

AUTRIMPUS SAMBIORUM GEN. AND SP. NOV. FROM EOCENE BALTIC AMBER AND NOTES ON MNEMOSYNINI STAT. NOV. (HEMIPTERA: FULGOROIDEA: CIXIIDAE)

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Abstract.— *Autrampus sambiorum* gen. et sp. nov. to comprise fossil from Eocene Baltic amber is described. The characters of Cixiidae planthoppers ascribed to subtribe Mnemosynina of tribe Pentastirini are discussed and new rank of the group as tribe Mnemosynini stat. nov. is proposed. The status of the extinct and extant taxa ascribed to Mnemosynini and characters of the tribe are discussed.



Key words.— *Autrampus*, *Autrampus sambiorum*, Mnemosynini, new rank, Cixiidae, fossil, Eocene Baltic amber, taxonomy.

INTRODUCTION

The family Cixiidae Spinola, 1839, is a group of planthoppers with over 1500 described species comprised in 146 genera (which may be about 40 percent of the actual world fauna) and cosmopolitan distribution (Larivière 1999, Holzinger et al. 2002). Within the family three subfamilies: Bothriocerinae Muir, 1923, Borystheninae Emeljanov, 1989 and Cixiinae Spinola, 1839 are recognized (Emeljanov 1997, 2002). Emeljanov (1989, 2002) discussed the problem of the higher classification of Cixiidae, but still there is no universally adopted tribal classification of this family. In addition, it is very probable that Cixiidae are not a monophylum and within this paraphyletic unit up to six different lineages are included (Holzinger et al. 2001, Holzinger and Bourgoin personal communication).

Subfamily Cixiinae is the most numerous and differentiated comprising 15 tribes. One of them – Pentastirini was separated by Emeljanov (1971) and comprise two tribes Oliarina and Pentastirina. The subtribe Mnemosynina was subsequently added by Emeljanov (1993). Later (Holzinger et al. 2002) Oliarina was synonymized under Pentastirina.

The fossil record of Cixiidae is not very rich and numerous fossil taxa previously ascribed to Cixiidae are excluded from this family or need to be re-considered and revised (Szwedo et al. 2004). The oldest fossils are known since Lower Cretaceous deposits of England and Brazil, and from Lebanese amber (Fennah 1961, 1987;

Martins-Neto 1988, Hamilton 1990). Cixiidae are quite common in Eocene Baltic amber inclusions (Szwedo and Kulicka 1999a, b, Szwedo et al. 2004).

Fossil taxa ascribed to Pentastirini were mentioned several times. *Oliarus oligocenus* Cockerell, 1910, ascribed to cixiids (Cockerell 1910) can not be placed in the extant genus *Oliarus* Stål, 1862 and according to the original description and drawing should be placed in Achilidae, but with an unresolved position until the type material will be accessible and revised. The other fossil representatives of Pentastirini are known from the Palaeogene, but undescribed forms ascribable to this group are reported from Lower Cretaceous Burmese amber (Grimaldi et al. 2002). The genus *Perunus* Szwedo et Stroiński, 2002, with two species, was described from Eocene Baltic amber (Szwedo and Stroiński 2002). A few other taxa related to Pentastirini were described from Oligocene strata of Germany (Statz 1950) and Dominican amber (Szwedo 2000). The fossil ascribed to the genus *Mnemosyne* Stål, 1866 was identified on the basis of the partly preserved tegmen by Fennah (1963), from Oligocene/Miocene Mexican amber.

SYSTEMATIC PART

Nomenclature of veins is used according to data provided by Emeljanov (1977), Dworakowska (1988) and Kukulová-Peck and Brauckmann (1992). Costal margin

is composed structure, the basal part, often thickened and/or tucked up is called epipleuron by Dworakowska (1988) *per analogiam* to the name applied for this area in beetle elytron. However, term 'epipleuron' or 'epipleura' is applied also for other structures in insects, i.e. basal and subalar sclerites of pleurites forming wings articulation, lateral margins of abdominal segments II and III in Hymenoptera: Ichneumonidae and bent ventrad lateral margins of beetle pronotum (Razowski 1996, Zombori and Steinmann 1999). The term 'basicostal field' is proposed to name this area in hemipteran hemelytron. Vein M in hemipterans hemelytron is composed only of vein MP, as MA is fused with RP (this character is regarded as apomorphy of Hemineoptera = Paraneoptera). Terminology of female genitalia structures follows Bourgoïn (1993).

Autrimpus gen. nov.

Type species. *Autrimpus sambiorum* sp. nov., here designated.

Etymology. "Autrimpus" — name of the god of sea and lakes in Old Prussian mythology. Gender: masculine.

Diagnosis. The genus described below is similar in general habitus to the extant species ascribed to the genus *Mnemosyne* Stål, 1866, which seems to be paraphyletic unit, a complex of genera. For this reason the characters are compared with the type species of the genus *Mnemosyne* — *M. cubana* Stål, 1866. *Autrimpus* gen. nov. in general habitus is similar to extant species of the genus *Mnemosyne* Stål, 1866, but differs by a set of characters from particular species ascribed to this genus. The lower transverse carina delimiting vertex and frons weakly visible (distinct in *Mnemosyne cubana* Stål, 1866); median carina of frons distinct (obsolete in *M. cubana*), postclypeus with median keel distinct (lacking in *M. cubana*). Posterior part of mesonotum distinctly elongate caudad (anterior and posterior portions of mesonotum of similar length in *M. cubana*). Tegmen branch M_{4+5} not coalescent with CuA_1 , connected with the latter by the transverse veinlet (vein M_{4+5} coalescent with CuA_1 at some part then separated in *M. cubana*, no veinlet present); vein RA with two terminals (single terminal in *M. cubana*); RP with 3 terminals (4 in *M. cubana*) and M with 6 terminals (5 in *M. cubana*). Hind coxae shifted caudad at distance exceeding length of mid trochanters (hind coxae at distance not exceeding length of midtrochanters in *M. cubana*); membranous area placed between hind coxa and 3rd sternum with disc parallel to longitudinal axis of the body (disc of this area oblique in *M. cubana*); posteroventral portion of epimerum 3 concave (convex in *M. cubana*). Anal tube relatively short, shorter than lateral appendages of pygofer (anal tube elongate, longer than lateral lobes of pygofer in *M. cubana*).

Description. Quite large cixiid, body length about 10 mm and wingspan about 20 mm, with some colour

markings on the tegmina and wings. Vertex concave with lateral carinae elevated, median portion of the disc flat, lateral portions elevated; apical transverse carina very obsolete, base of vertex arcuate, at posterior angles about as wide as vertex length

Face elongate, about 2.3 times as long as wide at widest point at level of antennae, with lateral margins elevated. Frons 1.6 times as wide as long in mid line; slightly convex; with distinct median carina; median carina bifurcate in upper portion, just below junction with vertex; transverse carina obsolete; median ocellus present. Frontoclypeal suture distinctly bent upward. Postclypeus very slightly convex, with median carina and distinct lateral carinae. Anteclypeus with median carina. Clypellus quite long. Rostrum very long, distinctly exceeding hind coxae, reaching almost to end of pygofer, subapical segment 1.75 times as long as apical one.

Pronotum with distinct postocular carinae, reaching posterolateral margin, median carina absent.

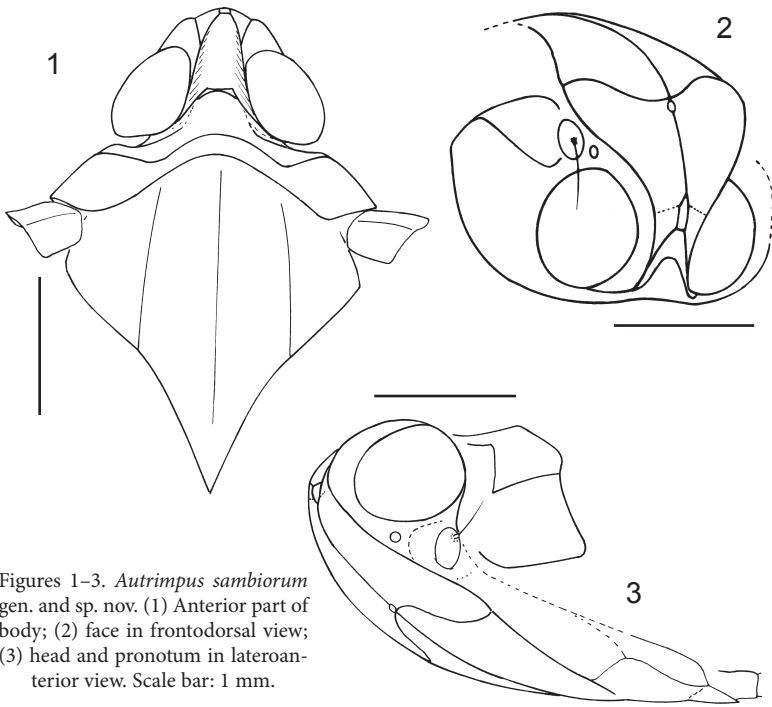
Mesonotum longer than wide, distinctly elongate in posterior portion, caudad of level of tegulae, with three obsolete median keels.

Tegmina hyaline, veins without distinct granules and setae, setiferous granules present only in apical cells; costal margin thickened; stigma about 3.5 times as long as wide; $ScRA_1$ forked basad of apex of clavus; RA with 2 terminals, RP with 3 terminals; M with 6 terminals, with M_{3+4} with a short common stalk, then bifurcated at level of cephalad margin of stigma, then forked in apical portion; CuA bifurcate at level of junction of claval veins, with two terminals; clavus quite long, reaching $\frac{2}{3}$ of tegmen's length, with veinlet pcu-cup present, claval veins Pcu and A_1 joined at half of length of claval commissural border (vein A_2). Tubercles with sensory setae present in subapical and apical cells.

Hind wings wide, fumose in apical portion, RP with 2 terminals, M with 4 terminals, CuA with 3 terminals; veinlet r-m quite long, veinlet m-cu distinctly oblique.

Fore and mid legs slender, fore and mid trochanters placed near each other. Hind coxae shifted caudad at distance 1.5 times exceeding length of mid trochanters, hind coxa with distinct posteriad spine (meracantha); hind tibia with two distinct lateral spines, first near base and the second just below half of hind tibia's length; hind basitarsomere longer than combined length of mid and apical tarsomeres, tarsal claws relatively small, arolium small. Tibio-metatarsal formula 1+2+3 : 5 : 5.

Abdomen flattened dorsoventrally, sternites IV–VII separated medially, sternites VI and VII with rows of distinct trichobothria at posterior margin, sternite VIII relatively big; pygofer slightly laterally flattened, with long, lateral, delicately carinated, caudad projections exceeding length of anal tube; ventral margin of pygofer with median process; anal tube with distinct apical ventrad process, genital styles seem to be asymmetric, distinctly curved dorsad, with subapical projection.



Figures 1–3. *Autrimpus sambiorum* gen. and sp. nov. (1) Anterior part of body; (2) face in frontodorsal view; (3) head and pronotum in lateroanterior view. Scale bar: 1 mm.

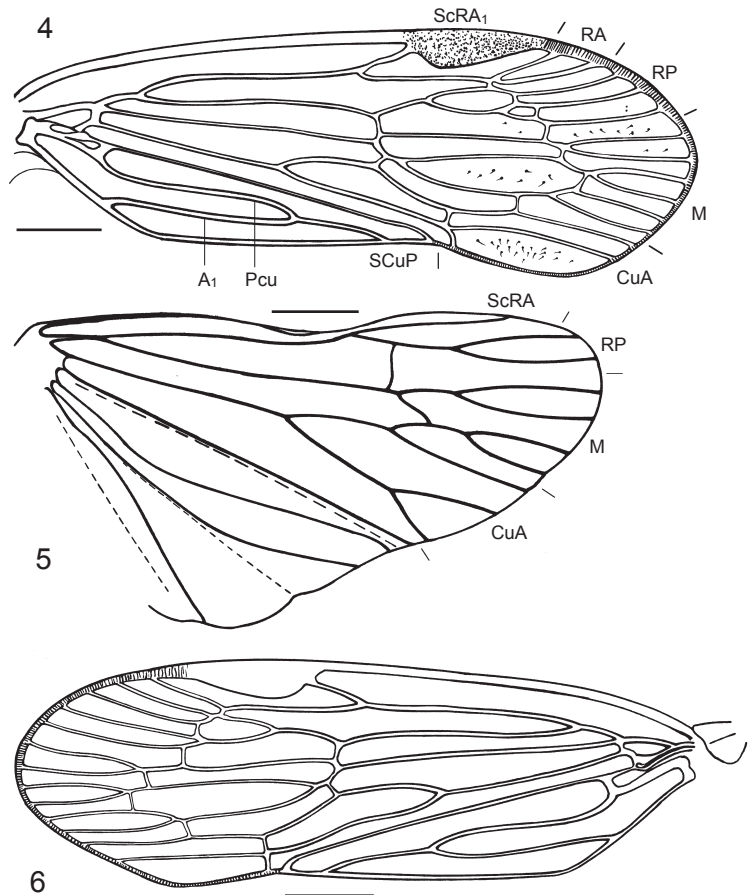
Autrimpus sambiorum sp. nov.
(Figs 1–13, 32–37)

Diagnosis. Posterior margin of pygofer with distinct rounded median process, lateral process of pygofer distinct, very long, exceeding length of anal tube, slightly carinate, this projection with distinct dorsad subbasal process and indistinct dorsad subapical process. Apical process of anal tube long, distinctly curved downwards, with slightly asymmetric, spatulate lower portion, reaching to ventral margin of pygofer. Genital styles asymmetric with subapical process, strongly curved dorsad. Dark marking on claval field near claval suture, indistinct darker marking in subapical portion, on claval apex and reaching to vein RP at level of veinlet r-m, indistinct marking in apical portion on radial and medial cells. Setiferous granules on apical field rp₃, subapical field ma₂ and apical cell cua₂.

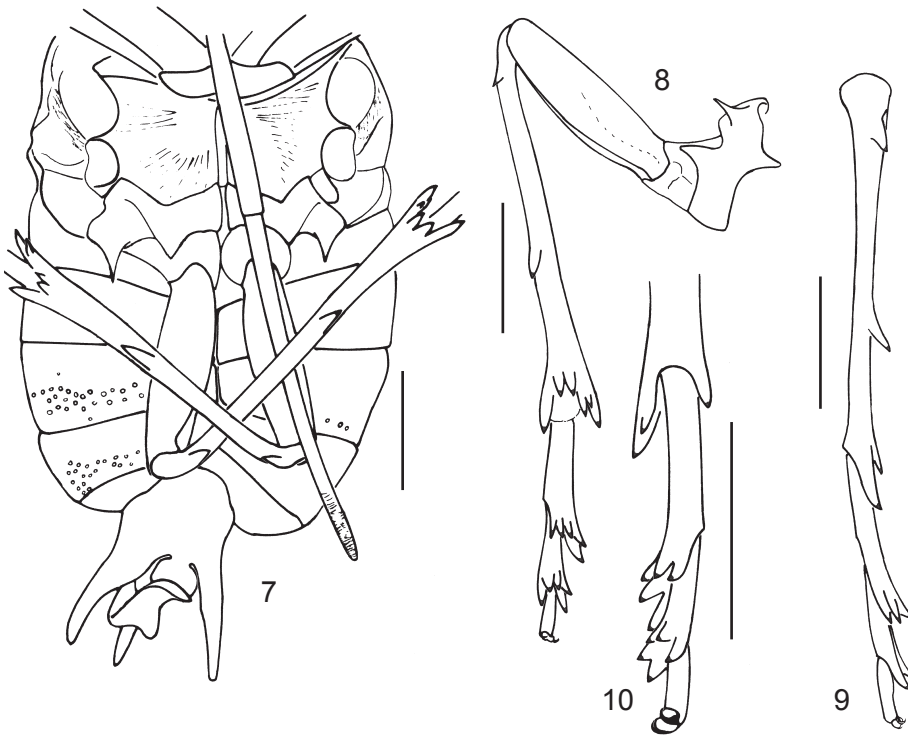
Description. Total length of body 8.2 mm, wingspan 19.3 mm. Body slightly dorsoventrally flattened (Fig. 32).

Head (Fig. 1) with compound eyes 1.53 mm wide, distinctly narrower than pronotum, compound eyes big, bulging. Vertex narrower than long, anterior margin slightly curved, lateral margins elevate, posterior margin distinctly concave; disc of vertex concave in median portion, distinctly elevate in lateral portions, without median carina; length of vertex in mid

line 0.6 mm, width of vertex 0.37 mm at anterior border, 0.5 mm at posterior border (posterior angles) of disc, 0.9 mm at lateral angles; lateral carinae of vertex 0.49 mm long to the point of connection with latero-mediad carinae. Face (Figs 2, 3 and 35) shifted ventrad, distinctly elongated, with lateral carinae elevated, median carina of frons and postclypeus distinct; frontoclypeal suture distinctly arcuate; median ocellus small, not very distinct; lateral carinae of postclypeus converging at junction with anteclypeus; face 3.2 mm long in mid line, 1.41 mm wide at widest point at the level of bases of antennae. Frons 0.87 mm long in mid line, 1.19 mm long at lateral border; postclypeus in mid line 1.53 mm long, 0.91 mm long at lateral margin; anteclypeus in mid line 1.04 mm long, clypellus 0.25 mm long; lateral ocelli distinct; antenna 0.94 mm long, scape short, pedicel globular, (not knob-like in shape), without median concavity, flagellum 0.72 mm long; base of antenna sunk in a quite deep concavity below the level of



Figures 4–6. *Autrimpus sambiorum* gen. and sp. nov. (4) Right tegmen; (5) right wing; (6) left tegmen. Scale bar: 1 mm.



Figures 7–10. *Autrimpus sambiorum* gen. and sp. nov. (7) Posterior part of thorax and abdomen in ventral view; (8) right hind leg; (9) right hind leg in lateral view; (10) hind tarsus. Scale bar: 1 mm.

lateral ocellus; rostrum 4.7 mm long, distinctly elongated, reaching almost to the end of pygofer, subapical segment 2.72 mm long, about 1.75 times as long as apical segment (1.55 mm).

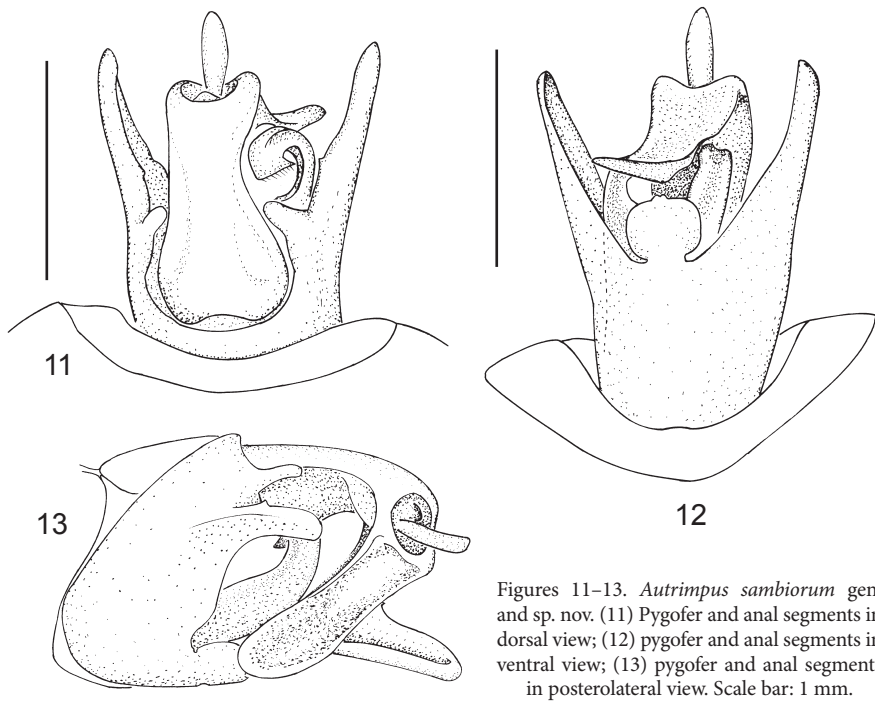
Pronotum (Figs 1, 3, 32 and 34) 2.44 mm wide, 0.4 mm long in mid line; anterior portion slightly protruded anteriorly, posterior margin concave, postocular carinae distinct, reaching posterolateral margin, median carina absent.

Mesonotum (Figs 1, 32 and 34) irregularly diamond shaped, elongated posteriorly, with disc convex, 2.47 mm long in mid line, 2.22 mm wide. Three indistinct lateral carinae present, median carina reaching from the anterior margin of mesonotum to the scutellum, lateral carinae reaching from anterior to posterior margins of mesonotum.

Tegulae slightly wider than long (0.54 mm : 0.47 mm), delicately carinate in the middle.

Tegmina (Figs 5, 6 and 33) 8.1 mm long, 2.7 mm wide at widest point, 2.5 mm wide at the end of clavus, elongate, semitransparent with indistinct colour pattern. Costal margin thickened; slightly

bent at base, almost straight in median portion to the level of end of stigma; widened in apical portion with acute apex; clavus long, reaching $\frac{2}{3}$ of tegmen length; veins with only a few setiferous tubercles, stigma triangular, elongate, with indistinct shagreen sculpture, about 3.5 times as long as wide; costal cell long, with subequal width along; basal cell about 3.5 times as long as wide. Costal margin slightly curved at base, then almost straight up to the end of stigma, costal margin with CP distinct (anterior margin) and CA shifted downwards, with basicostal field not widened at base; veins Sc+R and M begin with the common stem, R bifurcated close to the basal cell, ScRA₁ terminate in the cephalad margin of stigma, RA with two terminals, RP with three terminals; transverse veinlets between RA and RP₁, RP₁ and RP₂ present, right tegmen with veinlet between RP_{2a} and RP_{2b}. Vein M bifurcate before the claval angle, anterior branch bifurcate in apical portion, posterior branch bifurcate twice, near the first bifurcation and in apical portion, all these bifurcations create six terminals; first transverse veinlet r-m placed cephalad of claval angle, slightly anterior of anterior



Figures 11–13. *Autrimpus sambiorum* gen. and sp. nov. (11) Pygofer and anal segments in dorsal view; (12) pygofer and anal segments in ventral view; (13) pygofer and anal segments in posterolateral view. Scale bar: 1 mm.

margin of stigma, second transverse veinlet r-m in apical portion, delimiting apical cell; first transverse veinlet m-cu at the same level as first r-m veinlet, second transverse veinlet m-cu placed apicad; vein CuA bifurcate in about half of tegmen length, with two terminals in apical margin, short veinlet present near the claval angle; transverse veinlet icu placed slightly apicad of claval angle; vein CuP united with Pcu on the clavus slightly apicad of basal cell, with distinct veinlet cup-pcu. Pcu united with A₁ at $\frac{2}{3}$ of length of clavus, at half of length of commissural border, at level of CuA first forking

Wing (Figs 5 and 33) wide, elongate; costal margin thickened, undulate, apex relatively acute; wing membranous, fumose at external margin, more distinctly at apex; veins Sc+R and M begin with a short common stem; vein ScRA₁ long, terminate apicad of RP bifurcation, RP with two terminals, M with four terminals, forked at the same level as RP; transverse veinlet r-m long, perpendicular to veins R and M; vein CuA with three terminals, first forking at about half of wing length, distinctly basad of transverse veinlet r-m, transverse veinlet m-cu oblique, placed slightly apicad of veinlet r-m; CuP, Pcu and anal veins not bifurcated.

Fore legs (Fig. 35) slender; fore coxa elongate, fore trochanter short, fore femur 1.65 mm long, longer than fore tibia (1.25 mm); fore tarsus 0.62 mm long; tarsomeres subequal in length (0.25 mm), apical tarsomere merely longer, measured with claws 1.1 times as long as cumulative length of basal and mid tarsomeres. Mid legs slender, mid coxa elongate, mid trochanter short, mid femur 1.65 mm long, shorter than mid tibia (1.83 mm), mid tarsus and tarsomeres as in fore tarsus.

Bases of fore and mid legs close each other, bases of hind legs (hind coxae) distinctly shifted caudad at distance 1.5 times exceeding length of mid trochanters; membranous area placed between hind coxa and 3rd sternum with disc parallel to longitudinal axis of the body, 0.72 mm long in mediad margin, maximal length 1.04 mm, 0.98 mm wide; disc of this area flat, limited at lateral border by convex margin of 3rd episternum and convex margin of 3rd epimerum, epimerum at ventral portion with distinct concavity (Figs 7 and 35).

Hind coxa with quite long (0.46 mm long) caudad meracantha, trochanter ring-like, short, hind femur as long as mid femur, but slightly more massive, hind tibia (Figs 8 and 9) 3.25 mm long, slender with two big lateral spines, the first near base, the second at half of tibia length, with six (arranged 1+2+3) apical teeth with diastemma; hind tarsus 2.1 mm long, basal tarsomere as long as cumulative length of mid and apical tarsomeres, 1.48 mm long. Basal and mid tarsomeres relatively thick, with five apical teeth, mid tarsomere (0.95 mm) distinctly shorter than basitarsomere, apical tarsomere small and thin, 0.7 mm long with tarsal claws, tarsal claws small, arolium small (Fig. 10); tibio-metatarsal spinal formula of hind leg 1+2+3 : 5 : 5.

Abdomen (Figs 7, 32, 34 and 35) measured with pygofer in dorsal line 4.39 mm long, 2.83 mm wide, dorsoventrally flattened, with indistinct dorsal crest, connected to the thorax on all its width, caudal borders of tergites almost straight; abdominal sternites IV–VII separated medially, sternite VIII relatively big; sternites with caudal borders almost straight in basal portion, only slightly protruded cephalad in apical portion near pygofer; abdominal sternites VI and VII with distinct three rows of trichobothria in caudal portion (Figs 7 and 17).

Pygofer (Figs 11–13, 32, 34–37) 1.6 mm long, 1.28 mm wide at widest point at level of apices of lateral processes, subquadrate, distinctly narrower than pregenital segments of abdomen; lateral portions of pygofer elongated posteriad, creating two long, delicately carinate, lateral processes; each process provided with two additional dorsad process: long subbasal process and indistinct tooth at about of half of its length (Figs 11 and 13); pygofer in ventral view 1.04 mm long in mid line, medioventral process 0.27 mm long, oval, narrow at base, with additional, small, apical median process (Fig. 12). Anal tube elongate, 1.14 mm long in mid line, 1.48 mm long with anal style, 0.6 mm wide at widest point near base, 0.35 mm wide at the narrowest point, lateral margins concave mediad; apical portion in form of long, ventrad, spatulate, slightly asymmetric process, reaching lower margin of pygofer (Figs 11–13, 16 and 18). Anal style elongate, 0.37 mm long. Genital styles probably asymmetric, left style elongate, distinctly bent dorsad with short triangular, subapical process (Figs 11–13 and 36).

Etymology. The species name refers to the indigenous tribe “Sambi” inhabiting the Sambian Peninsula in the Early Middle Ages.

Material examined. Holotype. Eocene, Baltic amber inclusion, No. P. 8834, Ln 11927, Friedrich Adolf Paneth collection, Manchester Museum of Natural History, United Kingdom. Male, well preserved with tegmina and wings spread, and details of genital block visible.

DISCUSSION

The fossil genus *Autrimpus* gen. nov. described above is very close in external appearance and general habitus to the extant genus *Mnemosyne* Stål, 1866. The latter is distributed in the tropical zone of the New and Old World and recorded in the fossil state only by a part of the tegmen preserved from Oligocene/Miocene Mexican amber (Fennah 1963). It differs by the structures of the male genital block with lateral projections of pygofer exceeding length of anal tube, which is contrary to extant species of *Mnemosyne*, in which anal tube is always longer than lateral projections of pygofer. Regarding the structure of the male genital block, the most similar to *Autrimpus sambiorum* sp. nov. among

extant species ascribed to the genus *Mnemosyne* are some Neotropical ones. *M. braziliensis* Van Stalle, 1987 is characterized by the pygofer with two caudad process, but these are distinctly shorter than the anal tube; the ventral process of anal tube is short; and the postero-ventral process of pygofer is narrow and slightly bifurcate at apex; also the structure of the genital style is similar. The tegmen venation pattern of *M. braziliensis* is different, with 2 terminals of RP. The tegmen venation with 2 terminals of RA and 3 terminals of RP is present in some Afrotropical species ascribed to the genus *Mnemosyne*: *M. evansi* Muir, 1923 and *M. lamabokoensis* Synave, 1978, but Afrotropical species are characterized by 5 terminals of M vein. The structure of the male genitalia of *M. evansi* is quite similar, particularly the male genital style. However, this similarity could be artificial.

Taxonomic status of Mnemosynini Emeljanov, 1983 stat. nov.

The tribe Pentastirini of the subfamily Cixiinae was erected by Emeljanov (1971), with the set of characters as follows: five longitudinal carinae on mesonotum and ovipositor reduced or, if elongated, gonapophysis VIII (valvula I) not corrugated and gonapophyses IX (valvulae II) not fused together. Van Stalle (1986b) added to this set also the connection of aedeagus with the pygofer. Pentastirini were divided by Emeljanov (1971) into two subtribes: Oliarina Emeljanov, 1971, with vertex with subapical keel forming a sharp angle and hind tarsi with a single row of teeth, and Pentastirina Emeljanov, 1971, characterized as follows: subapical keels of vertex fused together to form an obtuse angle and hind tarsi with a double row of teeth. Subsequently, Emeljanov (1993) added a new subtribe Mnemosynina Emeljanov, 1993, with the combination of characters as follows: five keels on mesonotum, ovipositor reduced, and direct articulation between anal tube and theca.

Van Stalle (1986b) proposed to determine the limits of Pentastirini on the base of apomorphy: the separation of anal tube base from theca and articulation of theca with pygofer. From this point of view the genus *Mnemosyne* Stål does not fit the limits of the tribe, as the aedeagus is connected to the anal tube, not to the pygofer. This was argued by Emeljanov (1993: 25). He stated that general habitus and pattern of structure and the transformation of the male genitalia in *Mnemosyne* Stål make it related to other Pentastirini. The hypothesis that the five keeled mesonotum and reduced ovipositor are true synapomorphies for *Mnemosyne* Stål and Pentastirini is also preferable in his opinion. He also added that the configuration of wax plates on abdominal tergites VI–VIII in nymphs of *Mnemosyne* Stål and *Oliarus* Stål s.l. is similar, and that these taxa are also related by punctate anastomosis of M and CuA₁ on the hind wing (but this character is also present in other,

unrelated genera of Cixiinae). The other characters against placement of *Mnemosyne* Stål in Pentastirini mentioned by Van Stalle (1986a: 400) are: the tegminal venation, viz. the different pattern of furcation of the median sectors; the apical spinulation of the hind tibia which shows three unequal outer spines, the median one of this group being small instead of subequal in length to the others; and the medioventral process of the pygofer fairly different from Pentastirini. In his opinion (Van Stalle 1986b: 121) the five keeled condition of the mesonotum in *Mnemosyne* Stål could probably be the case of parallel evolution, as in these large, robust species with good ability to fly, two additional keels could serve as a further support for the wing muscles. The five keeled mesonotum is also observed in the genus *Oecleus* Stål (Cixiinae: Oecleini Muir, 1922) and representatives of Delphacidae Leach, 1815 – a family related to Cixiidae. He also stated that absence of a connection between aedeagus and pygofer suggest that *Mnemosyne* Stål has evolved along a separate line, although the structure of the female genitalia is close to the Pentastirini type (Van Stalle 1986b).

In the review of Cixiidae (Holzinger et al. 2002) Oliarina are synonymized under Pentastirina. Thus, Pentastirina comprise 35 genera and Mnemosynina sole genus *Mnemosyne* Stål.

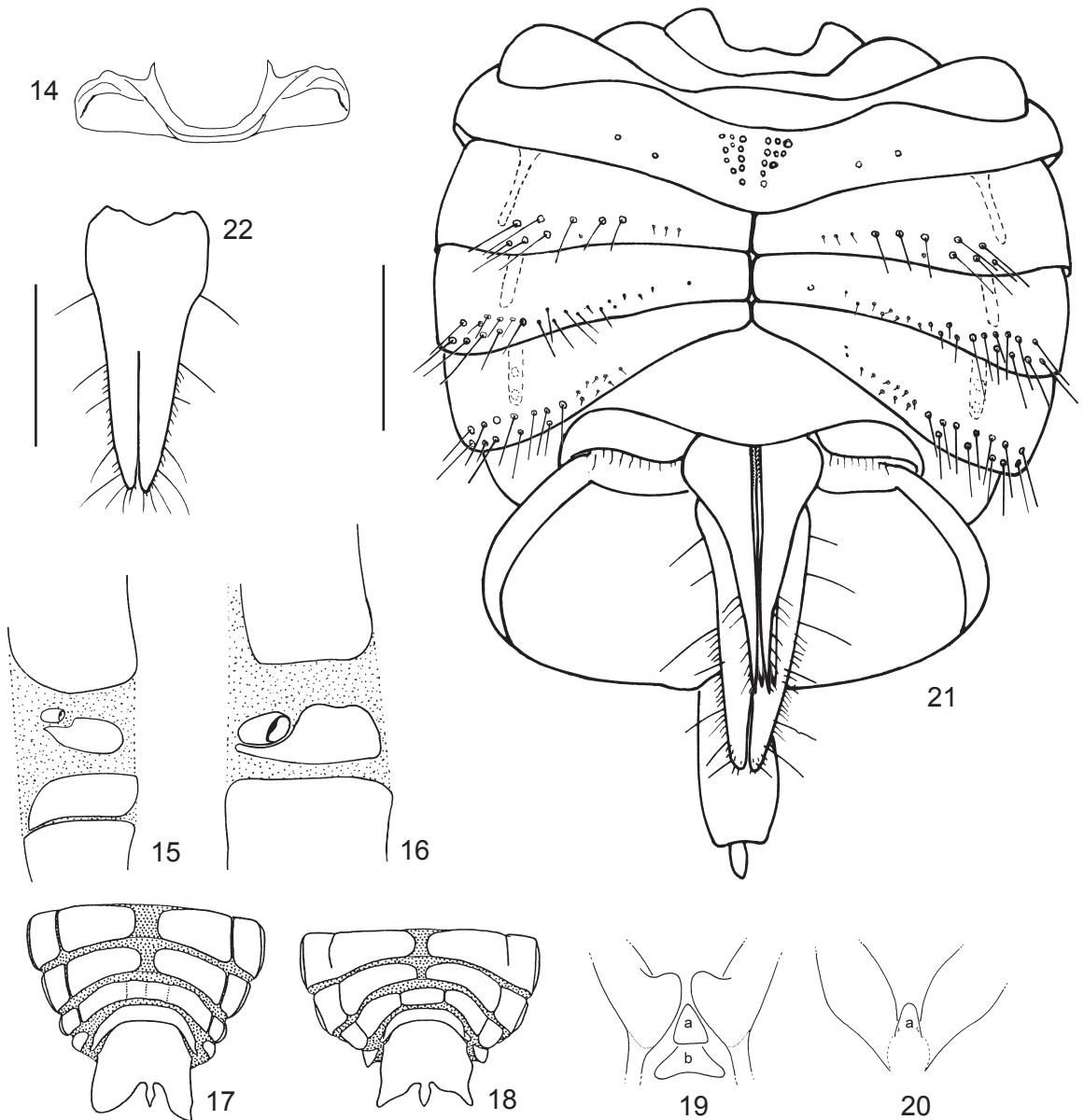
The genus *Mnemosyne* Stål, 1866, seems to be paraphyletic, a complex of genera rather than a compact genus, but further research is necessary to resolve this question. The extant species of *Mnemosyne* Stål were reviewed by Van Stalle (1986a, 1987, 1988) and Van Stalle and Lauterer (1985). The known species ascribed to the genus are known from the African continent (6 species), Oriental Region (17 species) and Neotropical Region (23 species).

Placement of the genus within recognized tribes of Cixiinae still remains controversial. Van Stalle (1986a, b) believed that this genus should not be placed within Pentastirini, but he did not propose any other placement. Emeljanov (1993, 2002) placed *Mnemosyne* Stål within Pentastirini, and proposed the subtribe Mnemosynina for this genus (Emeljanov 1993).

In my opinion, species ascribed to the genus *Mnemosyne* Stål, together with the extinct *Autrimpus sambiorum* Szwedo should be placed in separate tribe Mnemosynini stat. nov. of Cixiinae.

Mnemosynini Emeljanov, 1993 stat. nov.

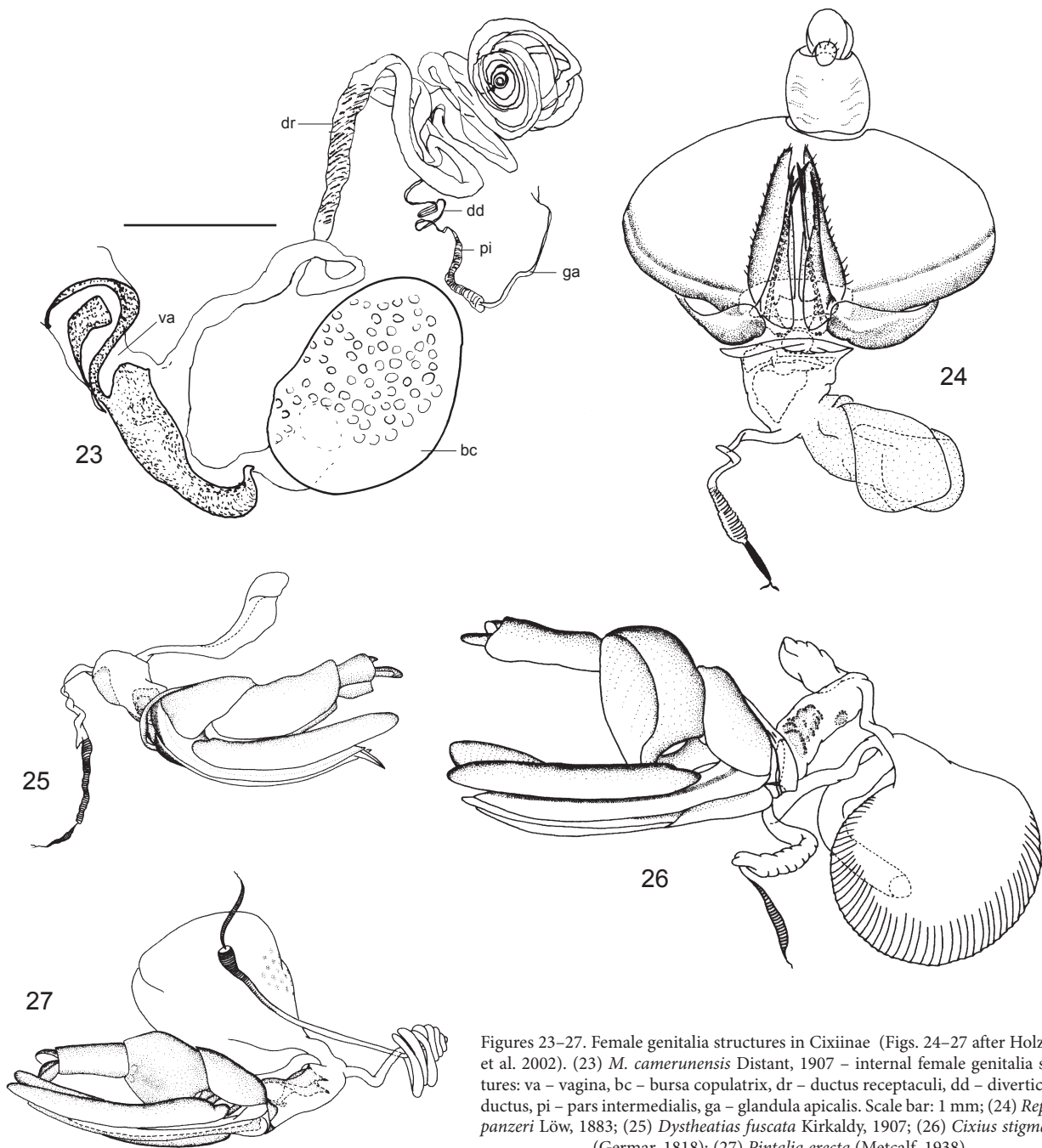
Diagnosis. Pronotum and mesonotum (even whole body) often covered with short hairs. Mesonotum usually with five keels, but in some species only three keels are distinct, or keels obsolete; posterior margin of mesonotum markedly elongate caudad. Tegmina with lines of setiferous tubercles on cells between veins; veins M₃₊₄



Figures 14–22. Mnemosynini and Pentastirini. (14) *Mnemosyne cubana* Stål, 1866 – chitinized part of tymbal organ in anterior view (After Van Stalle 1987); (15) Abdominal pleural region in Pentastirini: *Pentastiridius leporinus* (Linnaeus, 1761), semidiagrammatic; (16) Abdominal pleural region in Mnemosynini: *Mnemosyne camerunensis* Distant, 1907, semidiagrammatic; (17) male abdominal segment of Pentastirini: *Pentastiridius* Kirschbaum, 1868 (after Emeljanov 2002); (18) the same: *Reptalus* Emeljanov, 1971 (after Emeljanov 2002); (19) *M. cubana* – fused base of genital styles with (a) the unpaired median process, and (b) the dorsal part of the connectivum (after Van Stalle 1987); (20) *M. pernambucoensis* Van Stalle, 1987 – fused base of genital styles with (a) the unpaired median process (after Van Stalle 1987); (21) *M. camerunensis* – female abdomen in ventral view; (22) *M. camerunensis* – gonoplac in dorsal view. Scale bar: 1 mm.

always bifurcated basad of vein M_{1+2} bifurcation. Hind tibia with single row of spines in formula 1+2+3, hind basitarsomere and mid tarsomere with single row of spines, usually 5 : 5. Tymbal organ with a short apodeme on each side present in both males and females (Fig. 14). Abdomen with distinct rows of trichobothria on posterior margin of sternites V–VII, each socket provided with long, threadlike trichome (Fig. 21). Median sclerite of male VII sternite not developed. Abdominal hypopleur-

ites IV–VII fused with sternites. Epipleurites of segments IV–VII with parastigmal area quite big, but not distinctly delimited. Spiracles relatively big, placed in anterodorsal corner of the parastigmal area. Female sternite VIII with posterior margin almost straight, curved or provided with median process. Ovipositor reduced (Fig. 21); gonoplac fused at base (Fig. 22), gonapophysis IX fused at base. Vagina very long, with sclerotizations, bursa copulatrix globular with sclerotized ornamentations, ductus recepta-



Figures 23–27. Female genitalia structures in Cixiinae (Figs. 24–27 after Holzinger et al. 2002). (23) *M. camerunensis* Distant, 1907 – internal female genitalia structures: va – vagina, bc – bursa copulatrix, dr – ductus receptaculi, dd – diverticulum ductus, pi – pars intermedialis, ga – glandula apicalis. Scale bar: 1 mm; (24) *Reptalus panzeri* Löw, 1883; (25) *Dystheatis fuscata* Kirkaldy, 1907; (26) *Cixius stigmaticus* (Germar, 1818); (27) *Pintalia erecta* (Metcalf, 1938).

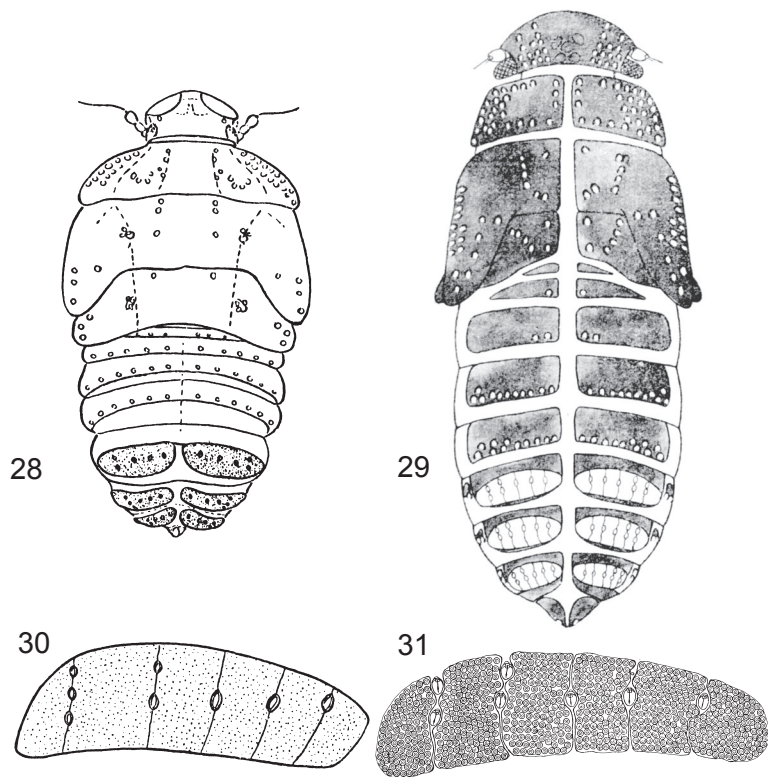
culi very long, strongly convolute with helicoid sculpture, diverticulum ductus very long, strongly helicoidal convolute, pars intermedialis short, glandula apicalis longer than pars intermedialis (Fig. 23). Male genital styles fused at base and a small unpaired process is present at place of their fusion (Figs 19 and 20). Aedeagus fused to anal tube, not fused with pygofer.

Comparing Mnemosynini with Pentastirini and other Cixiinae, the following apomorphic and plesiomorphic characters of the tribe could be suggested.

Furcation model of the M vein on tegmen, with veins M_{3+4} forking basad of M_{1+2} forking seems to be apomorphy for Mnemosynini; in Pentastirini the forking is opposite, similar condition is to be found among other Cixiinae, with exception of Brixiini Emeljanov, 2002 and some Oecleini. However, latter two tribes represent other lineages within Cixiinae, according to Emeljanov (2002). In Pentastirini, regarded as one of the most advance tribes, double rows of teeth and subapical setae on both tarsomeres (basitarsomere and mid tarsomere)

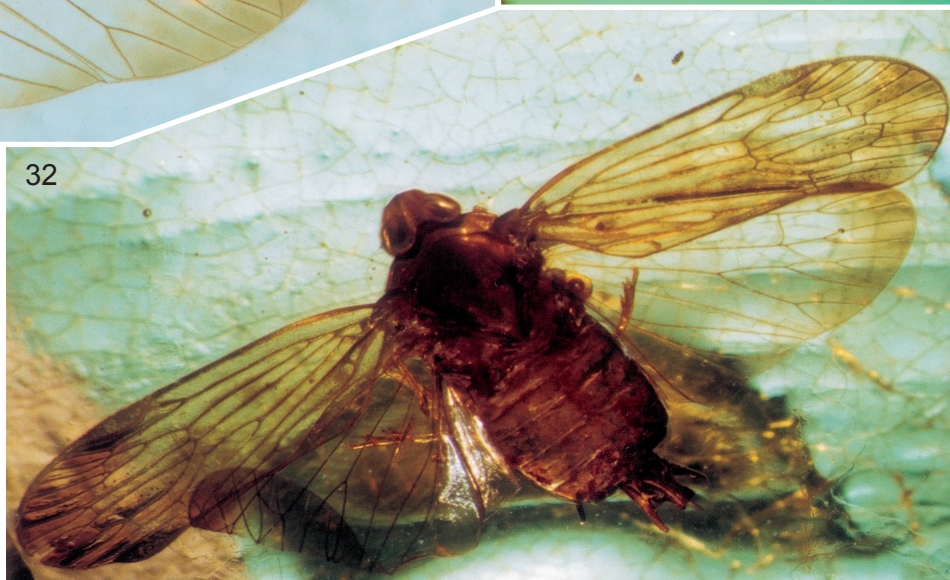
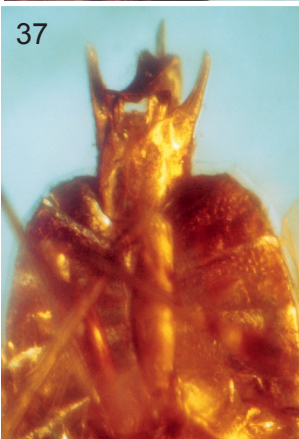
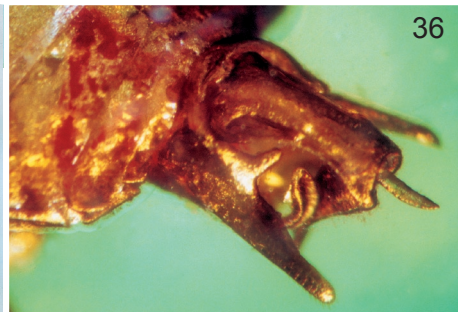
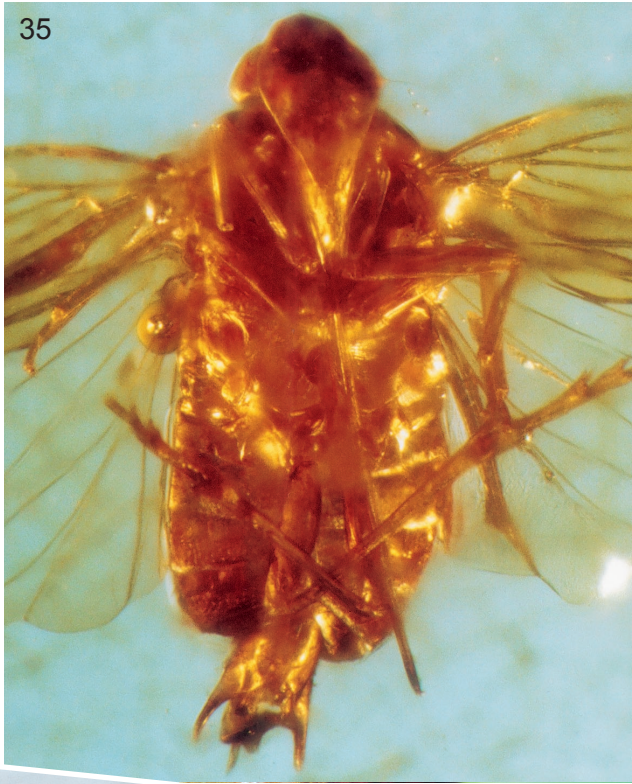
or with single row of teeth on basitarsomere and double row of teeth and subapical setae on mid tarsomere is present. Basitarsomere and mid tarsomere without subapical setae is regarded as plesiomorphic condition within Cixiidae and Fulgoroidea as well (Emeljanov 1982). On the other hand, Van Stalle (1986b) postulated that chaetotaxy of the hind tarsomeres with a double row of a variable number of teeth and setae as plesiomorphic condition. The presence of tymbal apodeme has not been studied among Cixiidae, but it seems probable that this is an apomorphic character of Mnemosynini. Cixiidae as other Fulgoroidea communicate by substrate-borne vibrations (Howarth et al. 1990; Tishechkin 1997). Distinct rows of a few abdominal trichobothria are without doubt an apomorphy of Mnemosynini. In Pentastirini only a few abdominal trichobothria in a single row are present, single row of a few trichobothria is also noted in abdominal sternites of *Pintalia* Stål, 1862 (Sweet 1996). The appearance of middle sternal sclerite on the male VII abdominal segment is believed an apomorphy of Pentastirini (Emeljanov 2002), so this state seems to be in Mnemosynini in a plesiomorphic condition (Figs 7, 17, 18 and 35). The divided VII and VIII abdominal sternites are regarded as plesiomorphic. This condition is found among Mnemosynini.

Also the fusion of hypopleurites with sternites IV–VII should be probably regarded as plesiomorphic. Hypopleurites in Pentastirini are separated by a long posteriorly incomplete suture. It is noteworthy that an isolated hypopleurite on pregenital abdominal segments is present in *Pintalia delicata* (Fowler, 1904) of the Pintalini Metcalf, 1938 (Sweet 1996). A large and not distinctly delimited parastigmal area on the epipleurite also seems to be an important character, probably apomorphic. In Pentastirini, the parastigmal area is small, not distinctly delimited, but this character should be analyzed in other Cixiinae (Figs 15 and 16). Reduction of ovipositor in Pentastirini and Mnemosynini seems to be homoplastic character. Fusion of the gonoplasts at their base in Mnemosynini is without doubt an apomorphic character of the tribe. Pentastirini are characteristic of separated gonoplasts, which is probably symplesiomorphic character with other Cixiinae. The fusion of gonapophyses IX is regarded as an apomorphy of Fulgoroidea (Bourgoin 1993); one of the postulated apomorphies of Pentastirini is separation of gonapophyses IX (Emeljanov 1971). The structure of internal female genitalia in Mnemosynini also differs distinctly from Pentastirini (Figs 23 and 24). The vagina about as long as wide seems to be a feature of Pentastirini,



Figures 28–31. Nymphs and nymphal wax pores in Mnemosynini and Pentastirini. (28) *M. cubana* – last instar nymph (after Myers 1929); (29) *R. panzeri* – last instar nymph (after Šulc 1928); (30) scheme of arrangement of nymphal wax-pores in *M. cubana* (after Myers 1929); (31) scheme of arrangement of nymphal wax-pores in *R. panzeri* (after Šulc 1928).

as in Mnemosynini this structure is very long. Also the ductus receptaculi is short in Pentastirini and distinctly convolute, particularly in the apical portion, in Mnemosynini. The diverticulum ductus is distinctly convolute in Pentastirini and its diameter is similar to the diameter of the antecedent part; in Mnemosynini this part is very long, convolute, with distinctly smaller diameter than ductus receptaculi; the situation is similar to this in Cixiini, Pintalini and Eucarpini (Figs 25–27). Another apomorphic character of Mnemosynini is the fusion of male genital styles at base, with a small unpaired process at place of their fusion (Van Stalle 1986a). The aedeagus fused to the anal tube observed in Mnemosynini is a plesiomorphic condition (symplesiomorphic state within Cixiinae); in Pentastirini the aedeagus is connected to the pygofer, not to the anal tube, which character was postulated as an apomorphy for Pentastirini by Van Stalle (1986b). Nymphal characters need further research, as only a single species – *Mnemosyne cubana* Stål was described by Myers (1929), with some notes on the biology, and this nymph is ant attended by Ponerinae ants (*Odontomachus insularis* Guérin-Méneville, 1844). Emeljanov (1993, 2001) stated that the wax-pore plates on abdominal tergites of nymphs of genera placed in Pentastirini – *Reptalus*



Figures 32–37. *Autrimpus sambiorum* gen. and sp. nov., holotype, coll. Manchester Museum. (32) Specimen in dorsal view; (33) right tegmen and wing in dorsal view; (34) body in dorsal view; (35) body in ventral view; (36) pygofer and anal segments in dorsolateral view; (37) pygofer in ventral view.

panzeri Löw, 1883 (Šulc 1928), *Pentastiridius pachyiceps* Matsumura, 1914, *Oliarus* sp. (Yang and Yeh 1994) and Mnemosynini – *Mnemosyne cubana* Stål, 1866 (Myers 1929) are very similar (Figs 28–31). According to his opinion division of wax-pore area onto six islands and placement of sensory pits at anterior border is a plesiomorphic condition in Cixiidae. Division of wax area is to be observed among Pentastirini and Mnemosynini as well, but sensory pits are placed more caudad, near middle. Also the number of sensory pits between wax-pore areas is different: plesiomorphic condition is 1 : 1 : 1 : 1 : 1, in Pentastirini this formula is 1 : 1 : 1 : (1)2 : 2, in Mnemosynini this formula is 1 : 1 : 1 : 2 : 3. It seems that nymphal characters must be studied more both for morphological and phylogenetic knowledge.

It seems that Mnemosynini is well separated from Pentastirini and share some characters with other tribes of Cixiinae, so the placement of this tribe in evolutionary scenario remains unclear. The available data suggest that together with Pentastirini, Mnemosynini represent the old and early separated lineages within Cixiinae. To resolve the phylogenetic scheme of Cixiinae and Cixiidae as whole, further data on taxonomically valuable supra-generic characters are necessary, previously known and new ones, from both fossil and extant forms.

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REFERENCES

- Bourgoin, Th. 1993. Female genitalia in Hemiptera Fulgoromorpha, morphological and phylogenetic data. *Annales de la Société Entomologique de France* (N.S.), 29(3): 225–244.
- Cockerell, T.D.A. 1910. Some insects in Baltic Amber. *Entomologist*, 43: 153–155
- Dworakowska, I. 1988. Main veins of the wings of Auchenorrhyncha (Insecta, Rhynchota:Hemelytrata). *Entomologisches Abhandlungen der Staatliches Museum für Tierkunde Dresden*, 52(3): 63–108.
- Emeljanov, A.F. 1971. Novye rody tsikadovykh fauny SSSR iz semejstv Cixiidae i Isiidae (Homoptera, Auchenorrhyncha). *Entomologicheskoe Obozrenie*, 50(3): 619–627. (In Russian). Published in English as: Yemel'yanov A.F. 1971. New genera of leafhoppers of the families Cixiidae and Issidae (Homoptera, Auchenorrhyncha) in the USSR. *Entomological Review*, 50(3): 350–354.
- Emeljanov, A.F. 1977. Gomologia krylovykh struktur u tsikadovykh i primitivnykh Polyneoptera. *Nomenklatura i gomologia zhilok u nasekomykh*. [Homology of wing structures in Cicadina and primitive Polyneoptera. Terminology and homology of venation in insects.] *Trudy Vsesoyuznogo Entomologicheskogo Obshchestva*, 58: 3–48. (In Russian).
- Emeljanov, A.F. 1982. Stroenie i evolyutsiya lapok u nosatok (Homoptera, Dictyopharidae). *Entomologicheskoe Obozrenie*, 61(3): 501–516. [In Russian] Published in English as: Yemel'yanov, A.F. 1982. Structure and evolution of the tarsus in the Dictyopharidae (Homoptera). *Entomological Review*, 61(3): 44–59.
- Emeljanov, A.F. 1989. K voprosu o podrazdelenii sem. Cixiidae (Homoptera, Cicadina). *Entomologicheskoe Obozrenie*, 68(1): 93–106. [In Russian] Published in English as: Emel'yanov, A.F. 1989. On the problem of division of the family Cixiidae (Homoptera, Cicadina). *Entomological Review*, 68(4): 54–67.
- Emeljanov, A.F. 1993. Planthoppers of family Cixiidae from vicinity of Ambo, Ethiopia (Homoptera, Cicadina). *Zoosystematica Rossica*, 1992. 1(1): 20–36.
- Emeljanov, A.F. 2002. Contribution to classification and phylogeny of the family Cixiidae (Hemiptera, Fulgoromorpha). *Denisia*, 04, zugleich Kataloge des OÖ. Landesmuseums, Linz, Austria, N.F., 176: 103–112.
- Fennah, R.G. 1961. The occurrence of a Cixiinae Fulgoroid (Homoptera) in a Weald Clay. *Annals and Magazine of Natural History*, 13(4): 161–163.
- Fennah, R.G. 1963. New fossil fulgorid Homoptera from the amber of Chiapas, Mexico. *University of California Publications In Entomology*, 31: 43–48.
- Fennah, R.G. 1987. A new genus and species of Cixiidae (Homoptera, Fulgoroidea) from Lower Cretaceous amber. *Journal of Natural History*, London, 21(5): 1237–1240.
- Grimaldi, D.A., Engel, M.S. and P.C. Nascimbene. 2002. Fossiliferous Cretaceous Amber from Myanmar (Burma): Its Rediscovery, Biotic Diversity, and Paleontological Significance. *American Museum Novitates*, No. 3361: 1–71.
- Hamilton, K.G.A. 1990. Homoptera. In: Grimaldi, D.A. (ed.) *Insects from the Santana Formation, Lower Cretaceous, of Brazil*. *Bulletin of the American Museum of Natural History*, 195: 82–122.
- Holzinger, W., Emeljanov, A. F. and I. Kammerlander. 2002. The family Cixiidae – A Review. *Denisia*, 04, zugleich Kataloge des OÖ. Landesmuseums, Linz, Austria, N.F., 176: 113–138.
- Holzinger, W., Kammerlander, I., Bourgoin, Th., Chan, K.L. and B.C. Campbell. 2001. Towards a phylogeny of the Cixiidae (Fulgoromorpha) and its major subgroups: preliminary results. *Abstracts of the 2nd European Hemiptera Congress*, Fiesca, Slovenia, June 20–24, 2001: 19.
- Howarth, F.G., Hoch, H. and M. Asche. 1990. Duets in darkness: species-specific substrate-borne vibrations produced by cave-adapted cixiid planthoppers in Hawaii (Homoptera Fulgoroidea). *Mémoires de Biospéologie*, 17: 77–80.
- Kukalová-Peck, J. and C. Brauckmann. 1992. Most Paleozoic Protorthoptera are ancestral hemipteroids: major wing braces as clues to a new phylogeny of Neoptera (Insecta). *Canadian Journal of Zoology*, 70: 2452–2473.
- Larivière, M.-C. 1999. Cixiidae (Insecta: Hemiptera: Auchenorrhyncha). *Fauna of New Zealand. Ko te Aitanga Pepeke o Aotearoa*, 40: 1–93.
- Martins-Neto, R.G. 1988. A new fossil insect (Homoptera, Cixiidae) from the Santana Formation (Lower Cretaceous), Araripe Basin, Northeast Brasil. *Interciencia*, 13(6): 313–316.

- Myers, J.G. 1929. Observation on the biology of two remarkable cixiid plant-hoppers (Homoptera) from Cuba. *Psyche*, 36(4): 283–292.
- Razowski, J. 1996. Słownik morfologii owadów. PWN, Warszawa – Kraków. i–xi + 1–431. (In Polish)
- Sweet, M.H. 1996. Comparative external morphology of the pre-genital abdomen of the Hemiptera, 119–158. *In*: Schaefer, C.W. (Ed.). *Studies on Hemiptera Phylogeny*. Entomological Society of America Lanham.
- Statz, G. 1950. Cicadariae (Zikaden) aus den oberoligocänen Ablagerungen von Rott. *Palaeontographica*, 98(1-4): 1–46.
- Szwedo, J. 2000. *Oliarus kulickae* sp. n. from Dominican amber (Hemiptera: Fulgoroidea: Cixiidae). *Polskie Pismo Entomologiczne*, 69(2): 161–166.
- Szwedo, J., Bourgoin, Th. and F. Lefebvre. 2004. Fossil Planthoppers (Hemiptera: Fulgoromorpha) of the World. An annotated catalogue with notes on Hemiptera classification. *Studio 1*, Warszawa: 1–208.
- Szwedo, J. and R. Kulicka. 1999a. Auchenorrhyncha (Insecta, Homoptera) in Baltic amber from the collection of the Museum of the Earth, Warsaw. *Estudios del Museo de Ciencias Naturales de Alava*, 14, Numero especial 2: 175–178.
- Szwedo, J. and R. Kulicka. 1999b. Inclusions of Auchenorrhyncha in Baltic amber (Insecta: Homoptera). *Estudios del Museo de Ciencias Naturales de Alava*, 14, Numero especial 2: 179–199.
- Szwedo, J. and A. Stroiński. 2002. First fossil Pentastirini from Eocene Baltic amber (Hemiptera: Fulgoromorpha: Cixiidae). *Annales Zoologici*, 52(1): 173–179.
- Šulc, K. 1928. Voskové žlázy a jejich výrobky u larev sbf. Cixiinae (Homoptera). *Biologické Spisy Vysoké Školy Zvěrolekařské*, B 108, VII, 13: 149–180. [1–32.] [Wax glands and their products in nymphs of subfamily Cixiinae (Homoptera)] (In Czech with German summary).
- Tishechkin, D.Yu. 1997. Prizyvnye signaly samtsov tsikadovykh semeïstva Cixiidae (Homoptera, Cicadinea) v sravnenii s signalami nekotorykh drugikh fulgoroidov (Homoptera, Cicadinea, Fulgoroidea). [Calling signals in males of Cixiidae (Homoptera, Cicadinea) compared with acoustic signals in some other Fulgoroidea (Homoptera, Cicadinea, Fulgoroidea)]. *Zoologicheskii Zhurnal*, 76(9): 1016–1024. (In Russian).
- Van Stalle, J. 1986a [1985]. A review of the Afrotropical species of the genus *Mnemosyne* Stål (Homoptera, Fulgoroidea, Cixiidae). *Annales de la Société entomologique de France*, 21(4): 399–405.
- Van Stalle, J. 1986b. Revision of Afrotropical Pentastirini (Homoptera: Cixiidae) IV: Description of *Peartolus* gen. nov., *Dorialsus* gen. nov., *Narravertus* gen. nov., *Kibofascius* gen. nov., *Afropreptalus* gen. nov. and *Pseudoliarus hudeibensis* n. sp., with notes on phylogeny and systematics. *Academiae Analecta, Mededelingen van de Koninklijke Academie voor Wetenschappen, Letteren en Schone Kunsten van België, Klasse der Wetenschappen*, 48(3): 101–129.
- Van Stalle, J. 1987. A revision of the Neotropical species of the genus *Mnemosyne* Stål (Homoptera, Cixiidae). *Bulletin de l'Institut royal des Sciences Naturelles de Belgique, Entomologie*, 57: 121–139.
- Van Stalle, J. 1988. Revision of the Oriental species of *Mnemosyne* Stål, 1866 (Homoptera, Cixiidae). *Annales Entomologici Fennici*, 54: 33–47.
- Van Stalle, J. and P. Lauterer. 1985. On two African Cixiidae (Homoptera, Fulgoroidea) described by L. Melichar. *Bulletin et Annales de la Société royal belge d'Entomologie*, 121: 261–268.
- Zombori, L. and H. Steinmann. 1999. *Dictionary of Insect Morphology*. *Handbuch der Zoologie*, IV, 34. DeGruyter, Berlin New York, 405 pp.

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