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Revision of the genus *Palaeopoecilostola* MEUNIER, 1899 (Diptera: Limoniidae) from Baltic amber (Upper Eocene)

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ABSTRACT. A revision of the genus *Palaeopoecilostola* MEUNIER, 1899 (Diptera: Limoniidae) from Baltic amber (Upper Eocene) is presented. Redescriptions of four species of this genus are given and documented with photographs and drawings. The taxonomic ranks of two subspecies – *Palaeopoecilostola longicornis longicornis* MEUNIER, 1906 and *Palaeopoecilostola longicornis parallela* ALEXANDER, 1931 – are elevated to species: *P. longicornis* stat. n. and *P. parallela* stat. n. *Anepsiomyia atterraneus* NAZAROV, 1994 is recognized as new junior synonym of *Palaeopoecilostola speciosa* MEUNIER, 1906.

KEY WORDS: *Palaeopoecilostola*, Limoniidae, Diptera, Baltic amber, Upper Eocene, taxonomy, *Anepsiomyia atterraneus* NAZAROV, 1994 syn., *Palaeopoecilostola speciosa* MEUNIER, 1906.

INTRODUCTION

The oldest representatives of crane flies (Diptera) are known from fossil records dating back as far as the Lower/Middle Triassic (KRZEMIŃSKI et al. 1994, BLAGODEROV et al. 2007). Representatives of Limoniidae can be found also among the Upper Triassic Diptera (KRZEMIŃSKI 1992, SHCHERBAKOV et al. 1995, KRZEMIŃSKI & KRZEMIŃSKA 2003). Limoniidae are well represented in the fossil faunas of the Jurassic, Cretaceous and Tertiary (KRZEMIŃSKI & EVENHUIS 2000, KRZEMIŃSKI & KOVALEV 1988, LUKASHEVICH 2009). The bulk of the information about fossil Limoniidae is to be found in the 'Catalogue of fossil flies' by EVENHUIS (1994).

The earliest information about the fossil representatives of the family Limoniidae in Baltic amber (Upper Eocene) was published by LOEW (1850, 1851, 1861), who described the first species from this fossil resin. Thereafter, MEUNIER (1894, 1895, 1899a, 1899b, 1906a, 1906b, 1906c, 1916, 1917) described a number of new species, both from Limoniidae and other families of crane flies. ALEXANDER (1931) carried out a critical revision of the taxa previously described and provided descriptions of new species. The monograph by ALEXANDER (1931) covers over 100 species from Limoniidae.

Research into Limoniidae was taken up again after World War II. SAVCHENKO (1967, 1983), KRZEMIŃSKI (1985, 1990a, 1990b, 1993, 1998a, 1998b, 2000a, 2000b, 2001), KRZEMIŃSKI et al. (2010) and PODENAS (1999a, 1999b, 2001, 2002, 2003a, 2003b, 2003c, 2003d, 2005, 2006) described new species, made revisions and supplemented the previous descriptions of species by LOEW, MEUNIER and ALEXANDER. Research to date has shown that most Limoniidae species from Baltic amber are in fact representatives of present-day genera.

Acknowledgements

We would like to express our gratitude to the well-known private collectors, Christel and Hans Werner Hoffeins from Hamburg and M. Kutscher from Bitterfeld. We are very grateful to the curators of public collections at the Museum of the Earth, Polish Academy of Sciences in Warsaw, the Museum of Amber Inclusions at the University of Gdańsk, the Museum of Natural History Institute of Systematic and Evolution of Animals Polish Academy of Sciences, Kraków (ISEA PAS) as well as the Institute and Museum of Geology and Palaeontology at the University of Göttingen for lending us the material. We would also like to thank Joseph Ohimor for his proof-reading of the material.

MATERIAL AND METHODS

The study is based on materials from the collections of the Museum of Natural History, Institute of Systematic and Evolution of Animals, Polish Academy of Sciences, Kraków (18 specimens), the collection of the University of Göttingen (4 specimens), the Museum of the Earth, Polish Academy of Sciences, Warsaw (3 specimens), the collection of the well-known German collectors, Christel and Hans Werner Hoffeins (3 specimens), 2 specimens from Kutscher's collection, 2 specimens from the Museum of Amber Inclusions of the University of Gdańsk.

The specimens were studied using a Nikon SMZ 1500 stereomicroscope. The photographs were taken with a Nikon DS-Fi1 camera equipped with a microscope. The drawings were produced on the basis of specimens and photographs.

SYSTEMATIC PALAEONTOLOGY

Order: Diptera LINNAEUS, 1758
Family: Limoniidae SPEISER, 1909

Genus: *Palaeopoecilostola* MEUNIER, 1899

Type species: *Palaeopoecilostola longicornis* MEUNIER, 1906 – Baltic amber, Upper Eocene.

The genus *Palaeopoecilostola* assumes a special position within the family Limoniidae. The species from this genera are known only from Baltic amber (Upper Eocene − approximately 40 Ma). The wing venation and presence of tibial spurs indicate that this genus belongs to the subfamily Limnophilinae. The representatives of the genus *Palaeopoecilostola* have a much elongated vein R2+3+4 (Figs 2D, E, 3 A-C, 8D, 9D) and a characteristic hypopygium structure (Figs 2B, 8B, 9C). These features distinguish the genus *Palaeopoecilostola* from all other genera in Limoniidae.

In 1899, MEUNIER identified the distinctive individuality of the genus *Palaeopoecilostola* among Limoniidae, but because of the prevailing state of knowledge it was impossible to establish the exact systematic position of this group. Later, in his monograph of 1906, he synonymized and coined the generic name *Palaeopoecilostola* as a synonym of the genus *Lasiomastix* OSTEN SACKEN. However, in his monograph of Limoniidae from Baltic amber, ALEXANDER (1931) became the first reviewer to propose restoring the earlier name *Palaeopoecilostola*. ALEXANDER (1931) postulated that the representatives of the genera he examined resembled representatives of *Epipragmaria* from the subfamily Limnophilinae, not the genus *Lasiomastix*. Nevertheless, *Palaeopoecilostola* differs from the other genera of Limoniidae in the elongated vein R2+3+4. Vein R2+3+4 is usually much longer than R3 in members of this genus, but in *P. parallela* this vein is elongated and typical of the genus, even though it is slightly shorter than R3. In addition to the type species *Palaeopoecilostola longicornis* MEUNIER (1906), ALEXANDER (1931) reclassified two more species, previously described by MEUNIER (1906) as members of *Limnophila*, i.e. *P. speciosa* and *P. fastuosa*, into the genus *Palaeopoecilostola*.

ALEXANDER (1931) also distinguished two subspecies *P. longicornis longicornis* and *P. longicornis parallela* within the species *Palaeopoecilostola longicornis*. However, meticulous revision showed that the specimens of *P. longicornis parallela* differed subtly from those *P. longicornis longicornis* in antennal morphology and wing venation. The differences are so evident that the elevation of these two subspecies to the taxonomic rank of species is proposed here.

Palaeopoecilostola longicornis MEUNIER, 1906
(Figs 1-3)

Palaeopoecilostola MEUNIER, 1899; Bull. Soc. Ent. France: p. 334, fig. (wing).

Lasiomastix longicornis MEUNIER, 1906; Mon. Tipulidae ambre Baltique, pp. 377-378, pl. 13, fig. 14 (male antenna).

Limnophila robusta MEUNIER 1906; Mon. Tipulidae ambre Baltique, pp. 383-384, pl. 14, fig. 8 (female antenna).

Material examined

Coll. Hoffeins, No. 1463 (male); No. 1490 (male); Coll. University of Göttingen, No. K. 1832 (male); Coll. ISEA PAS No. MP/1675, (male), No. MP/3107 (male), No. MP/3108 (male), No. MP/3109 (two specimens male and female), No MP/3110 (male), No. MP/3111 (male), No. MP/3112 (male); Coll. Museum of the Earth PAS, 13570 (male); Saxonian amber Coll. Kutscher, No. 22 (male), No. 26 (male).

Diagnostic characters

Antennae covered by wispy, tiny hairs, each flagellomere with two elongate setae; outer dististylus curved, narrow and long, obtuse at apex and strongly sclerotized; inner dististylus narrow at base, cordate, strongly extended in the middle part, with long, thick setae at hind margin, longer than outer dististylus.

Redescription

Head (Fig. 1A): slender with characteristic huge eyes; antennae (Figs 1B, 2A) 16-segmented; flagellomeres curved backwards extending to mid-length of the abdomen, usually dark brown; scape almost cylindrical, small; pedicel laterally swollen, cylindrical in shape; antennal flagellomeres elongate, cylindrical, covered by tiny, wispy hairs, each flagellomere with two elongate setae; the last flagellomere clearly shorter.

Palpi (Fig. 2C): 4-segmented, 0.37-0.6 mm length (male), the last segment twice as long as the penultimate one.

Wings (Figs 1A, C, 2D, E): wing length 4.54-6.1 mm (male), 5.18 mm (female), width 1.15-1.58 mm (male) and 1.57 mm (female), strongly dark, matt, stigmata slightly separated; Sc ends before the bifurcation of vein Rs into R2+3+4 and R5; Rs slightly shorter than R2+3+4; R2+3+4 approximately 1/3 longer than R3; R1 very elongate, ending opposite 1/4 of R3 length; r-r (R2) before the end of R1; R3 as long as half of R4; cross vein m-cu approximately half or 2/3 as long as d-cell base; A1 straight and long; A2 sinuous for half of its length, the distal part of this vein strongly curved to the wing margin.

Hypopygium (Fig. 2B): elongated, tapering, basistylus covered by wispy setae; outer dististylus curved, narrow and long, obtuse at apex and strongly sclerotized; inner dististylus narrow at the base, cordate, strongly extended in the middle part, with long, thick setae at the hind margin, longer than outer dististylus.

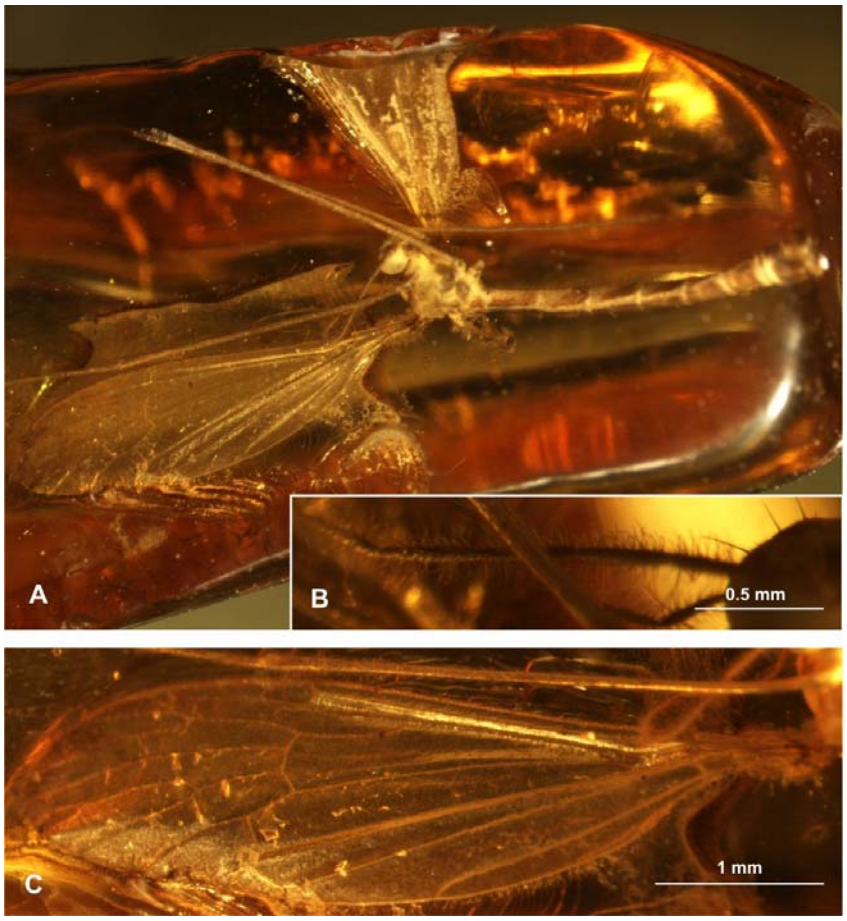

Fig. 1. *Palaeopoecilostola longicornis* MEUNIER, 1906, male, specimen No. MP/1675: A – ventral view, B – antennae, C – wing venation.

Comments

As regards the sex, the distinct differences in antennal length are conspicuous. In the female the antennae are curved backwards extending to the second abdominal segment. In the male the antennae are curved and extend towards the midpoint of the abdomen. There are also differences between female and male wing venation. In *P. longicornis* vein Rs in the male sometimes exhibits a small appendix at the base, while in the female it is arched at the base without an appendix; however, this is not a feature correlated with sex, because there are also males without a developed appendix at the base of Rs; m-cu behind or at 2/3 the length of the discal cell base (Figs 2D, E, 3A-C).

Among the specimens examined by ALEXANDER in the Collection of the University of Göttingen, we found one specimen No. 1832 (K. 1832) (male), which had previously been identified by MEUNIER (1906) as *Limnophila robusta*. ALEXANDER (1931) later defined this species as *P. longicornis*. We failed, however, to find the holotype designated by ALEXANDER in 1931.

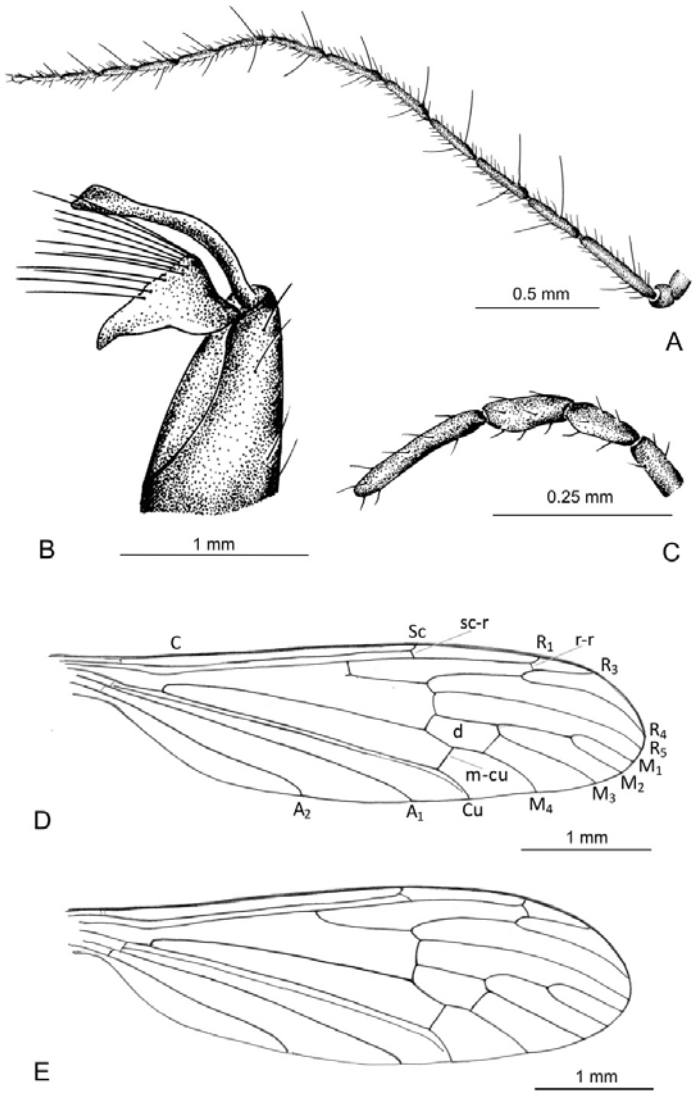

Fig. 2. *Palaeopoecilostola longicornis* MEUNIER, 1906, specimen No. MP/3109: A – antennae, B – basistylus, dististylus, C – palpi, D – male, wing venation, E – female, wing venation.

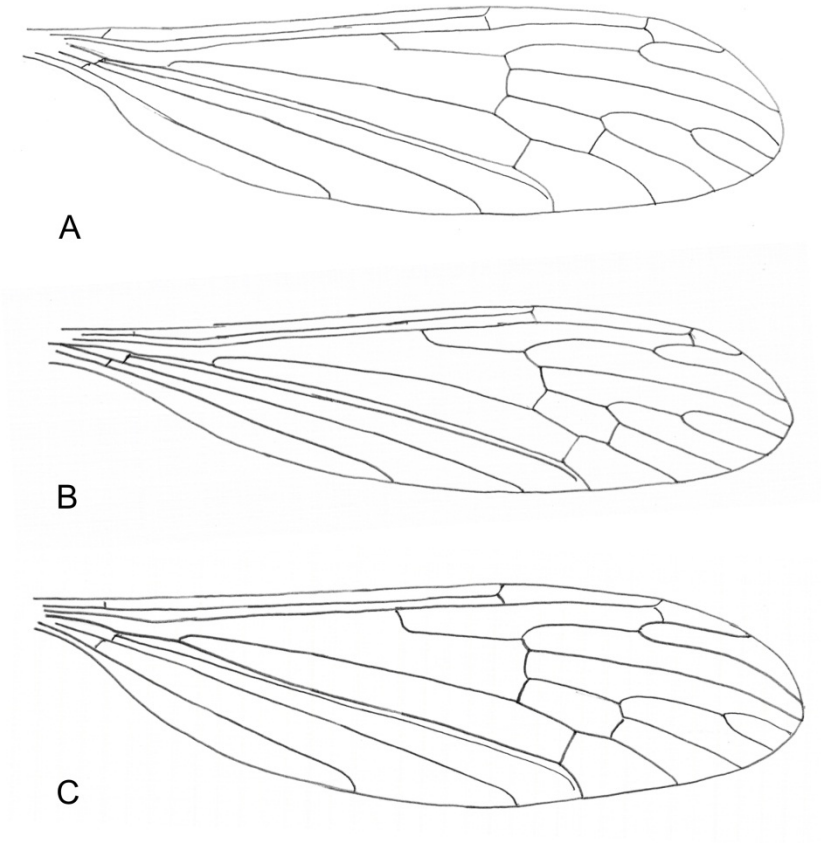

Fig. 3. *Palaeopoecilostola longicornis* MEUNIER, 1906, variation of male wing venation: A – specimen No. 1490, B – specimen No. 1463, C – specimen No. MP/3112.

Palaeopoecilostola parallela ALEXANDER, 1931
(Figs 4, 5)

Palaeopoecilostola longicornis parallela ALEXANDER, 1931 Bernstein-Forschungen: p. 48, fig. 50.

Material examined

Coll. University of Göttingen, No. 319 (sex indefinite); Coll. ISEA PAS, No. MP/1641 (male).

Diagnostic characters

Antennae covered by numerous and long setae; the bases of all flagellomeres with two very elongate setae and numerous shorter setae, sometimes reaching half the length of the elongate setae.

Redescription

Head (Fig. 4A): small, with huge eyes; antennae (Figs 4B, 5A) 16-segmented; scape narrow, nearly cylindrical; pedicel short, oval; flagellomeres narrow, cylindrical, covered by long setae, additionally the base of all flagellomeres with elongate setae, the last flagellomere half the length of the penultimate one.

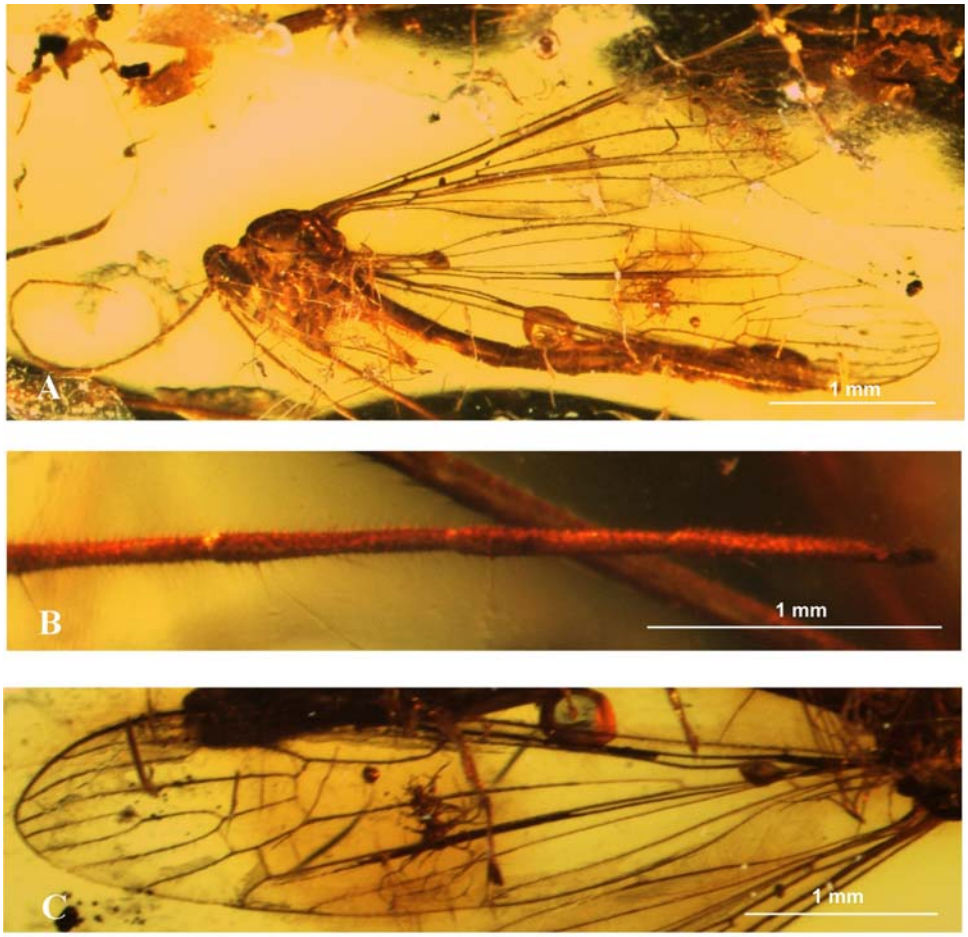

Fig. 4. *Palaeopoecilostola parallela* ALEXANDER, 1931, male, specimen No. MP/1641: A – lateral view, B – antennae, C – wing venation.

Palpi: not visible in the material examined.

Wings (Figs 4C, 5B): wing length 5.2-5.93 mm, width 1.43 mm; vein Sc ends before the bifurcation of Rs; R1 elongate; r-r (R2) almost at the end of R1; R2+3+4, approximately the same length as Rs, R2+3+4 half as long as than R3; R4 approximately 1/5 longer than R3; M1 nearly twice as long as petiola; petiola the same length as the fore margin of discal cell; cross vein m-cu at 2/3 the length of the discal cell base.

Hypopygium: not visible in the material examined.

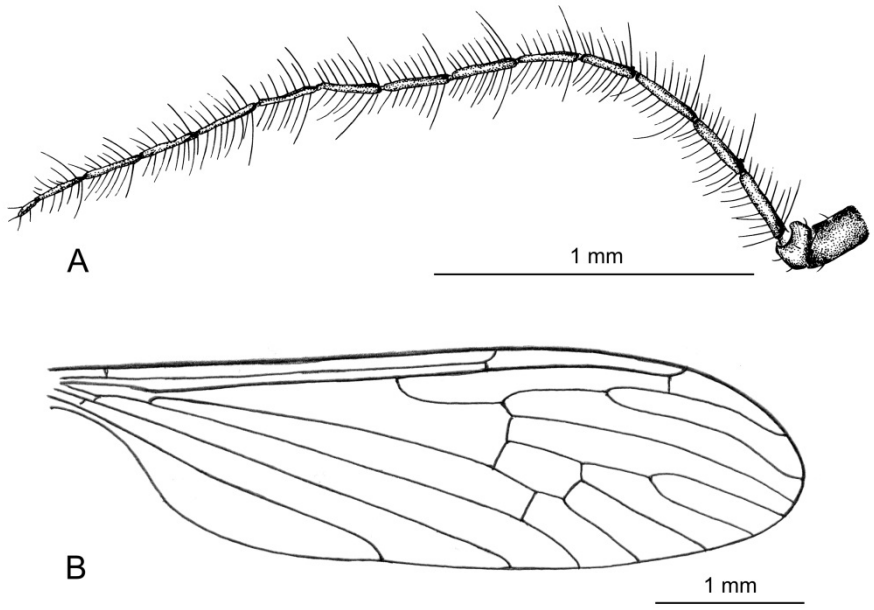

Fig. 5. *Palaeopoecilostola parallela* ALEXANDER, 1931, sex indefinite, specimen No. 319: A – antennae, B – wing venation.

Comments

This taxon was revised by ALEXANDER (1931), who distinguished two subspecies – *P. longicornis longicornis* and *P. longicornis parallela*. In his opinion, the separated subspecies were similar in morphology but differed subtly in wing venation. In *P. longicornis parallela* vein R2 is slightly longer; R3 is slightly (approximately 1/5) longer than R4, in *P. longicornis longicornis* R4 is twice as long as R3. In contrast to the interpretation of ALEXANDER (1931), comparison of the length of cells R1 and R2 shows that these features are variable among all species of this genus.

Our research has shown that both subspecies distinctively differ in antennal morphology (in *P. parallela* the antennae are covered by numerous, elongate setae; in *P. longicornis* the

setae are short and wispy) and in the length of vein R2+3+4 (in *P. longicornis* the vein R2+3+4 is as long as R2+3 or very slightly longer; in *P. parallela* this vein is distinctly shorter than R2+3). Unfortunately, the hypopygium of these taxa was not visible in the material examined.

ALEXANDER (1931) classified only one specimen No. SD 328 (female) in this species, which he designated as the holotype. We did not find the holotype in the collection of the University of Göttingen, but we did find specimen No. 319 (sex indefinite), which was classified by ALEXANDER (1931) as *P. longicornis parallela*.

Palaeopoecilostola speciosa MEUNIER, 1906.
(Figs 6-8)

Limnophila speciosa MEUNIER, 1906; Mon. Tipulidae Ambre Baltique, p. 384, pl. 13, fig. 22 (hypopygium), pl. 14, fig. 3 (wing), fig. 4 (male antenna)

Anepsiomyia atterraneus NAZAROV, 1994; Vesci Akademii Nauk Belorusi: Seria Biologichnykh Nauk, **2**: 104-108 (fig. 2 g □ antennae, v □ specimen), syn. n.

Material examined

Coll. University of Göttingen, No. K. 25, lectotype (male); Coll. Hoffeins, No. 1195 (male); Coll. ISEA PAS, No. MP/1657 (male), No. MP/3113 (male), No. MP/3114 (male), No. MP/3115 (male), No. MP/3116 (male), No. MP/3117 (male), No. MP/3118 (female), No. MP/3119 (male), No. MP/3120 (female), No. MP/3122 (male), Museum of Amber Inclusions, University of Gdańsk (MBI), No. 828 (female), No. 1425 (male), Coll. Museum of the Earth PAS, No. 469/23 (sex indefinite), No. 21137 (sex indefinite).

Diagnostic characters

Outer dististylus strongly expanded into wide lobe at the end, outer margin of this lobe with long setae; inner dististylus small, narrow, strongly sclerotized.

Redescription

Head (Figs 7A, B): not large, but with huge, distinctly separate eyes; antennae (Figs 7B, 8A) curved backwards, extending towards the base of the abdomen; scape almost cylindrical, short, pedicel small, oval; flagellomeres bottle-shaped, tapering upwards, covered by numerous short setae; additionally, 2-4 long setae are visible on all flagellomeres, slightly longer than the length of the flagellomere on which they occur. The last four flagellomeres are distinctly shorter than the others, and the apical one is slightly shorter than the sub-apical one.

Palpi (Fig. 8C): 0.43 mm length, the last segment twice as long as the penultimate one.

Wings (Figs 7A, 8D): 4.85-6.16 mm length, 1.24-1.43 mm width, slightly darker and narrow at the base; vein Sc long, ending at the bifurcation or after the bifurcation of Rs on

R2+3+4 and R5; R1 elongated, extending to about 1/3 length of vein R3; r-r (R2) almost before the end of R1; R2+3+4 the same length as Rs and 2/3 as long as R3; R4 twice as long as R3; discal cell small, rectangular; M1 approximately 1/3 longer than petiola; cross vein m-cu before the midpoint of discal cell base; A1 elongated and straight; A2 elongated, slightly sinuous to about half of its length, strongly curved at the end wing margin.

Hypopygium (Fig. 8B): with elongated and narrow basistylus; outer dististylus narrow at the base, strongly expanded into wide lobe at the end, outer margin of this lobe with long setae; inner dististylus small, lobe shaped, of simple structure.

Female differs from male in the shorter antennae and in the wing venation details: vein m-cu at or beyond the midpoint of the discal cell base. Ovipositor tiny, slightly curved at the end.

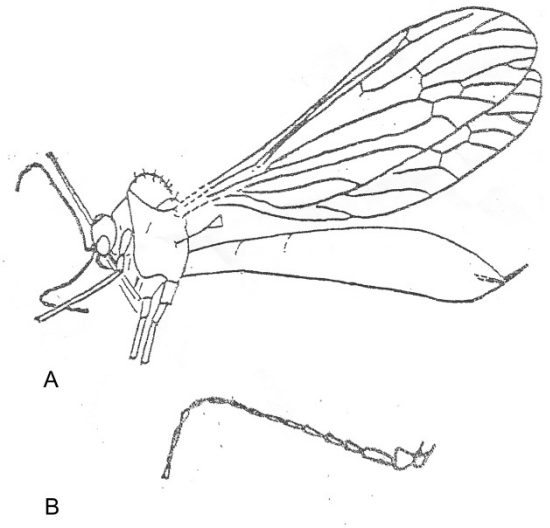

Fig. 6. *Palaeopoecilostola speciosa* MEUNIER, 1906, female (after NAZAROV et al. 1994): A – lateral view, B – antennae.

Comments

NAZAROV (in NAZAROV et al. 1994) described the new species *Anepsiomyia atterraneus* (Figs 6A, B) based on an amber inclusion from Belarus. Among the examined material, in the absence of the holotype but based on NAZAROV'S drawings, we can claim that the insect examined by this author is a specimen of *Palaeopoecilostola speciosa* described by MEUNIER (1906) from Baltic amber. This specimen does not differ from *Palaeocilostola speciosa* either in wing venation or in antennal morphology. Amber from Belarus thus belongs to the Baltic amber group.

Among the specimens classified by ALEXANDER as this species we found specimen No. 25 (K. 25) male, earlier marked by ALEXANDER as a lectotype.

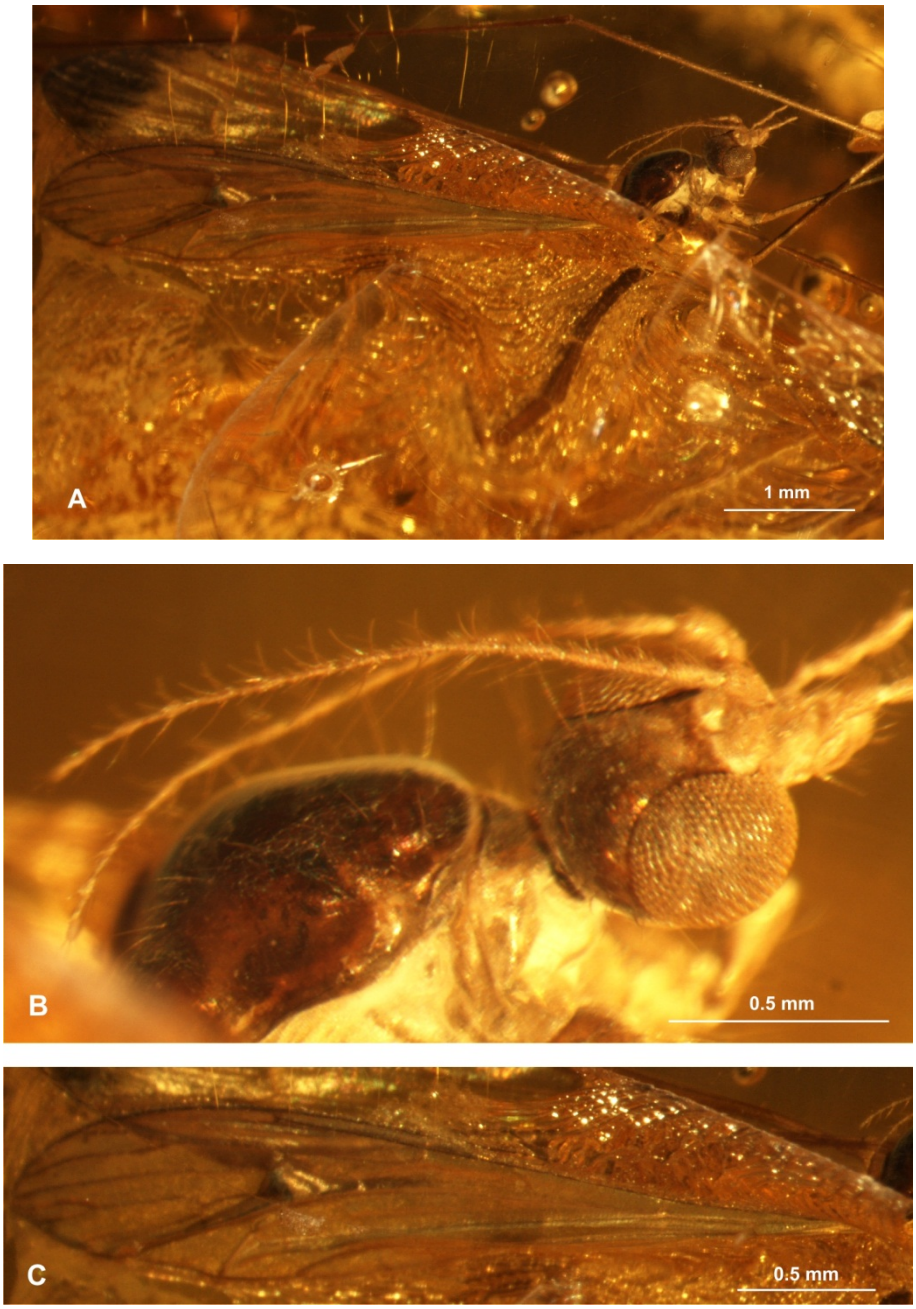

Fig. 7. *Palaeopoecilostola speciosa* MEUNIER, 1906, male, specimen No. MP/3119: A – lateral view, B – head with antennae, C – wing venation.

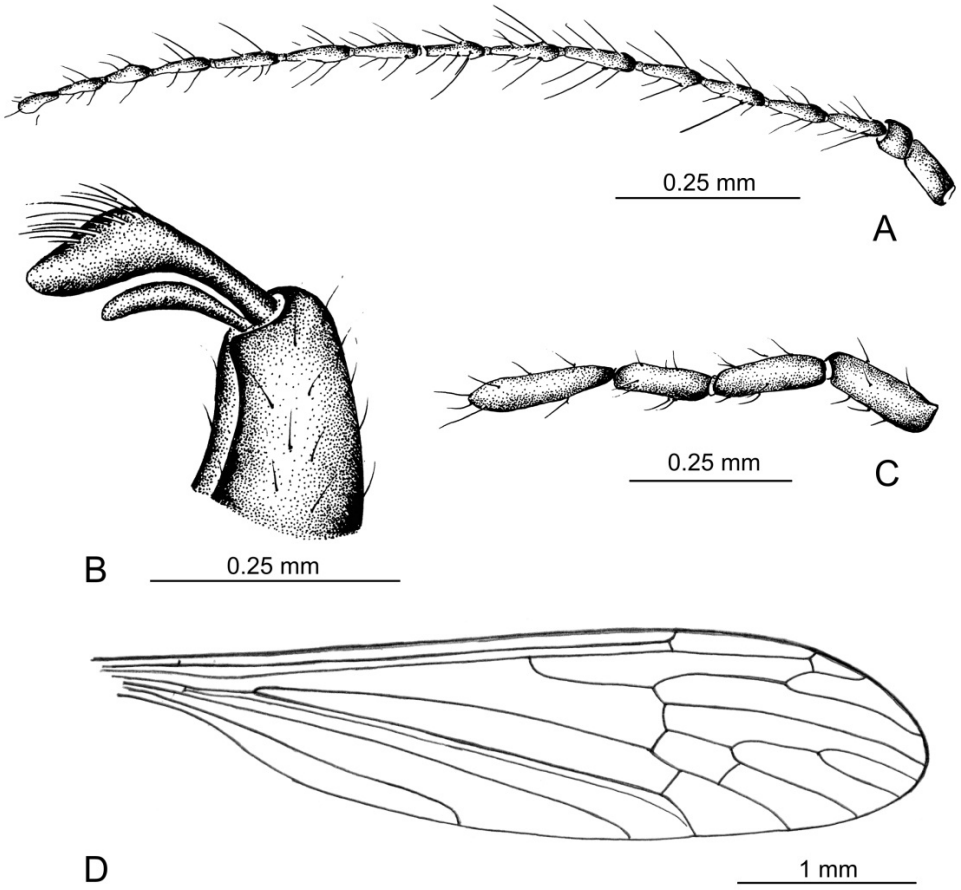

Fig. 8. *Palaeopoecilostola speciosa* MEUNIER, 1906, male, specimen No. MP/3119: A – antennae, B – basistylus, dististylus, C – palpi, D – male, specimen No. MP/3114, wing venation.

Palaeopoecilostola fastuosa MEUNIER, 1906
(Fig. 9)

Limnophila fastuosa MEUNIER 1906; Mon. Tipulidae ambre Baltique, pp. 384-385, pl. 14, fig. 5 (male antenna), fig. 6 (wing apex), fig. 7 (hypopygium).

Material examined

Coll. University of Göttingen, No. K-90 (male), holotype.

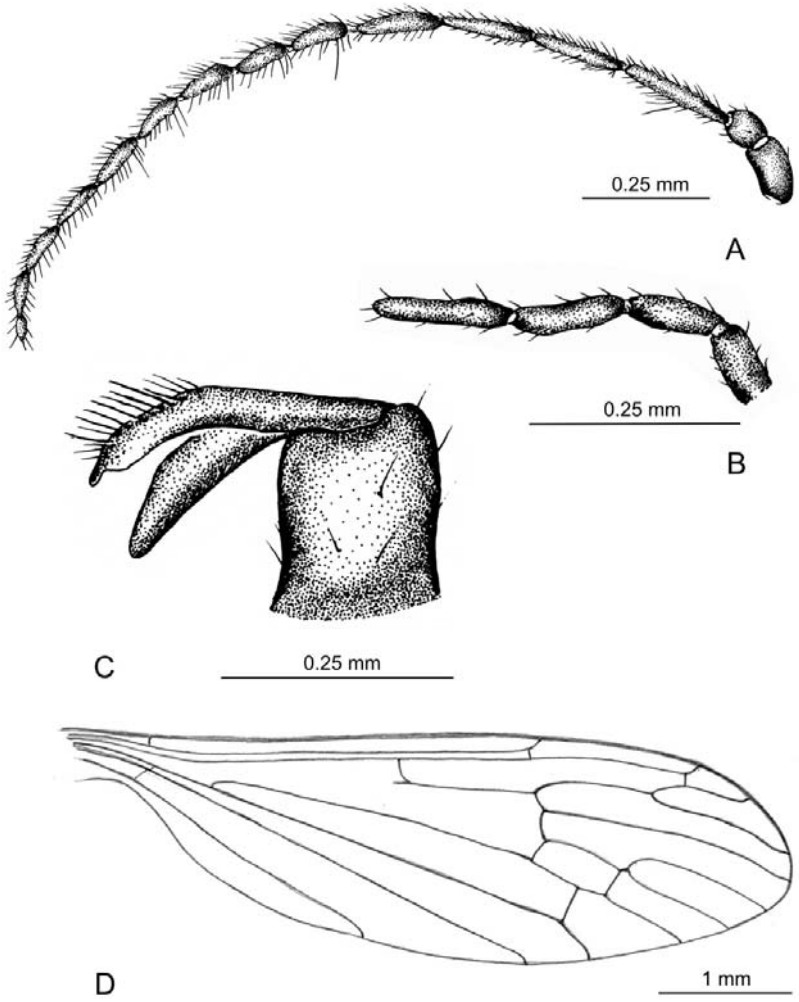

Fig. 9. *Palaeopoecilostola fastuosa* MEUNIER, 1906, male, specimen No. K-90, holotype: A – antennae, B ─ palpi, C – basistylus, dististylus, D – wing venation.

Diagnostic characters

Antennae 15-segmented; throughout its length M3 is joined with vein M4, forming a single vein M3+4; the last antennal segment is twice as long as the penultimate one.

Redescription

Head: rather small with huge eyes on the larger part of its surface. Antennae (Fig. 9A) 15-segmented; scape elongated, nearly cylindrical; pedicel short, round shape;

flagellomeres almost cylindrical, somewhat extended at the base, with short setae; elongated setae visible on some flagellomeres, but shorter than the length of a flagellomere.

Palpi (Fig. 9B): the last segment slightly longer than the penultimate one.

Wings: (Fig. 9D) vein Sc ends opposite the bifurcation of Rs into R2+3+4 and R5; Rs with small denticle at the base; vein r-r (R2) before the end of R1; R2 at 1/3 length of R3; R2+3+4 approximately 1/5 shorter than Rs and about 1/4 longer than R3; R4 approximately 3/4 longer than R3; discal cell relatively small and rectangular; cross vein m-cu at 2/3 the length of the discal cell base; short petiola is by M1 and M2; M1 almost twice as long as upper part of discal cell; throughout its length M3 is joined to vein M4, forming a single vein M3+4; A1 elongate, straight; A2 slightly sinuous.

Hypopygium: (Fig. 9C) basistylus elongated, tubular; outer dististylus narrow for 2/3 of its length, strongly curved with short, narrow denticle at the end; fairly short and wispy setae at its outer margin; inner dististylus wide at the base, tapered at the top.

Comments

The representatives of Limoniidae are usually characterized by the presence of 16-segmented antennae, although some members of this family have the number of antennal segments reduced to 4, e.g. the genus *Niphadobata*. The number of flagellomeres in Limoniidae is usually constant. The presence of 15-segmented antennae in *P. fastuosa* MEUNIER, 1906 can be regarded as a permanent feature of this species. Originally, MEUNIER (1906) incorrectly placed this species in the genus *Limnophila*. According to MEUNIER (1906) the cross vein r-r (R2) does not occur in *P. fastuosa*; however, detailed examination of more specimens shows that this vein is always present. The most characteristic feature in the wing venation of *P. fastuosa* is the occurrence of veins M3 and M4 joined throughout their length as M3+4. This feature is unknown in other species of the genus *Palaeopoecilostola.*

DISCUSSION

In view of the special position of the genus *Palaeopoecilostola*, it is a very good leading genus among Limoniidae in Eocene Baltic amber. Until recently, no similar species ascribable to the genus *Palaeopoecilostola* had been found in either contemporary or fossil sites. Specimens of different species of this genus are frequent in Baltic amber, but they are highly variable. The visible differences, e.g. in the morphological structures of *P. longicornis*, enabled ALEXANDER (1931) to describe two subspecies: *P. longicornis longicornis* and *P. longicornis parallela*. However, the specimens ascribable to *P. longicornis parallela* are rare, and no specimen with a well preserved and well visible hypopygium has been found to date. The differences in antennal morphology and in wing venation suggest that this taxon is a valid species.

We also found two specimens of the genus *Palaeopoecilostola* among the Saxonian amber in Kutscher's collection. Detailed analysis confirmed the similarity of these inclusions with those of *P. longicornis* from Baltic amber and confirmed the identity of these Eocene fossil ambers. The species described from Belarus amber by NAZAROV as *Anepsiomyia atterraneus* NAZAROV, 1994, is conspecific with *P. speciosa* from Baltic amber. It also confirms that Belarus amber belongs to the Baltic amber group.

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