

First fossil representatives of the limoniid dipteran *Rhabdomastix* with extremely elongate antennae from Eocene ambers

WIKTORIA JORDAN-STASIŁO, IWONA KANIA-KŁOSOK, and WIESŁAW KRZEMIŃSKI



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The first representatives of the genus *Rhabdomastix* (Diptera, Limoniidae) with extremely long antennae (much longer than the body) is discovered in the fossil record. The paper presents new data on Eocene species of the genus *Rhabdomastix* including a new species with surprisingly long and tiny antennae with characteristic almost black spots on individual flagellomeres from Bitterfeld amber: *Rhabdomastix* (*Rhabdomastix*) *wootoni* sp. nov. Two other species have been discovered and described based on inclusions in Baltic amber: *Rhabdomastix* (*Rhabdomastix*) *setosa* sp. nov. and *Rhabdomastix* (*Rhabdomastix*) *rafali* sp. nov. Antennae with similar morphology are characteristic for the American Recent species collectively known as “*Rhabdomastix illudens*”. New nomenclature decisions include a transfer of three species from Baltic amber with antenna longer than the body to the subgenus *Rhabdomastix*. These species: *Rhabdomastix* (*Rhabdomastix*) *grussica* Podenas, 2006 comb. nov., *Rhabdomastix* (*Rhabdomastix*) *mastix* Podenas, 2006 comb. nov. and *Rhabdomastix* (*Rhabdomastix*) *setix* Podenas, 2006 comb. nov., were not previously classified to any subgenus. New discovery of a species of *Rhabdomastix* with extremely elongate, very narrow antennae, sheds new light on the evolutionary history of this genus. The paper also presents interpretations of the ecological preferences of some modern representatives of the genus and their Eocene ancestors.

Key words: Insecta, Diptera, Limoniidae, inclusions, taxonomy, evolution, Baltic amber, Bitterfeld amber, Eocene.

Wiktoria Jordan-Stasiło [wjordan@ur.edu.pl; ORCID: <https://orcid.org/0000-0001-5621-6917>] and Iwona Kania-Kłosok [ikania@ur.edu.pl; ORCID: <https://orcid.org/0000-0002-2325-4308>] (corresponding author), Institute of Biology, University of Rzeszów, Zelwerowicza 4, 35-601 Rzeszów, Poland.

Wiesław Krzemiński [wieslawk4@gmail.com; ORCID: <https://orcid.org/0000-0001-5685-891X>], Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Sławkowska 17, 31-016 Kraków, Poland.

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Introduction

The representatives of the genus *Rhabdomastix* Skuse, 1890, are currently distributed worldwide and all its 131 known Recent species and subspecies are classified to two subgenera only: *Rhabdomastix* Skuse, 1890, and *Lurdia* Starý, 2003. Sixty eight species and subspecies of *Rhabdomastix* are known from the Holarctic region, 24 species occur in the Neotropic region, 23 in the Australasian/Oceanian region, 15 in the Oriental region, and only three species of the genus *Rhabdomastix* occur in the Afrotropic (Table 1).

Three subgenera of the genus *Rhabdomastix* are known from the fossil record: *Lurdia* Starý, 2003, with one extinct species (Podenas 2006), entirely extinct *Myanmamastix* Kania-Kłosok et al., 2021, with five species (Kania-Kłosok et al. 2021) and *Rhabdomastix* Skuse, 1890, with two species known only from the fossil record (Meunier 1906; Podenas

2006). All five species of the subgenus *Myanmamastix* are described from the Cretaceous Myanmar amber (Table 2) (Kania-Kłosok et al. 2021). Sixteen species of genus *Rhabdomastix* out of the 24 known from the fossil record, have not been classified into any subgenera (Table 2) (Cockerell 1920; Statz 1944; Scudder 1894; Meunier 1906; Alexander 1931; Evenhuis 1994; Podenas 2006; Kania-Kłosok et al. 2021; Jordan-Stasiło et al. 2023). Additionally, two groups without subgeneric attribution were distinguished by Starý (2003): “*Rhabdomastix caudata*” with species complex centred around *Rhabdomastix caudata* (Lundbeck, 1898). It’s interesting that this group is distinguished by its partially developed crossvein R_2 (r-r), while “*Rhabdomastix illudens*”, is characterized by extremely elongate antenna, even five times longer than the body. The similar structure of the body occur in the Recent Bolivian *Rhabdomastix* (*Rhabdomastix*) *illudens* Alexander, 1914b. This is group

Table 1. Species and subspecies diversity of the limoniid dipteran *Rhabdomastix* Skuse, 1890, in zoogeographical regions (Oosterbroek 2024; Jordan-Stasiło et al. 2023).

Zoogeographical regions	Number of species and subspecies	Number of species and subspecies of subgenera		
		<i>Lurdia</i>	<i>Rhabdomastix</i>	unplaced to subgenus
Palaearctic	39	10	28	1
Nearctic	29	3	21	5
Neotropical	24	0	24	–
Afrotropic	3	0	3	–
Oriental	15	0	15	–
Australasian/Oceanian	23	0	23	–

which includes five Neotropical, five Oriental and one Nearctic species *Rhabdomastix* (*Rhabdomastix*) *nuttingi* Alexander, 1950 (Oosterbroek 2024). In 1914, Alexander described the first Neotropical species *R. (R.) illudens*, whose antenna were extremely elongate approximately three to five times longer than the body (Alexander 1914b; Starý 2003; Jordan-Stasiło et al. 2023), then Starý (2003) mentions a group of species centered around “*R. illudens*” with antennae much longer than the body.

Hitherto, *Rhabdomastix* with this type of antennae was unknown from the fossil record. The new discovery of a new species with extremely elongate antenna (much longer than the body) in Eocene Bitterfeld amber is the first record of this type of antennae in fossil *Rhabdomastix*.

We report here three new species of *Rhabdomastix* from Eocene fossil resins displaying antennae longer than the body length, including one with extremely long antennae, and transfer to the subgenus *Rhabdomastix* three other already described species.

Institutional abbreviations.—SDEI, Senckenberg Deutsches Entomologisches Institut, Germany; GMUG, University of Göttingen, Germany; ISEA PAS MP, Natural History Museum of the Institute of Systematics and Evolution of Animals, PAS, Kraków, Poland.

Other abbreviations.— A_1 – A_2 , anal veins; C, costal vein; Cu, cubital vein; d, discal cell; h, humeral vein; I–IV, palpomeres 1–4; M_{1+2} to M_4 , medial veins; m-cu, medial-cubital crossvein; R_1 – R_5 , radial veins; Rs, radial sector; Sc, subcostal vein; sc-r, subcostal radial crossvein.

Nomenclatural acts.—This published work and the nomenclatural acts it contains have been registered in Zoobank: urn:lsid:zoobank.org:pub:45A50B90-72C3-44AF-B5F4-7FA090BF142A.

Material and methods

The study was based on ten specimens attributed to the genus *Rhabdomastix* Skuse, 1890, preserved as inclusions in Eocene Baltic amber (nine specimens) and Bitterfeld

amber (one specimen). The examined material is deposited at the Institute of Systematics and Animal Evolution of the Polish Academy of Sciences Kraków, Poland (ISEA PAS) (seven specimens) and at the Senckenberg Deutsches Entomologisches Institut (SDEI) Müncheberg, Germany (the collection of Christel and Hans Werner Hoffeins) (two specimens) (Table 3). One specimen examined herein belongs to the Manfred Kutscher’s collection, stored at the University of Göttingen (GMUG).

The specimens were examined using a Nikon SMZ 1500 stereomicroscope equipped with a Nikon DS-Fil camera. The measurements were performed with NIS-Elements D 3.0 software in the University of Rzeszów. The drawings were made by tracing specimens and photographs by WJ-S. The map was built using the map Maps-For-Free (<https://maps-for-free.com>) and modified with the CorelDraw 2018 software. We follow the nomenclature of wing venation of Krzemiński (2002), the designations of hypopygium and ovipositor were adapted from McAlpine et al. (1981), Podenas (2006), Krzemiński and Krzemińska (2003).

Systematic palaeontology

Order Diptera Linnaeus, 1758

Infraorder Tipulomorpha Rohdendorf, 1961

Family Limoniidae Speiser, 1909

Subfamily Chioneinae Rondani, 1861

Genus *Rhabdomastix* Skuse, 1890

Subgenus *Rhabdomastix* Skuse, 1890

Type species: *Rhabdomastix ostensackeni* Skuse, 1890; Australian/Oceanian, extant; by monotypy.

Emended diagnosis.—Antenna of various length; tip of Sc in half or beyond half length of wing; r-r (R_2) completely reduced; sc-r present or reduced; Rb bifurcation Rb before half length of wing; Rs elongate, usually longer than half of Mb; d-cell hexagonal, small, shorter or equal to length of M_3 ; R_3 more or less oblique; distal part of M_{1+2} and M_3 clearly arched; outer gonostylus longer than inner one.

Rhabdomastix (*Rhabdomastix*) *rafali* sp. nov.

Figs. 1, 2.

ZooBank LSID: urn:lsid:zoobank.org:act:D8C77073-6D92-4683-A92C-173E623D5DE5.

Etymology: The name of the new species is dedicated to Rafał Stasiło, the husband of WJ-S.

Holotype: ISEA PAS MP/3092, well preserved male imago lacking some legs, the mouthparts not visible.

Type locality: Baltic area, the Blue Earth (Blaue Erde).

Type horizon: Secondary deposit found mainly in glauconitic marine sediments of middle Eocene age (Lutetian Stage; 47.8–41.3 Ma), deposited along the paleo-North Sea margin (Wolfe et al. 2016).

Material.—Holotype and ISEA PAS MP/3948a, male, well-preserved specimen, hypopygium poorly visible; ISEA PAS

Table 2. List of fossil species of the limoniid dipteran *Rhabdomastix* Skuse, 1890, known from the fossil record with the stratigraphic range, age, type of fossil and division into subgenera.

Species	Age	Type of fossil
Subgenus <i>Lurdia</i> Starý, 2003		
<i>Rhabdomastix (L.) ratix</i> Podenas, 2006	middle Eocene (Lutetian); 47.8–41.3 Ma	inclusion/Baltic amber
Subgenus: <i>Myanmamastix</i> Kania-Kłosok et al., 2021		
<i>Rhabdomastix (M.) asiatica</i> Kania-Kłosok et al., 2021	Late Cretaceous; 98.79 ± 0.62 Ma	inclusion/Burmese amber
<i>Rhabdomastix (M.) cretatica</i> Kania-Kłosok et al., 2021	Late Cretaceous; 98.79 ± 0.62 Ma	inclusion/Burmese amber
<i>Rhabdomastix (M.) jarzembowskii</i> Krzemiński, 2004	Late Cretaceous; 98.79 ± 0.62 Ma	inclusion/Burmese amber
<i>Rhabdomastix (M.) krzeminskae</i> Kania-Kłosok et al., 2021	Late Cretaceous; 98.79 ± 0.62 Ma	inclusion/Burmese amber
<i>Rhabdomastix (M.) myanmae</i> Kania-Kłosok et al., 2021	Late Cretaceous; 98.79 ± 0.62 Ma	inclusion/Burmese amber
Subgenus <i>Rhabdomastix</i> Skuse, 1890		
<i>Rhabdomastix (R.) elegantula</i> (Meunier, 1906)	middle Eocene (Lutetian); 47.8–41.3 Ma	inclusion/Baltic amber
<i>Rhabdomastix (R.) grussica</i> Podenas, 2006 comb. nov.	middle Eocene (Lutetian); 47.8–41.3 Ma	inclusion/Baltic amber
<i>Rhabdomastix (R.) lutix</i> Podenas, 2006	middle Eocene (Lutetian); 47.8–41.3 Ma	inclusion/Baltic amber
<i>Rhabdomastix (R.) mastix</i> Podenas, 2006 comb. nov.	middle Eocene (Lutetian); 47.8–41.3 Ma	inclusion/Baltic amber
<i>Rhabdomastix (R.) rafali</i> sp. nov.	middle Eocene (Lutetian); 47.8–41.3 Ma	inclusion/Baltic amber
<i>Rhabdomastix (R.) setix</i> Podenas, 2006 comb. nov.	middle Eocene (Lutetian); 47.8–41.3 Ma	inclusion/Baltic amber
<i>Rhabdomastix (R.) setosa</i> sp. nov.	middle Eocene (Lutetian); 47.8–41.3 Ma	inclusion/Baltic amber
<i>Rhabdomastix (R.) woottoni</i> sp. nov.	middle–late Eocene	inclusion/Bitterfeld amber
Unplaced to subgenus		
<i>Rhabdomastix borussica</i> (Meunier, 1906)	middle Eocene (Lutetian); 47.8–41.3 Ma	inclusion/Baltic amber
<i>Rhabdomastix brevis</i> Alexander, 1931	middle Eocene (Lutetian); 47.8–41.3 Ma	inclusion/Baltic amber
<i>Rhabdomastix frigida</i> Scudder, 1894	Oligocene; 37.2–33.9 Ma	imprint/Florissant
<i>Rhabdomastix hoffeinsi</i> Jordan-Stasiło et al., 2023	middle Eocene (Lutetian); 47.8–41.3 Ma	inclusion/Baltic amber
<i>Rhabdomastix klebsi</i> Alexander, 1931	middle Eocene (Lutetian); 47.8–41.3 Ma	inclusion/Baltic amber
<i>Rhabdomastix labefactata</i> Scudder, 1894	Oligocene; 37.2–33.9 Ma	imprint/Florissant
<i>Rhabdomastix oligocaenica</i> Statz, 1944	Oligocene; 28.4–23.0 Ma	imprint/Rott Formation
<i>Rhabdomastix praecursor</i> Cockerell, 1927	Oligocene; 37.2–33.9 Ma	imprint/Florissant
<i>Rhabdomastix primogenitalis</i> Scudder, 1894	Oligocene; 37.2–33.9 Ma	imprint/Florissant
<i>Rhabdomastix profundi</i> Scudder, 1894	Oligocene; 37.2–33.9 Ma	imprint/Florissant
<i>Rhabdomastix pulcherrima</i> (Meunier, 1906)	middle Eocene (Lutetian); 47.8–41.3 Ma	inclusion/Baltic amber
<i>Rhabdomastix redophilax</i> Podenas, 2006	middle Eocene (Lutetian); 47.8–41.3 Ma	inclusion/Baltic amber
<i>Rhabdomastix scudderi</i> Cockerell, 1920	Eocene; 50.3–46.2 Ma	imprint/Rocky Mountains

Table 3. List of materials examined herein, with sex, type of resin and repository indicated.

Species	Number of specimen	Status of the material	Sex	Type of material	Collection
<i>Rhabdomastix (R.) mastix</i> Podenas, 2006 comb. nov.	MP/3321	additional material	♀	Baltic amber	ISEA PAS
<i>Rhabdomastix (R.) rafali</i> sp. nov.	MP/3092	holotype	♂	Baltic amber	ISEA PAS
	MP/3948a	additional material	♂	Baltic amber	ISEA PAS
	MP/3948b	additional material	♂	Baltic amber	ISEA PAS
	MP/3948c	additional material	♂	Baltic amber	ISEA PAS
<i>Rhabdomastix (R.) setosa</i> sp. nov.	CCHH 1462-2	holotype	♂	Baltic amber	SDEI/coll. Ch. and H.W. Hoffeins
	MP/3472	additional material	♂	Baltic amber	ISEA PAS
	CCHH 1471-2	additional material	♂	Baltic amber	SDEI/ coll. Ch. and H.W. Hoffeins
	MP/3945	additional material	♂	Baltic amber	ISEA PAS
<i>Rhabdomastix (R.) woottoni</i> sp. nov.	GMUG 80	holotype	♂	Bitterfeld amber	GMUG/coll. M. Kutscher

MP/3948b, male, well-preserved specimen, hypopygium poorly visible; ISEA PAS MP/3948c, male, well-preserved specimen, hypopygium poorly visible; all from Baltic amber (Lutetian, middle Eocene, 47.9–41.3 Ma).

Diagnosis.—Antenna elongate, thin, longer than body by about 0.3 times of its length, longer than wing, without color

pattern; flagellomeres 1–13 narrow, elongate, first flagellomere 5 times as long as wide, flagellomeres 2–13 6, 7 times as long as wide, last flagellomere approximately 0.16 times of penultimate one, 2 times of its width; setae on antennae relatively sparsely distributed, shorter than length of segments bearing them; Sc terminating beyond half length of

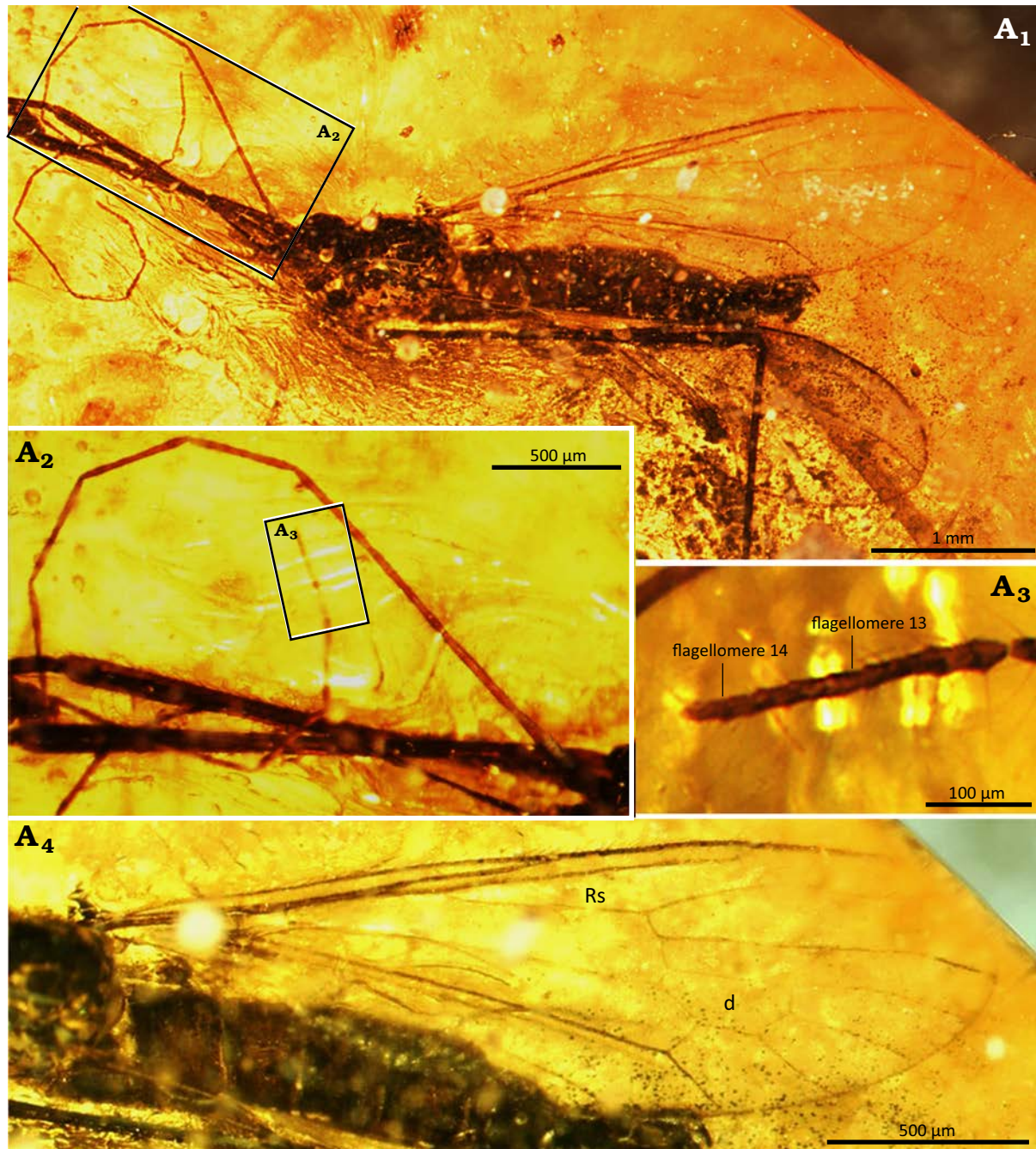


Fig. 1. Limoniid dipteran *Rhabdomastix (Rhabdomastix) rafali* sp. nov., holotype (male) ISEA PAS MP/3092 from Baltic amber, 47.8–41.3 Ma, Lutetian. Body in latero-dorsal view (A₁), antenna in latero-dorsal view (A₂), antenna, last flagellomere in lateral view (A₃), wing (A₄). Abbreviations: d, discal cell; Rs, radial sector.

wing, just beyond half of Rs; Rs shorter than R_{2+3+4} and R_4 combined, about 0.2 times of its length; tip of R_1 beyond half length of d-cell, opposite approximately 0.75 times of R_{2+3+4} ; R_4 3 times as long as R_3 , R_4 shorter than R_{2+3+4} ; distance between tips of R_1 and R_3 longer than R_3 ; M_3 and d-cell of comparable length, m-cu situated just before half length of d-cell; d-cell 2.5 times its width, narrow at base, slightly expanded distally; anal angle unexpanded; distance between tips of A_1 and A_2 correspondence to approximately 2 times distance between tips of Cu and A_1 ; tip of A_2 before

fork of Rb; tip of A_1 before fork of Rs; haltere less than 0.25 times of wing length.

Description.—*Body*: 3.28–3.87 mm long, wing without color pattern, pterostigma absent, haltere slightly elongate (Fig. 1A₁, A₂).

Head: 0.30–0.41 mm wide; antenna (Figs. 1A₁–A₃, 2A₂) with scape slightly elongate, scape 2 times as long as wide; pedicel narrow at the base, only slightly wider in the distal part, as long as wide; setae on the flagellomeres 3–15 times shorter than half the length of the segment bearing them,

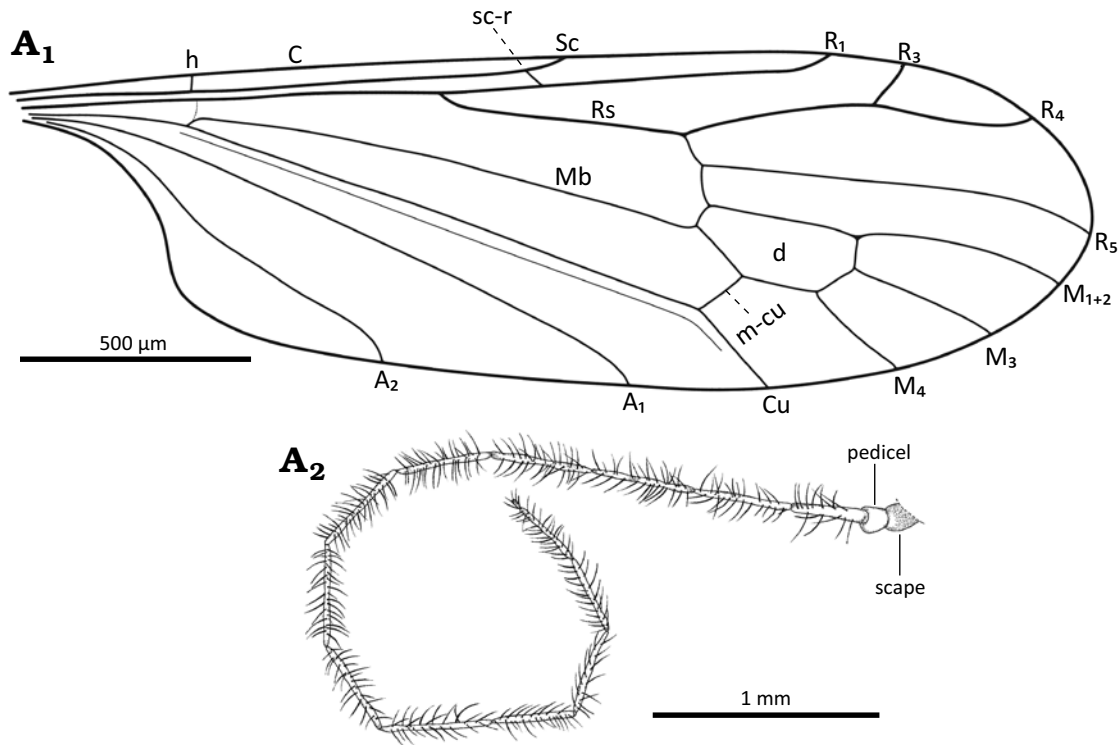


Fig. 2. Limoniid dipteran *Rhabdomastix* (*Rhabdomastix*) *rafali* sp. nov., holotype (male) ISEA PAS MP/3092 from Baltic amber, 47.8–41.3 Ma, Lutetian. Wing venation (A₁), antenna (A₂). Abbreviations: A₁, A₂, anal veins; C, costal vein; Cu, cubital vein; d, discal cell; h, humeral vein; M₁₊₂ to M₄, medial veins; Mb, medial-basal vein; m-cu, medial-cubital crossvein; R₁–R₅, radial veins; Rs, radial sector; Sc, subcostal vein; sc-r, subcostal radial crossvein.

only slightly longer than its width; setae occur perpendicular to the surface of flagellomere; the last flagellomere with numerous setae at the tip; antenna 4.29 mm long: scape 0.07 mm long, pedicel 0.08 mm long; flagellomeres: 1, 0.26 mm; 2, 0.29 mm; 3, 0.34 mm; 4, 0.34 mm; 5, 0.34 mm; 6, 0.34 mm; 7, 0.34 mm; 8, 0.34 mm; 9, 0.35 mm; 10, 0.33 mm; 11, 0.29 mm; 12, 0.27 mm; 13, 0.27 mm; 14, 0.04 mm.

Thorax: Wing 3.30–3.50 mm long, 0.77–0.95 mm wide, 3.5 times as long as wide (Figs. 1A₁, A₄, 2A₁); crossvein (h) situated at 0.2 times the length of the wing from its base; crossvein sc-r occurs at the distance from the tip of the vein Sc equal to 2 times its length; the distance between tips of Sc and R₁ 3.5 times longer than the distance between tips of R₁ and R₃; R₃ short, slightly shorter than the distance between tips of R₁ and R₃; vein M₁₊₂ 1.3 times longer than d-cell; M₄ short, shorter than d-cell; Mb 3 times as long as M₃; Cu from the point of connection with crossvein m-cu to the edge of wing straight; the distance between the tips of M₁₊₂ and M₃ shorter than the distance between tips of M₃ and M₄; the distance between the tips of M₃ and M₄ shorter than the distance between tips of M₄ and Cu; the distance between the tips of M₄ and Cu and also the tips of Cu and A₁ comparable; distance between the tips of A₁ and A₂ and also the tips of M₄ and A₁ comparable; A₁ almost straight, A₂ slightly sinusoidal.

Haltere: 0.68–0.72 mm long, stem short 1.5 times as long as wide, as massive knob.

Hypopygium: 0.63–0.88 mm long.

Remarks.—The features which allow to include the species within the subgenus *Rhabdomastix* are as follows: elongate antennae, longer than body length, crossvein well developed, d-cell hexagonal, distal part of M₁₊₂ and M₃ arched, outer gonostylus longer than inner gonostylus. Antenna in *Rhabdomastix* (*R.*) *rafali* sp. nov. are longer than the body length. Antenna longer than the body length also occur in the following species: *Rhabdomastix* (*R.*) *grussica* Podenas, 2006 comb. nov., *Rhabdomastix* (*R.*) *mastix* Podenas, 2006 comb. nov., *Rhabdomastix* (*R.*) *setix* Podenas, 2006 comb. nov., *Rhabdomastix* (*R.*) *setosa* sp. nov., and *Rhabdomastix* (*R.*) *woottoni* sp. nov. In the remaining species represented in Cenozoic fossil resins belonging to the subgenus *Rhabdomastix*, antennae are shorter than the body length. In contrast to *R. (R.) woottoni* sp. nov. a species with the antennae very thin and the very elongate flagellomeres with a few and short setae, antennae are longer than the length of the body by about half its length, in *R. (R.) rafali* sp. nov. the antennae are longer than the body by only 0.3 times of its length, they are not as thin as in *R. (R.) woottoni* sp. nov. and the setae are numerous, although they are relatively sparsely distributed on each segment and more elongate in contrast to those occurring in *R. (R.) woottoni* sp. nov. In *R. (R.) setosa* sp. nov. setae on each of the flagellomeres are much longer and more dense, often longer than half the length of the segment on which they occur, in *R. (R.) rafali* sp. nov. the setae are always shorter.

In *R. (R.) rafali* sp. nov. the vein M₃ is as long as d-cell, unlike in *R. (R.) grussica* Podenas, 2006 comb. nov., *R. (R.)*

mastix Podenas, 2006 comb. nov., *R. (R.) setix* Podenas, 2006 comb. nov., *R. (R.) setosa* sp. nov. and *R. (R.) woottoni* sp. nov., in which the vein M_3 is much longer than d-cell. Moreover, the vein Sc in *R. (R.) mastix* Podenas, 2006 comb. nov. is very short, ending before half the length of Rs, and in *R. (R.) rafali* sp. nov. it ends just beyond half the length of Rs, measured from the fork of Rb. In contrast to *R. (R.) grussica* Podenas, 2006 comb. nov. the distance between the tips of A_1 and A_2 is 2.5 times longer than the distance between the tips of Cu and A_1 , in *R. (R.) rafali* sp. nov. this distance is 2 times longer than the distance between the tips of the Cu and A_1 . Moreover, in a species described from the Eocene sediments of the Green River, USA, *Rhabdomastix scudderi* Cockerell, 1920, the Sc vein is very elongate, ending just before the Rs bifurcation, and the vein A_2 just before the fork of Rs, while in *R. (R.) rafali* sp. nov. Sc connect with C just behind half of Rs, vein A_2 ends before the fork of Rb, measured from the base of the wing.

Stratigraphic and geographic range.—Baltic amber is dated by some authors to middle Eocene age (Lutetian Stage; 47.8–41.3 Ma) (Wolfe et al. 2016), but the age range of this fossil resin is still under debate, dated by Grimaldi and Ross (2017) as Priabonian, based on pollen, spores and phytoplankton of the amber-bearing layer, the so-called Blue Earth. The specimen was collected in the Baltic area from the Blue Earth (Blaue Erde) (Wolfe et al. 2016).

Rhabdomastix (Rhabdomastix) setosa sp. nov.

Figs. 3, 4.

ZooBank LSID: lsid:zoobank.org:act:E6B70F17-F77B-40DE-B319-13B9E8DCA87E

Etymology: From Latin *saetae*, setaceous, bristly. Adjective.

Holotype: SDEI CCHH 1462-2, male, specimen well preserved, only some of the legs are not preserved (coll. Ch. and H.W. Hoffeins).

Type locality: Baltic area, the Blue Earth (Blaue Erde).

Type horizon: Secondary deposit found mainly in glauconitic marine sediments of middle Eocene age (Lutetian Stage; 47.8–41.3 Ma), deposited along the paleo-North Sea margin (Wolfe et al. 2016).

Material.—ISEA PAS MP/3472, male, specimen very poorly preserved; ISEA PAS MP/3945, male, specimen poorly preserved, only the wing and antennae were well visible; SDEI CCHH 1471-2, male, specimen well preserved, only some of the legs are not preserved; all from Baltic amber, Lutetian, middle Eocene, 47.9–41.3 Ma.

Diagnosis.—Antennae elongate, thin, longer than body by about 0.3 times of its length, longer than wing, without color pattern; flagellomeres elongate, first flagellomere almost 5 times as long as wide, flagellomeres 2–10, 7 times as long as wide, flagellomeres 11–13, 5 times as long as wide, last flagellomere half length of penultimate one; long setae on flagellomeres elongate, only slightly shorter than length of segments bearing them; tip of Sc beyond half length of wing, opposite 0.6 times of Rs; Rs shorter than R_{2+3+4} and R_4 combined, by about 0.3 times of its length; R_1 ends beyond half length of d-cell, opposite approximately 0.6 times

of R_{2+3+4} ; R_4 4 times as long as R_3 , R_4 longer than R_{2+3+4} ; distance between tips of R_1 and R_3 longer than R_3 ; M_3 2 times longer than d-cell, m-cu situated beyond half length of d-cell, at level of approximately 0.6 times of d-cell length; d-cell 2 times as long as wide, narrow at base, widened in distal part; anal angle unexpanded; distance between tips of A_1 and A_2 2.5 times longer than distance between tips of Cu and A_1 ; tip of A_2 before Rb bifurcation; tip of A_1 before Rs fork; outer gonostylus elongate, narrow, only slightly longer than inner gonostylus; haltere arrange less than 0.25 times of wing length.

Description.—**Body:** 3.12–3.36 mm long, dark brown (Fig. 3A₁), wing without color pattern, pterostigma absent, haltere slightly elongate (Fig. 3A₂).

Head: 0.24 mm wide (Fig. 3A₁); antennae elongate (Figs. 3A₁, A₆, 4A₄) scape narrower at the base, slightly widened distal; pedicel 2 times as long as wide, in the middle of the pedicel there are single, relatively short setae; flagellomeres very narrow, thin, elongate. Antenna 3.61–4.23 mm long: scape 0.09–0.10 mm long; pedicel 0.10 mm long; flagellomeres: 1, 0.14–0.21 mm; 2, 0.27–0.32 mm; 3, 0.28–0.32 mm; 4, 0.28–0.34 mm; 5, 0.28–0.34 mm; 6, 0.28–0.34 mm; 7, 0.28–0.35 mm; 8, 0.28–0.37 mm; 9, 0.28–0.36 mm; 10, 0.26–0.32 mm; 11, 0.25–0.28 mm; 12, 0.25–0.26 mm; 13, 0.22–0.17 mm; 14, 0.05–0.07 mm. Palpus (Figs. 3A₁, A₅, 4A₂) 0.32–0.47 mm long (1, 0.05–0.11 mm; 2, 0.08 mm; 3, 0.08–0.11 mm; 4, 0.11–0.17 mm); palpomeres elongate; the last palpomere 2 times as long as penultimate one, 6 times as long as wide, other palpomeres 2 times as long as wide; on each palpomeres several setae of varying length, 1.5–3 times longer than the width of the segment on which they occur.

Thorax: Wing 3.23–3.50 mm long, 0.79–0.91 mm wide, 3.5 times as long as wide (Figs. 3A₁, A₇, 4A₁); crossvein (h) positioned at 0.2 times the length of the wing from its base; crossvein sc-r terminating 2 times its own length from the tip of Sc; the distance between tips of Sc and R_1 2.5 times longer than the tips of R_1 and R_3 ; M_{1+2} over 2 times longer than d-cell; M_4 short, slightly longer than d-cell; Mb 3 times as long as M_3 ; Cu from the point of connection with crossvein m-cu to the edge of wing straight; A_1 slightly bent at the edge of the wing; A_2 sinusoidal. The distance between the tips of M_{1+2} and M_3 shorter than the distance between the tips of M_3 and M_4 ; the distance between the tips of M_3 and M_4 and the tips of M_4 and Cu, and the distance between the tips of M_4 and Cu and also the tips of Cu and A_1 comparable; the distance between the tips of A_1 and A_2 slightly longer than the distance between the tips of M_4 and A_1 ; A_1 almost straight, A_2 slightly sinusoidal.

Haltere: 0.48–0.53 mm long, stern long, narrow 2 times as long as knob (Fig. 3A₂).

Hypopygium: 0.63 mm long, gonocoxites very elongate, rather narrow, outer gonostylus elongate, narrow, inner gonostylus slightly widened at the base, narrowed distally, numerous setae on the outer and inner gonostylus (Figs. 3A₁, A₃–A₅, 4A₃).

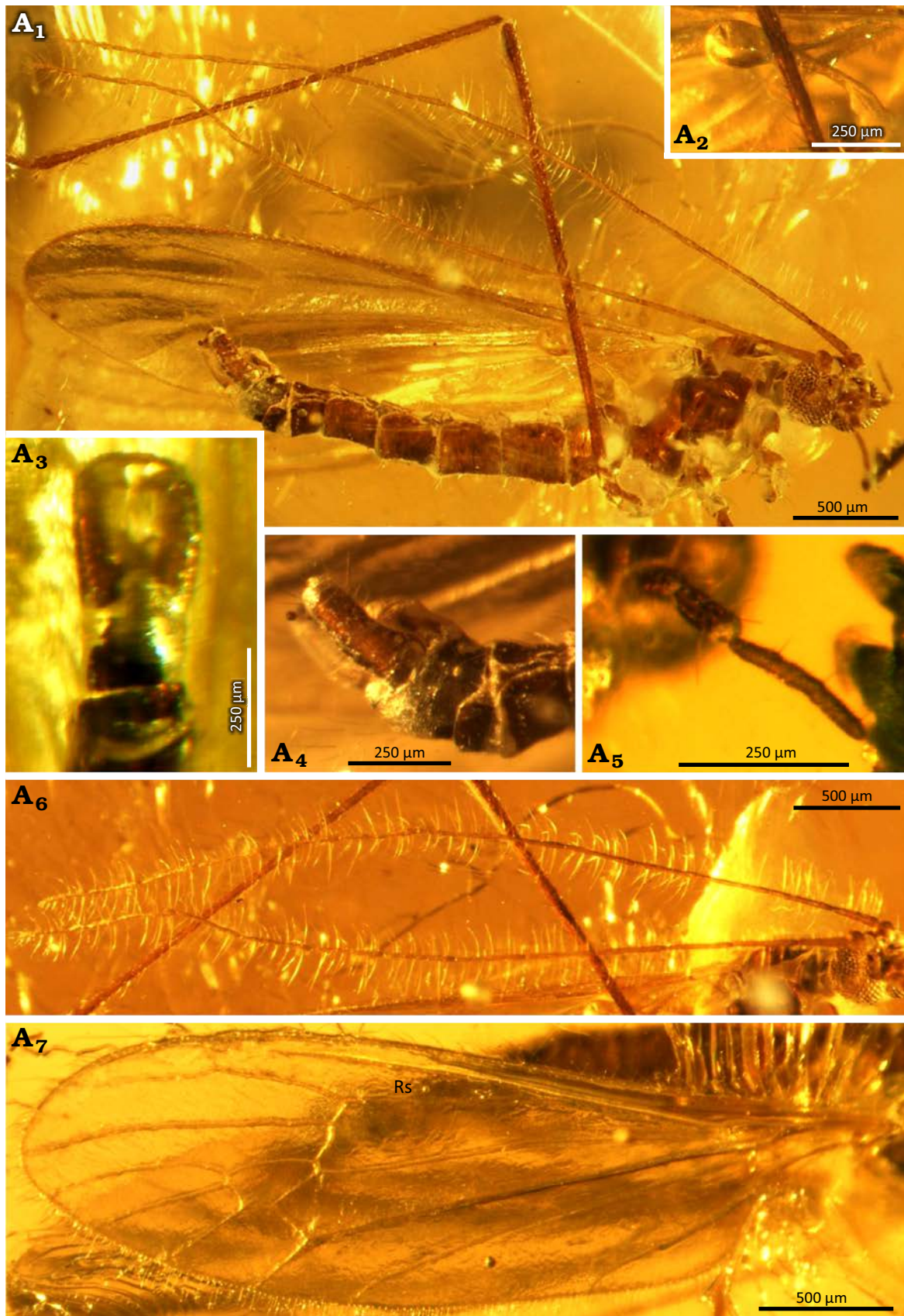


Fig. 3. Limoniid dipteran *Rhabdomastix* (*Rhabdomastix*) *setosa* sp. nov., holotype (male) SDEI CCHH 1462-2 from Baltic amber, 47.8–41.3 Ma, Lutetian. Body in lateral view (A₁), haltere in ventral view (A₂), hypopygium in ventral (A₃) and lateral (A₄) views, palpus in latero-ventral view (A₅), antenna in lateral view (A₆), wing (A₇). Abbreviation: Rs, radial sector.

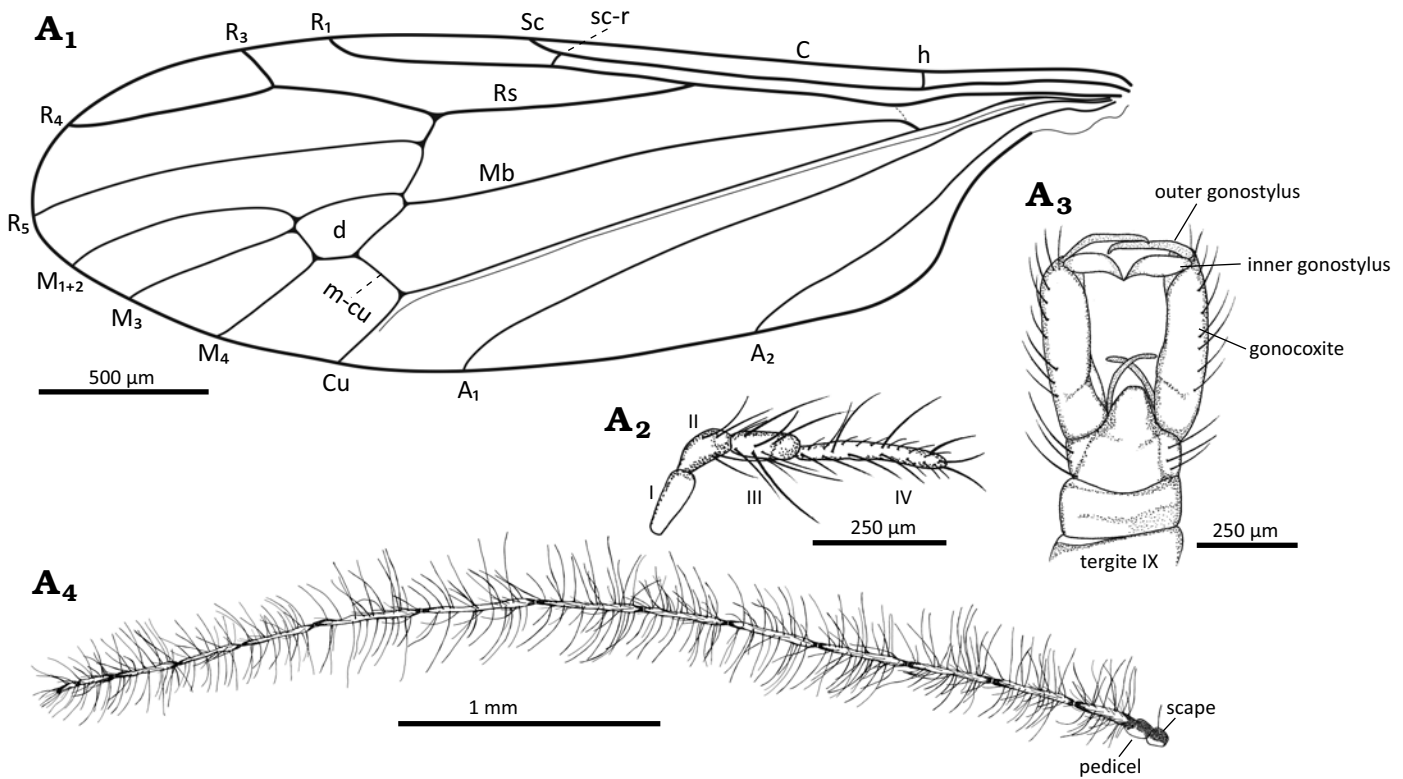


Fig. 4. Limoniid dipteran *Rhabdomastix* (*Rhabdomastix*) *setosa* sp. nov., holotype (male) SDEI CCHH 1462-2 from Baltic amber, 47.8–41.3 Ma, Lutetian. Wing venation (A₁), palpus (A₂), hypopygium in ventral view (A₃), and antenna (A₄). Abbreviations: A₁, A₂, anal veins; C, costal vein; Cu, cubital vein; d, discal cell; h, humeral vein; I–IV, palpomeres 1–4; M₁₊₂ to M₄, medial veins; Mb, medial-basal vein; m-cu, medial-cubital crossvein; R₁–R₅, radial veins; Rs, radial sector; sc-r, subcostal radial crossvein.

Remarks.—The features which allow to include the species within the subgenus *Rhabdomastix* are: elongate antennae, longer than body length, crossvein well developed, d-cell hexagonal, distal part of M₁₊₂ and M₃ arched, outer gonostylus longer than inner gonostylus.

The antennae in *Rhabdomastix* (*R.*) *setosa* sp. nov. are longer than the body length. Antennae longer than the body length also occur in the following species: *Rhabdomastix* (*R.*) *grussica* Podenas, 2006 comb. nov., *Rhabdomastix* (*R.*) *mastix* Podenas, 2006 comb. nov., *Rhabdomastix* (*R.*) *rafali* sp. nov., *Rhabdomastix* (*R.*) *setix* Podenas, 2006 comb. nov., and *Rhabdomastix* (*R.*) *woottoni* sp. nov. In other species known from Cenozoic resins, belonging to the subgenus *Rhabdomastix*, the antennae are shorter than the body length. In *R. (R.) woottoni* sp. nov. antennae are 1.5 times as long as the body and are very narrow, flagellomeres are very elongate with numerous, short setae. In *R. (R.) setosa* sp. nov. antenna are not so elongate, flagellomeres are much shorter than their length, only 7 times as long as wide. The setae on each flagellomere are much longer and more dense. Moreover, the *R. (R.) setosa* sp. nov. differs from other Cenozoic species within the subgenus *Rhabdomastix* in its wing venation and morphology of the hypopygium. Unlike the *R. (R.) grussica* Podenas, 2006 comb. nov., setae occur on the antennae constitute even more than half the length of the segment bearing them, in *R. (R.) grussica* Podenas, 2006 comb. nov. they are never longer than half the length of the

flagellomeres bearing them. The d-cell in *R. (R.) setosa* sp. nov. is small, 1.5 times as long as wide, vein M₃ is 2 times as long as the d-cell. In *R. (R.) grussica* Podenas, 2006 comb. nov. d-cell is 2 times as long as wide, vein M₃ is only slightly longer (1.5 times). In *R. (R.) mastix* Podenas, 2006 comb. nov. the setae are shorter than half the length of the flagellomeres on which they occur, d-cell is 2 times as long as wide. Vein Sc in *R. (R.) mastix* Podenas, 2006 comb. nov. is very short, ending before half the length of Rs, while in *R. (R.) setosa* sp. nov. this vein ending just beyond half the length of Rs, measured from the fork of Rb. In contrast to *R. (R.) setix* Podenas, 2006 comb. nov. in *R. (R.) setosa* sp. nov. crossvein m-cu is situated beyond half the length of the d-cell, measured from the fork of Mb, R₃ is shorter than the distance between the tips of R₁ and R₃, almost straight vein R₄ is 4 times as long as R₃. *R. (R.) setix* Podenas, 2006 comb. nov. crossvein m-cu is situated beyond half the length of d-cell, R₃ is shorter than the distance between the tips of R₁ and R₃, almost straight vein R₄ is 4 times as long as R₃. In *R. (R.) setix* Podenas, 2006 comb. nov. m-cu situated before d-cell, R₃ is longer than the distance between the tips of R₁ and R₃, R₄ is arched and is only 3 times longer than R₃. Moreover, in a species described from the Eocene of the Green River, USA *Rhabdomastix scudderi* vein Sc is very elongate, ending just before the bifurcation of Rs, tip of vein A₂ is just before the bifurcation of Rs, while in *R. (R.) setosa* sp. nov. Sc ending just beyond half the length of Rs, and vein A₂ terminating before fork of Rb.

Stratigraphic and geographic range.—Baltic amber is dated by some authors to middle Eocene age (Lutetian Stage; 47.8–41.3 Ma) (Wolfe et al. 2016), but the age range of this fossil resin is still under debate, dated by Grimaldi and Ross (2017) as Priabonian, based on pollen, spores and phytoplankton of the amber-bearing layer, the Blue Earth. The specimen was collected at the Baltic area, the Blue Earth (Blaue Erde) (Wolfe et al. 2016).

Rhabdomastix (Rhabdomastix) woottoni sp. nov.

Figs. 5, 6.

ZooBank LSID: lsid:zoobank.org:act:92A02AC5-1693-4BC0-AB01-CBE1560931CD

Etymology: Dedicated to the outstanding invertebrate researcher, Robin J. Wootton (Department of Biological Sciences, University of Exeter, UK).

Holotype: GMUG 80, male, the specimen is poorly preserved, the head is not well visible, partially damaged. (coll. Manfred Kutscher).

Type locality: Bitterfeld, Upper Saxony (Sachsen-Anhalt), Germany.

Type horizon: Cottbus Formation, “Glimmersand”, middle–upper Eocene.

Material.—Holotype only.

Diagnosis.—Antennae very elongate, thin, much longer than body, 1.5 times longer; almost black, small spots usually present at base and distal part of flagellomeres, longer than wing; flagellomeres very narrow, significantly elongate, length of flagellomeres 1–3 corresponding to approximately 5 times (first flagellomere) or 6 times (second and third flagellomere) width of each of them, with numerous short setae, flagellomeres 4–9 elongate, corresponding to approximately 26 times their width, flagellomeres 10–14 shorter than others, length of last segment corresponds to half of penultimate one and 3 times its width, the setae of flagellomeres 4–9 very few and short, much shorter than length of segment on which they occur; tip of Sc beyond half length of wing, beyond half of Rs; Rs shorter than R_{2+3+4} and R_4 combined by about 0.2 times of its length; tip of R_1 opposite half of d-cell, opposite approximately half length of R_{2+3+4} ; length of R_4 4 times length of R_3 , R_4 only slightly shorter than R_{2+3+4} ; distance between tip of R_1 and R_3 longer than R_3 ; M_3 1.5 times longer than d-cell; m-cu just behind half of d-cell; d-cell length corresponding to 1.5 times its width, only slightly narrowed at base, slightly widened in distal part; anal angle expanded; distance between the tips of A_1 and A_2 corresponds to almost 5 times distance between tips of Cu and A_1 ; tip of A_2 before Rb fork; tip of A_1 beyond Rs fork; outer gonostylus elongate, narrow, sharply tipped, with one thick setae in apical part, only slightly longer than inner gonostylus, pointed at the end, with two thick setae at the end; haltere less than 0.25 times of wing length.

Description.—*Body:* 2.54 mm long, dark brown, wing without color pattern, pterostigma absent, haltere significantly elongate.

Head: 0.35 mm wide (Fig. 5A₄); antenna elongate (Figs. 5A₁, A₃, 6A₁–A₄), very thin, scape pear-shaped, elongate,

longer than its width, significantly expanded distally; pedicel short and very wide, wider than its length, a few elongate setae in the distal part of the scape and pedicel; the last flagellomere bluntly ended with two setae on the tip; antenna 4.40 mm long; scape 0.12 mm long; pedicel 0.09 mm long; flagellomeres: 1/0.22 mm; 2/0.27 mm; 3/0.36 mm; 4/0.46 mm; 5/0.45 mm; 6/0.45 mm; 7/0.41 mm; 8/0.41 mm; 9/0.40 mm; 10/0.36 mm; 11/0.17 mm; 12/0.09 mm; 13/0.08 mm; 14/0.06 mm; palpus (Fig. 6A₆) 0.55 mm long (1/0.09 mm; 2/0.11 mm; 3/0.13 mm; 4/0.22 mm); palpomeres narrow and elongate, first and second palpomere of comparable length, approximately 2 times as long as wide, slightly expanded distally, the third palpomere longer than the first and the second but shorter than the last one, third palpomere 4 times as long as wide, the last palpomere 6 times as long as wide; each palpomeres with a few setae, slightly longer than the width of segments bearing them and much shorter than the length of the segments on which they occur.

Thorax: Wing 4.45 mm long, 1.52 mm wide, almost 3 times as long as wide (Figs. 5A₂, 6A₅); crossvein (h) positioned at the distance of 0.1 times of the length of the wing, measured from its base; crossvein sc-r occurs at the distance from the tip of the vein Sc corresponding to 3 times of its length; the distance between the tips of Sc and R_1 slightly longer than the distance between the tips of R_1 and R_3 ; R_3 short, shorter than half the distance between the tips of R_1 and R_3 ; M_{1+2} more than 2 times as long as the d-cell; M_4 short, as long as d-cell; Mb 3 times as long as M_3 ; the section of the Cu from the point of connection of the Cu with crossvein m-cu to the edge of the wing almost straight; the distance between the tips of M_{1+2} and M_3 shorter than the distance between the tips of M_3 and M_4 ; distances between the tips of M_3 and M_4 and the tips of M_4 and Cu comparable; the distance between the tips of M_4 and Cu 0.3 times longer than the distance between the tips of Cu and A_1 ; the distance between the tips of A_1 and A_2 2 times longer than the distance between the tips of M_4 and A_1 ; A_1 slightly curved, A_2 sinusoidal.

Haltere: 0.57 mm long, stem massive, only slightly longer than knob.

Hypopygium: 0.84 mm long, gonocoxites massive, elongate 2 times as long as wide with numerous long and thick setae (Figs. 5A₅, 6A₇, A₈).

Remarks.—The features which allow to include the species within the subgenus *Rhabdomastix* are: elongate antennae, much longer than body length, crossvein well developed, d-cell hexagonal, distal part of M_{1+2} and M_3 arched, outer gonostylus longer than inner gonostylus.

Rhabdomastix (R.) woottoni sp. nov. differs from the other species belonging to the subgenus *Rhabdomastix* represented in Cenozoic fossil resins by the proportions of the length of the antennae in relation to the length of the body. The antennae of this species are much longer than the body, about half its length, very elongate and thin. The individual flagellomeres are very elongate and narrow, the scape and pedicel are wide, massive, much wider than the other

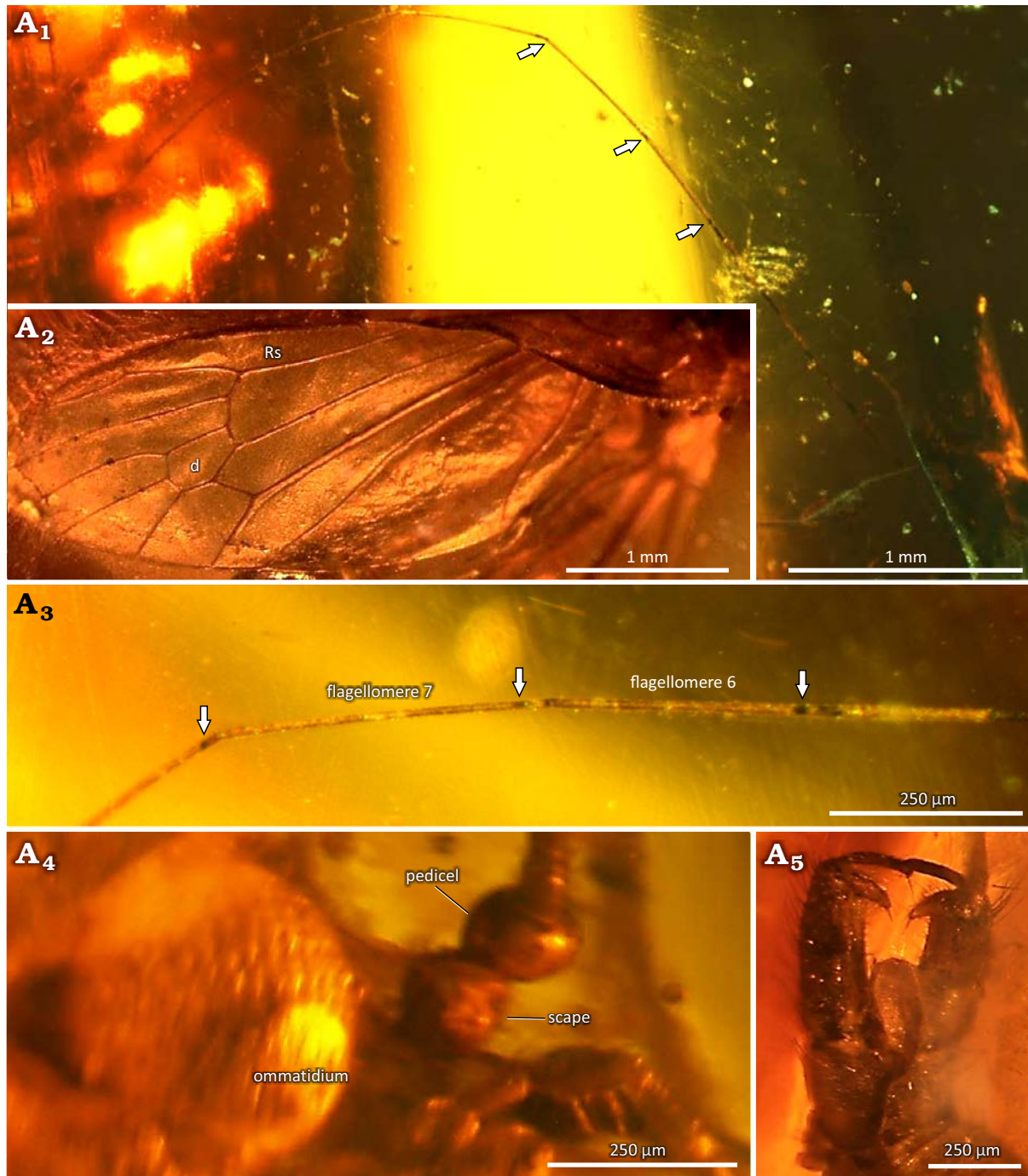


Fig. 5. Limoniid dipteran *Rhabdomastix (Rhabdomastix) woottoni* sp. nov., holotype (male) GMUG 80 from Bitterfeld amber, middle–upper Eocene. Antenna (A₁), wing (A₂), middle flagellomeres (A₃), head detail in lateral view (A₄), hypopygium in ventral view (A₅). Arrows indicate dark spots on flagellomeres. Abbreviations: d, discal cell; Rs, radial sector.

flagellomeres. In addition, there are single, clear, almost black color spots on the antenna and relatively short, sparse setae. So far, no fossil species of the *Rhabdomastix* genus have had this type of antennae. In other species belonging to the subgenus *Rhabdomastix*, represented in Cenozoic fossil resins, no color spots are observed on flagellomeres, the setae of this part of the body are more pronounced, usually numerous and more elongate. The shape of the scape and pedicel are also slightly different in the remaining

species within the subgenus *Rhabdomastix* represented in Cenozoic fossil resins, they are not so massive in relation to the flagellomeres, unlike in *R. (R.) woottoni* sp. nov. Moreover, *R. (R.) woottoni* sp. nov. differs from the species described from Eocene sediments from Green River, USA *R. scudderi* in the wing venation. Vein Sc in *R. scudderi* is very elongate, ending just before the Rs fork, and the vein A₂ achieves the edge of the wing just before the Rs fork, while in *R. (R.) woottoni* sp. nov. it is much shorter, ended

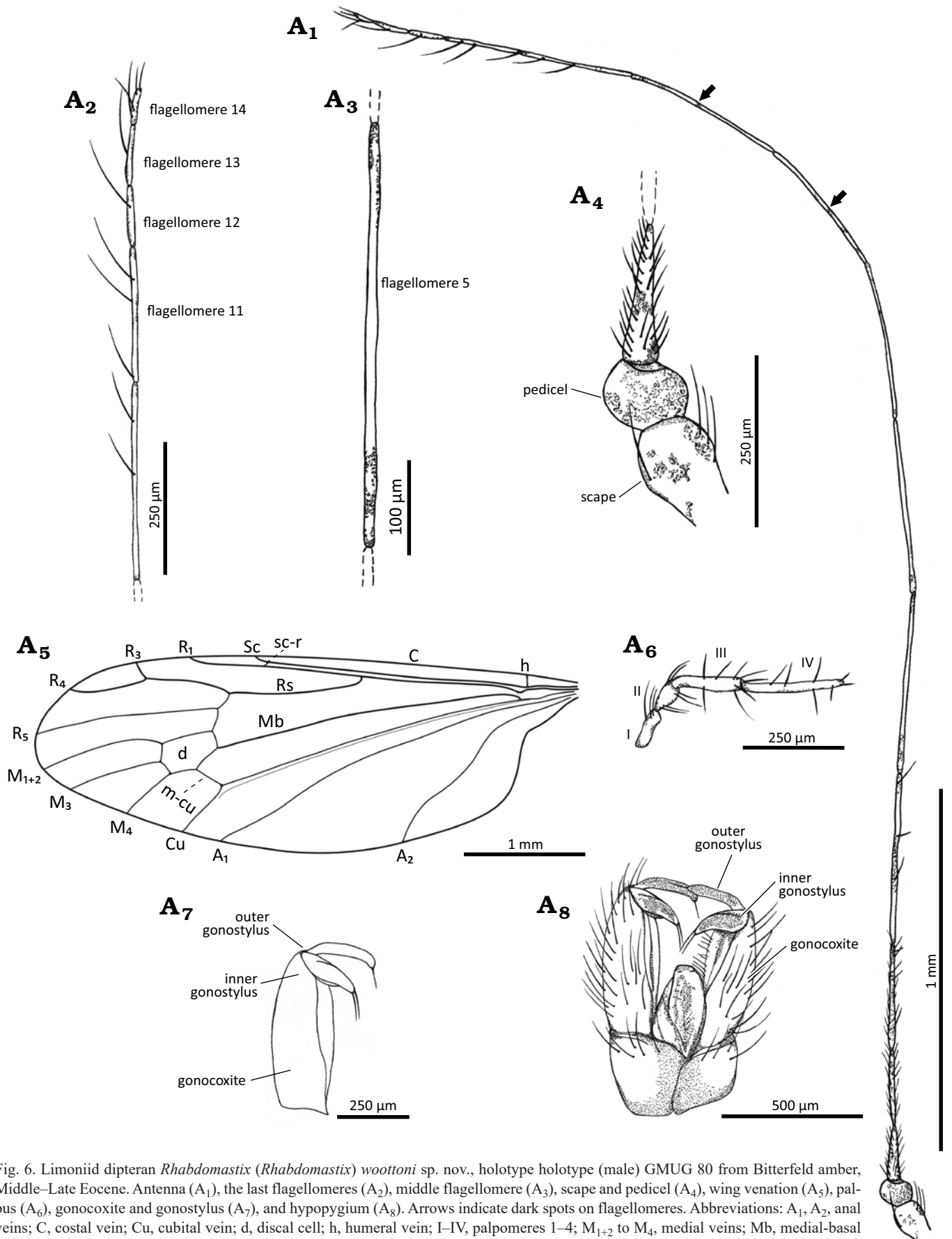


Fig. 6. Limoniid dipteran *Rhabdomastix (Rhabdomastix) woottoni* sp. nov., holotype holotype (male) GMUG 80 from Bitterfeld amber, Middle–Late Eocene. Antenna (A₁), the last flagellomeres (A₂), middle flagellomere (A₃), scape and pedicel (A₄), wing venation (A₅), palpus (A₆), gonocoxite and gonostylus (A₇), and hypopygium (A₈). Arrows indicate dark spots on flagellomeres. Abbreviations: A₁, A₂, anal veins; C, costal vein; Cu, cubital vein; d, discal cell; h, humeral vein; I–IV, palpomeres 1–4; M₁₊₂ to M₄, medial veins; Mb, medial-basal vein; m-cu, medial-cubital crossvein; R₁–R₅, radial veins; Rs, radial sector; sc-r, subcostal radial crossvein.

in half the length of Rs, and the end of the A₂ vein is situated far before the fork of Rb, measured from the base of the wing.

Stratigraphic and geographic range.—Bitterfeld amber is believed to be approximately the same age as Baltic amber (Szwedo and Sontag 2013), but it came probably from distinct ecosystems. Bitterfeld amber belongs to the same group of ambers as Baltic amber, with an age similar to that of Baltic amber, as indicated by the dipteran species similarity preserved in these fossil resins. The similarity of the species preserved as an inclusions in this fossil resin contradicts the large age difference of these fossil resins. The differences found seem to reflect differences ecological conditions, not age (Standtke 2008). Some recent geochronological efforts (Knuth et al. 2002; Blumenstengel 2004) date deposits of Bitterfeld amber as the late Oligocene (Chattian; 23.0–28.1 Ma), some authors date the deposits of this fossil resin as Early Miocene (e.g., Barthel and Hetzer 1982; Rikkinen and Poinar 2000). But, some have argued that Bitterfeld amber being merely a younger redeposited fraction of primary Eocene Baltic amber (Szwedo and Sontag 2013; Wolfe et al. 2016), the resin can be dated on middle–late Eocene (Drohojowska et al. 2024). The specimen was collected at the Cottbus Formation near the town of Bitterfeld in Upper Saxony (Sachsen-Anhalt) (Wolfe et al. 2016).

Some species were previously described by Podenas (2006) and have not been classified into any of the subgenera. Features such as the complete atrophy of r-r (R₂), presence of sc-r, the bifurcation of Rb before half the length of the wing, the presence of small, hexagonal d-cell shorter than the length of the vein M₃, a clearly arched distal part of part M₁₊₂ and M₃, and the inner gonostylus shorter than the outer gonostylus, allow the following three species: *Rhabdomastix (R.) grussica* Podenas, 2006 comb. nov., *Rhabdomastix (R.) setix* Podenas, 2006 comb. nov., *Rhabdomastix (R.) mastix* Podenas, 2006 comb. nov., all from the Baltic amber, to be included into the subgenus *Rhabdomastix*.

Rhabdomastix (Rhabdomastix) grussica Podenas, 2006 comb. nov.

2006 *Rhabdomastix* (?) *grussica*; Podenas 2006: 46.

Remarks.—The species is characterized by elongate antennae, elongate flagellomeres with numerous setae and a very small apical segment, antennae longer than the body and wings. The wings of this species are typical for the genus. Hypopygium is characterized by straight elongated gonocoxites and long, slender outer gonostylus, many setae occur on inner gonostylus, interbase are long, with a straight aedeus ending before tip of interbase and by slightly extended at mid-posterior margin ninth sternite (after Podenas 2006).

Rhabdomastix (Rhabdomastix) setix Podenas, 2006 comb. nov.

2006 *Rhabdomastix* (?) *setix*; Podenas 2006: 50.

Remarks.—The species is characterized by long antennae, longer than the body, with many long setae and a small apical segment, much smaller than the previous one. The wings are typical for the genus. Hypopygium of this species is characterized by long, slender bare outer gonostylus, without apical spine, fleshy inner gonostylus with straight posterior margin and slightly curved apex (after Podenas 2006).

Rhabdomastix (Rhabdomastix) mastix Podenas, 2006 comb. nov.

Figs. 7, 8.

2006 *Rhabdomastix* (?) *mastix* sp. nov.; Podenas 2006: 47, figs. 27–30.

Material.—ISEA PAS MP/3321, female from Baltic amber, Lutetian, middle Eocene, 47.9–41.3 Ma.

Emended diagnosis.—Antennae longer than body, shorter than wings, without color pattern; flagellomeres 1–13 narrow of length corresponding to approximately 7 times their width, last flagellomere approximately 0.3 times shorter than penultimate one; setae shorter than flagellomeres bearing them, densely spaced; Sc terminating before half length of wing, opposite 0.3 times of Rs; Rs shorter than R₂₊₃₊₄ and R₄ combined, approximately 0.2 times of its length; R₁ terminating opposite end of d-cell, opposite of 0.8 times of R₃₊₄; length of R₄ corresponds to 4 times length of R₃; R₄ longer than R₂₊₃₊₄ by about 0.2 times of its length; distance between tips of R₁ and R₃ longer than R₃; M₃ 1.5 times longer than d-cell; m-cu situated in the middle of length of d-cell, d-cell length corresponding to 2 times its width, narrow at base, extended in the distal part; anal angle unexpanded; distance between tips of A₁ and A₂ correspond to almost 2.5 times distance between tips of Cu and A₁; tip of A₂ before Rb fork; A₁ before Rs fork; posterior edge of outer gonostylus serrated; haltere elongate, as long as 0.2 times wing length.

Description.—*Body*: 3.39 mm long, brown (Fig. 7A₁), wing without color pattern, pterostigma absent, haltere significantly elongate (Fig. 7A₂).

Head: 0.30 mm wide (Fig. 7A₁); antenna with cylindrical scape, narrowed at the base, slightly wider in the distal part (Figs. 7A₁, 8A₂), scape and pedicel slightly longer than their width; pedicel with a few setae; flagellomeres 1–13 of comparable length; the last flagellomere with two setae at the tip, penultimate one 3 times longer than last one; setae on flagellomeres 3–15 longer than the width of the flagellomeres bearing them, shorter than half the length of these segments; antenna 1.09 mm long: scape 0.06 mm; pedicel 0.09 mm; flagellomeres: 1, 0.07 mm; 2, 0.07 mm; 3, 0.07 mm; 4, 0.07 mm; 5, 0.07 mm; 6, 0.07 mm; 7, 0.07 mm; 8, 0.07 mm; 9, 0.07 mm; 10, 0.07 mm; 11, 0.07 mm; 12, 0.07 mm; 13, 0.07 mm; 14, 0.03 mm).

Palpus: 0.36 mm long (1, 0.06 mm; 2, 0.08 mm; 3, 0.08 mm; 4, 0.14 mm, Figs 7A₁, 8A₃), palpomeres elongate, palpomeres 1–3 of comparable length, the last palpomere 2 times longer than penultimate one; first palpomere 3 times



Fig. 7. Limoniid dipteran *Rhabdomastix (Rhabdomastix) mastix* Podenas, 2006 comb. nov., (female) ISEA PAS MP/3321 from Baltic amber, 47.8–41.3 Ma, Lutetian. Body in latero-dorsal view (A₁), haltere in lateral view (A₂), ovipositor in lateral view (A₃).

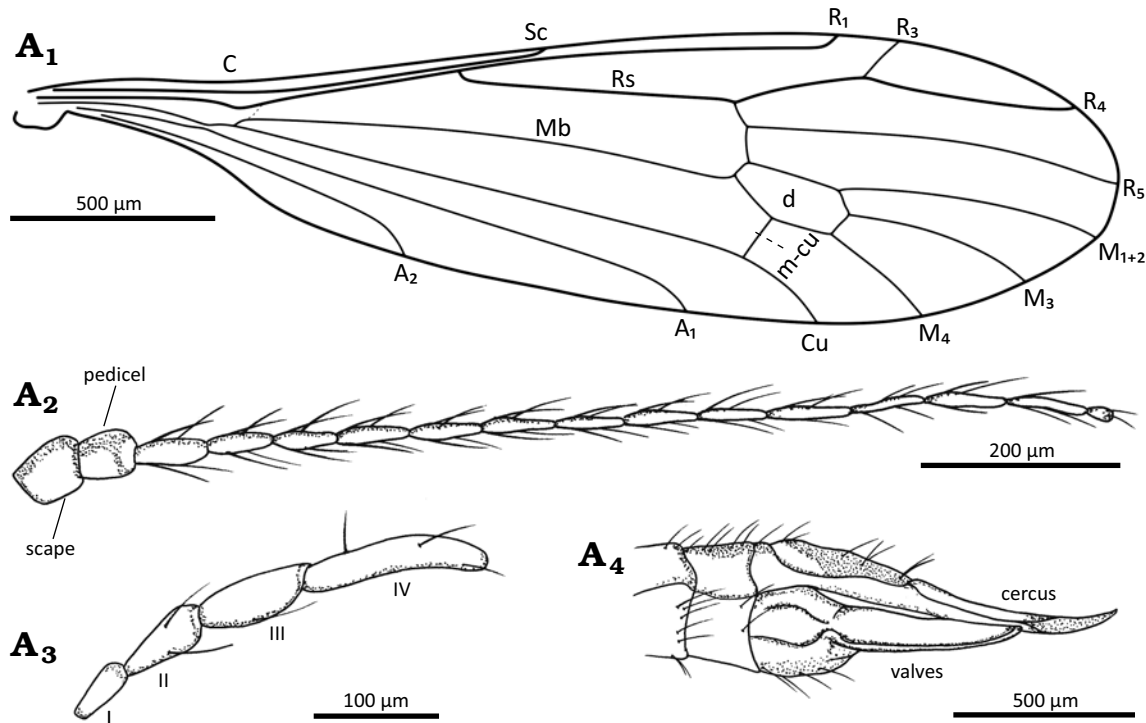


Fig. 8. Limoniid dipteran *Rhabdomastix (Rhabdomastix) mastix* Podenas, 2006 comb. nov., (female) ISEA PAS MP/3321 from Baltic amber, 47.8–41.3 Ma, Lutetian. Wing venation (A₁), antenna (A₂), palpus in lateral view (A₃), ovipositor in lateral view (A₄). Abbreviations: A₁, A₂, anal veins; C, costal vein; Cu, cubital vein; d, discal cell; I–IV, flagellomeres 1–4; M₁₊₂ to M₄, medial veins; Mb, medial-basal vein; m-cu, medial-cubital crossvein; R₁–R₅, radial veins; Rs, radial sector; Sc, subcostal vein; sc-r, subcostal radial crossvein.

as long as wide, second palpomere 2 times as long as wide, third palpomere 2.5 times as long as wide; the last palpomere elongate, 5 times as long as wide; each palpomere

with a few elongate setae, longer than wide but shorter than palpomeres bearing them.

Thorax: Wing 3.91 mm long, 0.79 mm wide, 3.5 times as

long as wide (Figs. 7A₁, 8A₁); the distance between tips of Sc and R₁ 5 times longer than the distance between the tips of R₁ and R₃; R₃ short, slightly shorter than the distance between the tips of R₁ and R₃; M₁₊₂ almost 2 times longer than length of d-cell; vein Mb approximately 2.5 times longer than the M₃; Cu from the point of connection with crossvein m-cu to the edge of wing slightly curved; the distance between the tips of M₁₊₂ and M₃ shorter than 0.25 times of its length, shorter than the distance between the tips of M₃ and M₄; the distance between the tips of M₃ and M₄ slightly longer than the distance between the tips of M₄ and Cu; the distance between the tips M₄ and Cu and the tips Cu and A₁ comparable length; the distance between the tips of A₁ and A₂ longer than 0.2 times the distance between the tips of M₄ and A₁; A₁ and A₂ almost straight.

Haltere: 0.60 mm long, stern narrow, 2 times longer than knob (Fig. 7A₂).

Ovipositor: 1.13 mm long, strongly sclerotized; cerci elongate, narrow and sharply ended; valves relatively short, narrow, 5 times as long as wide (Figs. 7A₁, A₃, 8A₄).

Remarks.—Characters of wing morphology (female wing venation is almost identical compared to the male's wing venation), as well as the ratio of the length of the haltere to the length of the wings of the first pair allowed to classify female as *Rhabdomastix (R.) mastix* Podenas, 2006 comb. nov. In the female, just like in the male, the halteres constitutes 0.25 times of the length of the wings and are very elongate.

In contrast to the other species within the subgenus *Rhabdomastix* represented in Cenozoic fossil resins in *R. (R.) mastix* Podenas, 2006 comb. nov. the haltere is as much as 0.25 times of the length of the wing, in other species haltere is shorter than 0.25 times of the wing length.

Stratigraphic and geographic range.—Baltic amber is dated by some authors to middle Eocene age (Lutetian Stage; 47.8–41.3 Ma) (Wolfe et al. 2016), but the age range of this fossil resin is still under discussion, dated by Grimaldi and Ross (2017) as Priabonian, based on pollen, spores and phy-

toplankton of the amber-bearing layer, the so-called Blue Earth. The specimen was collected at the Baltic area, the Blue Earth (Blaue Erde) (Wolfe et al. 2016).

Discussion

The internal classification system of the genus *Rhabdomastix* used by Alexander (1931), Savchenko (1976), Savchenko et al. (1992) and Krzemiński (2004) was based on differences related mainly to the proportion of the length of male antennae to the length of the body. It included three subgenera: *Rhabdomastix* sensu stricto, with antennae two to three times longer than the body, *Paleogonomyia* Meunier, 1899, with antennae reaching the length of the body or half of its length, and *Sacandaga* Alexander, 1911, where the antennae were much shorter than the body length.

According to results of the latest analysis of the genus *Rhabdomastix* the latter is divided into three subgenera, two of them represented in fossil and recent fauna: *Lurdia* Starý, 2003, *Rhabdomastix* Skuse, 1890, and one known only from the fossil record, i.e., *Myanmamastix* Kania et al., 2021, from the Cretaceous of Myanmar. Moreover, Starý (2003) distinguished two morphological groups of species “*Rhabdomastix caudata*” and “*Rhabdomastix illudens*” without including them into any of the subgenera. The “*Rhabdomastix caudata*” group is centred around the species of *Rhabdomastix caudata* Lundbeck, 1898, with six representatives recovered from Nearctic region: *Rhabdomastix leptodoma* Alexander, 1943, *Rhabdomastix monticola* Alexander, 1916, *Rhabdomastix subarctica* Alexander, 1933, *Rhabdomastix subcaudata* Alexander, 1927a, one Westpalaeartic species *Rhabdomastix parva* Siebke, 1863 and known from the fossil record *Rhabdomastix hoffeinsi* Jordan-Stasiło et al., 2023. All these species are characterized by more or less developed crossvein r-r (R₂) (Starý 2003; Oosterbroek et al. 2007; Jordan-Stasiło et al. 2023).

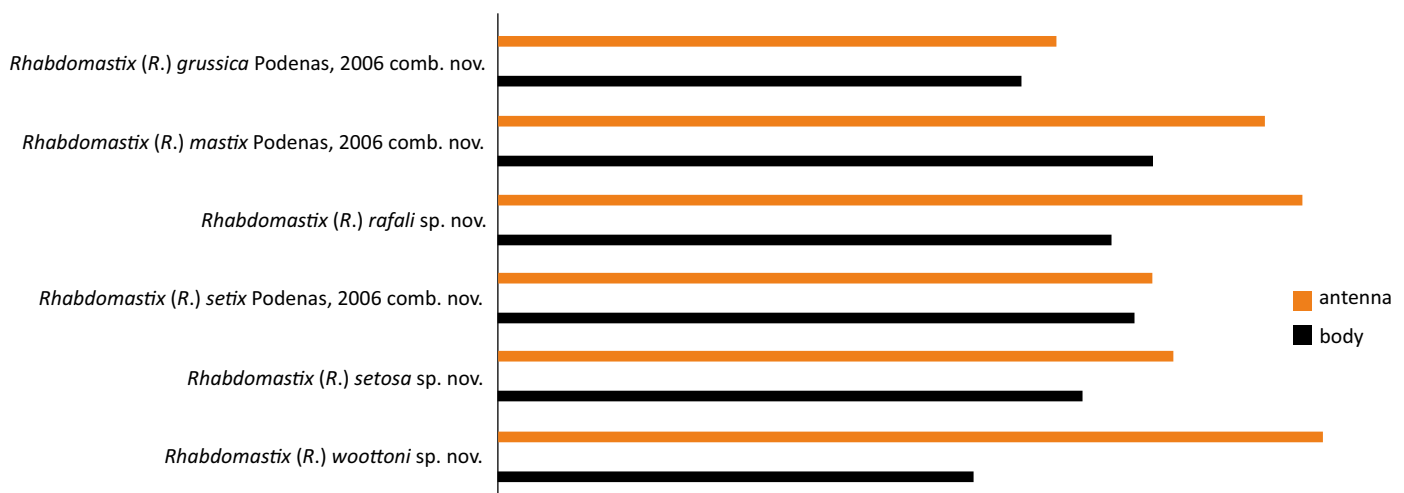


Fig. 9. Diagram showing the ratio of the length of the antennae to the body length of fossil representatives of subgenus *Rhabdomastix* Skuse, 1890, with the antenna longer than body.

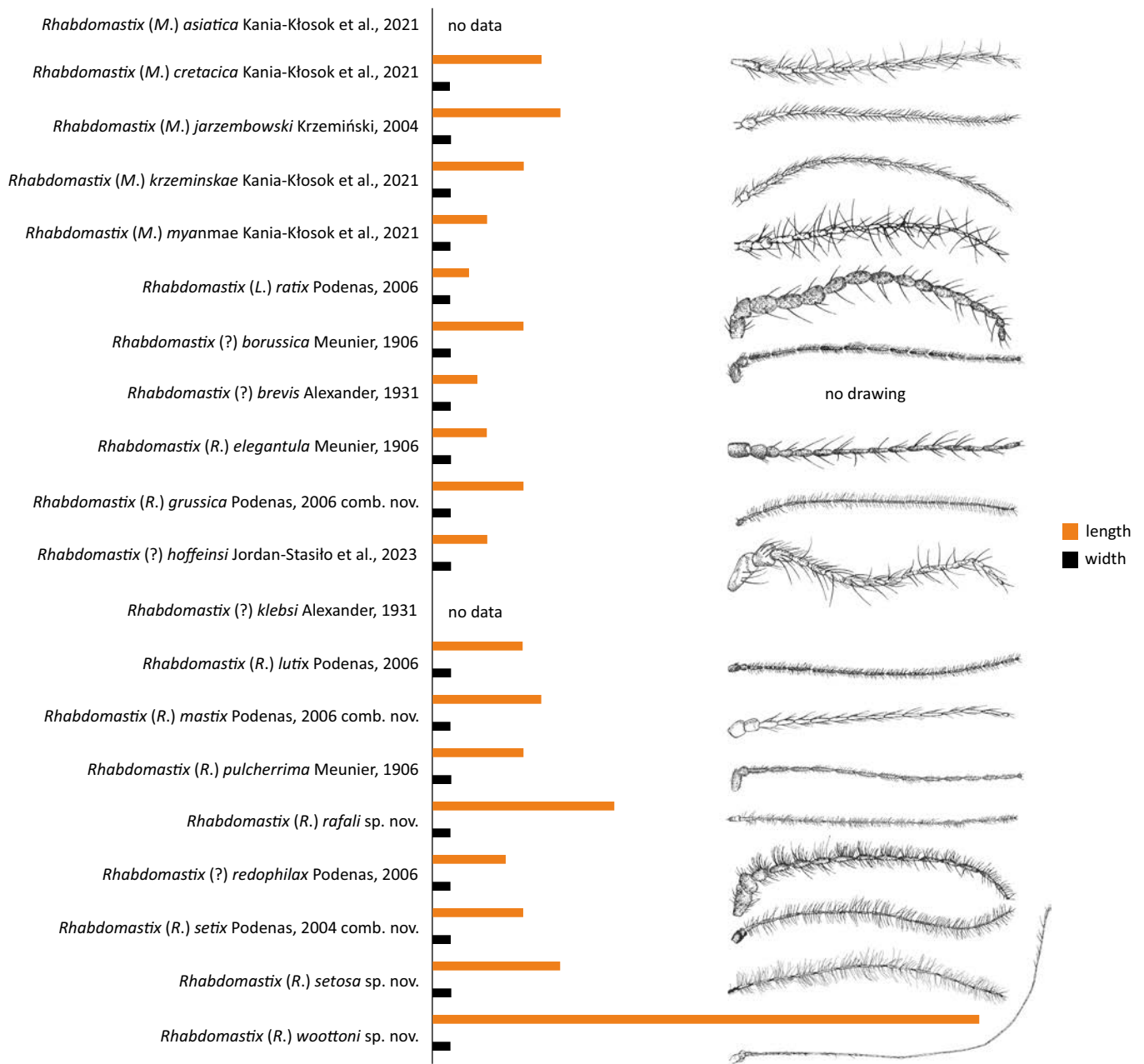


Fig. 10. Diagram showing the ratio of length to width of the flagellar antenna (F10). Antenna of *Rhabdomastix (Rhabdomastix) rafali* sp. nov., reconstructed; antennae of *Rhabdomastix (Rhabdomastix) grussica* Podenas, 2006 comb. nov., *Rhabdomastix (Rhabdomastix) setix* Podenas, 2006 comb. nov., redrawn after Podenas (2006).

The second group is represented by species centered around Neotropical *Rhabdomastix illudens* Alexander, 1914b, from Bolivia. The group comprises 11 Neotropical and Oriental species, and one from the Southern Nearctic, include also some species from Mexico like *Rhabdomastix isabella* Alexander, 1927b, *Rhabdomastix mexicana* Alexander, 1938 and also *Rhabdomastix longiterebrata* Alexander, 1938, from Costa Rica, such as *Rhabdomastix septentrionalis* Alexander, 1914b. Only one species classified to this group is recorded from Nearctic, i.e., *Rhabdomastix nuttingi* Alexander, 1950 from Arizona, USA (Alexander 1914a, b, 1927b, 1938, 1950; Starý 2003). All of these species are

characterized by extremely long male antennae which is three to five times longer than the body and much longer than wings. Scape of these very elongate antennae is enlarged in contrast to small and short pedicel, last flagellomere is longer than the penultimate one. Other differences in body structure, especially differences in wing venation, coloration of the body, trichation of the wings are also well visible, but the most characteristic feature of this group of insects are the proportion of male antennae relative to body and wing length respectively.

Although all species belonging to the group called “*Rhabdomastix illudens*” are classified in the subgenus *Rhab-*

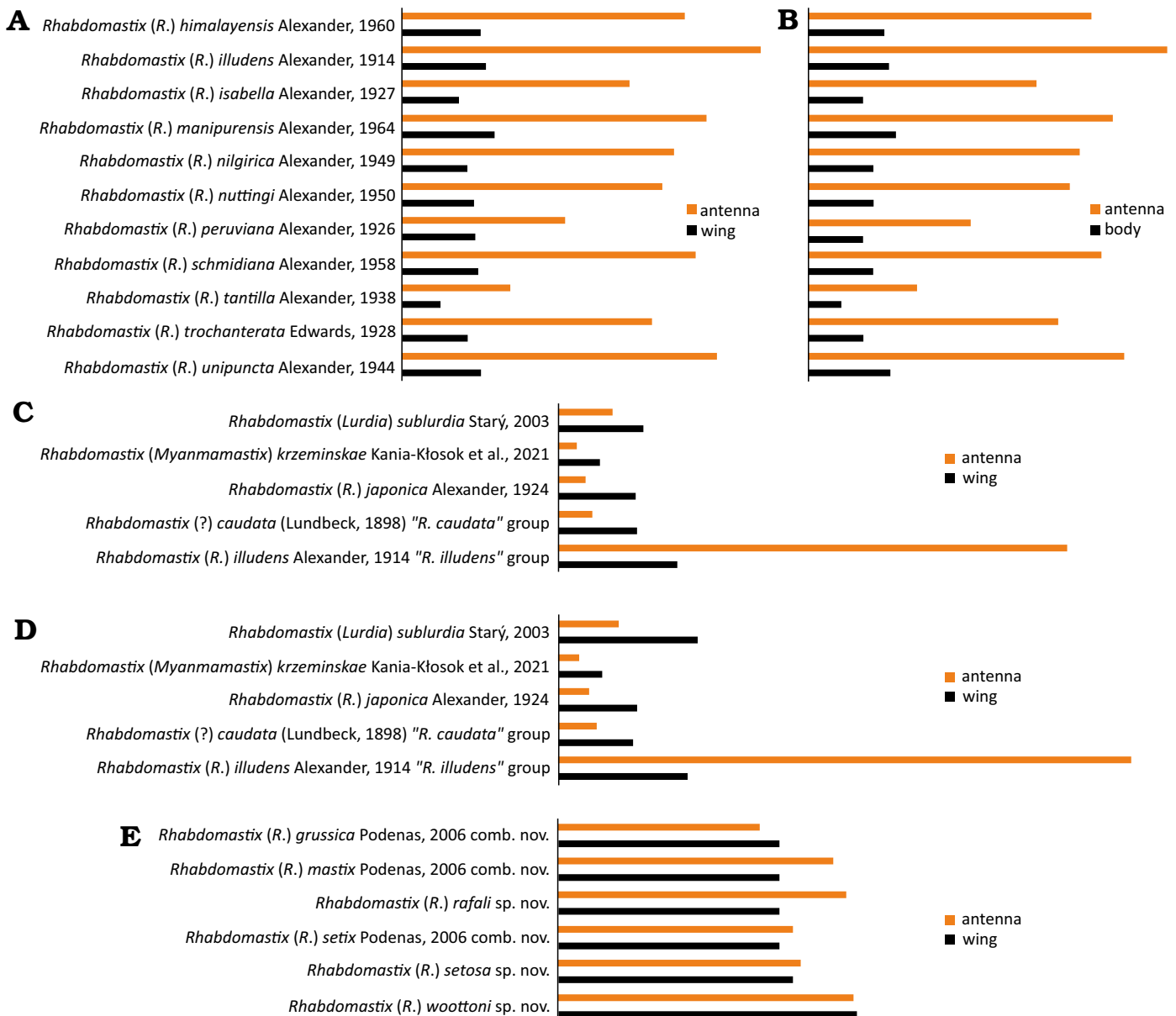


Fig. 11. Diagrams showing the ratio of the length of the antennae to the length of the body (B) and the length of the antennae to the length of the wing (A, C–E) of Recent representatives of the “*Rhabdomastix illudens*” group (A, B); representatives of subgenera and representatives of the groups “*Rhabdomastix caudata*” and “*Rhabdomastix illudens*” (C, D); fossil representatives of the “*Rhabdomastix illudens*” group (E).

domastix sensu stricto, the taxonomic status of this extralimital group still remains unresolved. As Starý (2003) emphasizes, this group is more closely related to *Rhabdomastix* sensu stricto than with the subgenus *Lurdia*. Moreover, it is considered to be a highly apomorphic evolutionary line of *Rhabdomastix* sensu stricto without subgeneric status (Starý 2003).

Starý (2003) proposed the extremely elongate antennae to be an apomorphic feature of the species belonging to “*Rhabdomastix illudens*” group, and we have an evidence that this feature appeared in the evolution of the group already in the Eocene. The antennae of all Cretaceous representatives of the genus *Rhabdomastix* are not so elongate, only slightly longer than the combined length of the head and body.

The species *Rhabdomastix* (*Myanmamastix*) *jarzembowski* Krzemiński, 2004, *Rhabdomastix* (*Myanmamastix*) *asiatica* Kania-Kłosok et al., 2021, *Rhabdomastix* (*Myanmamastix*) *cretacica* Kania-Kłosok et al., 2021, *Rhabdomastix* (*Myanmamastix*) *krzeminskae* Kania-Kłosok et al., 2021, and *Rhabdomastix* (*Myanmamastix*) *myanmae* Kania-Kłosok et al., 2021, belongs to one subgenus (Kania-Kłosok et al. 2021).

Between the Cretaceous and today, a group with this type of antennae morphology could have emerged, possibly as a result of the adaptation of these insects to the changing environment. The new discovery in Eocene certainly sheds new light on the evolution of this group of insects. The finding of representatives of the genus *Rhabdomastix* with very narrow and elongated antennae in fossil resins is the

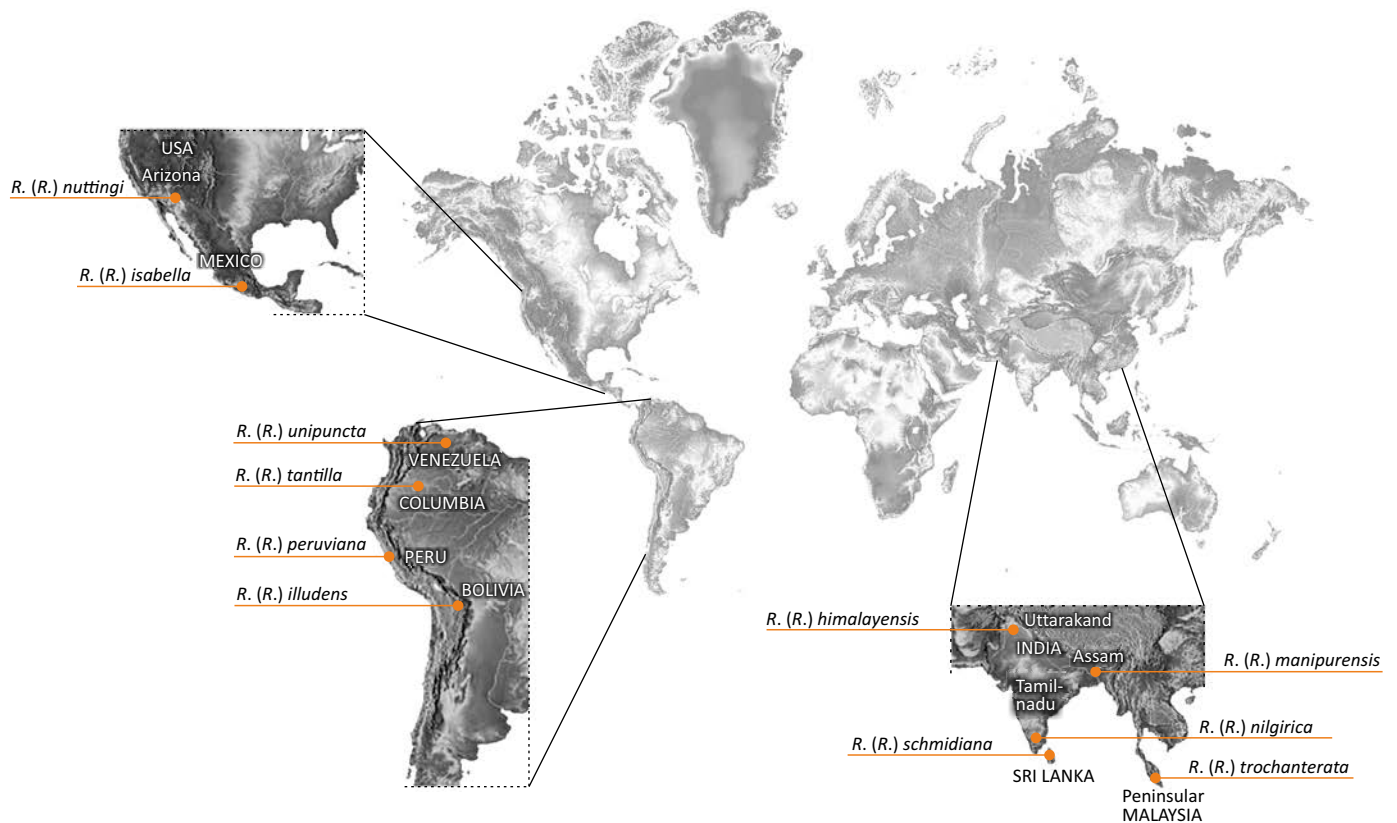


Fig. 12. Map of the distribution of representatives of the “*Rhabdomastix illudens*” group (the data used after Oosterbroek 2024).

first such evidence of their occurrence in the fossil record (Figs. 9, 10).

The representative of the genus *Rhabdomastix*, *R. (R.) woottoni* sp. nov. found in the Bitterfeld amber is very similar in morphology of antenna to the Bolivian “*R. illudens*” group, distinguished mainly on the basis of the criterion related to the proportions of the length of the antennae and the body, extremely elongate male antenna, even five times as long as the body (Figs. 10, 11). The newly described species is characterized by very narrow and elongate male antenna, which leads to the conclusion that it probably forms one group with modern American species with similar morphological characters. On the other hand, the elongate antennae may have appeared many times in evolution. It is also worth mentioning that the genus *Rhabdomastix* is more abundant in colder parts of the world, while fewer species of this genus occur in warmer zones (Fig. 12).

The group of species named by Starý (2003) “*R. illudens*”, which include species from Mexico, Bolivia, and Arizona in the USA, apparently prefer a warmer climate than majority of other species in *Rhabdomastix*.

Although both Baltic amber and Bitterfeld amber are believed to be approximately the same age (Szwedo and Sontag 2013), they came probably from distinct ecosystems. The differences found seem to reflect differences ecological conditions, not age (Standtke 2008).

Baltic and Bitterfeld ambers are compositionally distinct since each of them originates from different area of the

Eocene North Sea, i.e., Baltic amber from the north while Bitterfeld from the south (Wolfe et al. 2016). Generally, during the Eocene in northern Europe tropical and subtropical elements were gradually replaced by boreal forms (Weitschat 2008), and it is suggested that the Bitterfeld amber could have been deposited during a warm phase just after the Paleocene–Eocene Thermal Maximum (Westerhold et al. 2009) with mean annual temperatures in Central Europe of ~ 22 °C (Grein et al. 2011; Dunlop et al. 2018).

It is plausible that, similarly to modern species from the “*R. illudens*” group, occurring in warmer climates, the extinct species documented from Bitterfeld amber also preferred warm climatic conditions. This group is known not only from Bitterfeld amber, but also from all fossil resins known from the Baltic region. Nevertheless, further research is necessary to fully corroborate this hypothesis.

The discovery of a representative of the group “*R. illudens*” in Bitterfeld amber is important for the interpretation of the evolution of this group of insects, as well as their detailed biometrics and environmental preferences in the Eocene.

Conclusions

Although there is observed morphological diversity and disparity of extant and extinct representatives of the genus *Rhabdomastix*, specimens with features such as very elon-

gated antennae, much longer than body length, have not been known from the fossil record until now.

The new discovery shed new light on the evolution of this group of insects, indicating similarity to some modern representatives of the genus which occur in Nearctic, Neotropic and Oriental regions. Therefore, these and subsequent new discoveries may help resolving some taxonomic problems of this group of insects as the internal classification of the genus *Rhabdomastix* is not fully assessed, and the taxonomic position of the groups of “*Rhabdomastix illudens*” and “*Rhabdomastix caudata*” remains still undefined.

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Authors' contributions

WJ-S. conceived and designed the study, lead and performed the data analysis, interpretations and analysis, prepared photographs and drawings, wrote the manuscript and corrected the manuscript. IK-K conceived and designed the study, lead and performed the data analysis, interpretations and analysis, wrote the manuscript and corrected the manuscript. WK provided specimens, analyzed the data and corrected the manuscript. All authors edited and reviewed final version of the manuscript and agreed to the submitted version.

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