

The earliest find of Tropiduchidae (Homoptera: Auchenorrhyncha), representing a new tribe, from the Eocene of Green River, USA, with notes on the fossil record of higher Fulgoroidea

Древнейшая находка Tropiduchidae (Homoptera: Auchenorrhyncha), относящаяся к новой трибе, из эоцена свиты Грин Ривер, США, с замечаниями об ископаемых находках высших Fulgoroidea

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KEY WORDS: Fulgoroidea, Auchenorrhyncha, Tropiduchidae, Nogodinidae, Bladinini, Issidae, Tettigometridae, fossil, phylogeny, Cretaceous/Paleogene boundary, Paleocene, Eocene, Green River Formation, Baltic amber, Dominican amber, Neuroptera.

КЛЮЧЕВЫЕ СЛОВА: Fulgoroidea, Auchenorrhyncha, Tropiduchidae, Nogodinidae, Bladinini, Issidae, Tettigometridae, ископаемые, филогения, мел/палеогеновая граница, палеоцен, эоцен, свита Грин Ривер, балтийский янтарь, доминиканский янтарь, Neuroptera.

ABSTRACT. *Emiliana alexandri* gen. et sp.n. from the Middle Eocene of the Green River Formation, Colorado, USA is singled out in a new tribe of Tropiduchidae. Other fossil tropiduchids are discussed. '*Cixius*' *loculatus* and '*C.*' *succineus* from Baltic amber are transferred to *Jantaritambia* and *Jantaritambiini* gen. indet., respectively; diagnosis of this tribe is modified. Genus near *Neommatissus* is recorded from Dominican amber. Paleogene genera *Hammapteryx*, *Dilaropsis*, *Cotradechites* and *Lithopsis* are transferred to Nogodinidae s.l., and other Paleogene genera probably belonging to this family are listed. Eocene genera *Protoliarus* and *Scoparidea* are close to the origin of Issidae s.str. Eocene genera *Ricaniella* and probably *Callospilopteron* belong to Neuroptera.

The oldest higher Fulgoroidea attributable to Nogodinidae s.l. (i.e. including Bladinini) are recorded from the Early Paleocene of Amur Region. Nogodinidae s.l. are common since the Paleocene, Issidae s.str. and Tropiduchidae first found in the Eocene, Flatidae and Ricaniidae much later, and remaining higher fulgoroid families not recorded with certainty. Available fossil record agrees with suppositions that Issidae sensu Emeljanov are closest to the base of monophyletic higher Fulgoroidea, and that Tettigometridae constitute a distal lineage, and gives no arguments against monophyly of ricanoid group of families.

РЕЗЮМЕ. *Emiliana alexandri* gen. et sp.n. из среднего эоцена свиты Грин Ривер, Колорадо, США выделен в новую трибу семейства Tropiduchidae. Обсуждаются остальные ископаемые Tropiduchidae. '*Cixius*' *loculatus* и '*C.*' *succineus* из балтийского

янтаря отнесены к роду *Jantaritambia* и к трибе *Jantaritambiini* gen. indet. соответственно; диагноз данной трибы изменён. Род, близкий к *Neommatissus*, отмечен из доминиканского янтаря. Палеогеновые роды *Hammapteryx*, *Dilaropsis*, *Cotradechites* и *Lithopsis* перенесены в Nogodinidae s.l.; перечислены другие палеогеновые роды, вероятно, относящиеся к этому семейству. Эоценовые роды *Protoliarus* and *Scoparidea* близки к корням Issidae s.str. Эоценовые роды *Ricaniella* и, вероятно, *Callospilopteron* относятся к Neuroptera.

Древнейшие высшие Fulgoroidea, отнесенные к Nogodinidae s.l. (т.е. включая Bladinini) отмечены из раннего палеоцена Приамурья. Nogodinidae s.l. обычно начиная с палеоцена, Issidae s.str. и Tropiduchidae впервые найдены в эоцене, Flatidae и Ricaniidae много позже, а остальные семейства высших фулгориодов пока достоверно не отмечены в ископаемом состоянии. Имеющиеся ископаемые находки согласуются с мнениями о том, что Issidae sensu Emeljanov стоят в основании монофилетичных высших Fulgoroidea и что Tettigometridae составляют производную группу, и не дают аргументов против монофилии риканиоидной группы семейств.

Introduction

The family Tropiduchidae, one of smaller planthopper families comprising less than 400 described species, is quite diverse (more than 100 genera) in the overall structure and especially venation. Higher classification of the family was revised by Fennah [1982] who recog-

nized 15 tribes (three of them divided into subtribes), based on body structure and tegminal venation. Tropicuchidae are distributed in warmer regions across the world, some species are known as crop pests.

The fossil record of the family is restricted to the Cenozoic, like that of other families of higher Fulgoroidea [Shcherbakov, 2004]. The first undoubted fossil representative of Tropicuchidae was found in Baltic amber and singled out into the tribe [Szwedo, 2000]. The age of Baltic amber is Late Eocene, 40–35 Ma (million years ago).

The Green River Formation, an Eocene Lagerstätte in Colorado, Utah, and Wyoming, USA, yielded plants, vertebrates and above 100000 insect specimens (more than 22 orders); it had a temperate to subtropical climate and is dated to late Early to early Middle Eocene (53–48.5 Ma; ca. 49 Ma for Parachute Creek Member), including the transition between the moist Early Eocene climate and the slightly drier Middle Eocene [Santiago-Blay et al., 2004, and references herein]. In 1997 about one thousand Green River insects have been collected by David Kohls (Colorado Mountain College) and A.P. Rasnitsyn (Paleontological Institute RAS) from the Parachute Creek Member in Colorado. This collection, kept in the Paleontological Institute, Moscow (PIN), contains some 40 Auchenorrhyncha, including few small cercopoids, many small cicadellids and equally abundant, diverse, at average larger planthoppers, among latter a distinctive tegmen of Tropicuchidae. The Green River tropiduchid, about ten million years older than that from Baltic amber, represents the earliest fossil find of this family known up to date. It is peculiar enough to be separated into a new genus and new tribe described below.

Taxonomy

Tropicuchidae

Emilianini Shcherbakov **trib.n.**

TYPE GENUS. *Emiliana* Shcherbakov **gen.n.** (gender feminine).

DIAGNOSIS. Macropterous tegmen. All crossveins on remigium in two gradate series, nodal and subapical (*im* and *icua* present in nodal series); clavus with *cup-pcu* crossvein. Precostal carina very narrow, costal area narrow, both without crossveins. R and CuA forking much before nodal crossveins, CuA somewhat earlier. M forking basally, MA and MP forking before nodal crossveins, MP anastomosing with CuA for a distance. Clavus and cell Pcu short, Pcu+A1 joining posterior margin near acute apex of clavus. Several longitudinal folds between terminal branches of RP and M.

COMPOSITION. Type genus.

COMPARISON. Distinct from all other tribes in the M forking much earlier than CuA, and MP anastomosing with CuA. Similar only to another extinct tribe, Jantaritambiini in *cup-pcu* crossvein present (these tribes are also similar in precostal carina narrow, cell Pcu short, and all crossveins on remigium in two gradate series), but in the latter tribe clavus is long and costal area broader.

REMARKS. In the key of planthopper families based on tegmina [Shcherbakov, 1981] falls in Tropicuchidae on ac-

count of CuA forking earlier than R, all crossveins arranged in two gradate series (nodal series including not only *r-m* and *m-cu*), and Pcu+A1 joining margin near acute apex of clavus.

An alternative interpretation of the M+CuA anastomosis as a supernumerary *m-cu* crossvein between the bases of M and CuA stems seems hardly probable, because it results in extremely multibranching CuA occupying the area as large as R and M together (condition never found in fulgoroids).

Several subapical folds between RP and M branches and crossvein *cup-pcu* are known e.g. in the earliest member of Dictyopharidae + Fulgoridae group, Late Cretaceous *Netutela* Emeljanov, 1983 [Emeljanov, 1983].

Emiliana Shcherbakov **gen.n.**

TYPE SPECIES. *Emiliana alexandri* Shcherbakov **sp.n.**

DIAGNOSIS. Tegmen much widening distad, obliquely rounded apically, apex beyond RP, weak tornus at CuA, costal margin nearly straight. Five crossveins (*r-m*, *m-cu*, two *im*, *icua*) in subtransverse nodal series about 2/3 wing length; no *icua* crossvein in subapical series (i.e. single *icua* = only one cell CuA1 between CuA branches). Basal cell narrow, arched. R and CuA with 2 principal branches each; CuA forked just before, and R at wing midlength. RA running close to costal margin. M with 4 principal branches: MA forked just before nodal crossveins, MP forked earlier than CuA. Longitudinal veins nearly parallel beyond nodal crossveins; apical cells much shorter than subapical cells; most of principal branches with short forks near apical margin. Clavus less than 1/2 wing length; cell Pcu very short, less than 1/3 clavus length.

COMPOSITION. Type species.

ETYMOLOGY. The genus and species are named after Prof. Alexandr F. Emeljanov, the world authority in planthoppers and my teacher in hemipterology (Russian name Emel'yan was derived from Latin Emilian).

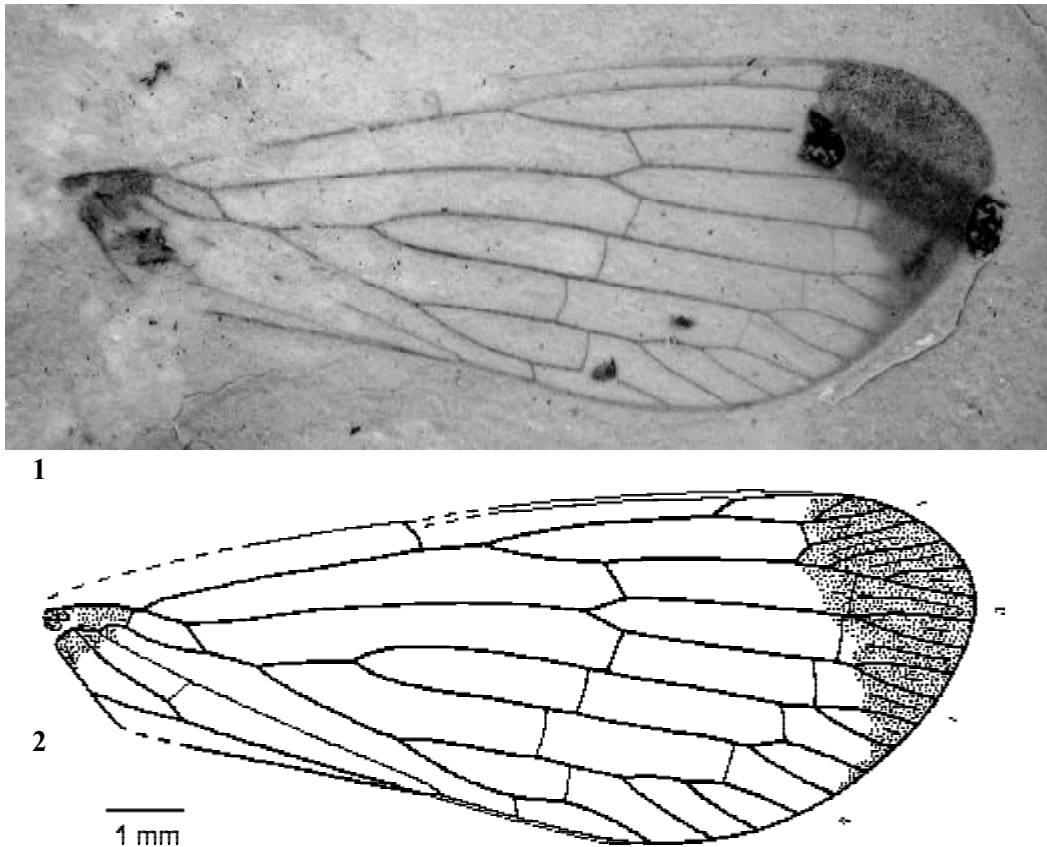
REMARKS. Similar only to a few extant tropiduchid genera, belonging to the tribes Neommatissini (*Neommatissus* Muir, 1913), Paricanini (especially *Paricana* Walker, 1857), Tropicuchini (*Pseudoparicana* Melichar, 1914) [Fennah, 1982: figs 3, 8, 23], and to the genus *Paricanoides* Liang, 2003 tentatively placed in Paricanini [Liang, 2003], in all crossveins on remigium arranged in two gradate series, clavus and cell Pcu short, precostal carina and costal area narrow and veinless. In addition, similar to *Neommatissus* in Pcu+A1 joining posterior margin, to *Pseudoparicana* in longitudinal veins distally parallel, and apical cells short, and to *Paricanoides* in RA close to margin, and crossvein *icua* single (and even colour pattern — see species description). All four latter genera differ clearly from the new genus in M forking at most slightly before R, and nodal *im* crossveins absent, and also *Paricana* in two *icua* crossveins, *Neommatissus* and *Pseudoparicana* in *icua* crossveins absent, and *Paricanoides* in nodal crossveins in basal wing third, apical cells long, and CuA–CuA2 running very close to CuP (the character neither mentioned nor illustrated in original description; observed in *Paricanoides* sp., Zoological Institute, St. Petersburg).

Emiliana alexandri Shcherbakov **sp.n.**

Figs 1–2.

MATERIAL. Holotype left tegmen PIN no. 4621/546 (part & counterpart) — Anvil Points Area, Piceance Creek Basin, Garfield Co., NW Colorado, USA; Middle Eocene (Lutetian), Parachute Creek Member, Green River Formation; coll. D. Kohls & A.P. Rasnitsyn, 1997; kept in Paleontological Institute, Russian Academy of Sciences, Moscow.

DESCRIPTION. Tegmen elongate (2.8 : 1), 12 mm long. Costal area with *c-r* crossvein before R bifurcation. RA



Figs 1–2. *Emiliana alexandri* gen. et sp.n. (Tropicuchidae), holotype, PIN no. 4621/546, Eocene, Green River Formation, Colorado, USA: 1 — left tegmen (mirrored); 2 — tegminal venation.

Рис. 1–2. *Emiliana alexandri* gen. et sp.n. (Tropicuchidae), голотип, ПИН № 4621/546, эоцен, свита Грин Ривер, Колорадо, США: 1 — левое переднее крыло (зеркально перевернуто); 2 — его жилкование.

beyond its midlength with short oblique anterior branch. Nodal *r-m* crossvein reclined. RA with two terminations; RP (pectinate anteriorly), MA, and MP (both dichotomous) with four terminations each; CuA1 (pectinate posteriorly) with three terminations. CuA2 at its midlength with short transverse posterior branch (closing lanceolate cell CuA2). Veins dark; main branches of M and CuA and ambient vein beyond claval apex sharply carinate. Rudimentary marginal membrane in CuA–CuP area. Wing membrane pale (hyaline?), wing base and wing apex darkened. About ten short folds within darkened apical area between RA2b and MP2a, five of them more distinct (posterior to RP1, RP2a, RP2b, MA1, MA2), some others very indistinct.

Other fossil Tropicuchidae

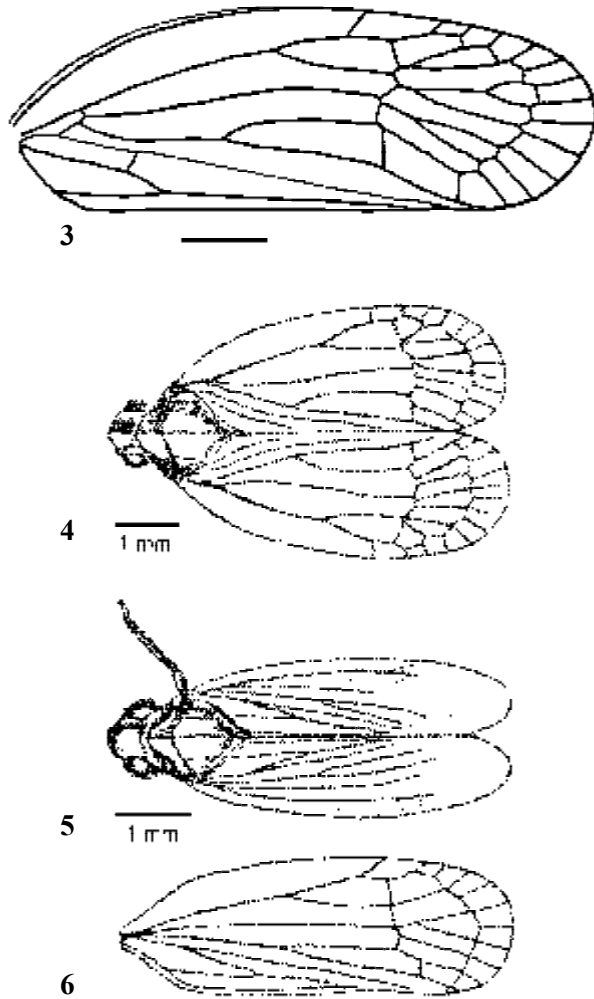
Baltic amber

'*Pseudophana*' (= *Dictyophara*) *reticulata* (Germar et Berendt, 1856). The younger of two nymphs ('larva') described under this name resembles Tropicuchidae [Emeljanov, 1983]. Two nymphs (types?) in Paläontologisches Institut Humboldt-Universität, Berlin [Szwedo et al., 2004: 88].

'*Cixius*' *loculatus* Germar et Berendt, 1856 (Fig. 4). According to Szwedo et al. [2004], could be a repre-

sentative of Tropicuchidae, related to the genus *Tambinia* Stål, 1859; type probably lost. In fact, the head and thorax in dorsal aspect, and especially tegminal venation of '*C.*' *loculatus* (including slight sigmoidal curvature of M stem) are very close to those of *Jantaritambia serafini* Szwedo, 2000 (Fig. 3). The differences of '*C.*' *loculatus* are: (1) small triangular subapical cell absent (present in different position in the left and right tegmen of the *J. serafini* holotype; such cells are developed in varying degree e.g. in different specimens of nogodinid *Tritophania patruelis* Jacobi, 1938 from Baltic amber [Szwedo & Stroinski, 1999: figs 1, 3, 5]); (2) postnodal part of tegmen shorter, *icua* crossvein in subapical series absent (not figured?); (3) hind tibia with 2 lateral spines (single in *J. serafini*; only other tropiduchid with single lateral spine is *Caffrommatissus* Fennah, 1967, placed by Fennah [1982] in Trypetimorphini along with genera having 2 spines [Szwedo, 2000]); (4) size smaller, ca. 6.3 mm (8.4 mm in *J. serafini*).

These two fossils are doubtless congeneric, so a new combination is proposed, *Jantaritambia loculata* (Germar et Berendt, 1856), **comb.n.** The diagnosis of Jantaritambiini should be modified as follows: "Hind tibia with 1–2 lateral spines. ..."



Figs 3–6. Baltic amber Jantaritambiini (Tropiduchidae): 3 — *Jantaritambia serafini*, right tegmen of holotype, redrawn from Szwedó [2000: fig. 8]; 4 — *Jantaritambia loculata*, habitus, dorsal view; 5–6 — *Cixius succineus* (5 — habitus, dorsal view; 6 — tegmen). 4–6 from Germar & Berendt, 1856: taf. 1, figs 23, 23b, 24.

Рис. 3–6. Jantaritambiini (Tropiduchidae) балтийского янтаря: 3 — *Jantaritambia serafini*, правое переднее крыло голотипа, перерисовано из Szwedó [2000: fig. 8]; 4 — *Jantaritambia loculata*, общий вид сверху; 5–6 — *Cixius succineus* (5 — общий вид, сверху; 6 — переднее крыло). 4–6 из Germar & Berendt, 1856: taf. 1, figs 23, 23b, 24.

'*Cixius succineus* Germar et Berendt, 1856 (Figs 5–6). According to Szwedó et al. [2004], could represent Achilidae or Cixiidae; type probably lost. In fact, similar to *Jantaritambia* Szwedó, 2000 in tegminal venation, but smaller (ca. 5.3 mm), with larger head, fewer apical and subapical cells, and nodal *icua* crossvein in more distal position (subapical *icua* present; number of metatibial spines not known). Fits diagnostic tegminal characters of Jantaritambiini [Szwedó, 2000] (nodal crossvein series transverse; CuA not meeting M basally; cell Pcu shorter than 1/2 clavus length; clavus exceptionally long) and could represent another genus of this tribe.

Dominican amber

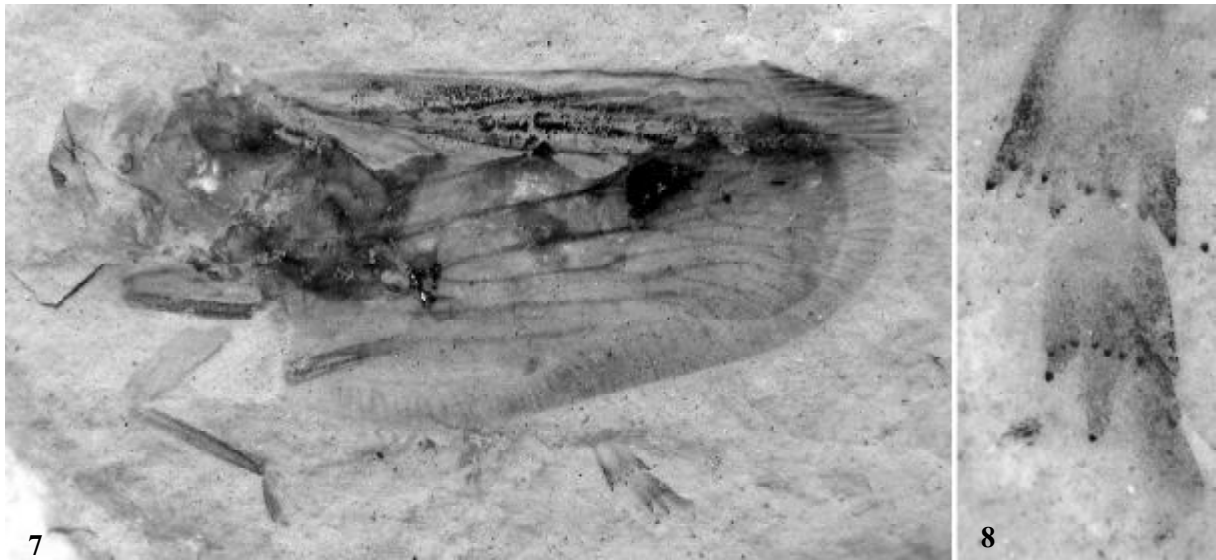
Specimen figured and identified as Cixiidae [Wu, 1996: 165, fig. F-346] represents Tropiduchidae [Szwedó et al., 2004: 150]. In tegminal venation it is very similar to *Neommatissus* (especially to the variant without nodal *ir* [Fennah, 1982: fig. 3]), but differs in the presence of short R+M stalk beyond basal cell and hind tibia with 3 spines laterally (no stalk and 2 spines in extant *Neommatissini*), and possibly merits generic separation. Dominican amber is dated Oligocene–Miocene (30–10 Ma) [Poinar, 2001], but the main amberiferous deposits were formed during the late Early Miocene through early Middle Miocene (20–15 Ma) [Iturralde-Vinent & MacPhee, 1996].

Some characters and family concepts in higher fulgoroids

The apical pecten on second metatarsal segment, complete in primitive fulgoroids, is reduced to a pair of lateral teeth in several families (Issidae, Nogodinidae, Acanaloniidae, Flatidae, Tropiduchidae, Tettigometridae) and lost in some others (Ricaniidae, Lophopidae, Eurybrachyidae, Gengidae, and also Hypochtonellidae). Three basic states in dentition of second metatarsomere (pectinate, bidentate, and toothless) are used as important family characters in classification of Fulgoroidea. In one more group, Caliscelidae, restored to the family rank by Emeljanov [1999], metatarsal dentition is unusually variable at the subfamily, tribe or genus level (second metatarsomere with 3, 2, 1 or 0 teeth; first with pecten, 2, 1 or 0 teeth) [Fennah, 1987; Emeljanov, 1999].

Many authors agree that the above 12 families (they may be termed 'higher Fulgoroidea') form a monophylum. Tettigometridae apparently belong there and do not form the most basal branch of fulgoroid family tree: this family has no reliable fossil finds, is dissimilar to basal fulgoroids [Shcherbakov, 2004], and appears close to Tropiduchidae or Issidae Hemisphaeriinae in the cladograms based on morphology, 16S or 18S rDNA [Bourgoin et al., 1997; Yeh et al., 2005]. Some authors consider the ricanioid group of families (Ricaniidae, Lophopidae, Eurybrachyidae, Gengidae) monophyletic as well; Hypochtonellidae belong rather near Flatidae and lost teeth on second metatarsomere independently due to neoteny [China & Fennah, 1952].

Other important characters used to construct higher fulgoroid phylogeny are in the structure of female genitalia and tentorium [Emeljanov 1990; Bourgoin, 1993]. Fennah [1978] divided Nogodinidae into tribes, based mainly on the structure of ovipositor and metatarsus. Emeljanov [1990] transferred one of these tribes, Bladinini Kirkaldy, 1907 to Issidae on account of similar ovipositor structure, and considered Issidae s.l. the most basal, and Nogodinidae s.str. the next basal paraphyletic groups in the higher Fulgoroidea lineage. Later Emeljanov [1999] divided Issidae s.l. into Caliscelidae, Issidae s.str., and Acanaloniidae (including Tonginae and Trienopinae). Gnezdilov [2003a] found that *Bladi-*



Figs 7–8. *Lithopsis* cf. *fimbriata* (Nogodinidae s.l.), specimen PIN no. 4621/64, Eocene, Green River Formation, Colorado, USA: 7 — habitus, laterodorsal view; 8 — hind tarsus and apex of tibia.

Рис. 7–8. *Lithopsis* cf. *fimbriata* (Nogodinidae s.l.), экземпляр ПИН № 4621/64, эоцен, свита Грин Ривер, Колорадо, США: 7 — общий вид, сверху-сбоку; 8 — задняя лапка с вершиной голени.

na Stål, 1859 is similar to Caliscelidae and Fulgoridae in the structure of ovipositor, and treated Bladinini as the tribe *incertae familiae*. In two cladograms based on 16S rDNA the subfamilies of Issidae s.str. (Issinae and Hemisphaeriinae) do not cluster together, as well as the tribes of Nogodinidae s.str. (Varciini and Pisachini) [Yeh et al., 2005: figs 3A, B], and the former of these trees is consistent with supposition on ‘paraphyletic Issidae s.l. → paraphyletic Nogodinidae → other higher Fulgoroidea’ sequence.

Based on venation and habitus, it seems impossible to make a distinction between Bladinini and Nogodinidae s.str., so for compression fossils, with ovipositor characters usually unknown, we can use only the concept of Nogodinidae s.l. (including Bladinini). The controversy over the Issidae/Nogodinidae boundary may be resolved by uniting them into paraphyletic Issidae in the broadest sense.

On the fossil record of higher Fulgoroidea

The genera *Hammapteryx* Scudder, 1890 (7 species, Paleocene–Eocene), *Dilaropsis* Cockerell, 1920 (Eocene) and *Cotradechites* Fennah, 1968 (latest Paleocene), all based on tegmina, were assigned to Ricaniidae, and this family was reported as having the longest fossil record among higher fulgoroids [Shcherbakov & Popov, 2002]. The genus *Henriksenopterix* Petrulievičius, 2005 (created for *Hammapteryx paucistriata* Henriksen, 1922, based on tegmen) and a monobasic tribe Celinapterixini were placed in Nogodinidae s.l. on account of bidentate second and long first metatarsomeres discovered in *Celinapterix* Petrulievičius, 2005 (Late Paleocene), and also RA not reaching tegminal apex, tornus remote from claval apex, and one or two RA–RP branches

sigmoidal [Petrulievičius, 2005]. However, excepting bidentate second metatarsomere, these characters could be found also in some Ricaniidae, all four of them in the primitive genus *Cotrades* Walker, 1858 [Fennah, 1949, 1968: fig. 3] that also lacks precostal lobe in hindwings, characteristic of Ricaniidae [Shcherbakov, 1982, and unpubl.]. Fennah [1968] compared Paleocene *Cotradechites* to existing genera of Nogodinidae and Ricaniidae, and found it to be closest to ricaniids *Semestra* Jacobi, 1916 and *Cotrades*, but in fact, its similarity to nogodinid *Mindura* Stål, 1862 (Varciini Sassulina) is greater. Numerous tegmina closely resembling *Cotradechites* and *Mindura* are found in the Early Paleocene (between 65 and 62 Ma, Middle Tsagayan Formation of Amur Region, Arkhara locality; undescribed).

Five Paleocene genera listed above are quite uniform in tegminal structure, including long, narrow apical cells and several RA–RP (and usually also several MP–CuA) branches sigmoidal in subapical zone, and similar to some Nogodinidae, especially to *Mindura*, differing e.g. in CuA–CuA2 more remote from CuP. Similarity of tegminal venation implies uniformity of metatarsal dentition; therefore *Hammapteryx*, *Dilaropsis* and *Cotradechites* are here transferred to Nogodinidae s.l. near (tribal status of the latter and generic status of *Henriksenopterix* is yet to be confirmed).

Three closely related Eocene species of six assigned to the genus *Lithopsis* Scudder, 1878 (*L. fimbriata* Scudder, 1878, *L. simillima* Cockerell, 1920, *L. dubiosa* Cockerell et Sandhouse, 1921) are similar in habitus and tegminal venation to narrow-winged Nogodinidae s.l., such as *Bladina* or some Epacriini. In a specimen of *L. cf. fimbriata* metatarsi are shaped like in *Celinapterix*, with first segment long and second bidentate, and tegmina show no trace of granules (Figs 7–8). Therefore the genus *Lithopsis*, formerly assigned to Flatidae, is

here transferred to Nogodinidae s.l. The genus *Thaumastocladius* Cockerell et Sandhouse, 1921 (based on incomplete tegmen) could be a synonym of *Lithopsis*.

Nogodinidae s.l. of typical appearance, with hyaline tegmina, pigmented pterostigma and strong *c-ra* crossvein(s) were found in the latest Paleocene–earliest Eocene (ca. 55 Ma) [Rust & Ansoerge, 1996: 359, right] and Eocene (*Ficarasites* Scudder, 1890, described in Flatidae, and specimen figured in Dayvault et al. [1995: fig. 25]).

Probable nogodinids are *Eoricania* Henriksen, 1922 (latest Paleocene–earliest Eocene; the type is represented by superimposed tegmen and hindwing similar to those of Nogodinidae – see fig. 28 in Szwedo et al. [2004]; '*Ormenis*' *furcata* Henriksen, 1922 is probably identical to *Eoricania*), and Eocene *Detyopsis* Cockerell, 1920, *Neoricania* Carpenter, 1990 (= *Eoricania* Haupt, 1956, non Henriksen, 1922), *Eobladina* Haupt, 1956, *Giselia* Haupt, 1956 (described in Flatidae), '*Aphaena*' *rotundipennis* Scudder, 1878 (described in Fulgoridae), and even '*Paralatinia*' *saussurei* Scudder, 1890 (described in Blattodea).

The structure of ovipositor, yet unknown for the genera listed above, may well be similar to that in Bladinini and Issidae (in the case they could be classified as Issidae *sensu* Emeljanov). Of three fossil nogodinid genera with known structure of ovipositor, the older one, *Tritophania* Jacobi, 1938 from Eocene Baltic amber, belongs to Bladinini (i.e. to Issidae *sensu* Emeljanov), and two younger, from Oligocene–Miocene Dominican and Mexican ambers, to Nogodinini.

Eocene genera *Protoliarus* Cockerell, 1920 (listed as probably not belonging to Fulgoroidea in Szwedo et al. [2004]) and *Scoparidea* Cockerell, 1920 (known from a tegmen without clavus; assigned to Lophopidae in Szwedo et al. [2004]) are basically similar in the tegminal structure to the extant issid genus *Colpoptera* Burmeister, 1835 (narrow tegmina with long clavus and short, membranous postnodal part, sharply delimited from convex, sclerotized 'corium' by reclined boundary; precostal carina narrow), differing in the tornus just beyond claval apex. In *Scoparidea* the postnodal part is more densely veined and contrasted to sparse prenodal venation. An undescribed fossil with similar tegmina (but tornus remote from claval apex as in *Colpoptera*, and precostal area apparently broader) from Dominican amber [Grimaldi & Engel, 2005: fig. 1.1] shows the hindwing characters immediately placing it into the tribe Colpopterini as defined by Gnezdilov [2003b: fig. 1]: hindwing not lobate; Pcu and A1 free; distal CuA2+CuP fusion fold-like, subparallel to anterior wing margin, and entering weak marginal incision. The hindwing of *Protoliarus humatus* Cockerell, 1920 (as seen on original photograph of holotype) looks dissimilar, nogodinid- rather than issid-like, and apparently lacks the CuA2+CuP fusion. *Protoliarus* and *Scoparidea* probably represent a group of Issidae *sensu* Emeljanov, intermediate between narrow-winged Nogodinidae s.l. (*Bladina*, *Lithopsis*) and Issidae Colpopterini, maybe even the earliest submacropterous Issidae s.str.

The tegmen of subbrachypterous Issidae s.str. is recorded in the Middle Eocene (*Issites* Haupt, 1956). Issid nymphs are common in ambers [Szwedo, 2002].

Having transferred into Nogodinidae s.l. most of putative fossil ricaniids and flatids, we left very few records for these two families. Eocene *Ricaniella antiquata* (Scudder, 1895), originally assigned to *Ricania* Germar, 1818, belongs to Polystoechotidae (Neuroptera), and Eocene *Callospilopteron ocellatum* Cockerell, 1920, described in Fulgoridae s.l., is probably a neuropteran as well (A.G. Ponomarenko, pers. comm.). '*Lechaea*' *primigenia* Henriksen, 1922 (latest Paleocene–earliest Eocene) shows no characters diagnostic of Flatidae. Flatid nymphs are reported from Mexican amber, but Ricaniidae are remarkably absent from ambers (except for subfossil copal), in contrast to nogodinids represented there with 3 genera [Szwedo, 2002]. Among compression fossils, *Scolypopites* Tillyard, 1923 (Miocene; RA far not reaching tegminal apex) belongs to Ricaniidae.

To clarify relationships of all listed and other Paleogene taxa (many of them based on isolated, often incomplete tegmina), revision of types and study of new material are needed, especially of numerous whole-bodied fossils from the Green River Eocene that are able to provide crucial information on the structure of hind legs and ovipositor. Diagnostics of broad-winged groups of higher Fulgoroidea based on venation and superficial characters is not easy, so one must be very cautious about the records of Cenozoic Ricaniidae, Flatidae etc. scattered over the literature.

If our considerations are true, the fossil record of higher fulgoroid families is very uneven: many finds for Nogodinidae s.l., especially in Paleogene rocks (including the earliest and most if not all Paleocene finds of higher Fulgoroidea); quite many finds for Issidae s.str., especially in ambers; several for Tropiduchidae; few, mostly recent ones for Flatidae and Ricaniidae; and no fossils for Caliscelidae, Acanaloniidae, Tettigometridae, Lophopidae, Eurybrachyidae, Gengidae, and Hypochtonellidae. To a certain degree these differences reflect the different age of these groups, as well as their different biology and geographic ranges, and broadly agree with the phylogenetic sequence 'Issidae s.l. → Nogodinidae s.str. → other families' proposed by Emeljanov [1990]. Rarity of subbrachypterous forms among compression fossils is explainable by that the record is biased toward macropters. Therefore one cannot exclude that the earliest higher fulgoroids were issid-like and subbrachypterous. Available fossils give no evidence on existence of known higher fulgoroid families in the Mesozoic, and such age estimates as 65 Ma for Lophopidae [Soulier-Perkins, 2000] seem too old.

Summing up the above:

- earliest higher Fulgoroidea are recorded just above the Cretaceous/Paleogene boundary, in the Early Paleocene;
- these are macropterous forms, attributable to Nogodinidae s.l. based on venation and metatarsal den-

tion, with female genitalia (yet unknown) presumably of issid type, i.e. Issidae *sensu* Emeljanov

– Nogodinidae s.l. are quite common and diverse in the Paleogene, Issidae s.str. and Tropicuchidae first found in the Eocene, Flatidae and Ricaniidae much later, and remaining higher planthopper families not recorded with certainty;

– the latest radiation of family-group fulgoroid taxa started after the Cretaceous/Paleogene crisis, but was not explosive;

– available fossil record agrees with ideas that Issidae s.l. are closest to the base of monophyletic higher Fulgoroidea [Emeljanov, 1990] and that Tettigometridae constitute a distal lineage [Bourgoin et al., 1997], and gives no arguments against monophyly of ricanioid group of families.

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