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A new species of *Palaeopoecilostola* Meunier, 1899 (Diptera: Limoniidae) from the Eocene Baltic amber

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Abstract

A new species of the genus *Palaeopoecilostola* Meunier, 1899 (Diptera: Limoniidae) from the Baltic amber (Upper Eocene) is described. The cladistic analysis of the species included in this genus is provided. The distributional pattern of the *Palaeopoecilostola* species is discussed. *Palaeopoecilostola* as numerous and remarkable representative of Limoniidae, can be treated as the marker genus of the Baltic amber in broad sense (including Bitterfeld and Ukrainian ambers). *Anepsiomyia atterraneus* Nazarov, 1994 is resurrected from synonymy with *Palaeopoecilostola speciosa* Meunier, 1906. *Ryta berestiana* Nazarov, 1994 appears a junior synonym of *Palaeopoecilostola speciosa* Meunier, 1906.

Key words: *Palaeopoecilostola*, Limoniidae, Diptera, Baltic amber, Upper Eocene, taxonomy, new species, *Palaeopoecilostola eocenica* sp. nov., synonymy

Introduction

The oldest representatives of the family Limoniidae are known in fossil records as far as from the Upper Triassic (Krzemiński 1992, Shcherbakov et al. 1995, Krzemiński & Krzemińska 2003). Limoniidae are numerous among the fossil representatives of Diptera in the Jurassic, Cretaceous and Paleogene fossil sites (Krzemiński & Evenhuis 2000, Krzemiński & Kovalev 1988, Lukashevich 2009). Limoniidae frequently representing also the present-day genera are known from the Baltic amber (Upper Eocene). Many taxa of these dipterans have been described from the Baltic amber by Loew (1850, 1851, 1861), who gave the earliest information about the fossil representatives of the family Limoniidae from the Baltic amber, by Meunier (1894, 1895, 1899a, 1899b, 1906a, 1906b, 1906c, 1916, 1917), who described a number of new species and by Alexander (1931), who also made a critical revision of the taxa described previously. Very important data about Cenozoic representatives of the Limoniidae from the Baltic amber can be found in the works of Savchenko (1967, 1983), Krzemiński (1985, 1990a, 1990b, 1993, 1998a, 1998b, 2000a, 2000b, 2001), Krzemiński et al. (2010) and Podenas (1999a, 1999b, 2001, 2003a, 2003b, 2003c, 2003d, 2005, 2006). The latter author described many new species, made a revision and supplemented the previous descriptions of species by Loew, Meunier and Alexander.

The extinct genus *Palaeopoecilostola* was described by Meunier in 1899a, but the exact position of this taxon was not given. In 1906c, Meunier, proposed to synonymize generic name *Palaeopoecilostola* under the genus *Lasiomastix* Osten Sacken (1864). Later, Alexander, in his monograph of Limoniidae from Baltic amber (1931), proposed to resurrect the genus *Palaeopoecilostola*, as having nothing in common with *Lasiomastix*.

The fossil record of the Eocene Limoniidae comprises representatives of the extinct genus *Palaeopoecilostola* Meunier, 1899, known exclusively from the resins of the Baltic amber group. Four species were known up so far, with *Palaeopoecilostola longicornis* described by Meunier (1906) as type-species. Within this species, Alexander (1931) distinguished two subspecies: *Palaeopoecilostola longicornis longicornis* Meunier, 1906 and *Palaeopoecilostola longicornis paralella* Alexander, 1931. Due to evident differences in morphology of antennae

and wing venation of these taxa, their taxonomic ranks have been elevated to species levels, resulting in *Palaeopoecilostola longicornis* Meunier, 1906 and *Palaeopoecilostola paralella* Alexander, 1931 (Kania et al., 2011). Two more species *Palaeopoecilostola speciosa* (Meunier, 1906) and *Palaeopoecilostola fastuosa* (Meunier, 1906) were described originally by Meunier (1906) as members of the genus *Limnophila*. They were subsequently transferred to the genus *Palaeopoecilostola* by Alexander (1931).

Anepsiomyia atterraneus Nazarov, 1994 was proposed as junior synonym of *Palaeopoecilostola speciosa* Meunier, 1906 (Kania et al., 2011). However, *Anepsiomyia atterraneus* Nazarov, 1994, from the Baltic amber of Belorussia appears a valid species of the family Dolichopodidae (Nazarov et al., 1994), and here it is resurrected from synonymy.

Ryta berestiana Nazarov, 1994, described by Nazarov (Nazarov et al., 1994) from the same locality and described in the same paper come out a junior synonym of *Palaeopoecilostola speciosa* Meunier, 1906.

In this paper we are describing a new species of the genus *Palaeopoecilostola*, which was found among inclusions in the collection of the Museum of the Earth, Polish Academy of Sciences, Warsaw. The cladistic analysis of the genus *Palaeopoecilostola* is also provided.

Material and methods

The study is based on material from the collection of the Museum of the Earth of Polish Academy of Sciences, Warsaw. 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.

Cladistic analysis was performed using the TNT software (Goloboff et al. 2008).

Systematic paleontology

Order: Diptera Linnaeus, 1758

Family: Limoniidae Speiser, 1909

Genus: *Palaeopoecilostola* Meunier, 1899

Type species: *Palaeopoecilostola longicornis* Meunier, 1906—Baltic amber, Upper Eocene.

Palaeopoecilostola eocenica sp. nov.

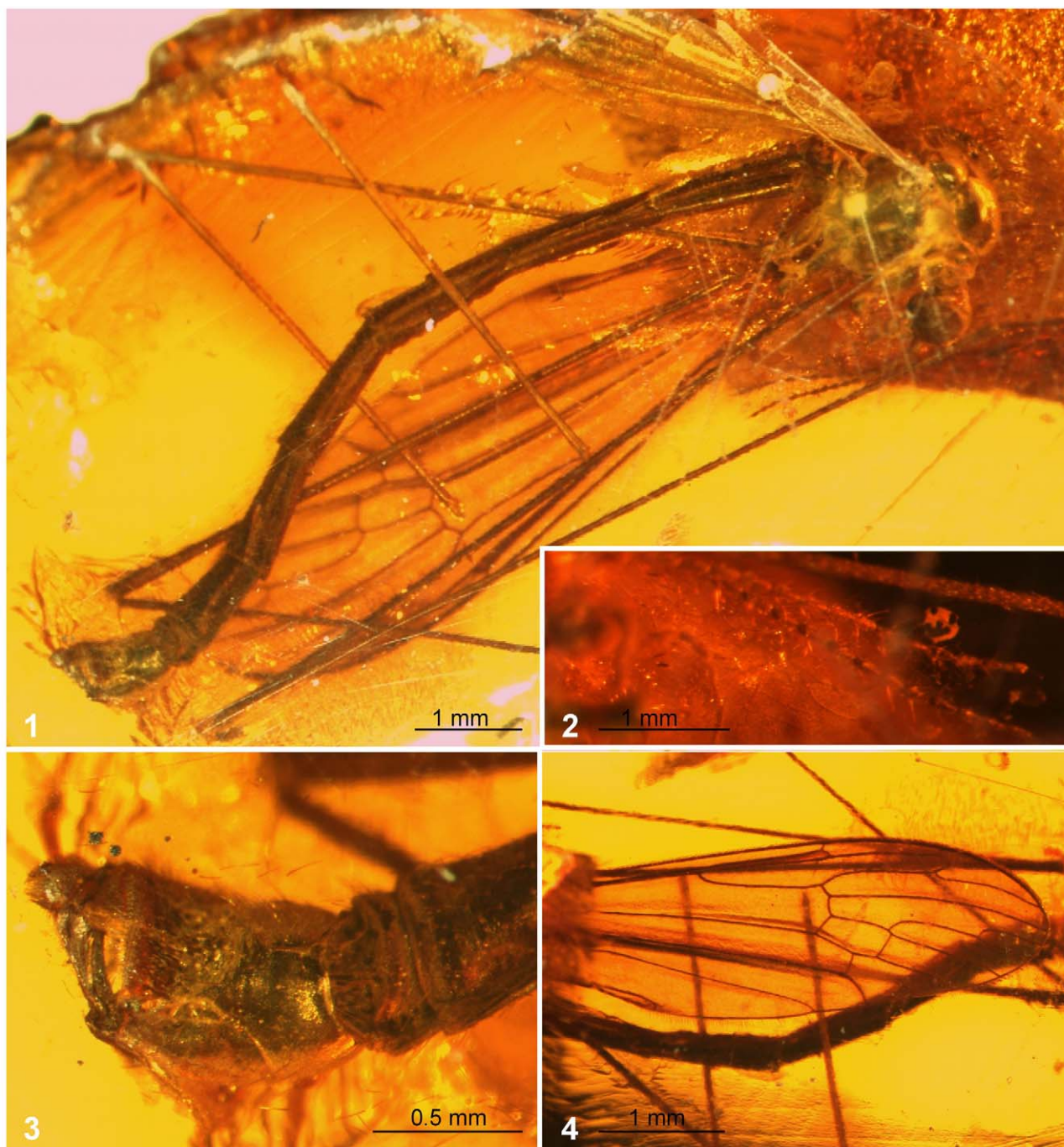
(Figs 1–8)

Diagnosis. Antennae 16-segmented, covered by long but not numerous setae, the base of each flagellomeres with two very elongated setae and rarely appearing shorter setae, usually reaching more than half the length of the elongated setae; outer dististylus wide and short, strongly expanded at the end, with short and thick setae; inner dististylus wide at the base, tapered at the top.

Description. The body length: 12.5 mm.; wing length 6.9 mm, width 4.1 mm, antennae 2.6 mm long. Head (Fig. 1): slender with characteristic huge eyes; antennae (Figs 1,2,5) shorter than mid-length of the abdomen, usually pale; shape almost cylindrical, small; pedicel laterally swollen, almost cylindrical in shape; antennal flagellomeres narrow, elongate, cylindrical, covered by tiny, wispy setae, each flagellomere with two elongated setae, additionally, a few 2–4 setae are visible on all flagellomeres, the same length or slightly longer than the length of the flagellomere on which they occur; the last segment almost as long as the sub-apical one, slightly shorter.

Palpi (Fig. 6): 4-segmented, the last segment subtly longer than the penultimate one.

Wings (Figs 1,4,7): strongly dark, stigma clearly separated; Sc long, ending a little bit past bifurcation of vein Rs into R2+3+4 and R5; Rs slightly longer than R2+3+4; R2+3+4 two times as long as R3; R1 ending opposite proximal ¼ of R3 length; r-r (R2) almost before the end of R1; R4 twice as long as R3; discal cell small, rectangular; M1 about 1/3 longer than petiola, cross vein m-cu behind the midpoint of discal cell base and approximately 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 towards the wing's edge.



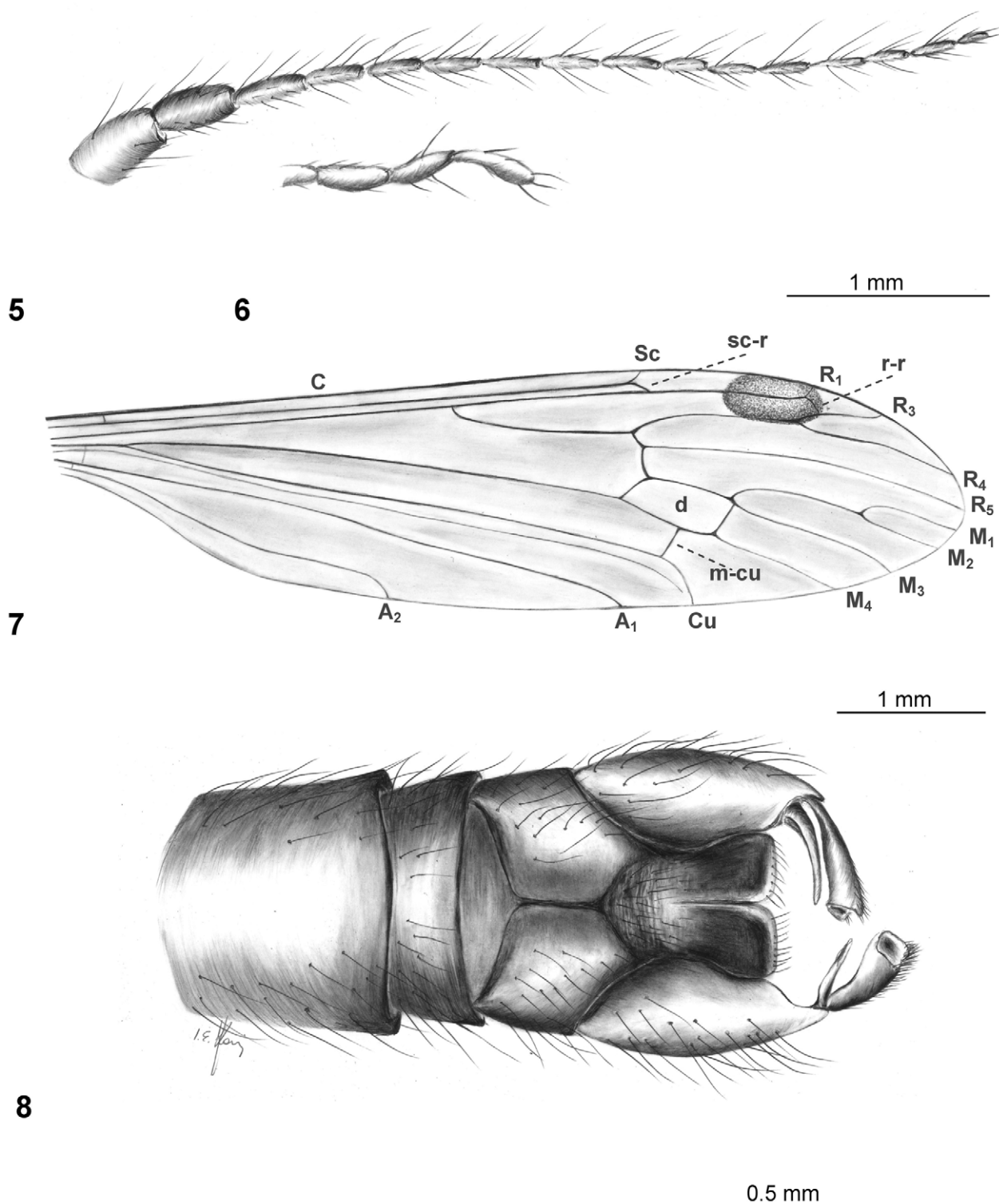
FIGURES 1–4. *Palaeopocilostola eocenica* sp. nov., holotype 1. Lateral view. 2. Antennae. 3. Hypopygium. 4. Wing venation.

Hypopygium (Figs 1, 3, 8): elongated, basistylus covered by wispy, elongate setae; outer dististylus wide, strongly expanded at the end, rather short with short and thick setae at outer edge; inner dististylus expanded at the base, narrow at the apex.

Age and occurrence. Baltic amber, Upper Eocene. The Baltic amber is aged within the range of 38–47 Ma (Ritzkowski 1997; Perkovsky et al. 2007). Absolute dating analyses of glauconites from Sambia Peninsula showed that the “blue earth” formation (amber bearing Prussian Formation) is allocated to the Middle Eocene (Lutetian: 44.1 ± 1.1 Ma) and is thus significantly older than previously assumed (Wappler 2003, 2005). Also Weitschat & Wichard (2010) suggested older age of the Baltic amber. However, assumptions on the Middle Eocene (or older) age of Baltic amber was argued by Perkovsky et al. (2007), and the Upper Eocene (Bartonian/Priabonian: 37.7 ± 3 Ma) age of Prussian Formation is preferred by these authors.

Etymology. Specific epithet after the geological period—the Eocene.

Material examined. Holotype, male. No. 19931, Coll. Museum of the Earth Polish Academy of Sciences, Warsaw, Poland.



FIGURES 5–8. *Palaeopoecilostola eocenica* sp. nov., holotype 1. Antennae. 2. Palpi. 3. Wing venation. 4. Hypopygium.

Discussion

Palaeopoecilostola eocenica sp. nov. clearly differs from the other species described in this genus, mainly by differences in the structure of antennae, details of venation and structures of the hypopygium. Presence of the dispersed shorter setae, usually reaching more than half the length of elongate setae is a unique character of this species. Antennal flagellomeres covered by numerous and short setae placed it close to the *P. speciosa* and *P. fastuosa*, and presence of 2–4 long setae visible on all flagellomeres, slightly longer than the length of the flagellomere on which they occur resembles the situation in the *P. speciosa*. The last segment of palpi slightly longer than penultimate one observable in *P. eocenica* sp. nov. resembles also the form present in *P. speciosa*. The combination of venational characters with Rs slightly longer than R2+3+4, R2+3+4 two times as long as R3 and cross vein m-cu behind the midpoint of discal cell base and approximately as long as d-cell base is a unique for *P. eocenica* sp. nov. Also the characters of hypopygium with outer dististylus wide and short, strongly expanded at the end, with short and thick setae, with inner dististylus wide at the base tapered at the top clearly separate *P. eocenica* sp. nov. from the other species of the genus *Palaeopoecilostola*.

Cladistic analysis

Taxa analysed

Palaeopoecilostola longicornis Meunier, 1906: 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); Bitterfeld (Saxonian) amber, Coll. Kutscher, No. 22 (male), No. 26 (male).

Palaeopoecilostoma parallela Alexander, 1931: Coll. University of Göttingen, No. 319 (sex indefinite); Coll. ISEA PAS, No. MP/1641 (male).

Palaeopoecilostola speciosa Meunier, 1906: lectotype, (male), Coll. University of Göttingen, No. K. 25; 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).

Palaeopoecilostola fastuosa Meunier, 1906: holotype, (male), Coll. University of Göttingen, No. K-90.

Palaeopoecilostola eocenica sp. nov.: holotype, (male), Coll. Museum of the Earth Polish Academy of Sciences, Warsaw, Poland, No. 19931.

Limnophila (*Limnophila*) *punctata* Schrank, 1781: (male and female), Coll. Department of Environmental Biology, University of Rzeszów.

The data matrix (Table 1) was analysed using TNT v.1.1 (Goloboff et al. 2008). Six species were included in this analysis. The genus *Limnophila* (Limoniidae) was chosen as the outgroup, using species *L. punctata* as representative members, because the genus *Limnophila* is one of the most primitive among Limoniidae and is also closely relative with *Palaeopoecilostola* (Savchenko 1983).

The analyses were performed using 'implicit enumeration', 'traditional search' and 'new technology search' of the TNT software to determine the most parsimonious tree for the data matrix. All 53 characters were treated as unordered and unweighted. Bremer support and bootstrap values (standard bootstrap; output—frequency differences; cut=1; 100 replicates) were computed using TNT.

All data were compiled into Nexus files using Mesquite v. 2.75 build 566 (Maddison & Maddison, 2011). Trees were viewed and their features studied using WinClada 1.00.08 (Nixon, 2002) and tree file received was adjusted using Corel PhotoPaint.

TABLE 1. The data matrix.

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TABLE 1. (Continued)

			<i>Limnophila punctata</i> SCHRANK, 1781	<i>P. eocenica</i> sp. nov.	<i>P. fastuosa</i>	<i>P. speciosa</i>	<i>P. paralella</i>	<i>P. longicornis</i>
R2+3+4 approximately 1/3 longer than R3	31	0	0	0	0	0	0	1
R2+3+4 about 1/4 longer than R3	32	0	0	0	1	0	0	0
R2+3+4 distinctly shorter than R3	33	1	0	0	0	0	0	0
R2+3+4 two times as long as R3	34	0	0	1	0	0	0	0
R2+3+4 half as long as R3	35	0	0	0	0	0	1	0
R2+3+4 2/3 as long as R3	36	0	0	0	0	1	0	0
R4 approximately 1/5 longer than R3	37	0	0	0	0	0	1	0
R3 as long as half of R4	38	1	0	1	0	1	0	1
R4 approximately 3/4 longer than R3	39	0	0	0	1	0	0	0
veins M3 and M4 forming a single vein M3+4	40	0	0	0	1	0	0	0
m-cu before the midpoint of discal cell base	41	0	0	0	0	1	0	0
cross vein m-cu approximately half or 2/3 as long discal cell base	42	0	0	0	0	0	0	1
m-cu at 2/3 the length of discal cell base	43	1	0	0	1	0	1	0
cross vein m-cu behind the midpoint of discal cell base and approximately as long as d-cell base	44	0	0	1	0	0	0	0
hypopygium elongated, tapering	45	0	0	1	?	0	?	1
basistylus covered by wispy setae	46	1	0	1	1	0	?	1
outer dististylus narrow for 2/3 of its length, strongly curved with short, narrow denticle at the end	47	0	0	0	1	0	?	0
outer dististylus curved, narrow, outer dististylus obtuse at apex and strongly sclerotised	48	1	0	0	0	0	?	1
outer dististylus wide, strongly expanded at the end, rather short	49	0	0	1	0	0	0	0
outer dististylus narrow at the base, strongly expanded into wide lobe at the end	50	0	0	0	0	1	?	0
outer dististylus with bunch of short and thick setae in the middle part at outer edge	51	1	0	0	0	0	0	0
inner dististylus narrow at the base, cordate, strongly extended in the middle part	52	0	0	0	0	0	?	1
inner dististylus small, lobe shaped, of simple structure	53	0	0	0	1	?	?	0
inner dististylus wide at the base tapered at the top	54	0	1	1	0	?	0	0

The characters

1. antennae
0–16-segmented
1–15-segmented
2. flagellomeres covered by numerous and long setae
0–no
1–yes
3. each flagellomere with two elongate setae
0–no
1–yes
4. flagellomeres covered by numerous and short setae
0–no
1–yes
5. 2–4 long setae are visible on all flagellomeres, slightly longer than the length of the flagellomere on which they occur
0–no
1–yes
6. the four flagellomeres are distinctly shorter than others
0–no
1–yes
7. elongated setae visible on some flagellomeres, but shorter than the length of a flagellomere
0–no
1–yes
8. rarely appearing shorter setae, usually reaching more than half the length of elongate setae
0–no
1–yes
9. numerous shorter setae, sometimes reaching more than half the length of elongate setae
0–no
1–yes
10. six first flagellomeres with 1 setae, the next one without numerous setae
0–no
1–yes
11. flagellomeres extending to mid-length of the abdomen
0–no
1–yes
12. flagellomeres shorter than mid-length of abdomen
0–no
1–yes
13. the last flagellomere clearly shorter than penultimate one
0–no
1–yes
14. the last flagellomere slightly shorter than penultimate one
0–no
1–yes
15. the last segment of flagellomere the same length as penultimate one
0–no
1–yes
16. antennal flagellomeres cylindrical
0–no
1–yes

17. flagellomeres bottle-shaped
0–no
1–yes
18. the last segment of palpi slightly longer than penultimate one
0–no
1–yes
19. the last segment of palpi elongated, twice as long as penultimate one
0–no
1–yes
20. Sc ends before the bifurcation of Rs into R2+3+4 and R5
0–no
1–yes
21. Sc ends at the bifurcation or after the bifurcation of Rs into R2+3+4 and R5
0–no
1–yes
22. Sc ends opposite of Rs into R2+3+4 and R5
0–no
1–yes
23. Sc ends after the bifurcation of Rs into R2+3+4 and R5
0–no
1–yes
24. Rs slightly shorter than R2+3+4Rs slightly longer than R2+3+4
0–no
1–yes
25. Rs slightly longer than R2+3+4
0–no
1–yes
26. Rs distinctly longer than R2+3+4
0–no
1–yes
27. Rs approximately 1/5 longer than R2+3+4
0–no
1–yes
28. Rs approximately the same length as R2+3+4
0–no
1–yes
29. r-r before the end of R1
0–no
1–yes
30. r-r almost at the end of R1
0–no
1–yes
31. R2+3+4 approximately 1/3 longer than R3
0–no
1–yes
32. R2+3+4 about 1/4 longer then R3
0–no
1–yes
33. R2+3+4 distinctly shorter than R3
0–no
1–yes

34. R2+3+4 two times as long as R3
0–no
1–yes
35. R2+3+4 half as long as R3
0–no
1–yes
36. R2+3+4 $\frac{2}{3}$ as long as R3
0–no
1–yes
37. R4 approximately $\frac{1}{5}$ longer than R3
0–no
1–yes
38. R3 as long as half of R4
0–no
1–yes
39. R4 approximately $\frac{3}{4}$ longer than R3
0–no
1–yes
40. veins M3 and M4 forming a single vein M3+4
0–no
1–yes
41. m-cu before the midpoint of discal cell base
0–no
1–yes
42. cross vein m-cu approximately half or $\frac{2}{3}$ as long discal cell base
0–no
1–yes
43. m-cu at $\frac{2}{3}$ the length of discal cell base
0–no
1–yes
44. cross vein m-cu behind the midpoint of discal cell base and approximately as long as d-cell base
0–no
1–yes
45. hypopygium elongated, tapering
0–no
1–yes
46. basistylus covered by wispy setae
0–no
1–yes
47. outer dististylus narrow for $\frac{2}{3}$ of its length, strongly curved with short, narrow denticle at the end
outer dististylus curved, narrow, outer dististylus obtuse at apex and strongly sclerotised
0–no
1–yes
48. outer dististylus curved, narrow, outer dististylus obtuse at apex and strongly sclerotized
0–no
1–yes
49. outer dististylus wide, strongly expanded at the end, rather short
0–no
1–yes
50. outer dististylus narrow at the base, strongly expanded into wide lobe at the end
0–no
1–yes

51. outer dististylus with bunch of short and thick setae in the middle part at outer edge
0–no
1–yes
52. inner dististylus narrow at the base, cordate, strongly extended in the middle part
0–no
1–yes
53. inner dististylus small, lobe shaped, of simple structure
0–no
1–yes
54. inner dististylus wide at the base tapered at the top
0–no
1–yes

Results

The parsimony analyses using all methods provided by TNT, yielded in one tree (Fig. 9) of 65 steps, with a consistency index of 0.81 and a retention index of 0.53. These analyses revealed that within the genus *Palaeopoecilostola* two clades could be recognized. The first consists of *P. longicornis* and *P. parallela*, supported by common synapomorphies as: each flagellomere with two setae, flagellomeres extending to mid-length of the abdomen, probably also antenna exceeding mid-length of abdomen, wing with vein Sc ends before the bifurcation of Rs into R2+3+4 and R5 and inner dististylus narrow at the base, cordate, strongly extended in the middle part. The second clade—(*P. fastuosa* + (*P. speciosa* + *P. eocenica*)) is supported by the synapomorphies as: antennae with flagellomeres covered by numerous and short setae, the last segment of palpi slightly longer than penultimate one, wing with Sc ends opposite of Rs into R2+3+4 and R5 and inner dististylus wide at the base and tapered at the top.

These results must be treated as preliminary, as not all features were available for examination. However, they seem to be reasonable and reduction of number of flagellomeres in *P. fastuosa* should be treated as apomorphy of this species (Fig. 9).

Bremer supports for the tree received and low bootstrap values for the nodes (*P. fastuosa* + (*P. speciosa* + *P. eocenica*)) and (*P. speciosa* + *P. eocenica*) (Fig. 9) probably are affected by the binary character coding and small number of characters supporting the nodes (Soltis & Soltis, 2003; Forey 2007).

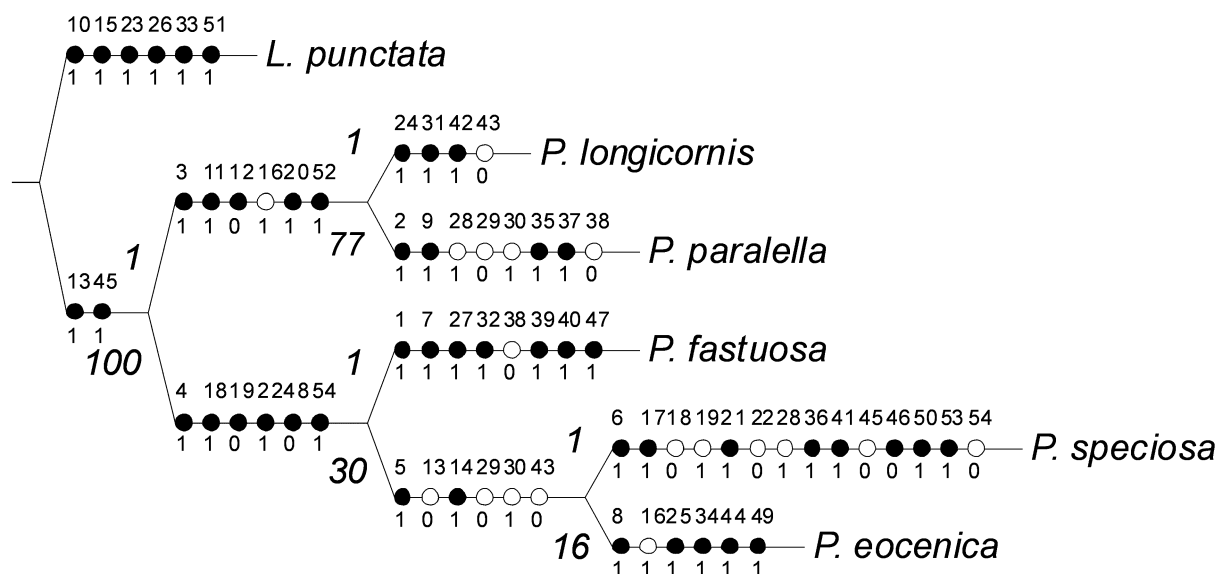


FIGURE 9. Relationships tree of *Palaeopoecilostola* species. Filled circles indicate synapomorphies or autapomorphies; open circles indicate homoplastic states; above branch, italics, Bremer support values; below branch, italics, bootstrap value.

Distribution

The genus *Palaeopoecilostola* Meunier, 1899 is believed to be a very good leading genus among Limoniidae in the Eocene Baltic amber (Kania et al. 2011). Until recently, no similar species ascribable to this genus had been found in either recent or fossil sites. However, it must be noted that fossils ascribed to the species of *Palaeopoecilostola* are very important for the discussion about the age, similarities and differences of the Eocene resins of Europe, especially Bitterfeld (Saxonian) and Ukrainian (Rovno) ambers.

The question of the Baltic amber age is still not resolved finally. There are several reasons for it: the biggest concentration in the deposit, in the Gdańsk Bay, is definitively secondary one; the other deposits, i.e. Górka Lubartowska amber, Rovno amber and with some reservations (Rascher et al. 2008) also Bitterfeld amber are also variously aged; same type of resin as Baltic amber was found also as far North as Spitsbergen and as far North-West as Axel Heiberg Island in the Canadian Arctic (Azar et al. 2011; Wolfe et al. 2009) and aged as older than Gdańsk Bay deposits.

The presence of the same species - *Palaeopoecilostola longicornis* - among the inclusions of Bitterfeld (Saxonian) and Gdańsk Bay amber gives a new point to discussion of the age and origin of the Baltic amber resins in broad sense. This fact proved rather Weitschat (1997) statement about close relationships of the Bitterfeld and Gdańsk Bay amber. The Bitterfeld amber was discovered in the Miocene deposits of Saxony-Anhalt, Germany and originally dated as its deposit (Barthel & Hetzer 1982). Later it was identified as redeposited Baltic amber (Weitschat 1997; Perkovsky et al. 2007), but some others treat it as a separate type of amber, of a considerably different, Oligocene age (Knuth et al., 2002; Fuhrmann 2005).

Inclusions of another species - *Palaeopoecila speciosa*—were found in the Gdańsk Bay amber and amber found in Polessiye (Belarussia). The amber of Belarussia seems to have the same origin as amber Ukrainian amber of Rovno (Perkovsky & Bogdasarov 2009). The Rovno amber forest is considered as representing flora of more xeric environments compared to that of the Baltic amber forest. Amber producing tree(s) was the same as for the Baltic amber (Perkovsky et al. 2010) and Rovno amber forest represents notophyllous evergreen forests (Kvaček 2010).

The recent analysis of faunal composition of various European ambers (Dlussky & Rasnitsyn 2009; Perkovsky 2009, 2010, 2011; Perkovsky et al. 2012) suggested that these faunas had formed autochthonously in different habitats of an approximately equal (on the geological scale) age. The faunal composition differences seem to reflect the differences in ecological conditions rather than in age, which could support also some paleogeographical and geological interpretations of the Bitterfeld amber forest and Rovno amber forest (Standtke 2008; Perkovsky et al. 2010). The presence of the species ascribed to the same genus in fossil resins of the Eocene in the resins originating from the Fennosarmatia and from the forests of the southern banks of the Eocene Paratethys sea gives new insights and data for these discussions. In addition it could be assumed that the genus *Paleopoecilostola*, known exclusively from Baltic amber (in broad sense), because of its very specific morphological features, especially wing venation, making identification quick and precise, could be used as a marker genus for this fossil resin.

Acknowledgements

We are deeply indebted to the curators of public collections at the Museum of the Earth, Polish Academy of sciences in Warsaw for lending the material of Limoniidae amber inclusions for our disposal. We wish to thank also Dr. Jacek Szewdo (Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw) for the discussions on amber and its inclusions and help with phylogenetic software. The TNT software was available thanks of the Willi Hennig Society (<http://www.cladistics.org/tnt.html>).

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