The first stage of the evolution of *Rhabdomastix* (Diptera, Limoniidae) and the taxonomic implications of genus

I. KANIA-KŁOSOK¹*, W. JORDAN-STASIŁO¹, K. KOPEĆ², K. JANISZEWSKA³, & W. KRZEMIŃSKI²

¹Department of Biology, Institute of Biology and Biotechnology, University of Rzeszów, Poland, ²Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Poland, and ³Institute of Paleobiology, Polish Academy of Sciences, Poland

(Received 9 July 2021; accepted 3 November 2021)

Abstract

A new subgenus *Myanmamastix* subgen. n. and four new species of *Rhabdomastix* from Cenomanian Burmese amber were described: *Rhabdomastix* (Myanmamastix) *asiatica* subgen. and sp. n., *Rhabdomastix* (Myanmamastix) *cretacea* subgen. and sp. n., *Rhabdomastix* (Myanmamastix) *krzeminskae* subgen. and sp. n., *Rhabdomastix* (Myanmamastix) *myanmae* subgen. and sp. n. The species *Rhabdomastix jarzembowskii* known from Burmese amber was reclassified to the new subgenus *Myanmamastix* subgen. n. An analysis of the morphological structures and taxonomical differences between the representatives of Cretaceous *Rhabdomastix* was carried out. The manuscript presents results of original research, including the first 3D reconstruction of a Dipteran preserved as an inclusion in Burmese amber using computer microtomography.

http://www.zoobank.org/urn:lsid:zoobank.org:pub:79C82852-2502-4A2F-B684-CCCE10D6C525

Keywords: fossil insects, Chioneinae, new subgenus, new species, Cenomanian

Introduction

Mesozoic Burmese amber (98.79 ± 0.62 Ma (Shi et al. 2012)) occurs in deposits in the state of Kachin in Myanmar (Burma) near Shwebo, Thayetmyo, Pakokku and Pegu provinces. This resin is found in the presence of thin-layer sandstone, silt, clay shale, micritic limestone and coal (Poinar & Brown 2003; Ross et al. 2010), in the form of lenses of various sizes or in the form of structures resembling small stalactites with circular cross-sections generally about 1 cm in diameter, though some larger pieces are known (Cruickshank & Ko 2003).

Intensive research on Burmese amber conducted in the twenty-first century has brought surprising discoveries. This fossil resin is characterized by an exceptional species diversity, including a large number and broad taxonomic diversity of insects preserved as inclusions. So far, representatives of over 290 families of invertebrates, mainly insects, arachnids, crustaceans and other arthropods, have been described from inclusions in Burmese amber (Ross 2020). The amber contains inclusions of flies from the family Culicidae Meigen 1818 along with representatives of many other insect groups, including species from the orders Embioidea Hagen, 1862, Strepsiptera Kirby, 1813, Zoraptera Silvestri, 1913, Archeognatha Börner, 1904, Zygometra Börner, 1904, Hemiptera Linnaeus, 1758 and Lepidoptera Linnaeus, 1758 (Engel & Grimaldi 2002, 2006; Borkent & Grimaldi 2004; Grimaldi et al. 2005; Ross 2020). However, the Diptera are one of the most numerous in terms of the number of species and specimens, as well as the one of the best known groups of insects represented in Burmese amber.
The representatives of the genus *Rhabdomastix* Skuse, 1890 described herein are medium-sized limoniids with 16-segmented antennae, 4-segmented palpus maxillaris, without ocelli or tibial spurs. They are characterized, like the other representatives of Limoniidae Speiser 1909 (Diptera, Nematocera), by termination of the subcostal vein into the costa. Wing venation also shows four radial veins and three medial veins well developed, while vein r-r (R2) is usually atrophied and d-cell is closed. Hypopygium of males is not large with massive gonoxoites and two pairs of gonostyles, while the ovipositor of females is not very elongate with two pairs of saber-like valves and one pair of cerci (Skuse 1890; Starý 2003; Szwedo et al. 2020).

In contemporary fauna the genus *Rhabdomastix* is represented by over 130 species and subspecies, which occur mainly in the Holarctic, with 68 species and subspecies, known across the region of these 40 species are represented in the Palearctic region, while 29 occur in the Nearctic region. Only a single species, *Rhabdomastix* (Rhabdomastix) borealis Alexander 1924 is known from both the Palearctic and Nearctic regions (Oosterbroek 2021). Beyond the Holarctic only three species of the genus *Rhabdomastix* occur in the Afrotropic region, 42 occur in the Neotropic region, 15 in the Oriental region, and 23 species in the Australasian region (Figures 1 and 2) (Oosterbroek 2021).

In the fossil record, the genus *Rhabdomastix* is represented by 19 species described mainly from inclusions in Eocene Baltic amber (11 species) (Meunier 1906; Alexander 1931; Podenas 2006) and Oligocene imprints in sediments (7 species) (Scudder 1894; Cockerell 1920, 1927; Statz 1944). To date only one species has been described from the Cretaceous, based on inclusion in Cenomanian Burmese amber, this is *Rhabdomastix jarzembovskii* Krzemiński, 2004, the oldest representative of the genus. Despite Diptera being among the most numerous insects represented in Burmese amber, to date, only 13 species within 11 genera of Limoniidae have been described from inclusions in Burmese amber and only the one species of *Rhabdomastix* (Table 1) (Ross 2020).

In Burmese amber we can find very well preserved specimens of insects, allowing for study of important taxonomic features at the same level as research of contemporary entomofauna. New findings of *Rhabdomastix* preserved as inclusions in Cretaceous Burmese amber shed new light on the early evolution of these insects.

The genus *Rhabdomastix* is recognized as a taxon with one of the most difficult internal classification systems. This is due to the slight degree of differentiation of the hypopygium, a structure that is usually highly distinctive and specialized for individual taxa at different levels within the family Limoniidae (Skuse 1890). However, study of the newly discovered fossil material highlights additional diagnostic features that give valuable insight on the classification within the genus *Rhabdomastix*, consistent for contemporary and fossil species.

The system of classification provided by Alexander (1914) included three subgenera of *Rhabdomastix*: *Rhabdomastix* s. str., *Sacandaga* Alexander, 1911, and *Palagonomyia* Meunier, 1899 and was based on the ratio of antennae length to body length. According to this system antennae longer than the body length

---

**Figure 1.** Worldwide distribution of subgenera and species of *Rhabdomastix* in recent fauna (data according to Oosterbroek (2021)).
characterized the representatives of subgenus *Rhabdomastix*, much shorter antennae than the body distinguished the subgenus *Sacandaga*, and only slightly shorter than the body — *Paleogonomyia*. This classification was used also by Savchenko in the Catalog of Palearctic Diptera (Savchenko et al. 1992). The Catalog of fossilized flies of the world (Insecta: Diptera) include 15 species, which were classified to the genus *Rhabdomastix*, *Paleogonomyia*, *Sacandaga* and 6 species unclassified to any subgenus (Evenhuis 1994; Starý 2003).

In 2003 Starý provided revision of European species, synonymizing the subgenera *Paleogonomyia* and *Sacandaga* with the subgenus *Rhabdomastix* and distinguished a new subgenus *Lurdia* Starý, 2003 which was characterized by an atrophied vein sc-r, an elongate subcostal vein always terminating beyond half the length of Rs, pentagonal discal cell, straight
distal section of M₁+₂ and M₃ and segment IX of abdomen widened distally, tergite with pale narrow midline interruption, posterior edge of the tergite existed medially, strongly sclerotized interbase, darkening distally part, and elongate cerci and hypogastral valvae, which constitute approximately twice the length of tergite X.

New discoveries in Burmese amber allow us to distinguish one new subgenus of *Rhabdomastix* and four new species, and to reclassify the species *R. jarzenbowski* Krzemiński, 2004 as belonging to the newly described subgenus.

**Material and methods**

The material examined included four specimens of fossil Diptera of the genus *Rhabdomastix* Skuse, 1890, preserved as an inclusion in Cretaceous Burmese amber (98.79 ± 0.62 Ma, Upper Cretaceous, Cenomanian) (Poinar & Brown 2003; Shi et al. 2012; Smith & Ross 2017). Burmese specimens were acquired in 2016, prior to the armed conflict and the escalation of the ethnic strife in the area (Szwedo et al. 2020).

All the studied specimens, erected as a new species, described, or figured are deposited in an accessible, permanent repository in public institutions: Institute of Systematics and Animal Evolution of the Polish Academy of Sciences in Krakow (ISEA PAS) (3 specimens) and Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (CAS) (1 specimen) (Table I).

The research was carried out using a Nikon SMZ 1500 stereomicroscope equipped with a Nikon DS-Fi1 camera, and the measurements were made using the NIS-Elements D 3.0 software. The drawings were made by W. J.-S. The specimen No. MP/3630 was visualised, using micro-computed tomography. MicroCT data were collected with Zeiss Xradia MicroXCT-200 imaging system equipped with a 90 kV/8 W tungsten X-ray source in the Laboratory of Microtomography, Institute of Paleobiology, Polish Academy of Sciences, Warsaw. The scans were performed using the following parameters: voltage: 133 kV, power: 4 W, exposure time: 30.00 s, voxel size: 3.85 μm. Radial projections were reconstructed with XMReconstructor software provided with the Xradia system. The 3D images of specimens and XMT sections were obtained with Avizo 7.1 Fire Edition software.

The wing venation nomenclature follows McAlpine et al. 1981, while the nomenclature of the male and female terminalia is in accord with later works (Krzemiński 2002; Podenas 2006). The classification system proposed by Starý 2003, covering both modern and extinct species, was adopted. The length of vein M₃ was measured from the point of its connection with the m-m cross-vein to the wing edge, and the length of the d-cell from its rear edge (from the wing base) to the cross-vein connection point of m-m with vein M₃. Measurements of individual parts of the body were given only when the measured morphological structures were not damaged.

**Acronyms**

ISEA PAS - Institute of Systematics and Animal Evolution of the Polish Academy of Sciences in Krakow; CAS - Nanjing Institute of Geology and Palaeontology, Chinese Academy of Science; BMNH – British Museum of Natural History.

**Results**

**Systematic palaeontology**

Ordo: Diptera Linnaeus, 1758

Subordo: Tipulomorpha Rohdendorf, 1961

Family: Limoniidae Speiser, 1909

Subfamily: Chioneinae Rondani, 1861

Genus: *Rhabdomastix* Skuse, 1890

Subgenus: *Myanmarmastix* subgen. n. Type species: *Rhabdomastix ostensackenii* Skuse, 1890; by monotype

Key to subgenera of *Rhabdomastix* and species of *Myanmarmastix* subgen. n.

1. Outer gonostylus shorter than inner gonostylus ...

2. Outer gonostylus longer than inner gonostylus ...

3. Cross-vein sc-r not far from the tip of Sc, the distance from Sc-r and the tip of Sc is approximately as long as 5x the length of sc-r; R₁ terminating beyond half the length of R₂+₃+₄;

4. Distance between the tips of Sc and R₁ longer than the distance between tips of R₁ and R₃ (6a; e; 7a; 12c) ...

5. Cross-vein sc-r not far from the tip of Sc, distance less than 3x the length of sc-r; R₁ terminating before half the length of R₂+₃+₄;

6. Distance between tips of Sc and R₁ less than or comparable length to the distance of tips of R₁ and R₃ ...

7. Cross-vein sc-r from the tip of Sc, distance less than 3x the length of sc-r; R₁ terminating before half the length of R₂+₃+₄;
3. Rs shorter than $R_{2+3+4}$ (9a, e-f; 10a; 12e) ...
   ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ... ......
setae, as long as the length of the palpomeres bearing them or longer.

Thorax: wing 2.68–3.21 mm long, 0.55–0.83 mm wide, 3.5–4.5 times as long as wide, cross-vein (h) positioned at one-fifth the length of the wing from its base; cross-vein sc-r positioned not far from the tip of Sc, approximately 2–5 times its own length from the tip of Sc; the distance between the tips of Sc and R1 of comparable length or 0.3 times its length longer than the distance between the tips of R1 and R3; M1+2 from straight to slightly arched, 0.25–0.3 times longer than d-cell; M4 short, shorter than length of d-cell; vein Mb equal to 2.5–5 times the length of M3; Cu from the point of connection with cross-vein m-cu to the edge of wing straight or slightly bent toward the wing margin. The distance between the tips of M1+2 and M3 approximately as long as the distance between the tips of M4 and M5 or 1.5 times longer; the distance between the tips of M3 and M4 shorter than the distance between the tips of M4 and Cu; the distance between the tips of M4 and Cu and the tips of Cu and A1 shorter, of comparable length or longer; the distance between the tips of A1 and A2 and the tips of M4 and A1 shorter, of comparable length or longer. Haltere: 0.28–0.54 mm long, stem very narrow, only slightly longer than knob. Abdomen: hypopygium 0.27–0.35 mm long; gonocoxite elongate, massive; outer gonostylus narrow, blunt or sharply terminated, strongly sclerotized, in some representatives with a small appendix in the apical part.

Comparison. In representatives of subgenus Myanamamastix subgen. n. the inner gonostylus is much longer than the outer gonostylus, while in representatives of the other subgenera within the genus Rhabdomastix the outer gonostylus is longer than the inner gonostylus. Contrary to the subgenus Lurdia, where cross-vein sc-r is absent (11(a)), in representatives of the subgenus Myanamamastix subgen. n. this vein is well developed (11(b) and 12(a–e)). In contrast to the representatives of other subgenera within the genus Rhabdomastix, in Myanamamastix subgen. n. the d-cell is elongate, 2.5 times as long as wide, as long, or longer, than the length of M3. In the species classified to the subgenus Lurdia (11(a)), as well as representatives of the subgenus Myanamamastix subgen. n. (11(b)) the d-cell is pentagonal (Starý 2003), while in representatives of the subgenus Rhabdomastix the d-cell is hexagonal (11(c)) (Starý 2004). Antennae of representatives of the subgenus Myanamamastix subgen. n. are usually only slightly longer than the length of the head and thorax combined, while the subgenus Rhabdomastix the antennae can vary from slightly longer than the head to much longer than the body.

New combination

Rhabdomastix (Myanamamastix) jarzembowskii Krzemiński, 2004 comb. n. Rhabdomastix (Paleogonomyia) jarzembowskii Krzemiński, 2004: Krzemiński, p. 124(12d

Remarks. The species, was first described and classified by Krzemiński in 2004 to the subgenus Paleogonomyia Meunier, 1899. However, features such as a complete atrophy of cross-vein r-r (R2), presence of cross-vein sc-r and a very short vein Rs, always shorter than half the length of Mb, presence of a large, elongate, pentagonal d-cell equal in length to vein M3, slightly arched veins M1+2 and M3 or inner gonostylus longer than characteristic, strongly sclerotized outer gonostylus all indicate inclusion of this species in the subgenus Myanamamastix subgen. n. and allow for its designation as the type species for the subgenus.

Rhabdomastix (Myanamamastix) asiatica subgen. and sp. n. (Figs 3; 12a)

Diagnosis. Vein Sc terminating just beyond half the length of Rs; cross-vein sc-r terminating 3 times its own length from the tip of Sc; fork of Rb before half the length of wing from wing base; R3 approximately one-third the length of R4; R4 equal to the length of R2+3+4; Rs longer than R2+3+4; R1 very short, terminate at about 0.3 of the length of R2+3+4; M3 equal to the length of the d-cell, very strongly bent toward thewing margin; d-cell 2.5 times as long as wide; the distance between the tips of Sc and R1 is slightly shorter than the distance between the tips of R1 and R3.

Material examined. Holotype: No. BA02-14379 (male), Coll. (CAS).

Etymology. The name of the new species is derived from the name of the continent “Asia”, on which the specimen was found.

Description. Body (Figure 3(a)) dark brown, wing without color pattern, pterostigma absent, haltere elongate (Figure 3 (b)). Thorax: wing (Figure 3 (c–e)) 3.21 mm long, 0.83 mm wide, 4.5 times as long as wide, cross-vein (h) positioned at one-fifth the length of the wing from its base in; R3 short, its length approximately 0.3 times the distance between the tips of R1 and R3. Vein M1+2 arched, 1.5 times longer than d-cell; length of Mb equal 4.5 times the length of M3; Cu from the point of connection with cross-vein m-cu to the edge of wing straight. The
distance between the tips of M_{1+2} and M_3 1.5 times the distance between the tips of M_3 and M_{4}; the distance between the tips of M_4 and Cu 2 times longer than the distance between the tips of M_3 and M_{4}; the distance between tips of M_4 and Cu slightly shorter than the distance between the tips of Cu and A_1; distance between tips of M_4 and A_1 1.5 times the distance between the tips of A_1 and A_2. Veins A_1 and A_2 slightly arched (12(a)). Haltere: (Figure 3(b)) 0.38 mm long, stem narrow and relatively short, about 1.5 times longer than the knob.

Comparison. R. (M.) asiatica subgen. and sp. n., in contrast to R. (M.) cretacea subgen. and sp. n. possesses a vein R_4 which is nearly three times longer than vein R_3 and about equal in length to vein R_{2+3+4}, and has vein M_3 about equal in length to the d-cell. While in R. (M.) cretacea subgen. and sp. n. vein R_4 is very short, barely twice the length of R_3 and only a trifle longer than half the length of R_{2+3+4}, and vein M_3 is much shorter than the d-cell. Compared to R. (M.) myanmae subgen. and sp. n., R. (M.) asiatica subgen. and sp. n. possesses a vein Rs which is longer than vein R_{2+3+4}, and has vein R_1 terminating at about one-third the length of R_{2+3+4}, while in R. (M.) myanmae subgen. and sp. n. vein Rs is shorter than R_{2+3+4}, and R_1 terminates just before half the length of R_{2+3+4}. In R. (M.) krzeminskae subgen. and sp. n. cross-vein sc-r terminates 5 times its own length from the tip of Sc, while in R. (M.) asiatica subgen. and sp. n. sc-r terminates 3 times its length from the tip of Sc. Moreover, in R. (M.) asiatica subgen. and sp. n. the distance between the tips of Sc and R_1 is shorter than the distance between the tips of R_1 and R_3, while in R. (M.) krzeminskae subgen. and sp. n. this distance is longer. Finally R. (M.) jarzembowskii Krzeminski, 2004 comb. n. vein Sc terminates before half the length of Rs. R_3 is one-quarter the length of R_4, and R_4 is longer than R_{2+3+4}. While in R. (M.) asiatica subgen. and sp. n. Sc terminates near half the length of Rs. R_3 is one-third the length of R_4 and R_4 is equal to R_{2+3+4}.

Remarks. A specimen without a well-preserved head and legs, a darkened field is visible in the place of the

---

![Figure 3. Rhabdomastix (Myanmarmastix) asiatica subgen. and sp. n., holotype No. BA02-14379 (male), Nanjing Institute of Geology and Palaeontology, Chinese Academy of Science (CAS): (a) body, latero-ventral view; (b) haltere, latero-ventral view; (c) base of the wing; (d) wing; (e) wing venation, drawing.](image-url)
head, making it impossible to examine the morphological features of this part of the body.

**Rhabdomastix (Myanamastix) cretacica subgen. and sp. n.** (Figs 4, 5, 12b)

**Diagnosis.** Vein Sc terminating just beyond half the length of Rs; cross-vein sc-r terminating at a distance of 3 times its own length from the tip Sc; fork of Rb positioned approximately at half the length of the wing; R3 half the length of R4; R3 very short, its length slightly longer than half of R2+3+4; Rs longer than R2+3+4; R1 very short, terminating about opposite one-third the length of R2+3+4; M3 much shorter than d-cell, only slightly bent toward the wing margin; d-cell 2.5 times as long as wide; distance between the tips of Sc and R1 and the tips of R1 and R3 of comparable length; on each flagellomere a few elongate, thick setae, longer than the flagellomeres bearing them, two of them on each flagellomere arranged almost perpendicular to the surfaces of the individual flagellomeres, the others at an acute angle; last flagellomere elongate, only slightly shorter than penultimate one; outer gonostylius short, narrow, sharply tipped, inner gonostylius broad basally then tapering to a blunt tip.

**Material examined.** Holotype: No. MP/3641 (male), Coll. (ISEA PAS).

**Etymology.** The name of the new species is derived from the name of the geological period “Cretaceous”/Latin: cretaceus.

**Description.** Body (Figure 4(a)) 3.48 mm long, dark brown, wing without color pattern, pterostigma absent, halter slightly elongate.

Head: (Figure 4(a)): head width 0.24 mm; antenna (Figures 4(a, d) and 5(b)) with pedicel narrow, elongate, only slightly extended distally, scape short, 1.5 times as long as wide; pedicel and scape with a few elongate setae in the distal part; flagellomeres rather narrow, cylindrical, gradually decreasing towards the apex of flagellum, 3 times as long as wide; the last flagellomere with four setae, two of them at the apex of flagellum. Antenna 1.29 mm long: pedicel 0.10 mm; scape 0.06 mm; flagellomeres: 1/0.10 mm; 2/0.08 mm; 3/0.08 mm; 4/0.07 mm; 5/0.08 mm; 6/0.07 mm; 7/0.10 mm; 8/0.10 mm; 9/0.10 mm; 10/0.08 mm; 11/0.07 mm; 12/0.08 mm; 13/0.07 mm; 14/0.05 mm). Palpus (Figures 4(c) and 5(e)) 0.26 mm long (1/0.05 mm; 2/0.07 mm; 3/0.07 mm; 4/0.07 mm); palpomeres 1–3 cylindrical, comparable length; the last palpomere elongate, only slightly longer than the penultimate one, rounded at the end, 4.5 times as long as wide; each palpomere with a few setae, these shorter or slightly longer than the segments bearing them.

Thorax: (Figure 4(a)) wing (Figures 4(a, e) and 5(a)) 2.68 mm long, 0.82 mm width, 3.5 times as long as wide; cross-vein (h) positioned at one-fifth the length of the wing from its base; R1 terminating at about opposite one-third the length of d-cell; R3 short, equal to 0.3 times the distance between the tips of R1 and R3. Vein M1+2 only slightly longer than the length of d-cell; M4 almost straight, nearly half the length of d-cell; vein Mb 5 times longer than the length M3; Cu from the point of connection with cross-vein m-cu to the edge of wing slightly bent. The distance between the tips of M1+2 and M3 and the tips of M3 and M4 of comparable length; distance between the tips of M3 and M4 shorter than the distance between the tips of M4 and Cu; distance between the tips of M4 and Cu slightly longer than the distance between the tips of Cu and A1; the distance between the tips of A1 and A2 slightly shorter than the distance between the tips of M4 and A1. A1 slightly bent toward the wing margins; A2 sinusoidal (12(b)). Haltere: (Figure 4(a, e)) 0.38 mm long, stem relatively short, only 1.5 times longer than the knob.

Abdomen: hypopygium (Figures 4(a, b) and 5(c, d)) 0.35 mm long, gonocoxite massive, wider at the basal part.

**Comparison.** A short and strongly arched vein R3, barely twice the length of the vein R3 and a very short vein M3, much shorter than the length of the d-cell, readily distinguish R. (M.) cretacica subgen. and sp. n. from all others species classified the subgenus Myanamastix subgen. n. In contrast to R. (M.) asiatica subgen. and sp. n., where the fork of Rb is positioned more or less at the midlength of the wing, R. (M.) cretacica subgen. and sp. n. has the fork of Rb positioned at less than half the length of the wing. R. (M.) cretacica subgen. and sp. n. cross-vein sc-r positioned 3 times its own length from the tip of Sc, while in R. (M.) krzeminskae subgen. and sp. n. this distance is much longer, equal to 5 times the length of the vein sc-r. In further contrast to R. (M.) krzeminskae subgen. and sp. n., R. (M.) cretacica subgen. and sp. n. has R3 short, ending opposite one third of the length of vein R2+3+4, while in R. (M.) krzeminskae subgen. and sp. n. this vein terminates just beyond half the length of vein R2+3+4. Moreover, in R. (M.) cretacica subgen. and sp. n. on each flagellomere several elongate, thick setae are visible, longer than the segments bearing them, two of them on each flagellomere arranged almost perpendicular to the surface of the individual
flagellomeres, the others arranged at an acute angle, and the last flagellomere is of moderate length, more than half the length of the penultimate one, completely different to R. (M.) krzeminskae subgen. and sp. n., where the setae on the flagellomeres are shorter than the length of segments bearing them, densely spaced, almost perpendicular to the surface of the individual flagellomere, and the last flagellomere is short, only half the length of the penultimate one. In R. (M.) myanmae subgen. and sp. n. the last flagellomere is also of moderate length, only slightly shorter than the penultimate one. Moreover, in R. (M.) myanmae subgen. and sp. n. vein Rs is shorter than R2+3+4, while in R. (M.) cretacea subgen. and sp. n. vein Rs is longer than R2+3+4. R. (M.) jarzem-bowskii Krzemiński, 2004 comb. n. shows vein Sc terminating before half the length of Rs, R3 one-quarter of the length of a vein R4, and R4 longer than R2+3+4, while in R. (M.) cretacea subgen. and sp. n. Sc terminates beyond half the length of Rs, R3 is about half the length of vein R4, and R4 is short and only slightly longer than half the length of R2+3+4.

Remarks. The condition of the specimen is good, only the legs are not preserved, the mouthparts are poorly visible.

**Rhabdomastix (Myanmamastix) krzeminskae** subgen. and sp. n. *(Figs 6–8, 12c)*

**Diagnosis.** Vein Sc terminating at approximately three-quarters of the length Rs; cross-vein sc-r
terminating at distance equal to 5 times of its own length from the tip Sc; fork of Rb positioned before half the wing length from its base; R3 one-third the length of R4; R4 equal in length to R2+3+4; Rs longer than R2+3+4; R1 terminating just beyond half the length of R2+3+4; M3 equal to the length of the d-cell, length of d-cell 2.5 times its width, the distance between the tips of Sc and R1 longer than the distance between the tips of R1 and R3; setae on the flagellomeres shorter than length of the flagellomere bearing them, densely spaced, almost perpendicular to the surface of the individual flagellomere; the last flagellomere half the length of the penultimate one; outer gonostylus narrow, strongly sclerotized, dark brown, blunt tipped, inner gonostylus relatively wide, pointed with a small appendage in the distal part.

**Material examined.** Holotype: No. MP/3630 (male) (ISEA PAS).

**Etymology.** The name of the new species is dedicated to Professor Ewa Krzemieńska (Polish Academy of Sciences, Kraków), the eminent specialist of fossil and recent Diptera.

**Description.** Body (Figures 6(a) and 8-video) 2.49 mm long, dark brown, wing without color pattern, pterostigma absent, haltere slightly elongate.

Head: (Figure 6 (a)): head width 0.24 mm; antenna (Figures 6 (a,c) and 7(b)) only slightly longer than the length of the head and thorax combined, with a cylindrical pedicel and a relatively wide scape, narrow at the base, strongly widened distally, about as long as wide; pedicel and scape with a few distal setae, flagellomeres cylindrical, widened basally, more slender in the distal part of the flagellum, becoming more slender towards the apex, comparable length, the last flagellomere elongate, half the length of the penultimate one, blunt ended; the last flagellomere with two bristles on its tip. Antenna 1.15 mm long; scape 0.06 mm long; pedicel 0.06 mm long; flagellomeres: 1/0.10 mm; 2/0.08 mm; 3/0.08 mm; 4/0.08 mm; 5/0.08 mm; 6/0.08 mm; 7/0.08 mm; 8/0.07 mm; 9/0.07 mm; 10/0.07 mm; 11/0.07 mm; 12/0.08 mm; 13/0.06 mm; 14/0.03 mm). Palpus (Figures 6(d) and 7(e)) 0.19 mm long (1/0.04 mm; 2/0.05 mm; 3/0.05 mm; 4/0.05 mm); palpomeres relatively narrow, palpomeres 1–3 of comparable length, the last one slightly longer than the penultimate one, rounded at the tip; approximately 4.5 times as long.
There are several setae on each palpomere, slightly longer or shorter than the length of the segments bearing them.

Thorax: (Figure 6(a)): wing (Figures 6(a, c) and 7(a)) 2.71 mm long, 0.64 mm width, 3.5 times as long as wide, cross-vein (b) positioned at one-fifth the length of the wing from its base; d-cell 2.5 times as long as wide. M₁+₂ significantly longer than M₃; M₄ short, almost straight, shorter than the d-cell; vein Mb slightly longer than 3 times the length of M₃; Cu from the point of connection with the cross-vein m-cu to the edge of the wing almost straight; cross-vein m-cu positioned distinctly before half the length of the d-cell from the fork Mb. Distance between the tips of M₁+₂ and M₃ and the tips of M₃ and M₄ of comparable length; the distance between the tips of M₃ and M₄ shorter than the distance between the tips of M₄ and Cu; distance between the tips of M₄ and Cu and the tips of Cu and A₁ of comparable length; distance between the tips of A₁ and A₂ significantly shorter than the distance between the tips of M₄ and A₁. A₁ and A₂ slightly bent toward the wing margin (12(c)). Haltere: 0.48 mm long, stem very narrow, only slightly longer than the knob. Abdomen: hypopygium (Figures 6 (a,b) and 7(c,d)) 0.27 mm long, gonocoxite relatively elongate, massive.

Comparison. In contrast to the species described by Krzemiński in 2004 R. (M.) jarzembowskii Krzemiński 2004 comb. n., R. (M.) krzeminskae subgen. and sp. n. has cross-vein sc-r positioned at
a considerable distance from the tip of vein Sc, equal to 5 times the length of sc-r, while in *R. (M.) jarzembowskii* Krzemiński, 2004 comb. n., this vein is positioned much closer to the tip of Sc, at a distance equal to only twice the length of sc-r (Krzemiński 2004). Moreover, vein Sc in *R. (M.) krzeminskae* subgen. and sp. n. ends at half the length of Rs, while in *R. (M.) jarzembowskii* Krzemiński, 2004 comb. n. Sc terminates before half the length of Rs. In the species *R. (M.) asiatica* subgen. and sp. n. the distance between the tips of Sc and R_1 is shorter than the distance between the tips of R_1 and R_3, and the cross-vein sc-r is positioned three times its own length from the tip of Sc, while in *R. (M.) krzeminskae* subgen. and sp. n. the distance between the tips of Sc and R_1 is longer than the distance...
between the tips of R₁ and R₃, and the cross-vein sc-r terminates five times its own length from the tip of Sc. In R. (M.) krzeminskiae subgen. and sp. n. the setae on the flagellomeres are shorter than the length of the segments bearing them, are densely spaced, almost perpendicular to the surface of individual flagellomeres, and the last flagellomere is only half the length of the penultimate one, while in both R. (M.) cretacica subgen. and sp. n. and R. (M.) myanmae subgen. and sp. n. the setae are very elongate and thick, longer than the flagellomeres bearing them, and the last flagellomeres of these species are elongate, only slightly shorter than the penultimate ones.

**Remarks.** The condition of the specimen is good, only the legs are partially not preserved.

**Rhabdomastix (Myanmamastix) myanmae** subgen. and sp. n. (Figs 9, 10, 12c)

**Diagnosis.** Vein Sc terminating opposite approximately three-quarters the length of Rs; cross-vein sc-r terminating at a distance equal to 3 times its own length from the tip Sc; fork of Rb positioned before half the wing length; Rs shorter than R₂+₃+₄; R₁ terminating just before half the length of R₂+₃+₄; M₃ equal in length to d-cell, slightly bent distally, d-cell 3 times as long as wide; distance between the tips of Sc and R₁ and the tips of R₁ and R₃ of comparable length; on each flagellomere several very long and thick setae, longer than the segment bearing them, almost perpendicular to the surface of individual flagellomeres; the last flagellomere, elongate but shorter than the penultimate one, more than half its length; outer gonostylus narrow, strongly sclerotized, dark colored, blunt ending, inner gonostylus relatively wide, pointed.

**Material examined.** Holotype: No. MP/3637 (male) (ISEA PAS).

**Etymology.** The name of the new species is derived from the name of the country of Myanmar (Burma), where the deposits of Burmese amber are located.

**Description.** Body (Figure 9(a)) 2.54 mm long, dark brown, wing without color pattern, pterostigma absent, haltere slightly elongate (Figure 9(a)).

Head: (Figure 9(a)): head width 0.31 mm; antenna (Figure 9(a, d) and 10(b)) shorter than half the length of the body, slightly longer than the length of the head and thorax combined, pedicel narrowed at the base, slightly widened distally, scape elongate, its length almost 1.5 times its width, distal part of pedicel and scape bearing several elongate setae; flagellomeres elongate, 2.5–3 times as long as wide, more slender towards the tip of flagellum, last flagellomere with two setae at the tip. Antenna 1.10 mm: scape 0.10 mm; pedicel 0.07 mm; flagellomeres: 1/0.09 mm; 2/0.07 mm; 3/0.06 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; 11/0.06 mm; 12/0.06 mm; 13/0.06 mm; 14/0.04 mm). Palpus (Figures 9(c) and 10(e)) 0.33 mm long (1/0.06 mm; 2/0.1 mm; 3/0.06 mm; 4/0.11 mm); palpomeres elongate, palpomeres 1–3 comparable in length, the last segment slightly longer than the penultimate one. Palpomeres with several very elongate, thick setae, slightly longer or shorter than segment bearing them, the last palpomere with two distinct setae near the apex. Thorax: (Figure 9(a)): wing (Figure 9(a,e–g) and 10(a)) 2.90 mm long, 0.55 mm wide, 4.5 times as long as wide; cross-vein (h) positioned at one-fifth the length of the wing from its base; R₁ terminating distinctly beyond half the length of the d-cell; R₃ short, equal to one-third of the distance between the tip of R₁ and the tip of R₃; d-cell 3 times as long as wide; vein Mb 4 times as long as M₃; Cu from the point of connection with the cross-vein m-cu to the edge of the wing almost straight; cross-vein m-cu positioned before half the length of the d-cell from the fork Mb. The distance between the tips of M₃ and M₄ shorter than the distance between the tips of M₄ and Cu; the distance between the tips of M₄ and Cu and the tips of Cu and A₁ of comparable length; distances between the tips of A₁ and A₂ and the tips of M₄ and A₁ of comparable length. A₁ and A₂ slightly bent toward the edge of the wing (Figure 11, Figure 12(e)).

Haltere: (Figure 9(a)) 0.54 mm long, stern elongate, approximately 1.5 times the length of the knob. Abdomen: hypopygium (Figure 9(a, b) and 10(c,d)) 0.42 mm long, gonocoxite massive, widened basally.

**Comparison.** R. (M.) myanmae subgen. and sp. n. differs from all other species within the Myanmamastix subgen. n. in antennae chetotaxy. In representatives of R. (M.) jarzembovskii Krzemiński, 2004 comb. n. and R. (M.) krzeminskiae subgen. and sp. n. setae on flagellomeres are shorter than the length of the segments bearing them, they are densely positioned and almost perpendicular to the surface of the individual flagellomeres, and the length of the last flagellomere is only half that of the penultimate one. In R. (M.) cretacica subgen. and sp. n. on all flagellomeres several elongate, thick setae are visible, longer than the segments bearing them, two on each flagellomere are arranged almost perpendicular to the surface of the individual
segment, the rest positioned a tan acute angle, and the last flagellomere is of moderate length, more than half the length of the penultimate one.

While in *R. (M.) myanmae* subgen. and sp. n. setae are very elongate and thick, longer than the length of segments bearing them, and the last flagellomere is elongate, only slightly shorter than the penultimate one.

Moreover, in *R. (M.) myanmae* subgen. and sp. n., *R. (M.) asiatica* subgen. and sp. n. and *R. (M.) cretacica* subgen. and sp. n. cross-vein sc-r is positioned at a moderate distance from the tip of vein Sc, nearly 3 times its own length, while in *R. (M.) krzeminskae* subgen. and sp. n. crossvein sc-r is positioned at a considerable distance from the tip of vein Sc, 5 times its own length, and in *R. (M.) jarzembowskii* Krzemiani, 2004 comb. n., this vein is positioned much closer to the tip of Sc, only twice own length.

Additionally, in *R. (M.) jarzembowskii* Krzemiani, 2004 comb. n. and *R. (M.) krzeminskae* subgen. and sp. n. the distance between the tips of Sc and R1 is greater than the distance between the tips of R1 and R3, while in *R. (M.) myanmae* subgen. and sp. n. and *R. (M.) cretacica* subgen. and sp. n. these distances are of near equal length, and in *R. (M.) asiatica* subgen. and sp. n. this distance is shorter.
Remarks. The condition of the specimen is good, only the legs are not preserved.

Discussion

The analysis of inclusions of *Rhabdomastix* flies preserved in Burmese amber has allowed for the distinction of a new subgenus, *Myanmamastix* subgen. n., and the description of four new species within this new subgenus. The new materials have allowed for the definition of clear boundaries regarding the differences in body morphology between taxonomic units at the species or subgeneric level, and an attempt to organize the systematic system within the genus, which has previously been insufficient to accommodate some fossil species. Described from inclusions in Burmese amber the species *R. (M.) jarzembowskii* Krzemiński, 2004 comb. n., was previously classified into the subgenus *Paleogonomyia* Meunier, 1899, according to the system used by Savchenko (1976, 1992).

Savchenko followed earlier work by Alexander (1914), whereby the genus *Rhabdomastix* was divided into three subgenera: *Rhabdomastix* s. str., *Palaeogonomyia* and *Sacandaga* Alexander, 1911, based on the ratio of antenial length to body length. The subgenera *Paleogonomyia* and *Sacandaga* were later synonymized with the subgenus *Rhabdomastix* s. str. by Starý (2003) and the subgenus *Lurdia* Starý, 2003 was distinguished, leaving the subgeneric placement of *R. jarzembowskii* uncertain. This classification system covering only two subgenera, *Rhabdomastix* s. str. and *Lurdia*, was also adopted in a study of *Rhabdomastix* flies from Australia (Theischinger et al. 2019). It is only now, in light of the material examined in this work, that a third subgenus, *Myanmamastix* subgen. n., can be recognised, and the species *R. (M.) jarzembowskii* Krzemiński, 2004 comb. n. can be placed as the type species.

The study of organisms preserved as inclusions in Mesozoic resins, such as Burmese amber, is important for many reasons. Particularly, they allow for the
Figure 11. Wing venation of representatives of known genera of Rhabdomastix. The tips of particular veins are marked with vertical lines. Line colors have been introduced to better distinguish the position of the tips of individual veins in relation to the length of other veins. The red dots show the fork of Rb vein and the position of the A₂ tip in relation to the Rb fork.

Figure 12. Wing venation of Cretaceous species of Rhabdomastix. The tips of particular veins are marked with vertical lines. Line colors have been introduced to better distinguish the position of the tips of individual veins in relation to the length of other veins. The red dots show the fork of Rb vein and the position of the A₂ tip in relation to the Rb fork.
The completion of data on the oldest representatives of many insect groups, including the genus *Rhabdomastix*.

The new discovery of some of the oldest *Rhabdomastix* species carries taxonomic implications for the subgenera and species within the genus. Based on the analysis of the oldest limonid inclinations, including representatives of the genus *Rhabdomastix* preserved in Burmese amber from the Cenomanian period, we can draw conclusions about the possible directions of evolution of this group of insects. The early occurrence of the subgenus *Myanmaramastix*, as much 50 million years before the oldest known species of *Rhabdomastix* s. str. and *Lurdia* found in Eocene Baltic amber (Podenas 2006), suggests the subgenus has a basal position within *Rhabdomastix*, with the other subgenera arising at a later period in the evolution of the genus.

Acknowledgements

We would like to thank two Anonymous Reviewers for very valuable comments and corrections of the text.

Funding

This work was supported by the National Science Centre of Poland under [Grant no. 2016/23/B/NZ8/00936].

Disclosure statement

No potential conflict of interest was reported by the author(s).

References

Alexander CP. 1911. Notes on two Tipulidae (Diptera). Entomological News 22:349–354.

Alexander CP. 1914. The Neotropical Tipulidae in the Hungarian national museum (Diptera). III. Entomological News 25:205–215.

Alexander CP. 1924. New species of two-winged flies from western North America belonging to the family Tipulidae. Proceedings of the United States National Museum 64 (10):1–16. DOI: 10.5479/si.0093801.64-2500.1.

Alexander CP. 1931. Crime–flies of the Baltic amber (Diptera). Bernstein–Forschung 2:1–135.

Borkent A, Grimaldi DA. 2004. The earliest fossil mosquito (Diptera: Culicidae), in Mid–Cretaceous Burmese amber. Annals of the Entomological Society of America 97:882–888. DOI: 10.1093/annr/97.0882. TEFMDJCJ2.0.CO;2.

Börner C. 1904. Zür Systematic der Hexapoden. Zoologischer Anzeiger 27:511–533.

Cockerell TDA. 1920. Eocene insects from the rocky mountains. Proceedings of the United States National Museum 57:233–260. DOI: 10.5479/si.00963801.57-2313.233.

Cockerell TDA. 1927. XVII.—Fossil insects from the Miocene of Colorado. Annals and Magazine of Natural History 19 (9):161–166. DOI: 10.1080/00222932708633587.

Cruickshank RD, Ko K. 2003. Geology of an amber locality in the Hukawng Valley, northern Myanmar. Journal of Asian Earth Sciences 21(5):441–455. DOI: 10.1016/S1367-9120 (02)00044-5.

Engel MS, Grimaldi DA. 2002. The first Mesozoic Zoraptera (Insecta). American Museum Novitates 3362:1–20. DOI: 10.1206/0003-0082(2002)362<0001:TFMZJ>2.0.CO;2.

Engel MS, Grimaldi DA. 2006. The earliest webspinners (Insecta: Embioidea). American Museum Novitates 3514 (1):1–15. DOI: 10.1206/0003-0082(2006)3514[1:TEWIEJ2.0.CO;2.

Evenhuis NL. 1994. Catalogue of the fossil flies of the world (Insecta: Diptera). Leiden: Backhuys. pp 1–600.

Grimaldi DA, Zhang L, Fraser NC, Rasnitsyn AP. 2005. Revision of the bizarre Mesozoic scorpion flies in the Pseudopolycentropodidae (Mecopteroidae). Insect Systematics & Evolution 36:443–458. DOI: 10.1163/18763120594761021.

Hagen KS. 1862. Biology and ecology of predaceous Coccinellidae. Annual Review of Entomology 7:289–326. DOI: 10.1146/annurev.en.07.010162.001445.

Kirby W. 1813. Streispitptra, a new order of insects proposed; and the characters of the order, with those of its genera, laid down. Transactions of the Royal Society of London 11:86–133.

Krzemiński W. 2002. Three new species of the genus *Helius* Lepeletier et Serville (Diptera, Liniomidae) from the Middle Miocene of Stavropol (northern Caucasus, Russia). Acta Zoologica Cracoviensia 35:597–601.

Krzemiński W. 2004. Fossil Liniomidae (Diptera, Tipulomorpha) from Lower Cretaceous amber of Myanmar. Journal of Systematic Palaeontology 2(2):123–125. DOI: 10.1080/147720104001257.

Linnaeus C. 1758. Systema Naturae per Regna tria Naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. T. 1. Holmiae: Impensis Direct. Laurentii Salvii, Sweden, Stockholm. pp 1–800.

McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, and Wood DM. 1981. Manual of Nearctic Diptera. Vol. 1. Research Branch, Agriculture Canada. Monograph No. 27, Canada, Ottawa, Ontario. pp 674.

Meigen JW. 1818. Systematische Beschreibung der bekannten europäischen zweiflügeligen Insekten. Systematisches Beschreibung der bekannten europäischen zweiflügeligen Insekten. Aachen: Erster Theil. F.W. Forstmann. pp 400.

Meunier F. 1899. Études de quelques Diptères de l’ambre tertiaire. Bulletin de la Société Entomologique de France 4 (17):334–335.

Meunier F. 1906. Monographie des Tipulidae et Dixidæ de l’ambre de la Baltique. Annales des Sciences Naturelles (Zoologie) 4(9):349–401.

Oosterbroek P. 2021. Catalogue of the crane-flies of the World. (Diptera, Tipuloidae: Pediidae, Liniomidae, Cylindrothomidae, Tipulidae). Available: https://ecw.naturalis. nl/ecw/index.php. updated Aug 2021 11. Accessed Oct 2021.

Podenas S. 2006. *Rhabdomastix* crane flies (Diptera: Liniomidae) in Baltic amber (Eocene). Proceedings of the Academy of the Natural Sciences of Philadelphia 155:41–66. DOI: 10.1635/ i0097-3157-155-1-41.1.
Cretaceous Rhabdomastix (Diptera, Limoniidae) 1169

Poinar GJ, Brown AE. 2003. A new genus of hard ticks in Cretaceous Burmese amber (Acari: Ixodida: Ixodidae). Systematic Parasitology 54:199–205. DOI: 10.1023/A:1022689325158.

Rohdendorf BB. 1961. The oldest infraorders of Diptera from the Triassic of Middle Asia. Palaeontologicheskoi Zhurnal 2:90–100.

Rondani C. 1861. Dipterologiae italicae prodomus. Vol. IV. Species Italicae ordinis Dipterorum in genera characteribus definita, ordinum collectae, metodo analatica distinctae, et novis vel minus cognitis descriptis. Pars tertia. Muscidae Tachininarum complementum. A. Stocco. Parmæ [= Parma]:174.

Ross AJ. 2020. Burmese (Myanmar) amber checklist and bibliography 2018. Palaeoentomology 2(1):22–84. DOI: 10.11646/palaeoentomology.2.1.5.

Ross AJ, Mellish C, York P, Crighton B. 2010. Burmese amber. In: Penney D, editor. Biodiversity of fossils in amber from the major world deposits. Manchester (UK): Siri Scientific Press. pp. 208–235.

Savchenko EN. 1976. On finding limoniid–flies (Diptera, Limoniidae) from the Palaeogonomyia Meunier subgenus of the Rhabdomastix Skuse genus in the USSR fauna. Dopovidi Akademi Nauk Ukrajinskoi RSR (B):561–564. (in Ukrainian).

Savchenko EN, Oosterbroek P, Starý J. 1992. Family Limoniidae. Catalogue of Palearctic Diptera 1:183–369.

Scudder SH. 1894. Tertiary Tipulidae, with special reference to those of Florissant, Colorado. Proceedings of the American Philosophical Society 32:163–245.

Shi G, Grimaldi DA, Harlow GE, Wang J, Wang J, Yang M et al. 2012. Age constraint on Burmese amber based on U–Pb dating of zircons. Cretaceous Research 37:155–163. DOI: 10.1016/j.cretres.2012.03.014.

Silvestri F. 1913. Descrizione di un nuovo ordine di insetti. Bollettino del Laboratorio di Zoolgia Generale e Agraria della R. Scuola Superiore d’Agricoltura in Portici 7:193–209.

Skuse FAA. 1890. Diptera of Australia. Part VII.—The Tipulidae brevipalpi. Proceedings of the Linnean Society of New South Wales 4(2):757–892.

Smith RDA, Ross AJ. 2017. Amberground pholadid bivalve borings and inclusions in Burmese amber: Implications for proximity of resin-producing forests to brackish waters, and the age of the amber. Earth and Environmental Science Transactions of the Royal Society of Edinburgh 239–247. DOI: 10.1017/S1755691017000287.

Speiser P. 1909. Orthoptera Nematocera. In: Wissenschaftliche W, editor. Schwedischen Zoologischen Expedition nach dem Kilimandjaro, dem Meru und dem umgebenden Massaisteppen Deutsch–Ostafrikas, Band 2, 10. Diptera, 4. Orthorapha. pp. 31–112.

Starý J. 2003. Revision of European species of the genus Rhabdomastix (Diptera: Limoniidae). Part 1: Introduction and subgenus Luridia subgen. n. European Journal of Entomology 100:587–608. DOI: 10.14411/eje.2003.089.

Starý J. 2004. Revision of European species of the genus Rhabdomastix (Diptera: Limoniidae). Part 2: Subgenus Rhabdomastix s. str. European Journal of Entomology 101:657–687. DOI: 10.14411/eje.2004.089.

Statz G. 1944. Neue Dipteren (Nematocera) aus dem Oberoligocän von Rott. III. Familie Limnobiidae (Stelzmücken). IV. Familie: Tipulidae (Schnaken). V. Familie: Culicidae (Stechmücken). Palaeontographica Abteilung B 95:93–120.

Szwedo J, Wang B, Sozyszyska-Maj A, Azar D, Ross A. 2020. International palaeoentomological society statement. Palaeoentomology 3:221–222. DOI: 10.11646/palaeoentomolgy.3.3.1.

Theischinger G, Billingham ZD, Martin J, Growns I. 2019. The genus Rhabdomastix Skuse in Australia (Diptera: Tipuloidae: Limoniidae). Zootaxa 4661(1):65–100. DOI: 10.11646/zootaxa.4661.1.3.