

New Mnemosynini taxa (Hemiptera, Fulgoromorpha: Cixiidae) from the Palaeogene of France with notes on their early association with host plants

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Abstract

Three new genera: *Stalisyne* **gen. nov.** comprising *S. lutetiorum* **sp. nov.** and *S. veromanduiorum* **sp. nov.**, *Mnaomaia* **gen. nov.** for *M. bellovaciorum* **sp. nov.**, both from the Lowermost Eocene (Sparnacian) amber of Oise, (Northern France) and *Mnasthaia* **gen. nov.** for *M. arverniorum* **sp. nov.** from the Palaeocene strata of Menat (Auvergne) are described. Characters of extant and fossil Mnemosynini are discussed also. Remarks on co-evolutionary processes of Mnemosynini, as well as Cixiidae and the host plants are presented. Eco-evolutionary processes affecting Mnemosynini and other Cixiidae lineages are presented.

Key words: Cixiidae, Mnemosynini, Oise amber, Menat, Palaeogene, France, co-evolution plant-insects

Introduction

The family Cixiidae Spinola, 1838 has been known in fossil record since the Lower Cretaceous, it is one of the most common groups in the Eocene Baltic amber, but most of species described need to be revised, as their taxonomic placement remain doubtful (Szwedo et al. 2004).

The tribe Mnemosynini Emeljanov, 1993 was recently discussed as well as extant and fossil taxa placed within (Szwedo 2004). The genus *Mnemosyne* was erected by Stål in 1866 to accommodate a species described from Cuba (Stål 1866). The extant species of the genus were revised by Van Stalle, in a series of papers dealing with species from particular geographic areas (Van Stalle 1985, 1987, 1988; Van Stalle & Lauterer 1985). Currently, 45

species are recognized, 17 in Oriental, 6 in Afrotropical and 22 in Neotropical regions respectively.

The only fossil record of this genus was presented by Fennah (1963) on the basis of partly preserved tegmen from the Oligocene/Miocene amber from Chiapas, Mexico. The second, fossil genus of the tribe, *Autrimpus* Szwedo, 2004 was recently described from the Eocene Baltic amber (Szwedo 2004).

The fossil genera and species described below are remarkably similar to extant and fossil forms. However, it is sure that the genus *Mnemosyne* Stål, 1866 is in fact a paraphyletic (or perhaps even polyphyletic) group, and further studies are necessary to separate monophyletic genera within. For this reason the type species: *Mnemosyne cubana* Stål, 1866 is used for comparison to define the concept of *Mnemosyne*.

Systematics

Order Hemiptera Linnaeus, 1758

Suborder Fulgoromorpha Evans, 1947

Superfamily Fulgoroidea Latreille, 1807

Family Cixiidae Spinola, 1838

Stalisyne gen. nov.

TYPE SPECIES: *Stalisyne lutetiorum* sp. nov.

ETYMOLOGY: Combination of the family name of the eminent Swedish hemipterologist Carolus Stål and the genus name “*Mnemosyne*”. Gender: feminine.

DIAGNOSIS: Longitudinal vein RP forked basad of nodal line (apicad of nodal line in *Mnemosyne cubana* Stål, 1866 and *Autrimpus* Szwedo, 2004), additional *irp* cell separate cells *ra-rp* and *r-m*; Whole tegmen, including veins covered with chaetae (only apical cells with scarce chaetae in *Mnemosyne cubana* and *Autrimpus*); Tegulae carinate (no tegular carinae in *M. cubana*, delicate carinae in *Autrimpus*); Female ovipositor with strongly reduced gonapophysis VIII (valve 1) (normally developed in extant *Mnemosyne cubana*), gonapophysis IX (valve 2) developed normally, with rows of distinct, stout chaetae on internal margin (no such chaetae in *M. cubana*), gonoplac (valve 3) wide with rows of long chaetae on margins (gonoplac 3 narrower, with shorter chaetae in *M. cubana*).

DESCRIPTION: Head wider than long; vertex with lateral margins elevated, longer in mid line than wide at base; border of vertex and frons with two longitudinal short carinae; frons, postclypeus and anteclypeus with distinct median carina, lateral carinae of frons

distinct, elevated, lateral carinae of postclypeus distinct, rostrum very long; pronotum relatively narrow, with postocular carinae distinct, and median carina; tegulae carinate; mesonotum five carinate; tegmen with basicostal field, stigma elongate; basal cell elongate, about twice as long as wide; RP forked basad of nodal line, *ir* cell elongate; CuA with two terminalia; clavus reaching about 2/3 of tegmen length; hind tibia with two lateral spines and 1 + 2 + 3 apical spines; anal tube long, anal style long; gonapophysis VIII short.

***Stalisyne lutetiorum* sp. nov.**

(Figs. 1–12)

MATERIAL: Holotype, female. Specimen MNHN PA 2427, 1/2; collection “Langlois-Meurinne / De Ploëg”, mounted in Canada balsam, deposited in Muséum national d’Histoire naturelle, Paris [MNHN]. State of preservation: anterior part of body partly hardly visible, covered with milky veil, left tegmen incomplete, only basal part and claval portion preserved. Facial portion partly covered with milky veil. Fore and mid femora, tibiae and tarsi missing.

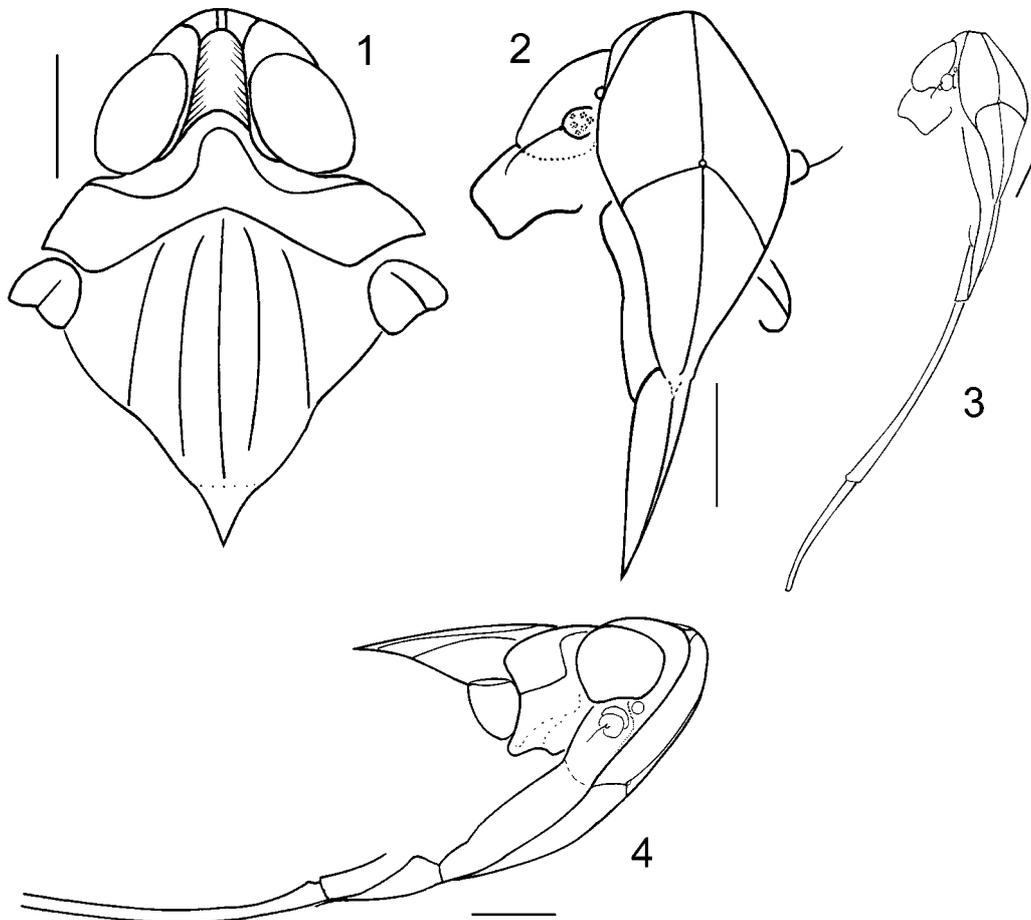
TYPE LOCALITY: Farm Le Quesnoy, Chevière, region of Creil, Oise department (Northern France).

STRATIGRAPHIC POSITION: Lowermost Eocene, circa 53 Ma, Sparnacian, level MP7, of the mammal fauna of Dormaal (Feugueur 1963; De Ploëg et al. 1998; Nel et al. 1999, Nel et al. 2004; Cavagnetto 2000).

ETYMOLOGY: Named after Gallo-Celtic tribe inhabiting environs of Paris—the Lutetes.

DIAGNOSIS: Vertex narrow at base, angulately incised, its anterior margin slightly before the level of compound eyes (in *M. cubana* vertex wide at base, with straight angle incision, almost straight in middle portion, anterior margin of vertex not exceeding level of anterior angles of compound eyes). Postocular carinae distinct (not distinct in *M. cubana*), placed more caudad to the compound eyes than in *Stalisyne veromanduiorum*. Mesonotum with five distinct carinae (carinae very weak in *M. cubana*, three carinae in *Autrimpus sambiorum*). basicostal field short and wide (no distinct basicostal field in *M. cubana*); first M forking apicad of ScRA and CuA forkings (M forked basad of ScRA forking in *M. cubana*); RA with three terminalia (two terminalia in *M. cubana* and *A. sambiorum*); RP with four terminalia (three terminalia in *M. cubana* and *A. sambiorum*); CuP and Pcu not connected with transverse veinlet at tegmen base (such veinlet present in *M. cubana*, *A. sambiorum* and *Mnasthaia arverniorum*).

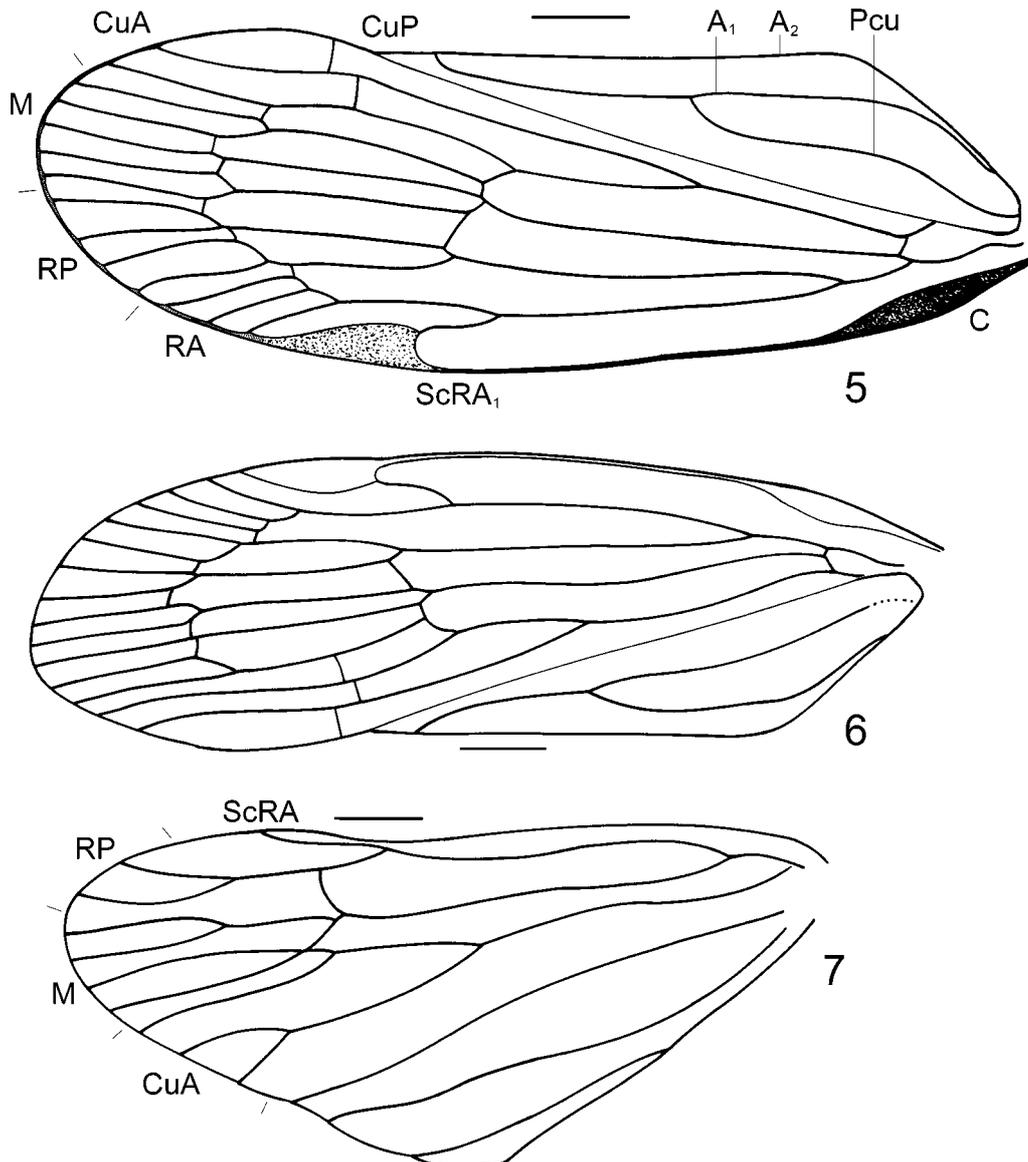
DESCRIPTION: General coloration in amber ochraceous, head, pronotum and mesonotum lighter, tegmina with dark brown, elongate spot at the base of clavus, incomplete transverse band in the median portion, not reaching costal margin and irregular spots in apical cells. Tegmen regularly covered with short setae, including veins.



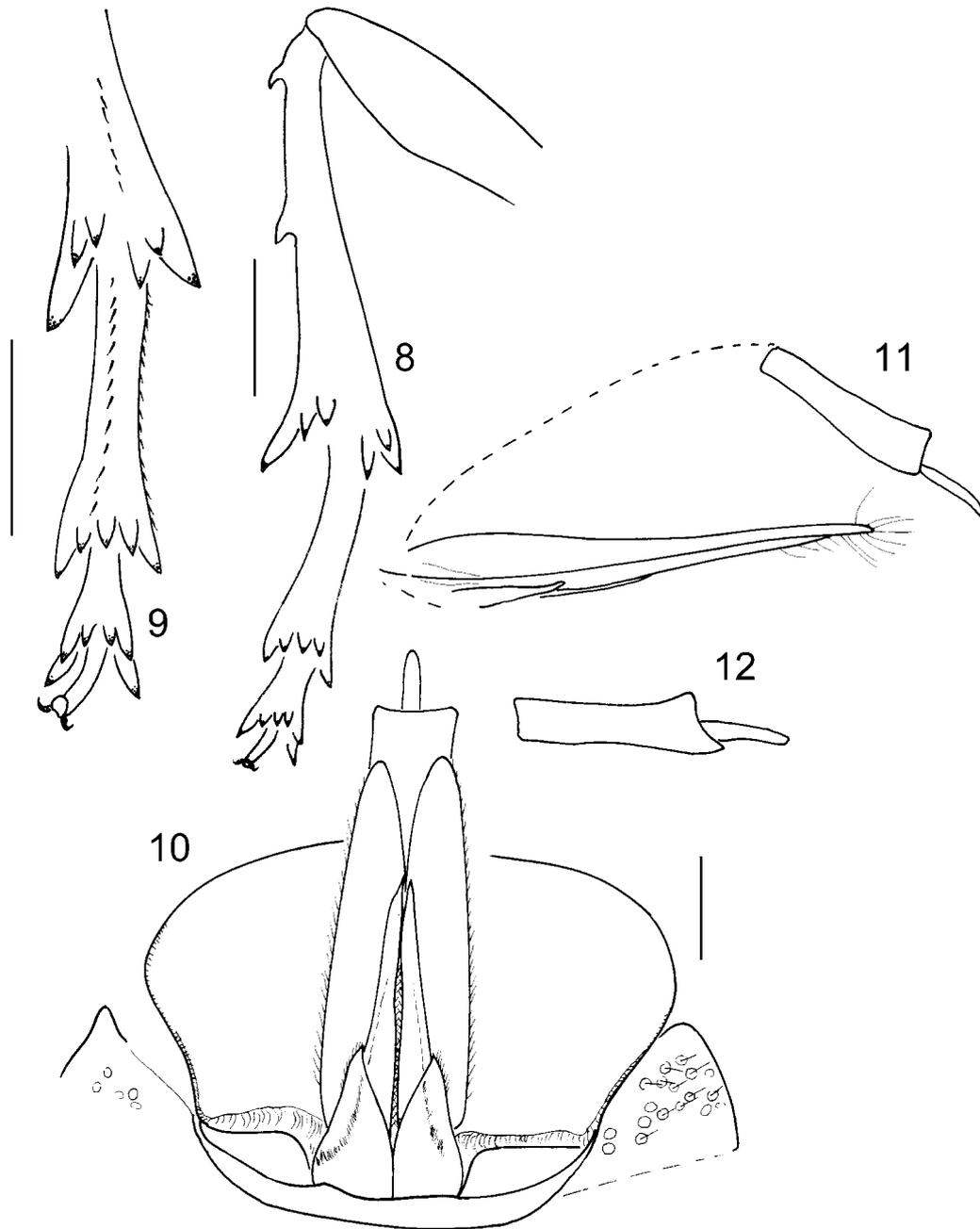
FIGURES 1–4. *Stalisyne lutetiorum* gen. et sp. nov. Fig. 1. Anterior part of body in dorsal view; Fig. 2. Face in ventrolateral view; Fig. 3. Face and rostrum in ventrolateral view; Fig. 4. Anterior part of body in right lateral view; Scale bar: 1 mm.

Total length (female) 12.3 mm. Head with compound eyes (2.2 mm) wider than long, Anterior margin of head in dorsal view rounded. Vertex with lateral margins distinctly elevate, posterior margin angulately incised; vertex at base (0.56 mm) slightly narrower than long in mid line (0.6 mm), narrowing apicad. Face very long (4.48 mm in mid line), with median carina and median ocellus. Two longitudinal carinae at the margin of frons and vertex, two transverse carinae, the upper delimiting vertex, and the lower uniting longitudinal carinae with lateral carinae present. Frons 1.12 mm long in mid line, 1.12 mm wide at widest point, at the level of antennae, with disc almost flat; Frontoclypeal suture distinct, arcuate; Postclypeus 1.68 long in mid line, convex, with distinct lateral carinae; Anteclypeus 1.48 mm long in mid line, with median carina; Labium long; Rostrum very

long (6.28 mm), reaching far beyond end of abdomen and tip of ovipositor, with anteapical segment almost two times as long as apical one; Bases of antennae sunk in lateral concavities of the head capsule, basal segment short, the second rounded, covered with sensillae, arista relatively long; Lateral ocelli distinct, placed just below the level of lower margin of the compound eye, close to the lateral carinae of frons.



FIGURES 5–7. *Stalisyne lutetiorum* gen. et sp. nov. Fig. 5. Right tegmen; Fig. 6. Left tegmen; Fig. 7. Hind wing; Scale bar: 1 mm. Abbreviations: C — costal margin; ScRA₁ — terminal of subcosta-radius anterior 1; RA — terminalia of radius anterior; RP — terminalia of radius posterior; M — terminalia of media; CuA — terminalia of Cubitus anerior; CuP — terminal of cubitus posterior; Pcu — postcubitus; A₁ — first anal vein; A₂ — second anal vein.



FIGURES 8–12. *Stalisyne lutetiorum* gen. et sp. nov. Fig. 8. Right hind leg; Fig. 9. Right hind tarsus; Fig. 10. End of female abdomen and ovipositor; Fig. 11. Ovipositor and anal tube in lateral view; Fig. 12. Anal tube. Scale bar: 1 mm.

Pronotum 3.16 mm wide, wider than head with compound eyes, 0.6 mm long in mid line, about as long in mid line as in lateral portion, with median carina and postocular

carinae distinct, posterior margin incised at wide angle; Tegula with median carina, about twice as wide as long.

Mesonotum slightly longer (2.72 mm) than wide (2.6 mm), with concave disc and with five longitudinal carinae, scutellum distinct, flat.

Tegmen 10 mm long, 3.04 mm wide at widest point, clavus long, reaching 2/3 of tegmen length, stigma distinct, elongately triangular; costal margin mildly curved at base, with distinct basicostal field, almost straight in the median portion, angulately rounded in apical portion of tegmen; basal cell about twice as long as wide, ScR forked near the base, ScRA₁ reaching the stigma, RA with three terminalia, RP forked basad of the level of nodal line, with four terminalia; M simple at base, forked slightly apicad of ScR and Cu forkings, with five terminalia, CuA forked apicad of ScR forking, at the half distance between ScR forking and PcuA₁ junction, CuA with two terminalia, CuA₁ branch distinctly curved; first row of transverse veinlets uniting RP and M and M and CuA₁ basad of nodal line, transverse veinlets of apical line not very regular, not forming distinct line; claval veins Pcu and A₁ united apicad of half of length of clavus.

Hind wing with venation typical of *Mnemosyne* spp., RP with two terminalia, M with four terminalia, CuA with three terminalia, transverse veinlet *r-m* long curved apicad.

Hind femur 2.12 mm long, hind tibia 3.84 mm long, quadrandular in cross section, with two distinct lateral spines, the first near the base and the second, bigger just above half of tibia's length, six apical spines organized in formula 1 - 2 - 3; hind tarsus 3.28 mm long, basitarsomere longer than combined length of mid and apical tarsomeres, 1.96 mm long with 5 apical spines, mid tarsomere shorter, 1.04 mm, with 6 apical spines, apical tarsomere, 0.72 mm long with small tarsal claws and pulvillus.

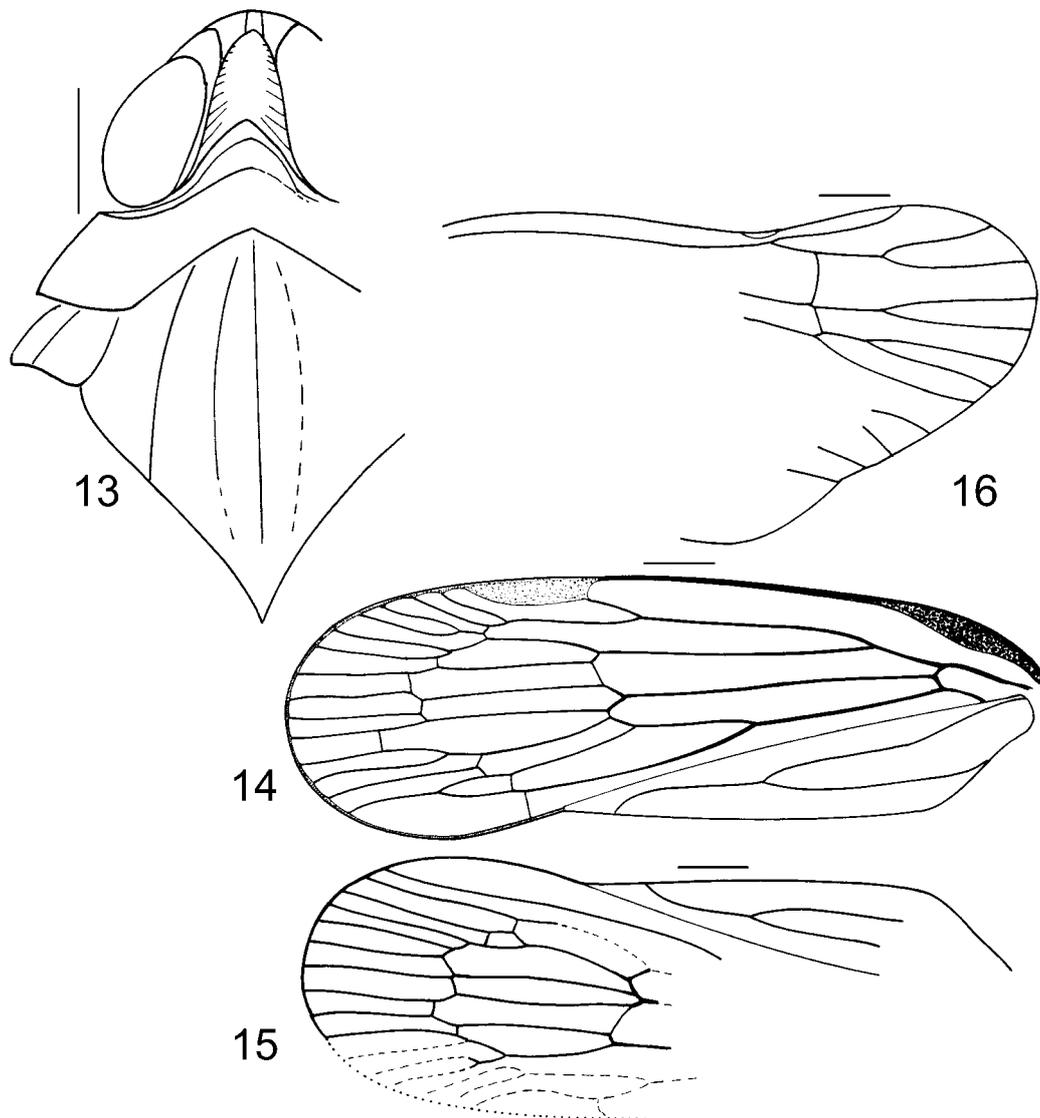
Female abdomen 4.36 mm wide, with distinct trichobothrial pits in lateral portion of sternites, pygofer capsule oblique in lateral view, concave, with wax pores; ovipositor elongate, not exceeding length of anal tube, gonapophysis VIII shortened, 1 mm long, with tip covered with a few setae, gonapophysis IX 2.04 mm long, with short, stout setae on internal margin, gonoplac foliaceous, 2.32 mm long, 0.48 mm wide, with margins covered with long setae.

Female anal tube 1.16 mm long, slightly flattened, anal style 1 mm long.

***Stalisyne veromanduiorum* sp. nov.**

(Figs. 13–18)

MATERIAL: Holotype, male. Specimen MNHN PA 2770; collection “Langlois-Meurinne / De Ploëg”, mounted in Canada balsam, deposited in Muséum national d’Histoire naturelle, Paris. State of preservation: right part of body partly destroyed, fore, mid and hind femora partly, preserved fore, mid and hind tibiae and tarsi missing, anterior part of body, face and part of tegmina covered with milky veil.

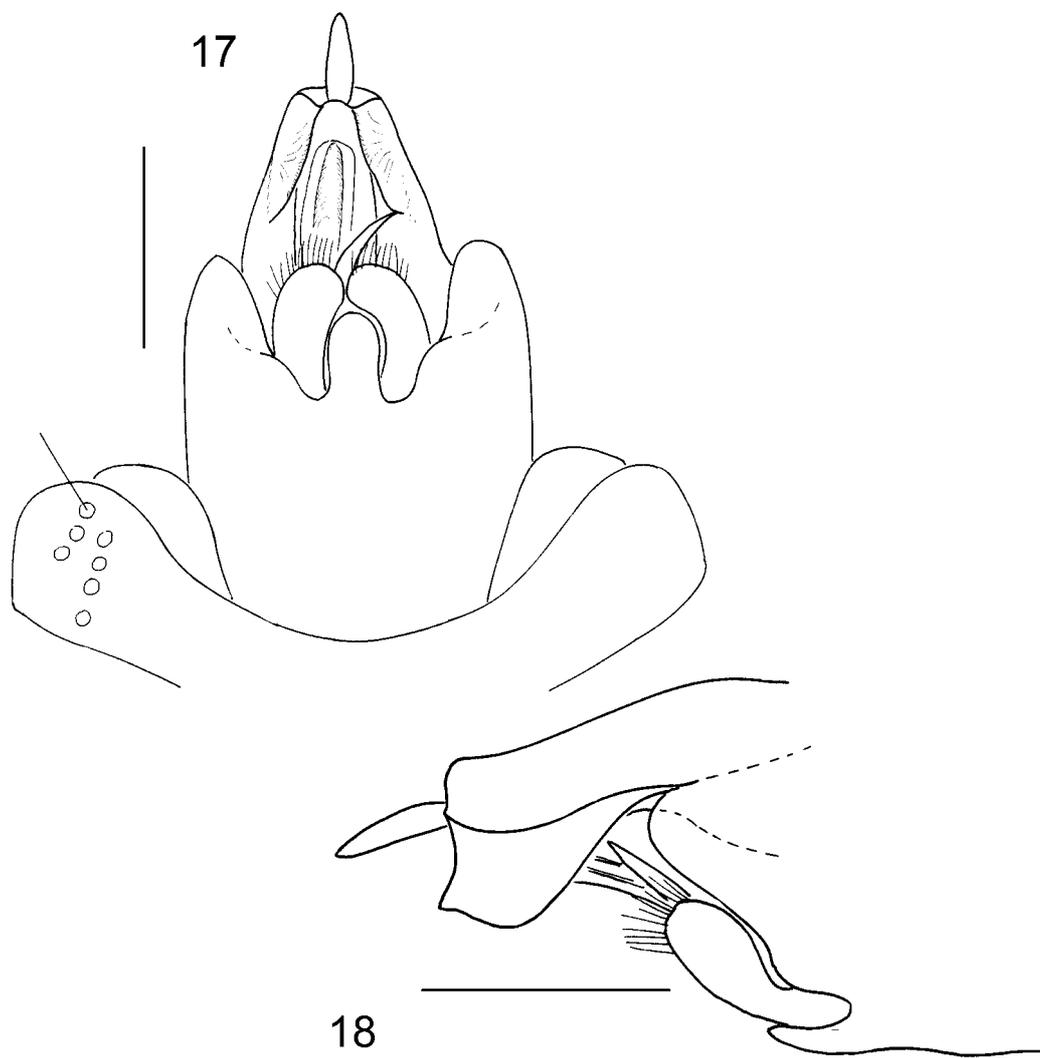


FIGURES 13–16. *Stalisyne veromanduiorum* gen. et sp. nov. Fig. 13. Anterior part of body in dorsal view; Fig. 14. Left tegmen; Fig. 15. Part of right tegmen; Fig. 16. Part of hind wing. Scale bar: 1 mm.

TYPE LOCALITY: Farm Le Quesnoy, Chevrrière, region of Creil, Oise department (Northern France).

STRATIGRAPHIC POSITION: Lowermost Eocene, circa 53 Ma, Sparnacian, level MP7, of the mammal fauna of Dormaal (Feugueur 1963; De Ploëg et al. 1998; Nel et al., 1999, Nel et al. 2004; Cavagnetto 2000).

ETYMOLOGY: Named after Gallo-Celtic tribe Veromandui, inhabiting area of river Oise valley.



FIGURES 17–18. *Stalisyne veromanduiorum* gen. et sp. nov. Fig. 17. Male pygofer in ventral view; Fig. 18. Male genital block in lateral view. Scale bars: 0.5 mm for 17, 1 mm for 18.

DIAGNOSIS: Bigger than *Stalisyne lutetiorum*; Vertex in mid line longer than wide at base (about as long as wide in *S. lutetiorum*); Postocular carinae close to the compound eyes; RA with two terminalia (three in *S. lutetiorum*), RP with five terminalia (four in *S. lutetiorum*) M with six terminalia (five terminalia in *S. lutetiorum*).

DESCRIPTION: General coloration in amber brownish, head, pronotum and mesonotum slightly lighter. Tegmina brownish, with darker spot in apical, external portion. Tegmina, both cells and veins covered with short chaetae.

Total length (male) 13.2 mm. Head with compound eyes (2.4 mm) distinctly wider

than long; Anterior margin of head rounded in dorsal view. Vertex with lateral margins distinctly eleviate, posterior margin angulately incised; vertex at base (0.6 mm) narrower than long in mid line (0.76 mm), narrowing apicad. Face very long (4.8 mm), with median carina and median ocellus. Two longitudinal carinae at the margin of frons and vertex, two transverse carinae, the upper delimiting vertex, and the lower uniting longitudinal carinae with lateral carinae present. Frons 1.52 mm long in mid line, with disc slightly concave; Frontoclypeal suture arcuate; Postclypeus 1.92 mm long in mid line, convex, with distinct lateral carinae; Anteclypeus 1.44 mm long in mid line, with median carina.

Pronotum about 3.44 mm wide, wider than head with compound eyes, 0.56 mm long in mid line, longer in lateral portion, with median carina and postocular carinae distinct, postocular carinae shifted anteriorly close to the compound eyes; posterior margin incised at wide angle; Tegula with median carina, wider than long.

Mesonotum longer (3.12 mm) than wide (about 2.72 mm), with disc concave and five longitudinal carinae, scutellum flat.

Tegmen 10.5 mm long, 3.5 mm wide, clavus long reaching 2/3 of tegmen length, stigma distinct, elongately triangular, costal margin mildly curved at base, with distinct, short basicostal field, almost straight in median portion, rounded in apical portion; basal cell about twice as long as wide, ScR forked near base, ScRA₁ reaching the stigma, RA forked apicad, with two terminalia, RP forked basad of nodal line, then forked apicad, with five terminalia; M simple at base, forked slightly apicad of ScRA₁ forking, with six terminalia; CuA with two terminalia, CuA₁ curved; CuA terminalia in left tegmen fused (aberrancy); first row of transverse veinlets uniting RP and M and M and CuA₁ basad of nodal line, transverse veinlets of apical line not very regular, not forming distinct line, additional transverse veinlet apicad of third M forking on right tegmen; claval veins Pcu and A₁ united apicad of half of length of clavus.

Hind wing with m-cu veinlet very short, and M branching slightly apicad of ir veinlet.

Male abdomen about 3.2 mm long; Pygofer 0.8 mm long in mid line, with median process, posterior margin incised lateral of median process, lobed of pygofer in lateral view without projections; Anal tube long (1.5 mm), wide and flattened, tapering apicad, with lateral carination, apical portion with distinct, wide ventrad lobes; Anal style long (0.48 mm); Genital styles quite short, without distinct widenings at apex, apical margin covered with chaetae. Aedeagus with a single long lateral spine (of periandrium?) visible.

***Mnaomaia* gen. nov.**

TYPE SPECIES: *Mnaomaia bellovaciorum* sp. nov.

ETYMOLOGY: From the Ancient Greek word “*mnaomai*”—remember. Gender: feminine.

DIAGNOSIS: *Mnaomaia* gen. nov. differs from *Mnemosyne*, *Autrimpus*, *Stalisyne* and *Mnasthaia* by single terminal of vein RA (two or three terminalia in the others), from *Stalisyne* it differs also by lack of basicostal field on tegmen, shorter rostrum, not exceeding end of pygofer, distinctly longer stigma and smaller size.

DESCRIPTION: Head with compound eyes distinctly wider than long; vertex about twice as long in mid line as at base; border of vertex and frons with two longitudinal short carinae; face long, with median carina, lateral carinae of postclypeus distinct, frontoclypeal suture distinctly arcuate; rostrum slightly exceeding base of pygofer; pronotum with postocular carinae visible; mesonotum five carinate; tegmen without basicostal field, stigma very long, about six times as long as wide; vein RA with single terminal, RP forked slightly basad of nodal line, *ir* cell elongate; CuA with two terminalia; clavus not exceeding 2/3 of tegmen length; hind tibia with two lateral spines and 1 + 2 + 3 apical spines; male pygofer with median process, anal tube quite long.

***Mnaomaia bellovaciorum* sp. nov.**

(Figs. 19–26)

MATERIAL: Holotype, male. Specimen MNHN PA 1781, 1/15; collection “Langlois-Meurinne / De Ploëg”, mounted in Canada balsam, deposited in Muséum National d’Histoire Naturelle, Paris. State of preservation: anterior part of body cracked, and covered with milky veil, ventral portion partly covered with milky veil, apical portion of tegmina partly destroyed, but traces of venation visible. Specimen probably parasitized, two round foramens visible on abdomen, one with remnants of parasite sac (Diptera: Pipunculidae?).

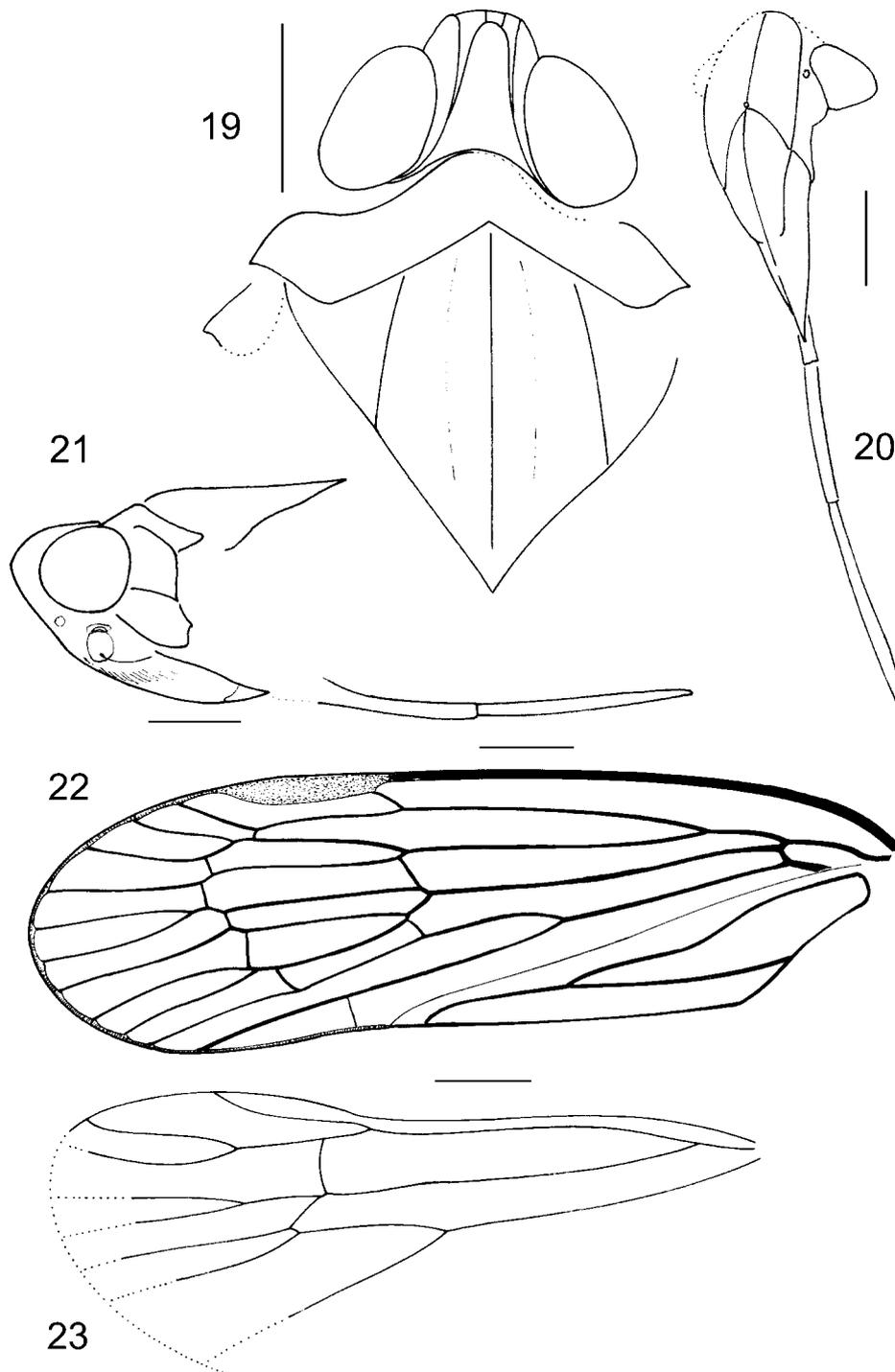
TYPE LOCALITY: Farm Le Quesnoy, Chevrrière, region of Creil, Oise department (Northern France).

STRATIGRAPHIC POSITION: Lowermost Eocene, circa 53 Ma, Sparnacian, level MP7, of the mammal fauna of Dormaal (Feugueur 1963; De Ploëg et al. 1998; Nel et al., 1999, Nel et al. 2004; Cavagnetto 2000).

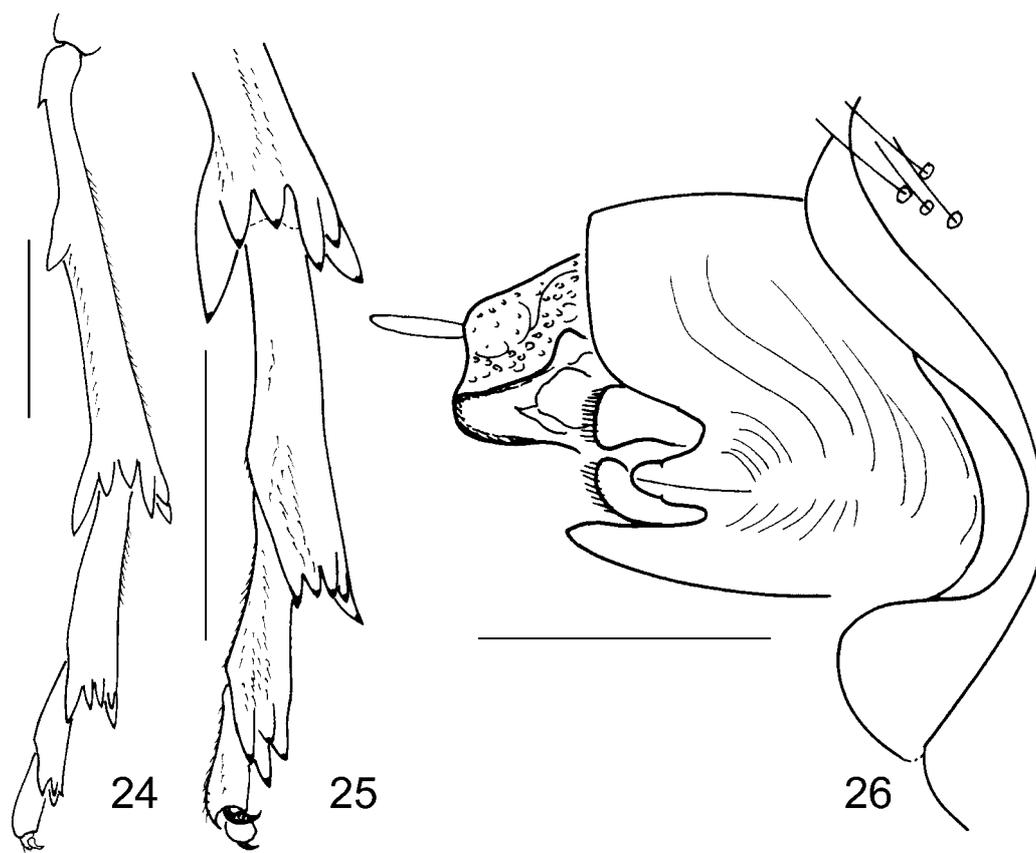
ETYMOLOGY: Named after Gallo-Celtic tribe Bellovaci, inhabiting river Oise valley.

DIAGNOSIS: Combination of characters: vertex in mid line about twice as long as wide at base; mesonotum about as long in mid line as wide; postclypeus in mid line about twice as long as frons in mid line, tegmen 3.6 times as long as wide, RA with single terminal, RP with three terminalia, M with five terminalia, CuA with two terminalia; tibio-metatarsal formula 3 + 2 + 1 : 5 : 4; male anal tube with lateral lobes, about twice as long as wide.

DESCRIPTION: Coloration in amber ochraceous, with slightly darker tegmina, and probably darker veins. Tegmina, both cells and veins covered with short chaetae.



FIGURES 19–23. *Mnaomaia bellovaciorum* gen. et sp. nov. Fig. 19. Anterior part of body in dorsal view; Fig. 20. Face and rostrum; Fig. 21. Anterior part of body in lateral view; Fig. 22. Right tegmen; Fig. 23. Part of hind wing. Scale bar: 1 mm.



FIGURES 24–26. *Mnaomaia bellovaciorum* gen. et sp. nov. Fig. 24. Left hind tibia and tarsus; Fig. 25. Left tarsus; Fig. 26. Male genital block in left ventrolateral view. Scale bar: 1 mm.

Total length 10.5 mm. Head with compound eyes 1.76 mm wide, distinctly wider than long, narrower than pronotum. Anterior margin of head angulate-arcuate in dorsal view. Vertex with lateral margins elevate, posterior margin arcuately incised; vertex at base (0.4 mm) distinctly narrower than long in mid line (0.72 mm), narrowing apicad. Face with median carina distinct and median ocellus visible. Two longitudinal carinae at the margin of vertex and frons. Frons about 1 mm long in mid line, with slightly concave disc; frontoclypeal suture distinctly arcuate. Postclypeus 1.35 mm long, with distinct lateral carinae. Anteclypeus about 0.9 mm long in mid line with median carina.

Pronotum slightly narrower in mid line (0.4 mm) than in lateral portions, with postocular carinae visible.

Mesonotum 2.2 mm long in mid line, 2.12 mm wide, with five longitudinal carinae.

Tegmen 9 mm long, 2.5 mm wide, clavus not exceeding 2/3 of tegmen length, stigma distinct, elongate, about six times as long as wide, costal margin mildly curved at base,

almost straight in median portion, rounded in apical portion; basal cell about twice as long as wide, ScR forked near base, ScRA₁ reaching the stigma, RA with single terminal, RP forked basad of nodal line, then RP₁ forked apicad, with three terminalia; M simple at base, forked slightly basad of ScRA₁ forking, with five terminalia; CuA with two terminalia; first row of transverse veinlets uniting RP and M and M and CuA₁ basad of nodal line, transverse veinlets of apical quite regular; claval veins Pcu and A₁ united apicad of half of length of clavus.

Hind wing with m-cu veinlet very short, and M branching slightly apicad of ir veinlet.

Fore femur 1.96 mm long, fore tibia quadrangular in cross section, 1.4 mm long, foretarsus 0.6 mm long, with tarsomeres subequal in length. Hind coxa with distinct spine, hind femur about 1.6 mm long, hind tibia 2.76 mm long, with two distinct lateral spines, basal one smaller and the second, bigger, placed basad of half of hind tibia length; hind tibial apical row of spines 3 + 2 + 1. Hind tarsus 2.12 mm long, basitarsomere 1.32 mm long with 5 apical spines, longer than combined length of mid and apical tarsomeres; mid tarsomere 1 mm long with four apical spines; apical tarsomere 0.68 mm long with distinct tarsal claws and pulvilla.

Male pygofer 1.4 mm long in mid line, with median process, posterior margin incised laterad of median process, lobes of pygofer in lateral view almost straight, without projections. Anal tube twice as long (1.2 mm) as wide (about 0.6 mm) flattened, apical portion with distinct, wide ventrad, punctate lobes; Anal style quite long (0.3 mm); Genital styles quite short, without distinct widenings at apex, apical margin covered with chaetae.

***Mnasthaia* gen. nov.**

TYPE SPECIES: *Mnasthaia arverniorum* sp. nov.

ETYMOLOGY: From the Greek verb “*mnâstha*” —to remember. Gender: feminine.

DIAGNOSIS: *Mnasthaia* gen. nov. differs from *Mnemosyne*, *Autrimpus*, *Stalisyne* and *Mnaomaia* by lack of forking of RP near the level of nodal line (always forked at or apicad of nodal line in the others), RP forked near the apex, with two terminalia (more terminalia in *Mnemosyne*, *Autrimpus* and *Stalisyne*, two terminalia also in *Mnaomaia*); CuA with three terminalia (two terminalia in *Mnemosyne* and *Stalisyne*); basicostal field not present (present in *Stalisyne*), veins CuP and Pcu connected by a veinlet at base.

DESCRIPTION: Face very long, with median carina; lateral carinae of postclypeus distinct; rostrum long; Costal border without basicostal field, stigma elongate; basal cell about twice as long as wide; RP with only apical forking; CuA with three terminalia; clavus long exceeding 2/3 of tegmen length; transverse veinlet between CuP and Pcu at base of tegmen present.

***Mnasthaia arverniorum* sp. nov.**

(Figs. 27–28)

MATERIAL: Holotype. No. MNHN-LPR 63851, preserved in Museum national d'Histoire naturelle, Paris: dorsoventral compression with face, end of rostrum, margin of pronotum, left tegmen, partly left wing and fragments of abdomen visible.

TYPE LOCALITY: Menat, Puy-de-Dôme, France.

STRATIGRAPHIC POSITION: Upper Palaeocene (circa 58 Ma), volcano-sedimentary, spongo-diatomite maar.

ETYMOLOGY: Named after Gallo-Celtic tribe Arverni, inhabiting Auvergne.

DIAGNOSIS: Combination of characters: postclypeus in mid line about twice as long as frons in mid line, tegmen 3.2 times as long as wide, RA with three terminalia, RP with two terminalia, M with five terminalia, CuA with three terminalia.

DESCRIPTION: Total length about 15 mm. Basal portion of tegmen light, with a few darker spots at longitudinal veins, distinct, arcuate, transverse band in apical portion; tegmen, including veins covered with chaetae.

Face long with median carina; Frons in mid line about 1.2 mm long; Postclypeus about 2.5 mm long in mid line, with distinct lateral carinae. Rostrum very long, distinctly exceeding hind coxae.

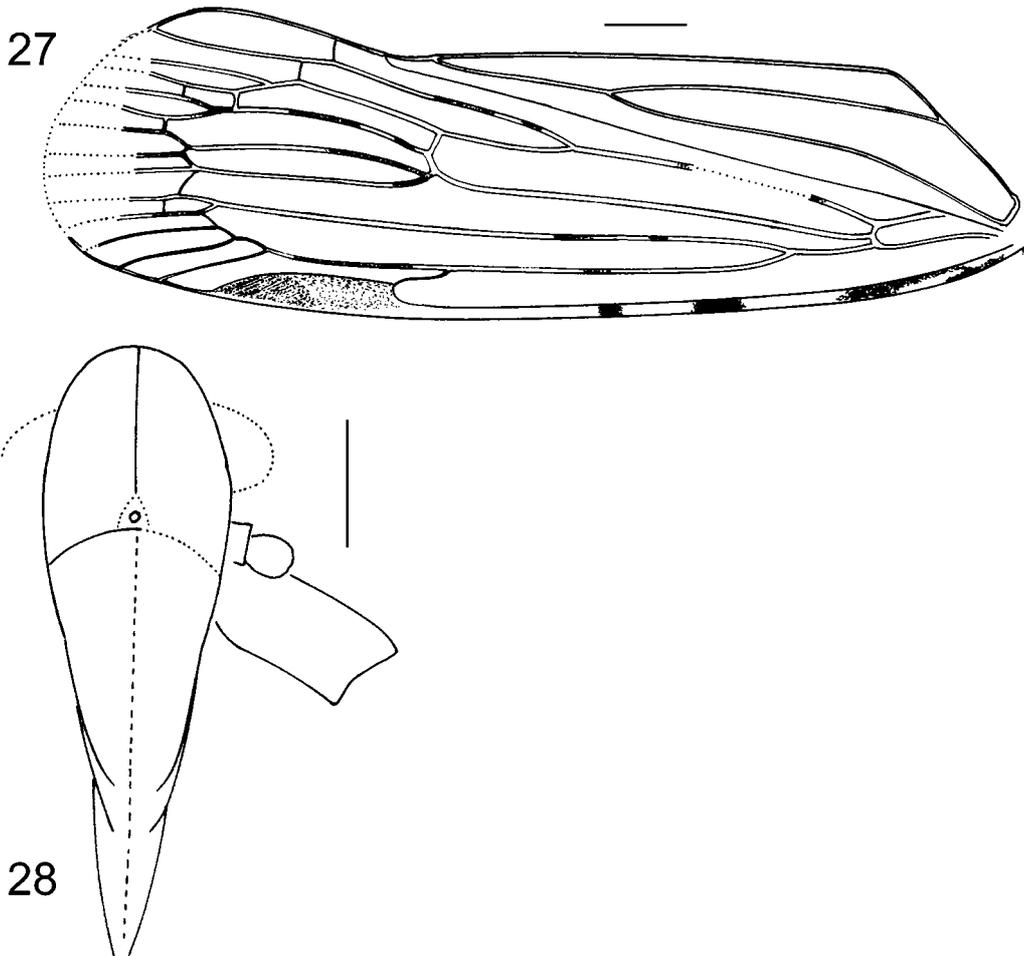
Tegmen about 10.5 mm long, with anterior margin mildly curved at base, without basicostal field, stigma elongate about six times as long as wide, clavus very long, slightly exceeding ? of tegmen length; ScR forked near basal cell, RA with three terminalia, RP forked in apical portion, with two terminalia; M forked at the level of nodal line, with five terminalia, CuA forked basad of half of tegmen length, branch CuA₁ forked in apical portion, CuA with three terminalia. Clavus with transverse veinlet between CuP and Pcu near base. transverse veinlet m-cu just apicad of M forking, second m-cu veinlet in apical portion, oblique, apical transverse veinlets do not form regular pattern.

Hind wing venation seems to be similar to pattern observed in *Mnemosyne* Stål.

Remarks

Extant species of *Mnemosyne* Stål, 1866 and fossil genus *Autrimpus* Szwedo, 2004, from Eocene Baltic amber were placed in tribe Mnemosynini Emeljanov, 1993 (Szwedo 2004). Also genera described above: *Stalisyne* Szw., Bour. et Lfb., *Mnaomaia* Szw., Bour. et Lfb., and *Mnasthaia* Szw., Bour. et Lfb. most likely belong to this tribe. The fossil record of Mnemosynini seems to be richer, as some undescribed taxa are to be found in Upper Palaeocene strata of Fur Formation in Denmark and Eocene/Oligocene strata of Bembridge Marls, Isle of Wight in United Kingdom (unpublished data). It seems that this group was relatively richly represented in various parts of Europe in the Palaeogene. The relationships within Mnemosynini are not clear and cannot be resolved until the

monophyletic units have been identified among recent taxa. As mentioned above, the genus *Mnemosyne* Stål is a complex of genera and thus a paraphyletic, if not polyphyletic unit. Preliminary results suggest that there are at least nine groups of species within this genus, but with the present state of knowledge it is premature to call them valid genera.



FIGURES 27–28. *Mnasthaia arverniorum* gen. et sp. nov. Fig. 27. Right tegmen (partly reconstructed); Fig. 28. Face. Scale bar: 1 mm.

The fossil taxa described above are very important in the reconstruction of phylogenetic scenarios among Cixiidae. The classification of Cixiidae was recently presented by Emeljanov (2002), but in his opinion Mnemosynini are sunk among Pentastirini as subtribe. Szwedo (2004) recognized Mnemosynini as a separate tribe, probably not directly related to Pentastirini, but with some characters in common with other Cixiinae. It seems that Mnemosynini together with Pentastirini belong to the oldest documented lineages among Cixiinae. The oldest Cixiidae are known from the Lower

Cretaceous of England (Fennah 1961), Lebanese amber inclusion (Fennah 1987) and Brazil (Martins-Neto 1988, Hamilton 1990), but these taxa can hardly be placed among recently recognized tribes of Cixiinae. The Pentastirini are recorded since the Lower Cretaceous, from the Upper Albian Burmese amber (specimen figured in Grimaldi et al. 2002). The other Cixiidae taxa from Palaeogene and Neogene deposits exceptionally are placed in particular tribes (Szwedo et al. 2004) and most of them need to be re-examined. It seems that Pentastirini and Mnemosynini have been separated since the end of the Lower Cretaceous, i.e. soon after the origination of Cixiidae as whole (end of Jurassic/beginning of Cretaceous?). Shcherbakov's (1996) opinion that Jurassic Fulgoridiidae should be regarded as one of subfamilies of Cixiidae remains controversial. Shcherbakov & Popov (2002) listed Fulgoridiidae as a separate family, extinct at the end of the Jurassic. Bourgoïn & Campbell (2002) mentioned Fulgoridiidae as sister group to Cixiidae (*sensu lato*). It is quite evident that the Jurassic/Cretaceous border and Early Cretaceous period were important times for the origination and diversification of Cixiidae (as well as other Fulgoroidea), but the fossil data from this period are very scarce.

During the Jurassic, the large supercontinent of Pangaea which was largely a single unit for much of the period, is likely to have experienced a considerable seasonal range of temperature (Hallam 1993). On the other hand there is no convincing evidence for any notable global temperature change through the course of this period. During the Jurassic, the western part of Pangaea in low to mid latitudes experienced an arid climate. The more easterly parts of Laurasia and Gondwanaland were more humid, at least seasonally, and higher latitudes were persistently humid. The principal change took place towards the end of the Jurassic, when arid conditions extended across the southern Eurasia area, because of orographic effects (Hallam 1993). The Cretaceous is marked by a sudden return to more humid conditions (seasonally wet) over a large region extending from North America via Europe and North Africa to the Middle East, although southern Central Asia remained dry (Hallam 1985). Fossil remains of several woody gymnosperms are recorded from the Triassic or earlier, but underwent diversification in the Jurassic and Early Cretaceous (Taylor 1988). Prior to the Cenomanian/Turonian boundary (circa 90 Mya), conifer occurrence decreased significantly (Boulter et al. 1998) and species diversity had declined by half of that in the Lower Cretaceous (Neocomian). The other seed plants were dramatically decreased to a few percent of megafossil taxa per flora (Crane 1987). The K/T boundary marked an approximate 75% reduction in overall species diversity (Upchurch & Wolfe 1987).

The Cretaceous was a period of profound vegetational change due largely to the evolutionary and geographic radiation of angiosperms (Spicer et al. 1993). Although the date of angiosperm origin is debated (e.g. Crane et al. 1995; Taylor & Hickey 1996; Sun et al. 1998, 2002), angiosperms were probably not significant components of the early Cretaceous flora, gaining a foothold first in herbaceous form in marginal, swampy, and unstable habitats (Taylor & Hickey 1992; Wing & Boucher 1998). Two major angiosperm

radiations in the Upper Cretaceous, at the Cenomanian/Turonian boundary and the Cretaceous/Palaeogene boundary (Boulter et al. 1998) are noted in the fossil record. In the Cretaceous, plant productivity was concentrated at middle and high latitudes. Polar cool temperate rain forests in coastal areas, were conifer-dominated and deciduous, winter temperatures there were ameliorated by the proximity of the ocean. In more continental high latitudes, winter temperatures probably fell below freezing, thermally depressing metabolic rates and allowing some plants to retain their leaves year round. Evergreen plants resistant to desiccation because of reduced leaf size and thick cuticles were growing there. At mid latitudes, open canopy woodlands and forests were dominated by a mixture of microphyllous conifers, moderately xeromorphic ferns, cycadophytes, pteridosperms and sphenophytes. Late Cretaceous broadleaved coriaceous angiosperms were mostly subordinate shrubs and small trees. Large angiosperm trees were comparatively rare. Low latitude vegetation tended to be xeromorphic and only patchily forested, and tropical everwet vegetation was (if present) highly restricted (Spicer et al. 1993).

Many families and genera of Jurassic insects died out or were greatly reduced in number of species by the Lower Cretaceous boundary (Whalley 1988, Carpenter 1992, Labandeira 1994), whereas Cretaceous species belong to extant groups. It is noteworthy that across the Cretaceous/Palaeogene boundary the morphology of the individuals, and to a large extent the faunal composition of the insects, have changed little. Cretaceous rapid radiation was noted for numerous other plant-sucking hemipterans (von Dohlen & Moran 2000). All these environment challenges — opening of new habitats, appearance of new host plants, opportunities to create new niches — are likely to have influenced also the ancestors of extant Cixiidae lineages. Interestingly, the data on gymnosperms as host plants of extant Cixiidae are very rare, and restricted to some Cixiini species (Wilson et al. 1994). Pentastirini seems to be restricted to angiosperm host plants, and the range of Mnemosynini host plants remains enigmatic. The evolutionary pattern of Cixiidae in relation to their host plants is not known, but it seems that the origin and two radiation periods of angiosperms also influenced Cixiidae. It could be hypothesized that the origin of Pentastirini, Mnemosynini and Cixiini appears to be related (rather) with the very early angiosperms (Jurassic/Cretaceous boundary). The radiation of Cixiini and Pentastirini could be related to both periods of angiosperm-plant radiation (fossils are known from Hauterivian to Aptian strata of Old and New Worlds), while the radiation of Mnemosynini probably took place at Cretaceous/Palaeogene border, or in Early Palaeogene (the oldest known fossils are restricted to Palaeogene of European continent). The reconstruction of an evolutionary scenario of Cixiidae, the limits and number of higher monophyletic units within the group, scheme of relationships among them, remain aims for the future. Further intensive research on morphology, palaeoentomology, molecular features and ecology of the group is necessary to achieve a better understanding of the evolutionary patterns in the Cixiidae.

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