Rostrum with last segments short, dark, reaching beyond hind coxae. Pronotum inverted V-shaped, trapezoidally produced between eyes, with deep acutangular posterior incision; each disc half with 12 sensory pits; jugal carina nearly straight; subocular carina vertical; pectoral lobe with a group of 4 pits. Mesonotum with small acutangular posterior incision; each half of mesonotum with a group of 4 sensory pits mediad of nearly straight jugal carina, 5th pit at this carina (that kinked outwards there and giving off a weak carina running anterolaterad and serially homologous to subocular carina of pronotum), 6th pit just laterad of jugal carina, and 2 pits on rudimentary forewing pad; mesonotum laterally about 1.5 times as long as pronotum (pectoral lobe) and much shorter than metanotum. Metanotum with posterior margin shallowly V-shaped, 2 small sensory pits near the centre of each half, hindwing pads not developed. Legs short, tibiae and tarsi with sparse setae (long lateral setae on tibiae), tarsi two-segmented, 2nd tarsomere with a pair of curved apical setae; claws simple, slender; arolium rounded; hind tibia 0.3 mm long, conspicuously widened towards apex in lateral aspect; 1st metatarsomere setose ventroapically; hind tibia and 1st metatarsomere with rudimentary uniserial apical pectens of few pale macrosetae, of which outer two and innermost one provided with dark, tooth-like bases (some 5 macrosetae in tibial and some 4 in tarsal pecten). Abdomen subtriangular in dorsal view, 2–5th tergites very short, 6–8th short, 3rd at



Figs 21–26. *?Cretargus emeljanovi* **gen.** et **sp.n.**, 1st(?) instar nymph PIN 3311/561: 21–22 —laterodorsal view: 21 — habitus; 22 — abdomen; 23 — head, anterior view; 24–25 — lateroventral view: 24 — habitus; 25 — hind leg; 26 — arrangement of sensory pits on dorsum and eumetope.

Рис. 21–26. *?Cretargus emeljanovi* **gen.** et **sp.n.**, нимфа 1-го(?) возраста PIN 3311/561: 21–22 — сбоку-сверху: 21 — общий вид; 22 — брюшко; 23 — голова, вид спереди; 24–25 — сбоку-снизу: 24 — общий вид; 25 — задняя нога; 26 — расположение сенсорных ямок на спинной стороне и эвметопе.

each side with one small, 4–7th with two sensory pits (large outer and small inner ones) separated by a groove (homologue of sublateral carina), 9th tergite twice longer, its posterior third depressed, separated by a row of 8 sensory pits faced caudad; abdominal venter concave, poorly sclerotized; laterotergites directed ventromediad; pregenital sternites slightly V-shaped; 9th sternite trapezoidal, with transverse groove at midlength, swollen before the groove. 10th segment (anal tube) cylindrical, about as long as wide, with three low rounded flaps (dorsal and paired lateral) at apical margin.

REMARKS. The nymph from Yantardakh, the best preserved of all perforissid specimens at hand, is strikingly similar (including the number and arrangement of sensory pits) to the nymph of *Perforissus muiri* **gen.** et **sp.n.** The latter probably represents the same instar and differs only in minor characters (eumetope less arched in profile, 6 pits on 9th abdominal tergite, size 20% smaller as measured across thorax), other differences being mostly explainable by shriveled condition of the specimen (seemingly more squat body and shorter coryphe, rostrum, abdomen and anal tube). Adults of two genera and species are known from Yantardakh: *Cretargus emeljanovi* **gen.** et **sp.n.** belonging to the same subfamily as *P. muiri* **gen.** et **sp.n.,** and *Cixitettix yangi* **gen.** et **sp.n.** from another subfamily (see below). On account of apically widened hind tibia, ventrally setose 1st metatarsomere and larger size of Yantardakh nymph, it is tentatively associated with adult of *C. emeljanovi* **gen.** et **sp.n.** that is larger than that of *P. muiri* **gen.** et **sp.n.** (whereas adult of *C. yangi* **gen.** et **sp.n.** is smaller than the latter). The nymph is probably 1st instar, because its forewing pad is no much larger than pectoral lobe of pronotum, and the nymph length is less than 1/3 of the length reconstructed for adult *C. emeljanovi* **gen.** et **sp.n.**

Cixitettiginae Shcherbakov, **subfam.n.**

TYPE GENUS. *Cixitettix* Shcherbakov, **gen.n.**

DIAGNOSIS. Hind tibia, 1st and 2nd tarsomere with uniserial apical pectens.

COMPOSITION. Three monobasic genera from the Late Cretaceous amber of Taimyr (*Cixitettix* **gen.n.**), Early Cretaceous Burmese amber (*Foveopsis* **gen.n.**), and the Early Cretaceous of Mongolia (*Tsaganema* **gen.n.**).

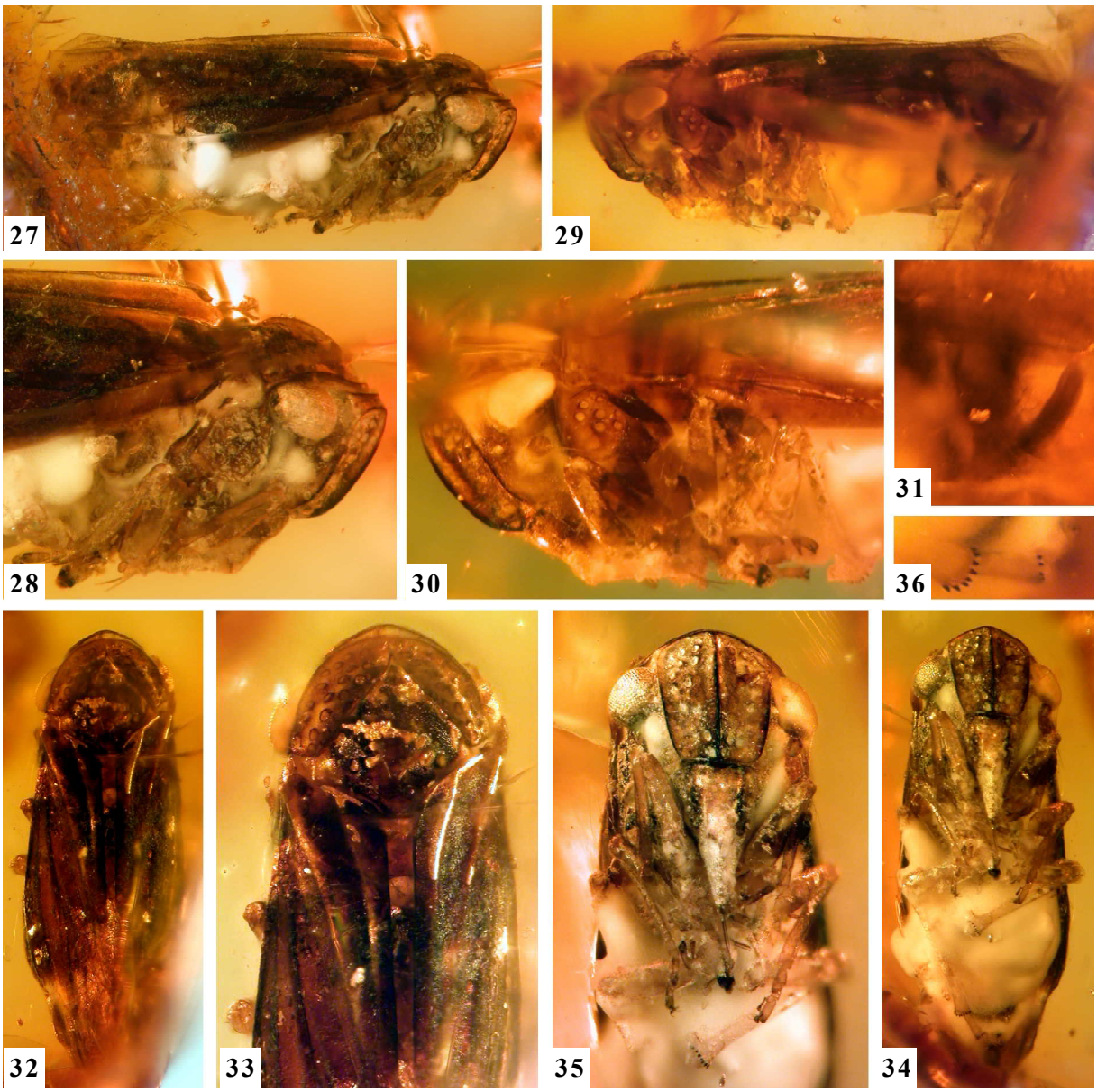
Cixitettix yangi Shcherbakov, **gen.** et **sp.n.**
Figs 27–36, 52

MATERIAL. Holotype: female PIN 3130/169 (abdomen covered with thick milky layer; specimen seems to be desiccated before burial in resin, probably spider's victim: left fore and hind tarsus and most of right fore tarsus missing; damaged right tegmen and left fore, mid and right mid legs at trochanterofemoral joint detached but preserved in nearly natural position, venter with some adherent debris and fine threads, presumably spider silk) — Yantardakh, Maimecha River, east of Taimyr Peninsula; Late Cretaceous, Santonian (ca. 85 Ma), Kheta Formation, retinite [Eskov, 2002]; coll. V.V. Zherikhin et al. 1970.

DIAGNOSIS. Tegmen unevenly darkened with pale markings, membranized about crossveins and beyond, conspicuously widened beyond basal cell up to beyond midlength, costal area moderately narrow, R and M leaving basal cell separately, M proximally nearer to CuA1, CuA stem longer than basal cell, CuA2 unforked, Pcu+1A not very short, and posterior vein stems pustulate. Mesonotum without conspicuous carinae. Hind tibia and 1–2nd tarsomere moderately widened apically, tibial pecten with less than 10 teeth. Ovipositor much shorter than hind tibia, slender, diverging from pygophore.

DESCRIPTION. Adult. Body with folded tegmina 3.2 mm long, 1.1 mm wide, gradually widening from eyes to about claval apices, then steeply narrowed towards tips of folded tegmina; mesonotum and prenodal tegmina dark; head, pronotum, venter and legs paler. Exposed part of coryphe shorter than acrometope; acrometope faced nearly forwards, its anterior margin steeply arched and slightly angulate at junction with median carina of eumetope; eumetope convex, each half with 13 fully developed sensory pits (10 dorsolaterally and 3 medioventrally) plus possibly few rudimentary ones; prominent median and lateral carinae of eumetope arched in profile (especially ventrally); eumetope separated from postclypeus by deep groove. Lateral ocelli well developed. Pedicel pyriform. Postclypeus without carinae, contiguous with lora; anteclypeus raised along midline, angulate in profile in anterior third; small or rudimentary sensory pits on maxillary plates, genae and postclypeus. Rostrum reaching hind trochanters, its apex black, stylets extracted from labial groove. Pronotum strongly arcuately produced anteriorly, very deeply cleft posteriorly; each half of disc with no less than 18 sensory pits faced chiefly backwards; collateral carina short; pectoral lobe posterodorsally with rounded group of 9 sensory pits (7 fully developed and 2 rudimentary), overlapping hypocostal carina in repose. Mesonotum without conspicuous carinae, with 3 sensory pits at each side, slightly depressed and transversely wrinkled towards scutellum, its tip obtuse. Mesepisternum with prominence below pectoral lobe. Tegula small. Tegmen 2.7 mm long, 0.8 mm wide, conspicuously widened beyond basal cell, widest beyond midlength; prenodal part dark (claval veins pale basally); postnodal part (as well as claval apex and apices of cubital areas) membranized, slightly suffused (veins paler) and transversely wrinkled, pale nodal band along crossvein series; costal margin steeply arched and with hypocostal carina near base, nearly straight and foliaceous beyond; R and M not forming a stalk, CuA stem longer than basal cell; M proximally diverging from R and running nearer to CuA1; 7 apical cells; R, M and with 2 branches each, CuA with 3 branches; *m-cu* distal to *r-m* and aligned with single *icua* and cubital veinlet; one faint *cup-pcu* seemingly present; claval furrow ending blind before desclerotized cubital veinlet; Pcu+1A short (shorter than clavus width at Pcu & 1A junction); 1A, Pcu+1A and marginal vein in nearly straight line; commissural area continued into narrow, crimpled marginal membrane continued somewhat beyond cubital veinlet and replaced with crimpled marginal vein about tegminal tip; claval veins and posterior stems minutely pustulate. Hindwing narrow (coupling lobe just beneath CuA1 of tegmen in repose), veins dark, membrane suffused and transversely wrinkled, few discernible details much as in *P. muiri* **gen.** et **sp.n.** Tibiae slightly flattened; fore tibia as long as femur, mid tibia longer than femur, hind tibia twice longer than femur. 3rd tarsomere with a pair of curved apical setae; claws simple, slender; arolium slighly surpassing 1/2 claw, seemingly bilobed. Hind tibia 0.8 mm long, unarmed laterally, about 1.5 times widened towards apex; tibial and tarsal pectens uniserial, tibial with 8 teeth, 1st tarsal with 6 teeth (diastema between 2 inner and 4 outer), 2nd tarsal with no less than 4 small teeth. Ovipositor somewhat reduced, short (0.4 mm long, 1/2 as long as hind tibia), slender, slightly upcurved, diverging from concavely truncate pygophore and not reaching anal tube.

ETYMOLOGY. The genus *Cixius* and Greek *tettix* (cicada); gender masculine. The type species is named after Prof Chun-tu Yang, distinguished hemipterologist from Taiwan.



Figs 27–36. *Cixitettix yangi* **gen.** et **sp.n.**, holotype female PIN 3130/169: 27–28 — right lateral view: 27 — habitus; 28 — head and thorax; 29–31 — left lateral view: 29 — habitus; 30 — head and thorax; 31 — ovipositor; 32–33 — dorsal view: 32 — habitus; 33 — head and thorax; 34–36 — ventral view: 34 — habitus; 35 — head and thorax; 36 — distal part of hind leg.

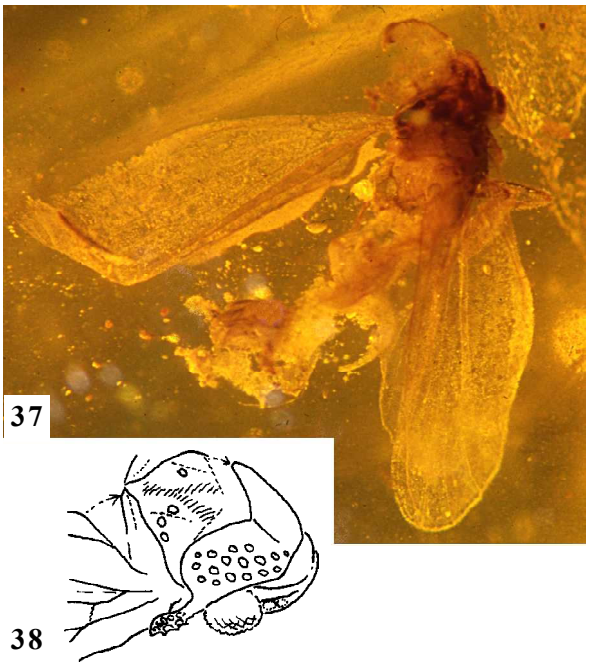
Рис. 27–36. *Cixitettix yangi* **gen.** et **sp.n.**, самка, голотип PIN 3130/169: 27–28 — с правой стороны: 27 — общий вид; 28 — голова и грудь; 29–31 — с левой стороны: 29 — общий вид; 30 — голова и грудь; 31 — яйцеклад; 32–33 — сверху: 32 — общий вид; 33 — голова и грудь; 34–36 — снизу: 34 — общий вид; 35 — голова и грудь; 36 — дистальная часть задней ноги.

Foveopsis fennahi Shcherbakov, **gen.** et **sp.n.**
Figs 37–38, 53–54

MATERIAL. Holotype: female NHM In. 20172 (pregenital abdomen fragmented) — Burmese amber; Early Cretaceous, Albian, ca. 112–100 Ma [Ross & York, 2004].

DIAGNOSIS. Tegmen unicolorous, costal margin gibbous about midlength, costal area very narrow distally, R+M stalk short, M proximally nearer to CuA1, CuA stem about as long as basal cell, CuA2 forked before crossveins, and Pcu+1A not very short. Mesonotum with rudimentary lateral carinae. Hind tibia and 1–2nd tarsomere slender, weakly widened apically. Ovipositor shorter than hind tibia, adpressed to pygophore.

DESCRIPTION. Adult. Body with folded tegmina ca. 3.6 mm long, unicolorous, slightly suffused. Coryphe appearing rather long; carina between coryphe and acrometope interrupted medially, acrometope very short there, its anterior margin steeply arched, not angulate; lateral carina of eumetope dorsally foliaceous, apparently foveolate. Rostrum reaching hind trochanters. Thorax 0.75 mm wide. Pronotum trapezoidally produced over the head, carinate medially, rather shallowly incised posteriorly (medially as long as laterally); each half of disc with at least 17 sensory pits, anteriorly arranged in oblique irregular rows; pectoral lobe densely covered with pits, foveolate. Mesonotum with shallow median depression and



Figs 37–38. *Foveopsis fennahi* **gen.** et **sp.n.**, holotype female NHM In. 20172, dorsal view: 37 — habitus; 38 — head and thorax.

Рис. 37–38. *Foveopsis fennahi* **gen.** et **sp.n.**, самка, голотип NHM In. 20172, сверху: 37 — общий вид; 38 — голова и грудь.

rudimentary lateral carinae; two sensory pits laterad and one(?) mediad of each lateral carina. Tegmen 2.75 mm long, 0.83 mm wide, opaque, uniformly sclerotized; costal margin shallowly sinuate subbasally, gibbous about midlength; hypocostal carina absent; R+M stalk as long as obsolete arculus, CuA stem about as long as basal cell; M proximally diverging from R and running nearer to CuA1; CuA2 forked nearly level with Pcu & 1A junction; 7 apical cells; R with 2 branches, M plus CuA1 with 3 branches; Pcu+1A stalk not very short, as long as clavus width at Pcu & 1A junction; marginal membrane developed from apex of Pcu+1A up to cubital veinlet, and continued with crimpled marginal vein around tegminal tip; veins raised, basal (Sc+)R and claval veins carinate. Hindwing with nearly straight anterior margin, coupling lobe about midlength, M straight proximally, and crimpled marginal vein (no marginal membrane). Tegmen and hindwing densely and evenly (including veins) covered with very short microtrichia. Tibiae carinate, setose (at least along carinae); fore and especially hind tibia elongate, fore tibia flattened and widened towards apex. Hind legs slender; tibia and first two tarsomeres weakly widened to apices; tibia ca. 0.7 mm long, in second quarter bearing a single, tiny lateral spine (seeming to consist of a socle mounted with a stout macroseta); tibia and first two tarsomeres with uniserial apical pectens of few teeth, tibial and 1st tarsal pectens setigerous, of 7 teeth, 2nd tarsal pecten of about 5 teeth (apparently with diastema). At least 8th abdominal tergite with sensory pits (no less than 10 in each half). Ovipositor ensiform with inner valvulae cutting, ca. 0.5 mm long (shorter than hind tibia), upcurved, adpressed to convex pygophore.

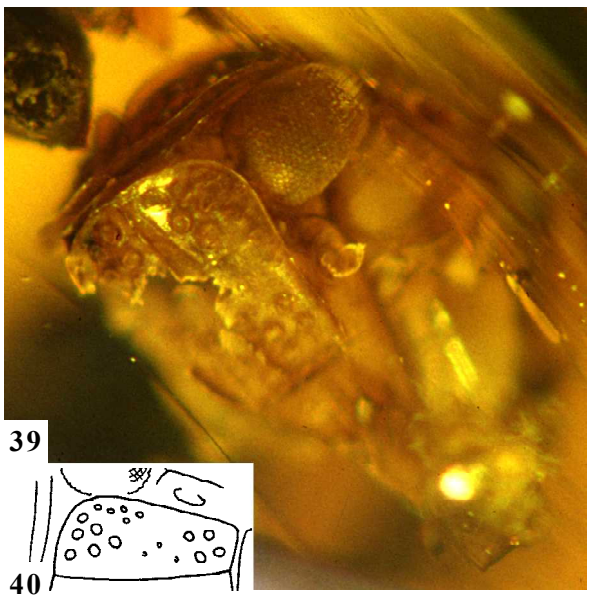
ETYMOLOGY. Latin *fovea* (pit) and the genus *Macropsis;* gender feminine. The type species is named after Ronald Gordon Fennah (1910–1987) who was the best expert in Fulgoroidea.

Cixitettiginae gen.sp.
Figs 39–40

MATERIAL. Adult NHM In. 20175 (fragmentary, gnawed by dermestid or other scavenger: most of wings, legs and abdomen missing) — Burmese amber; Early Cretaceous, Albian, ca. 110–100 Ma [Ross & York, 2004].

DESCRIPTION. Adult as preserved 3.3 mm long (reconstructed length with folded tegmina more than 4 mm). Face from acrometope to labrum 1.9 mm long; acrometope very short medially; eumetope with high, foliaceous carinae, median carina slightly arched in profile, lateral carinae nearly straight, lowering dorsally; each half of eumetope with 18 sensory pits: upper group of 6 large pits medially and 5 small ones laterally, middle group of 3 rudimentary pits (or rather tubercles) medially, and lower group of 4 large pits; ventral carinae of eumetope submarginal, cutting off a low triangular space adjacent to postclypeus. Oblique suture running above antennal pit. Scape very short; pedicel (grazed) apparently with very small sensillar rosettes. Post- plus anteclypeus about as long as eumetope; anteclypeus angulately produced in anterior 2/3, with median carina in anterior third (feebly continued onto postclypeus); lora dorsally not separated from postclypeus (tentorial pit visible on loroclypeal suture); anteclypeus truncate, overlapping anteromedial extremities of metacoxae; labrum as short triangle. Stylets (incomplete?) extended beyond ring-like hind trochanters (stylet base visible through the hole grazed in head capsule). Anterior pronotal margin carinate, overlapping upper margin of eye and almost entire coryphe. Narrow mesepisternum with rounded prominence just posterior of fore coxa. Hind tibia slender, setose, apparently unarmed laterally, a little widened towards apex, with uniserial apical pecten obliquely arched, faced inwards (partly grazed away). A pair of internal sound-producing apodemes inside the base of abdomen.

REMARKS. This specimen may well represent a sixth genus of the family, but preservation is too incomplete for the formal description.



Figs 39–40. Cixitettiginae gen.sp., adult NHM In. 20175: 39 — anteroventral view; 40 — arrangement of sensory pits on eumetope (schematized).

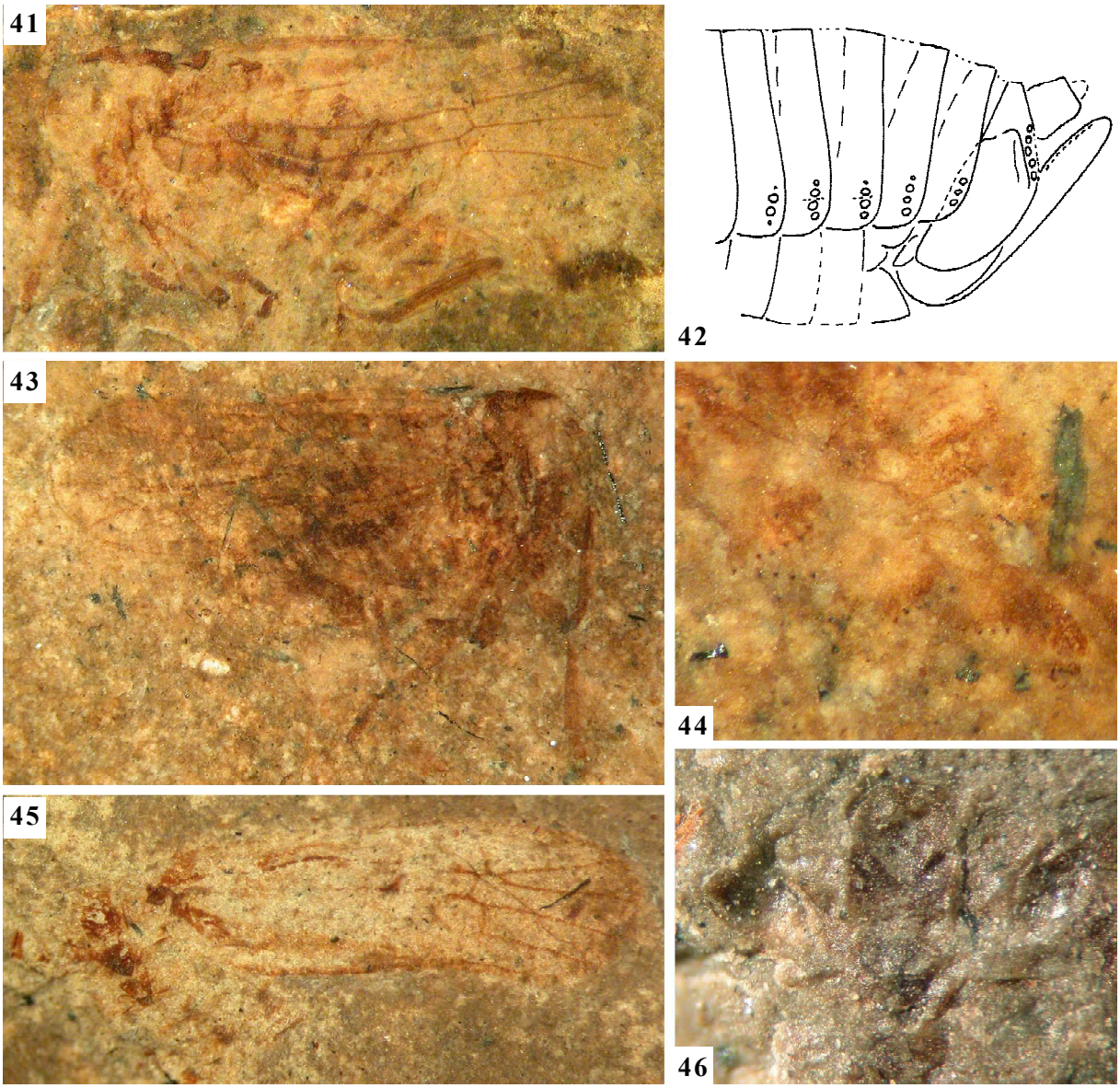
Рис. 39–40. Cixitettiginae gen.sp., adult NHM In. 20175: 39 — спереди-снизу; 40 — расположение сенсорных ямок на эвметопе.

Tsaganema oshanini Shcherbakov, **gen.** et **sp.n.**
Figs 41–46, 55–57

MATERIAL. Holotype: female PIN 3559/7455; paratypes: females PIN 3559/7457, 7458; males PIN 3559/7451, 7452, 7456; tegmen with meso- and metanotum and several abdominal tergites PIN 3559/7454; isolated tegmen with aberrant venation PIN 3559/7453 — outcrop 87/8, south of Bon-Tsagan-Nur (or Bon-Tsagaan-Nuur) Lake, Central Mongolia; Lower Cretaceous, ?Aptian, ca. 125–112 Ma [Sinitza, 1993; Rasnitsyn & Zherikhin, 2002].

DIAGNOSIS. Tegmen (as well as thorax) with contrasting pale and dark pattern, membranized about crossveins and beyond, not much widened beyond basal cell, costal area very narrow distally, R+M stalk short, M proximally running close to R, CuA stem longer than basal cell, CuA2 usually unforked, and Pcu+1A extremely short or undeveloped. Mesonotum with well developed submedian carinae and convex prescutum. Hind tibia and 1–2nd tarsomere much widened apically, tibial pecten with more than 10 teeth. Ovipositor longer than hind tibia, adpressed to pygophore.

DESCRIPTION. Body with folded tegmina 4.5–4.7 (males) to 4.9–5.1 mm (females) long, pro- and mesonotum dark medially and pale laterally, coryphe and tarsi dark, remaining body and legs paler. Eumetope with more than 10 sensory pits in each half. Rostrum reaching at least hind trochanters; apical segment dark, a little longer than wide.



Figs 41–46. *Tsaganema oshanini* **gen.** et **sp.n.**: 41 — holotype female PIN 3559/7455, habitus, lateral view; 42 — arrangement of sensory pits on female abdomen, based on paratype PIN 3559/7457; 43–44 — paratype male PIN 3559/7456, lateral view: 43 — habitus; 44 — distal part of hind leg with apical pectens; 45–46 — paratype PIN 3559/7454: 45 — tegmen with meso- and metanotum; 46 — mesonotum, dorsal view.

Рис. 41–46. *Tsaganema oshanini* **gen.** et **sp.n.**: 41 — самка, голотип PIN 3559/7455, общий вид сбоку; 42 — расположение сенсорных ямок на брюшке самки, по паратипу PIN 3559/7457; 43–44 — самец, паратип PIN 3559/7456, сбоку: 43 — общий вид; 44 — дистальная часть задней ноги с апикальными гребнями; 45–46 — паратип PIN 3559/7454: 45 — переднее крыло со средне- и заднеспинкой; 46 — среднеспинка, сверху.

Pronotum deeply incised posteriorly; pectoral lobe with more than 4 pits posterodorsally in a semicircle. Mesonotum with distinctly separated, convex prescutum and well developed submedian carinae in addition to weaker lateral ones, with no less than 2 sensory pits just posteromediad of each submedian carina, at the base of transversely wrinkled, acute scutellum. Tegmen 3.7–3.9 mm long, 1.2–1.3 mm wide (males) to 4.0–4.1 mm long, 1.3–1.4 mm wide(females), more or less parallel-sided in prenodal part, membranized about crossveins and beyond, suffused, with dark M, CuA1, distal CuA2, middle part of Pcu, and pale distal costal area, streak along claval furrow, and 1A; costal margin steeply arched basally, straight beyond; costal area very narrow distally; R+M stalk as long as arculus, CuA stem longer than basal cell; M proximally running close to R, then bent and running parallel to CuA1; CuA2 unforked; 6 apical cells, R and M with 2 branches (M forked either before or beyond crossveins; in an aberrant tegmen PIN 3559/7453 showing same size, shape, M course and colour pattern: 8 apical cells, CuA2 forked before crossveins, CuA2a joining CuA1, two *icua*, M and CuA with 3 branches each); Pcu+1A very short or undeveloped; claval furrow ending bling before cubital veinlet; marginal membrane crimpled, developed from apex of Pcu+1A (widest just beyond it) up to tegminal tip, and continued beyond with crimpled marginal vein. Legs rather stout, tibiae (especially fore) flattened; hind tibia 1.2 mm long, seemingly with one small lateral spine about midlength, nearly twice widened apically; tibial and tarsal pectens uniserial, with long and stout macrosetae, tibial transverse, 1st and especially 2nd tarsal oblique, tibial with about 13, 1st tarsal with about 10, 2nd tarsal with about 9 teeth. 4–8th abdominal tergites with about 3 (2–4) sensory pits laterally. Female pygophore (9th tergite) with at least 5 sensory pits laterally along posterior margin separated by groove. Ovipositor ensiform with inner valvulae cutting, 1.4–1.5 mm long (longer than hind tibia), nearly straight, directed obliquely caudad, adpressed to convex pygophore, extended just beneath anal tube.

ETYMOLOGY. The Bon-Tsagan-Nur and genus *Aphelonema;* gender neuter. The type species is named after Vassily Fyodorovich Oshanin (1844–1917), first Russian hemipterologist.

Systematic position of Perforissidae

Perforissidae are similar to Caliscelidae in many characters. Grex Caloscelides Amyot & Serville, 1843 was raised to the full family by Melichar [1906], then treated as a subfamily in Issidae by many authors, restored to the family rank by Hamilton [1981], and recently revised by Gnezdilov & Wilson [2006]. Some Caliscelidae likewise possess: sensory pits in adult on metope, pronotum (disc and paranota), sides of mesonotum, and abdominal tergites (full set only in some macropters; abdominal pits, when present, are clearly visible in brachypters but concealed with tegmina in macropters); rostrum reaching hind trochanters, with short last joint; anteclypeus angulate in profile; eumetope without submedian carinae; pronotum produced anteriorly and incised posteriorly; convex mesonotum with prescutellar depression (in macropters only); small tegula; narrow tegmen with small basal cell, (Sc+)R and M simple in prenodal part, very few crossveins (in nodal series only), membranized postnodal part (in macropterous *Asarcopus* Horváth [Fennah, 1949, fig. 6]), and narrow marginal membrane; hindwing with R unbranched like other veins (including CuA [Dworakowska, 1988, fig. 88]), only two crossveins, and distinct marginal membrane; tibiae (especially fore) flattened; hind tibia with single lateral spine; 1st and 2nd metatarsomere hairy on plantar surface; metatarsal dentition extremely variable; nymphs adult-like.

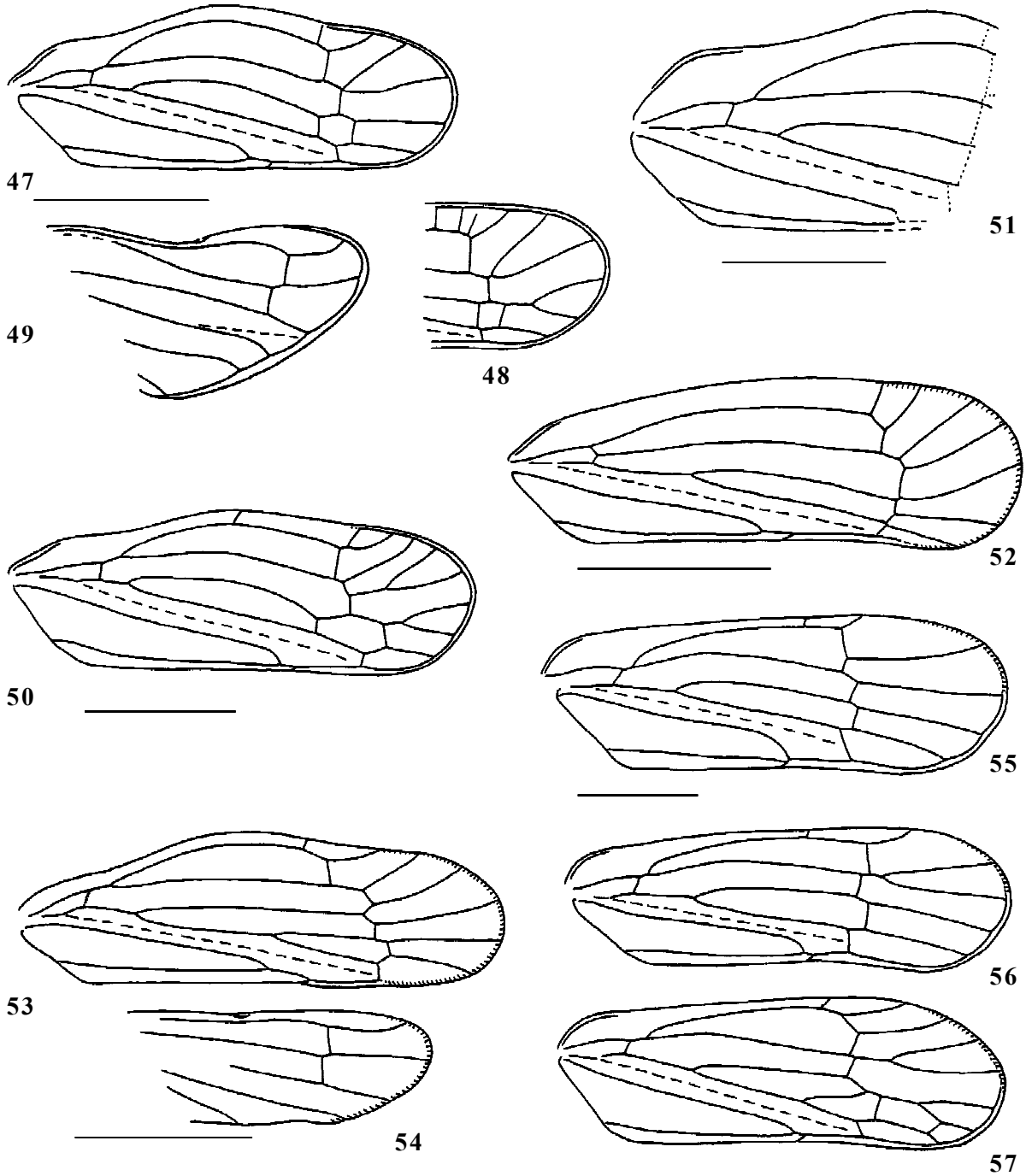
The apical pecten on 2nd metatarsomere, complete in lower Fulgoroidea (cixioid and dictyopharoid groups of families), is reduced to a pair of lateral teeth in issoid group and Tettigometridae, and lost in ricanioid group. The metatarsal dentition is stable at the family level in planthoppers, except for Perforissidae and Caliscelidae. In the latter, dentition is unusually diverse at the adult stage: 1st metatarsomere with 6–10, 2, 1 or 0 teeth; 2nd with 3, 2, 1 or 0 teeth [Fennah, 1987; Emeljanov, 1999; Gnezdilov & Wilson, 2006]. In Perforissidae hind leg dentition is likewise diverse, and the variants of *Perforissus* **gen.n.** and *Cretargus* **gen.n.** are similar to those found in two closely related families of ricanioid group, Lophopidae and Eurybrachyidae.

Nymphal sensory pits persist at the adult stage on the head and/or tegmen also in Meenoplidae, some Cixiidae (e.g. *Borysthenes* Stål), some Delphacidae (e.g. *Achorotile* Fieber), Derbidae [Emeljanov, 1994], Fulgoridae, and Flatidae, on the head, pronotum and abdomen in Orgeriinae (Dictyopharidae), and on abdominal sternites in Achilixiidae (3–4th or 3rd & 5th), some Cixiidae (on 4–6th in Bennarellini [Holzinger & Kunz, 2006], modified on 3rd in Bennini), some Mithymnini (Nogodinidae; on 6–7th) [Gnezdilov & Wilson, 2007], and Gaetuliini (transferred to Tropiduchidae [Gnezdilov, 2007]; on 6–7th), but only in some Caliscelidae the distribution of pits is the same as in Perforissidae.

The acrometope is not shortened medially in some Delphacidae (especially Ugyopinae), Cixiidae and in few Achilidae and Dictyopharidae. The pronotum strongly produced over the coryphe is found in some Flatidae.

Adult-like nymph is characteristic of dictyopharoid, issoid and ricanioid groups. Nymphs of most cixioid families are more dorsoventrally flattened and usually cryptobiotic (except in Delphacidae). Sensory pits are developed on the mesonotum mediad of jugal carina in several families of cixioid group: in Meenoplidae, Cixiidae, some Delphacidae (*Ugyops* Guerin-Meneville) and Derbidae (*Vekunta* Distant) [Yang & Yeh, 1994]. Perforissid nymphs are in some respects more adult-like than any other planthopper nymphs known: eumetope lacking submedian carinae; 9th abdominal segment as well as 10th (anal tube) subcylindrical, 9th not small and V-shaped, 10th not reduced. They are also unique in their mesonotum structure, similar to pronotum and dissimilar to metanotum.

The list of similarities between perforissids and caliscelids seems impressive, but we treat these two families as distantly related and their likeness homoplastic, resulting mainly from parallel neotenic transformations, on account of four important differences of Perforissidae from Caliscelidae:



Figs 47–57. Wing venation (left wings mirrored): 47–50 — *Perforissus muiri* **gen.** et **sp.n.**: 47–49 — holotype AMNH NJ-256: 47 — left tegmen; 48 — distal part of right tegmen; 49 — hindwing; 50 — paratype AMNH NJ-716, left tegmen; 51 — *Cretargus emeljanovi* **gen.** et **sp.n.**, holotype PIN 3311/562a, left tegmen; 52 — *Cixitettix yangi* **gen.** et **sp.n.**, holotype PIN 3130/169, tegmen (based on both tegmina); 53–54 — *Foveopsis fennahi* **gen.** et **sp.n.**, holotype NHM In. 20172: 53 — tegmen (based on both tegmina); 54 — hindwing; 55–57 — *Tsaganema oshanini* **gen.** et **sp.n.**: 55 — right tegmen of holotype female PIN 3559/7455; 56 — paratype tegmen PIN 3559/7454; 57 — paratype aberrant tegmen PIN 3559/7453. Scale bar 1 mm.

Рис. 47–57. Жилкование крыльев (левые изображены зеркально): 47–50 — *Perforissus muiri* **gen.** et **sp.n.**: 47–49 — голотип AMNH NJ-256: 47 — левое переднее крыло; 48 — дистальная часть правого переднего крыла; 49 — заднее крыло; 50 — паратип AMNH NJ-716, левое переднее крыло; 51 — *Cretargus emeljanovi* **gen.** et **sp.n.**, голотип PIN 3311/562a, левое переднее крыло; 52 — *Cixitettix yangi* **gen.** et **sp.n.**, голотип PIN 3130/169, переднее крыло (по обоим крыльям); 53–54 — *Foveopsis fennahi* **gen.** et **sp.n.**, голотип NHM In. 20172: 53 — переднее крыло (по обоим крыльям); 54 — заднее крыло; 55–57 — *Tsaganema oshanini* **gen.** et **sp.n.**: 55 — правое переднее крыло самки, голотип PIN 3559/7455; 56 — переднее крыло, паратип PIN 3559/7454; 57 — аберрантное переднее крыло, паратип PIN 3559/7453. Масштабная линейка 1 мм.

(i) Setigerous metatibial pectens, recorded also in Mesozoic Lalacidae [Hamilton, 1990] and presumed in Mesozoic Fulgoridiidae and other pre-Cenozoic planthopper families [Shcherbakov, 2004], further collectively referred to as pre-cixioids (metatibial pectens are asetigerous in all extant planthoppers).

(ii) Very proximal forking of CuA in tegmen, characteristic of Fulgoridiidae and some other pre-cixioids, but not of cixioid group (CuA is forked earliest also in some issoid families, e.g. Tropiduchidae, but unbranched before crossveins in Caliscelidae).

(iii) In *Tsaganema* **gen.n.,** mesonotum with distinctly separated, convex prescutum and ledge-shaped rather than rib-like submedian carinae, similar to Triassic and Jurassic fulgoroids (pers. obs.) and distinct from all extant planthoppers.

(iv) Ensiform ovipositor with cutting inner valvulae, known elsewhere in Cixiidae and Delphacidae of cixioid group, and in pre-cixioids (Caliscelidae in the structure of ovipositor are similar to Dictyopharidae, Fulgoridae and Bladinini s.str. of Nogodinidae [Gnezdilov, 2003, 2007]; all instances of partial reversal to cutting structure in issoid family group, e.g. in Tropiduchidae and Flatidae, are considered secondary). Like in Cixiidae, two variants of ovipositor structure are recorded in Perforissidae: primitive, known also in Delphacidae (ovipositor long, adpressed to convex pygophore), and modified (ovipositor short and diverging from concave pygophore).

The characters (i–iii) indicate that perforissids descended from the ancestors more primitive than Cixiidae, presumably from Fulgoridiidae. (An alternative placement of Perforissidae as closely related to Caliscelidae and possibly ancestral to the higher groups of Fulgoroidea will require hypothesizing much homoplasy in planthopper phylogeny, e.g. in transformations of the ovipositor.)

Among five perforissid genera, *Perforissus* **gen.n.** is the most advanced, and closely related *Cretargus* **gen.n.** shows the less modified hind leg dentition. Three genera of Cixitettiginae demonstrating the basic state of hind leg dentition are more disparate, each of them (especially *Cixitettix* **gen.n.**) retaining some autplesiomorphic features in the structure of tegmen (*Foveopsis* **gen.n.**, *Cixitettix* **gen.n.**) or mesonotum and ovipositor (*Tsaganema* **gen.n.**), and *Foveopsis* **gen.n.** appearing transitional to the nominate subfamily.

On the origins of Perforissidae and higher groups of Fulgoroidea

'Regressive' characters of Perforissidae and Caliscelidae (retention of sensory pits in adult; simplified venation; destabilization and underdevelopment of hind leg armature) indicate their neotenous (paedomorphic) nature (caliscelids show even greater reduction of teeth on 1st hind tarsomere, up to toothless in Augilini). Their metatarsal dentition is so diverse that classifying fulgoroids formally on the basis of this sole character one should place different genera of these families into different family groups.

Among higher Fulgoroidea (issoid and ricanioid family groups), the oldest family recorded up to now is Nogodinidae (since the Early Paleocene), but the compression fossil record is biased toward macropters, and Shcherbakov [2006] supposed that ancestors of higher fulgoroids might be issid-like and subbrachypterous. Caliscelidae are in some characters intermediate between issoid and ricanioid groups, and could be such ancestors, derivable from dictyopharoid group. If so, then higher fulgoroids originated through neoteny, and multi-veined wings re-evolved multiple times in many issoid and ricanioid families. It looks quite probable, because these latter never restore in full the basic venational pattern universal for cixioid group. In polyneurous caliscelids (subtribe Pteriliina of Adenissini [Gnezdilov & Wilson, 2006]) the multi-veined membranous precostal area looks like an alien fringe 'glued' to otherwise coriaceous tegmen, as if just evolved 'de novo'.

We interpret Perforissidae as an early (Early Cretaceous) attempt to create leafhopper-like forms ('quasi-leafhoppers') from typical planthoppers. Several later (Cenozoic), independent attempts of 'cicadellization' in planthoppers exist (e.g. Delphacidae, Orgeriinae, and several groups with subbrachypterous tegmina), and that of Issidae s.l. (incl. Caliscelidae) was the most prolific, if several offshoots of this latter indeed reversed to the more usual planthopper habitus and gave rise to all enormous diversity of higher fulgoroids. These attempts were presumably associated with colonization of angiosperms in the later Early (Perforissidae) and terminal Cretaceous. However, Fulgoroidea were less successful in constructing a 'leafhopper' than Membracoidea. Perforissidae seem more leafhopper-like than any other planthopper group (maybe except for Tettigometridae), and presumably went extinct being outcompeted by Cicadellidae (known since the Early Cretaceous [Shcherbakov & Popov, 2002]). Other possible cause of perforissid extinction is that they were trophically associated with some earliest angiosperm (or proangiosperm) lineages not surviving into the Cenozoic. The small size and compact build of perforissids allows us to speculate that they lived on low herbaceous and/or brachyphyllous plants. Some variants of hind leg armature in Perforissidae modeled and anticipated those which were later realized in ricanioid families.

Sensory pits of planthoppers, presumed hygroreceptors [Šulc, 1928], are usually retained in adults of extreme xerophiles (Orgeriinae, some *Aphelonema* Uhler) or hygrophiles (delphacids *Laccocera* Van Duzee and *Achorotile*, caliscelid *Ommatidiotus* Spinola; A.F. Emeljanov, pers. comm.). Multiple sensory pits in perforissid adults indicate that they inhabited biotopes with highly variable and/or extremal humidity, possibly coastal-littoral environments. Early Cretaceous xeromorphic bennettite-brachyphyll communities confined to these environments were rich in proangiosperms and are considered the cradle of angiosperms [Krassilov, 1997]. The earliest unequivocal angiosperms come from around

the Barremian–Aptian transition [Friis et al., 2006]. The perforissid *Tsaganema oshanini* **gen.** et **sp.n.** is regularly found (8 specimens) in the Aptian(?) lake sediments of the Bon-Tsagan locality and probably lived close to the paleolake shore, in the bennettite-brachyphyll community dominated with proangiosperm *Brachyphyllum densiramosum* (Hirmerellaceae, producing *Classopollis* pollen) and containing angiosperms (unidentified dicots, diaspores *Typhaera* similar to cattail follicles) [Krassilov, 1982; Sinitza, 1993; Ponomarenko, 2007]. Aptian Burmese amber that yielded *Foveopsis fennahi* **gen.** et **sp.n.** and another perforissid contains grass-like monocots [Poinar, 2004] and angiosperm flowers with entomophilous traits [Santiago-Blay et al., 2005]. The Upper Cretaceous beds where perforissids are recorded, the Santonian Kheta Formation of Taimyr and especially the Turonian Raritan Formation of New Jersey, have yielded diverse angiosperm megafossils and pollen [Zherikhin & Sukatsheva, 1973; Crepet & Nixon, 1998]. Evolution of proangiosperms into angiosperms (angiospermization) was ruled by neoteny [Ponomarenko, 1998], like that of their presumed trophic associates, Perforissidae.

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