

New Miocene limoniid craneflies from Dominican amber and their evolutionary importance

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Kopeć, K., Kania-Kłosok, I., Ross, A., Soszyńska, A., and Krzemiński, W. 2026. New Miocene limoniid craneflies from Dominican amber and their evolutionary importance. *Acta Palaeontologica Polonica* 71 (1): 119–132.

This paper describes three new species belonging to the genus *Styringomyia*, based on specimens preserved in Early Miocene (Burdigalian) Dominican amber: *Styringomyia caridadi* sp. nov., *S. caribean*a sp. nov., and *S. grimaldii* sp. nov. Previously, only five extinct species of *Styringomyia* were known, including two from Dominican amber. These new discoveries increase the total number of species known from fossils to eight. The genus *Styringomyia* is morphologically intriguing, characterized by the highly complex structure of the male and female terminalia, particularly the morphology of the gonostyles. The hypopygial features of the five Dominican amber species resemble those of certain extant *Styringomyia* species found in Australia. These findings contribute to our broader understanding of cranefly diversity and significantly enhance our knowledge of Miocene *Styringomyia* and this stage of evolution of the genus. Notably, despite the abundance of *Styringomyia* fossils in Dominican amber, the genus is not known to inhabit the island of Hispaniola today.

Key words: Diptera, Limoniidae, Chioneinae, fossil insects, taxonomy, evolution, Miocene, Dominican Republic, Hispaniola.

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Received 6 November 2025, accepted 8 January 2026, published online 26 March 2026.

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Introduction

The cranefly *Styringomyia* Loew, 1845, belongs to the family Limoniidae in the infraorder Tipulomorpha of the order Diptera. The Tipulomorpha includes the extant families Limoniidae, Pedicidae, Tipulidae, Cylindrotomidae, and Trichoceridae, as well as the extinct families Archilimoniidae and Psychotipidae. The latter two families were included in Tipulomorpha by Krzemiński and Krzemińska (2003), and all six families were assigned to the suborder Polyneura. Morphologically, *Styringomyia* is particularly distinctive differing significantly from most other Limoniidae in wing

venation, the structure of the male hypopygium, and the female copulatory organs. The genus comprises 176 described extant species distributed across the Neotropical, Ethiopian, Australian, and Palearctic regions, but it has not been recorded in the Nearctic region. The first fossil representatives of this genus were discovered by Hermann Loew preserved in East African copal and Baltic amber (Loew 1845, 1850). The first extant species, *Styringomyia didyma* Grimshaw, 1901, was described half a century later from Hawaii. Detailed information on the history of discoveries and research on this fascinating genus was provided by Edwards (1914) and Ribeiro (2003). A total of six fossil species have been described so far, although one was

subsequently synonymized: *Styringomyia venusta* Loew, 1845, from East African copal, *S. gracilis* Loew, 1850, from Baltic amber, *S. concinna* (Cockerell, 1917) (= *S. extensa* Cockerell & Haines, 1921, see Krzemiński et al. 2019) from the Bembridge Marls of the Isle of Wight, *S. dominicana* Podenas & Poinar, 1999, from Dominican amber and *S. optiva* Podenas & Poinar, 2001, also from Dominican amber (Table 1). These, along with the three new species described here, demonstrate that Dominican amber has yielded the most diverse known fauna of extinct *Styringomyia* species (Arillo and Ortuño 2005).

Dominican amber is mined in the Dominican Republic on the island of Hispaniola and is considered to be of Early Miocene (Burdigalian) age (Iturralde-Vinent and MacPhee 1996; Penney 2010; Grimaldi and Ross 2017). This stage ranges 20.45–15.98 Mya (International Chronostratigraphic Chart v.2024/12, <https://stratigraphy.org/chart>). The resin that fossilized into Dominican amber was produced by trees belonging to an extinct species of the genus *Hymenaea* (Seyfullah et al. 2018). A total of eight *Styringomyia* specimens preserved in Dominican amber are now known (Table 2). The new discoveries presented here enhance our understanding of the diversity and evolution history of these flies during the Miocene as well as shed light on the possible course of evolution of this group. Investigation of the morphological similarities between fossil representatives of the genus and extant species currently found in Australia may help clarify both the evolution pathways of this group and the development of its current geographical distribution.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York City, USA; ISEA PAS MP,

Natural History Museum of the Institute of Systematics and Evolution of Animals, PAS, Kraków, Poland; NMS, National Museums Scotland, Edinburgh, Scotland, UK; SI, Smithsonian Institution, Washington DC, USA.

Other abbreviations.—A₁, A₂, anal veins; C, costal vein; Cu, cubital vein; d, discal cell; h, humeral vein; M₁₊₂–M₄, medial veins; Mb, medial-basal vein; m-cu, medial-cubital crossvein; R₁–R₅, radial veins; r-m, radial-medial crossvein; Rs, radial sector; Sc, subcostal vein; sc-r, subcostal radial crossvein; I–IV, palpomeres 1–4.

Nomenclatural acts.—The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank. The LSID for this publication is: LSID urn:lsid:zoobank.org:pub:8BBAE62B-D78A-430F-8A7B-B66A264454DF.

Material and methods

The five specimens studied herein (the representatives of extinct species) are all preserved as inclusions in Dominican amber. Two specimens are housed in the collections of AMNH; one in SI; one in NMS; and one in ISEA PAS.

The specimens were examined with a Nikon SMZ 1500 stereomicroscope equipped with a Nikon DS-Fi1 camera and measured with NIS-Elements D 3.0 software, as well as a Nikon SMZ25 stereomicroscope equipped

Table 1. List of fossil species of *Styringomyia*, including their location, preservation material, and age.

Species	Locality	Type of material	Age
<i>Styringomyia venusta</i> Loew, 1845	East Africa	African copal inclusion	Quaternary
<i>Styringomyia caridadi</i> sp. nov.	Dominican Republic	Dominican amber inclusion	Miocene: Burdigalian
<i>Styringomyia caribea</i> sp. nov.	Dominican Republic	Dominican amber inclusion	Miocene: Burdigalian
<i>Styringomyia dominicana</i> Podenas & Poinar, 1999	Dominican Republic	Dominican amber inclusion	Miocene: Burdigalian
<i>Styringomyia grimaldii</i> sp. nov.	Dominican Republic	Dominican amber inclusion	Miocene: Burdigalian
<i>Styringomyia optiva</i> Podenas & Poinar, 2001	Dominican Republic	Dominican amber inclusion	Miocene: Burdigalian
<i>Styringomyia concinna</i> (Cockerell, 1917) (= <i>Styringomyia extensa</i> Cockerell & Haines, 1921)	England: Isle of Wight	compression fossil	Eocene: Priabonian
<i>Styringomyia gracilis</i> Loew, 1850	Baltic region	Baltic amber inclusion	Eocene: Priabonian

Table 2. List of specimens of species known from Dominican amber.

Number	Sex	Type	Collection	Species
NMS G.2019.6.3	male	holotype	NMS	<i>Styringomyia caridadi</i> sp. nov.
AMNH 11833	male	paratype	AMNH, coll. J. Brodzinsky	<i>Styringomyia caridadi</i> sp. nov.
MP/5259	male	holotype	ISEA PAS, coll. K. Kopeć	<i>Styringomyia caribea</i> sp. nov.
REG # 10937	male	paratype	SI, coll. J. Brodzinsky/M. Lopez-Penha	<i>Styringomyia caribea</i> sp. nov.
D-7-202	male	holotype	G.O. Poinar coll.	<i>Styringomyia dominicana</i> Podenas & Poinar, 1999
D-7-202A	male	paratype	G.O. Poinar coll.	<i>Styringomyia dominicana</i> Podenas & Poinar, 1999
AMNH DR-8-73	male	holotype	AMNH	<i>Styringomyia grimaldii</i> sp. nov.
D-7-39H	male	holotype	G.O. Poinar coll.	<i>Styringomyia optiva</i> Podenas & Poinar, 2001

with a Nikon DS-Ri2 digital camera. Measurements were taken only from undamaged structures. Drawings were created by tracing the specimen and photographs, prepared by IKK. Descriptive terminology follows McAlpine et al. (1981), Ribeiro (2003) and Podenas (2011).

Systematic palaeontology

Order Diptera Linnaeus, 1758

Infraorder Tipulomorpha Rohdendorf, 1961

Family Limoniidae Speiser, 1909

Subfamily Chioneinae Rondani, 1841

Genus *Styringomyia* Loew, 1845

Type species: Styringomyia venusta Loew, 1845, monotypic, Dominican amber, Miocene.

Styringomyia caridadi sp. nov.

Figs. 1–3.

ZooBank LSID: urn:lsid:zoobank.org:act:EF125B23-6307-4E88-AADD-8C6315DD9B5C.

Etymology: Dedicated to Jorge Caridad, Director of the Amber World Museum, in recognition of his donation of the holotype to National Museums Scotland.

Type material: Holotype: NMS G.2019.6.3, male, well preserved male imago lacking part of legs. Paratype: AMNH 11833, male, coll. Jacob Brodzinsky, an inclusion in Dominican amber, well preserved male imago lacking part of legs.

Type locality: Dominican amber, Dominican Republic.

Type horizon: Lower Miocene (Burdigalian).

Material.—Type material only.

Diagnosis.—Pedicel massive, bulbous, $1.5\times$ as long as wide; last palpomere longer than penultimate one; wing without petiole; r-m elongate, as long as basal section of R_{4+5} ; d-cell elongate, $5.5\times$ as long as wide; m-cu in $0.16\times$ of d-cell length from fork of Mb; hypopygium slender, narrow, $2\times$ as long as wide, basal part of gonocoxite broad, approximately $2\times$ as long as wide, distal part of gonocoxite narrow, elongate, approximately $1.5\times$ as long as its basal part; gonocoxite with two very elongate terminal bristle (b) at apex; four apical extensions of gonostylus present: extension I, tiny, not very elongate; extension II, narrow, angled toward the internal part of hypopygium, ending with a long, strongly sclerotized spine; extension III, narrowed and slightly bent at the apex toward the inner part of the hypopygium, strongly sinusoidal; extension IV, middle part widened, significantly broader than its distal part, slightly sinusoidal, apical part forming an almost right angle with the basal part with a narrowed, sharp apex; tergite IX elongate, approximately $2\times$ as long as wide, broad, and truncate at apex; sternite X triangular, tapering towards the tip.

Description.—Body (Fig. 1A₁, 1B₁) 6.8 mm long (holotype), 6.9 mm long (paratype), pale brown, wings without a color pattern, pterostigma absent.

Head (Fig. 1A₁, A₂, A₅): antenna (Figs. 1A₂, A₅, 2A₂) 1.7 mm long (1/0.2; 2/0.1; 3/0.1; 4–16/0.1) in both holotype and paratype; longer than head but shorter than head and thorax combined; longer than palpus; scape narrow, elongate, cylindrical, $1.5\times$ as long as wide; pedicel massive, spherical, much shorter than scapus, $1.5\times$ as long as wide, flagellomeres elongate, ovoid, approximately $2\times$ as long as wide, became more slender to the apex of antenna; last flagellomere as long as penultimate one, with two not very elongate setae at apex, flagellomeres with a few elongate setae, six of them very elongate, longer than segment bearing them; palpus (Figs. 1A₂, A₅; 2A₃) 0.4 mm long (1–4/0.1) (holotype), 0.6 mm long (1/0.2; 2–4/0.1) (paratype), palpomeres elongate, narrow, first palpomere longer than the rest, palpomeres 2–3 of equal length, approximately $2\times$ as long as wide, palpomeres with few not very elongate setae, not longer than segments bearing them.

Thorax (Fig. 1A₁, B₁): Wing (Figs. 1A₁, A₆, B₁, 2A₁) 4.6 mm long, 1.0 mm wide (holotype), 4.7 mm long, 1.0 mm wide (paratype), $4.5\times$ as long as wide; Rs almost straight, slightly arched basally, elongate, shorter than R_{4+5} , $3\times$ as long as R_{2+3} , R_1 ending just before fork of Rb; R_{4+5} $2\times$ as long as Rs; M_3 approximately $1.2\times$ the length of d-cell; d-cell 1.1 mm long (holotype and paratype); tip of Cu beyond fork of M_{3+4} on M_3 and M_4 , in approximately $0.3\times$ of M_4 ; A₁ and A₂ slightly waved, tip of A₁ just beyond level of R_{2+3} , tip of A₁ in approximately $0.5\times$ of Mb.

Abdomen (Fig. 1A₁, A₃, A₄, B₁): Hypopygium pale brown, with a brighter distal part of gonocoxite (Fig. 1A₃, A₄) 0.9 mm long (holotype), 0.7 mm long (paratype), elongate and slender, constituting approximately $0.2\times$ the body length; gonocoxite 0.8 mm long (holotype), 0.6 mm long (paratype), basal part approximately $2\times$ as long as wide; four apical extensions of gonostylus, aedeagus tubular, relatively narrow, interbases slightly elongate, narrow, angled toward the internal part of hypopygium, sternite X almost triangular in shape, gradually narrowing from base to tip, tergite IX broad, truncated at the apex.

Remarks.—*Styringomyia caridadi* sp. nov. is most similar to *S. caribeana* sp. nov.; however, in *S. caridadi*, the petiole is absent, whereas in *S. caribeana* it is elongate, as long as $0.15\times$ the length of M_3 . Additionally, the pedicel of *S. caridadi* is massive and bulbous, while in *S. caribeana* it is elongate and cylindrical. In *S. caridadi*, the d-cell is $5.5\times$ as long as wide, and the m-cu is situated at $0.16\times$ the length of d-cell from the fork of Mb; in contrast, in *S. caribeana*, the d-cell is $7\times$ as long as wide, with the m-cu located at $0.25\times$ the d-cell length from the fork of Mb. Sternite X in *S. caridadi* is broad and truncate at the apex, whereas in *S. caribeana* it is rounded apically. *S. caridadi* also lacks of a petiole, similar to *S. grimaldii* sp. nov., but differs in that the r-m vein in *S. caridadi* is well developed and as long as the basal section of R_{4+5} , while in *S. grimaldii* is nearly reduced. However, the most distinctive differences between these two species are visible in the morphology of the hypopygium. In *S. caridadi*,

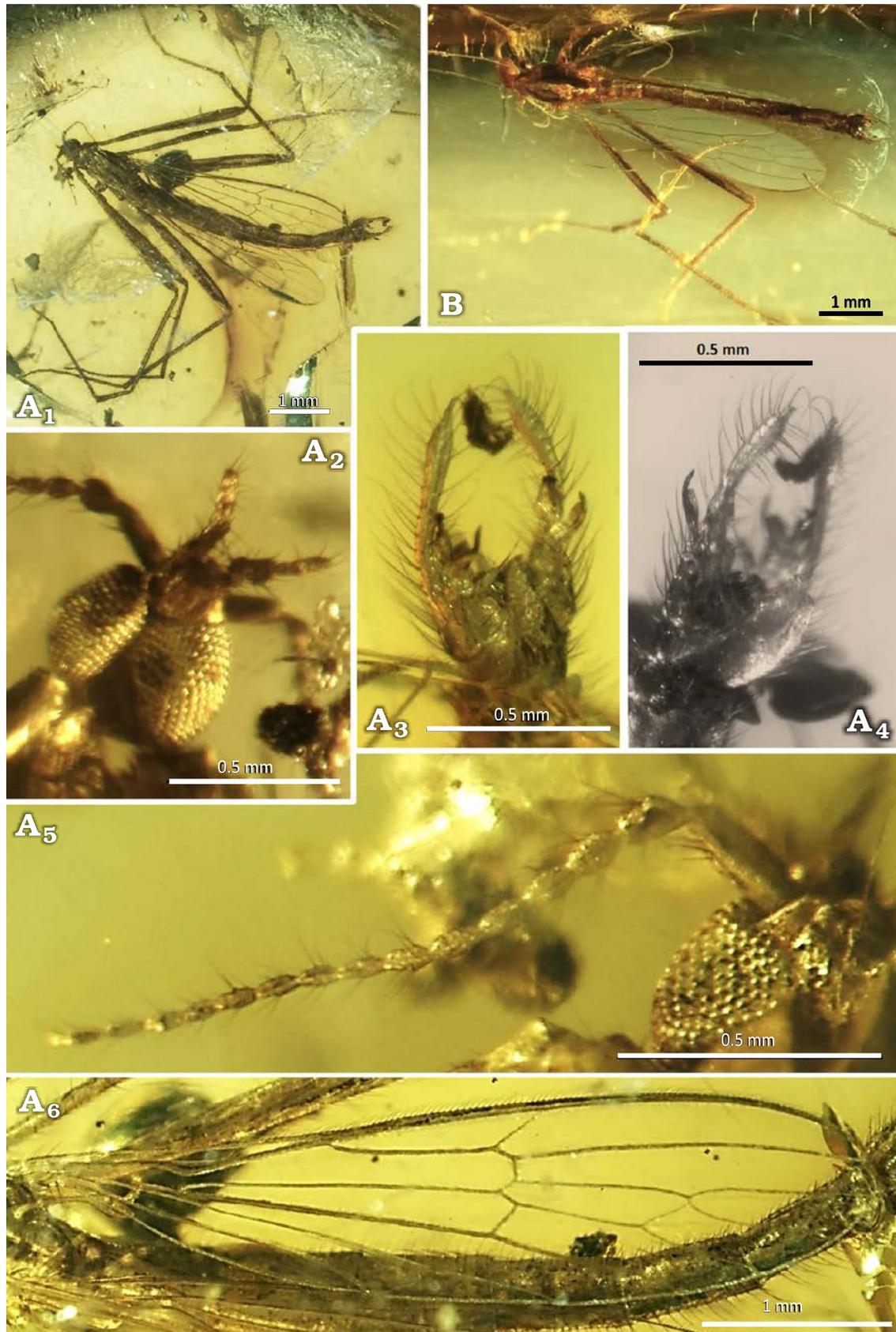


Fig. 1. Limoniid cranefly *Styringomyia caridadi* sp. nov. from Dominican amber, Dominican Republic, Lower Miocene (Burdigalian). A. Holotype NMS G.2019.6.3, male; body in ventral view (A₁), palpi in ventral view (A₂), hypopygium in dorsal (A₃) and ventral (A₄) views; antenna (A₅), wing (A₆). B. Paratype AMNH 11833, male; body in ventral view.

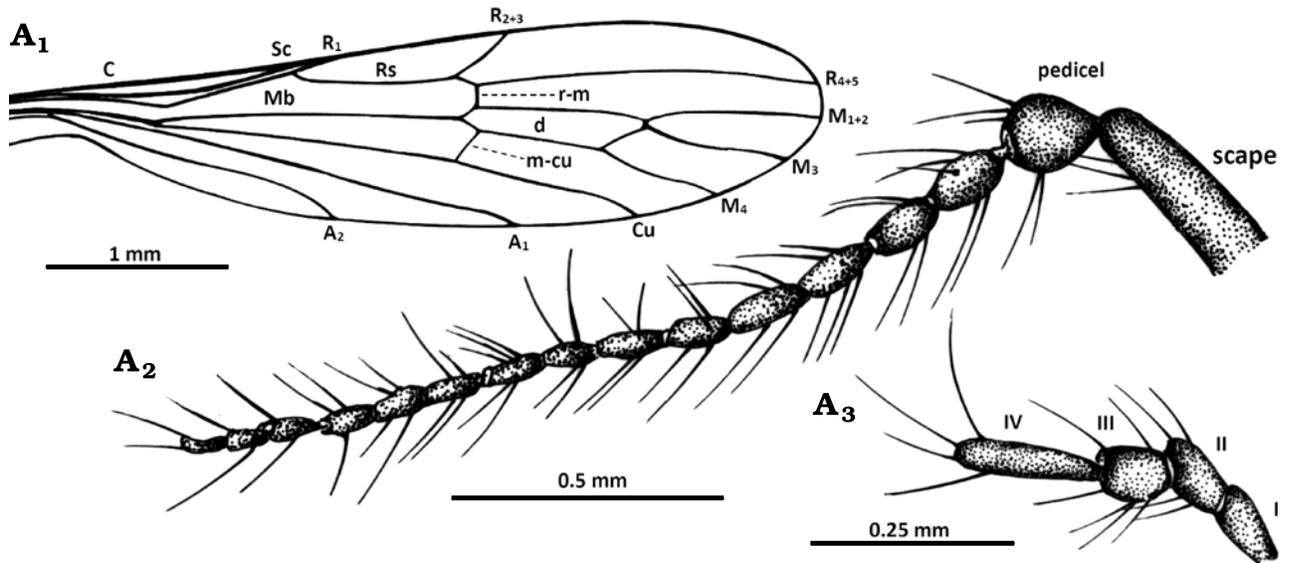


Fig. 2. Limoniid cranefly *Styringomyia caridadi* sp. nov. from Dominican amber, Dominican Republic, Lower Miocene (Burdigalian). Holotype NMS G.2019.6.3, male; wing (A₁), antenna (A₂), and palpus (A₃). Abbreviations: A₁, A₂, anal veins; C, costal vein; Cu, cubital vein; d, discal cell; M₁₊₂–M₄, medial veins; Mb, medial-basal vein; m-cu, medial-cubital crossvein; R₁–R₅, radial veins; r-m, radial-medial crossvein; Rs, radial sector; Sc, subcostal vein; I–IV, palpomeres 1–4.

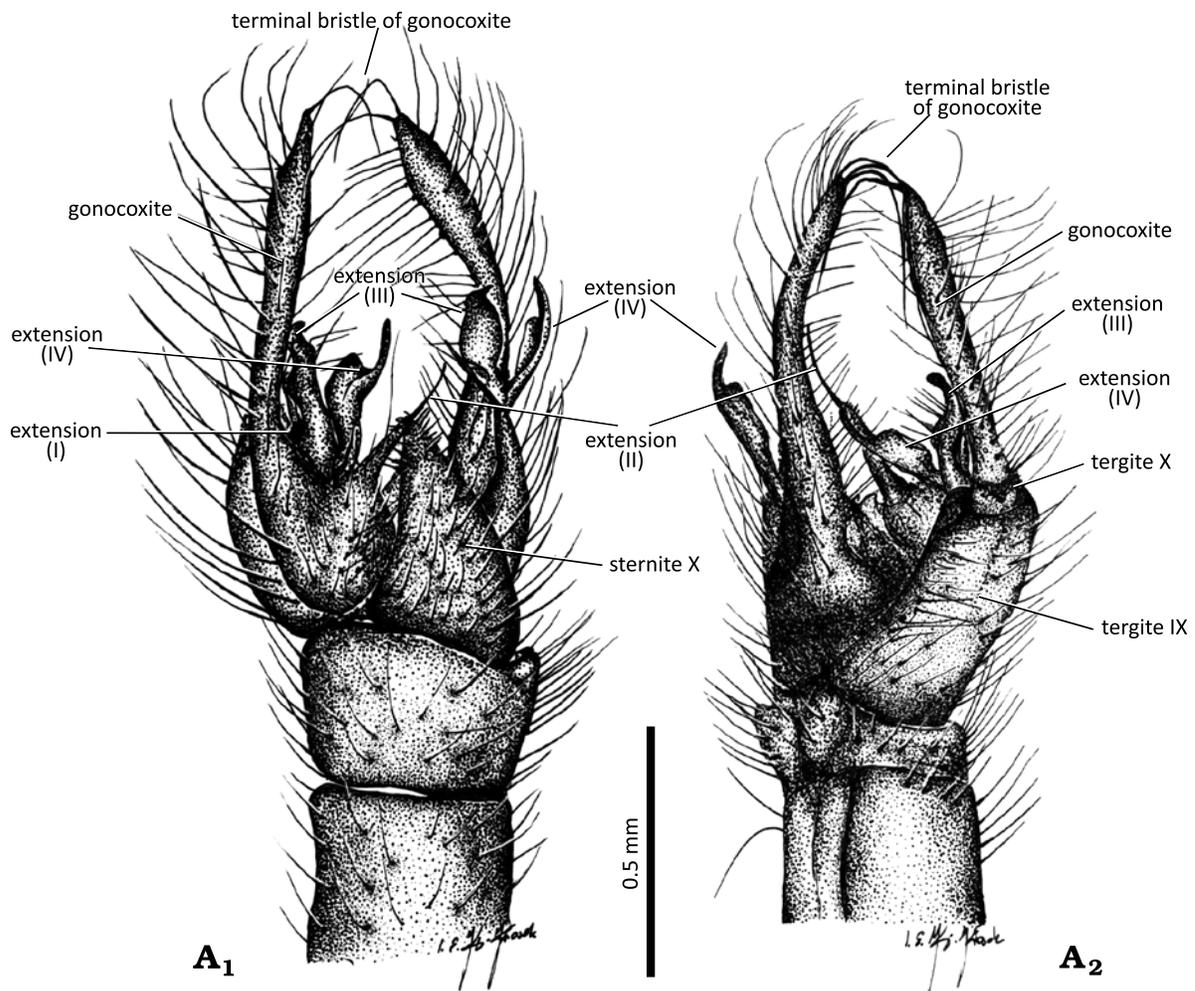


Fig. 3. Limoniid cranefly *Styringomyia caridadi* sp. nov. from Dominican amber, Dominican Republic, Lower Miocene (Burdigalian). Holotype NMS G.2019.6.3, male; hypopygium in latero-dorsal (A₁) and latero-ventral (A₂) views.

the hypopygium is relatively narrow and slender, while in *S. grimaldii* it is massive and broad. The gonocoxite of *S. caridadi* is elongate, with a very narrow distal portion bearing two long terminal bristles (b) at the apex. It also features four apical extensions of the gonostylus, with extension III narrowed, slightly bent apically toward the inner side of the hypopygium, and strongly sinusoidal in shape. The tergite IX of *S. caridadi* is elongate, approximately $2\times$ as long as wide, and truncate at apex; sternite X is triangular, tapering toward the tip. In *S. grimaldii*, the gonocoxite is less elongate, lacks the terminal bristle (b) at the apex, and extension III is flattened with an outward-pointing tip forming a right angle to the longitudinal axis of the gonostylus. Tergite IX is also elongate ($2\times$ as long as wide), but slightly rounded at the apex; the sternite is broad at the base, tapering strongly toward the tip to form a narrow, tongue-shaped structure.

In the two species described from Dominican amber by Podenas and Poinar (1999, 2001), *S. dominicana* and *S. optiva*, only one elongate terminal bristle (b) is present at the apex of the gonocoxite, whereas two are present in *S. caridadi* and *S. grimaldii*. Moreover, the hypopygium of *S. optiva* is quite distinct; it is rather short and massive than slender and is characterized by a flattened intermediate arm (extension III) with an outward-pointing tip forming a right angle with the longitudinal axis of the gonostylus. The inner arm (extension IV) with a basal part that is broader than the apical portion, slightly sinusoidal in shape, with the apical part forming an almost right angle with the basal part and terminating in an acute tip (Podenas and Poinar 2001). In *S. caridadi*, the hypopygium is slender; the tip of extension III does not point outwards, although it is bent, but is direct inward, toward the inner part of the hypopygium. It is narrowed at the apex and strongly sinusoidal. Extension IV has a middle part wider than the apex, is slightly sinusoidal, and its apical part forms an almost right angle with the basal part, ending in a sharp, strongly narrowed apex. However, this narrowed and sharp apex is distinctly shorter than that of *S. optiva*.

Geographic and stratigraphic range— Dominican amber, Dominican Republic, Lower Miocene (Burdigalian).

Styringomyia caribearia sp. nov.

Figs. 4–6.

ZooBank LSID: urn:lsid:zoobank.org: act:D2692737-E9EF-49BE-9D95-BE323DE2A3EA.

Etymology: Derived from Caribbean.

Type material: Holotype: ISEA PAS MP/5259, male, coll. KK, well preserved male imago lacking part of legs. Paratype REG. #10937, male, inclusion in Dominican amber, coll. Jacob Brodzinsky/ Marianela (Mañeña) Lopez-Penha, deposited in the Smithsonian Institution, well preserved male imago lacking part of legs.

Type locality: Dominican amber, Dominican Republic.

Type horizon: Lower Miocene (Burdigalian).

Material.—Type material only.

Diagnosis.—Pedicel elongate, cylindrical, $1.5\times$ as long as

wide; last palpomere longer than penultimate one; wing with petiole; petiole approximately $0.15\times$ the length of M_3 ; vein r-m elongate, as long as basal section of R_{4+5} ; d-cell elongate, $7\times$ as long as wide; crossvein m-cu located at $0.25\times$ the length of d-cell from fork of Mb; hypopygium slender and narrow, $2\times$ as long as wide; basal part of gonocoxite wide, approximately $2\times$ as long as wide, distal part narrow and elongate, approximately $1.5\times$ as long as the basal part; gonocoxite with two very elongate terminal bristle (b) at apex; four apical extensions of gonostylus present; extension I small, not elongate; extension II narrow, directed toward the internal part of hypopygium, ending in a long, strongly sclerotized spine; extension III narrowed and slightly bent at the apex toward the inner part of the hypopygium, strongly sinusoidal; extension IV with a widened middle part, much wider than its distal part, slightly sinusoidal, with the apical part forming an angle with the basal part and in a narrowed, sharp apex; tergite IX elongate, approximately $2\times$ as long as wide, rounded at the apex, with strongly sclerotized small spine-shaped structure at the tip; sternite X triangular, with strongly tapered tip.

Description.—Body (Fig. 4A₁, B₁) 8.2 mm long (holotype), 7.4 mm long (paratype), pale brown, wings without color pattern, pterostigma absent.

Head (Fig. 4A₁, B₁): Antenna (Fig. 4A₁, A₂, B₁, 5A₂) 1.7 mm long (holotype and paratype) (1/0.2; 2–16/0.1); longer than head and palpus; scape massive, elongate, widened distally, $2.5\times$ as long as wide, longer than pedicel; pedicel spherical $1.5\times$ as long as wide; flagellomeres elongate, ovoid, approximately $3\times$ as long as wide, becoming more slender towards the apex of antenna; last flagellomere as long as penultimate one, with three moderately elongate setae at apex, each flagellomere bears four elongate setae, slightly longer than the segment itself; palpus (Figs. 4A₄, 5A₃) not very elongate 0.4 mm long (holotype) (1–4/0.1), 0.8 mm long (paratype) (1–4/0.2), palpomeres elongate, almost cylindrical, palpomeres 1–3 of comparable length, with the last palpomere longer than the penultimate one; all palpomeres bears several elongate setae, not exceeding the length of the segments bearing them.

Thorax (Fig. 4A₁, B₁): Wing (Figs. 4A₁, A₃, B₁, B₂, 5A₁) 5.2 mm long, 1.0 mm wide (holotype), 5.0 mm long, 0.7 mm wide (paratype), approximately $5–7\times$ as long as wide; vein Rs almost straight, slightly arched basally, elongate, shorter than R_{4+5} but $3\times$ longer than R_{2+3} , vein R_1 ends beyond fork of Rs; vein M_3 shorter than d-cell; d-cell 1.11 mm long (holotype), approximately $7\times$ as long as wide; tip of M_4 reaches well beyond petiole and passes the halfway point of R_{4+5} ; tip of A_2 before fork of Rb.

Abdomen (Figs. 3A₁, A₂; 4A₁, A₅, A₆, B₁): Hypopygium pale brown (Figs. 4A₁, A₅, A₆, B₁, 6A₁, A₂) 1.0 mm long, with gonocoxite 0.9 mm long (both holotype and paratype), slender, elongate, comprising approximately $0.1\times$ of the total body length; gonocoxite elongate and small; gonostylus with four extensions.

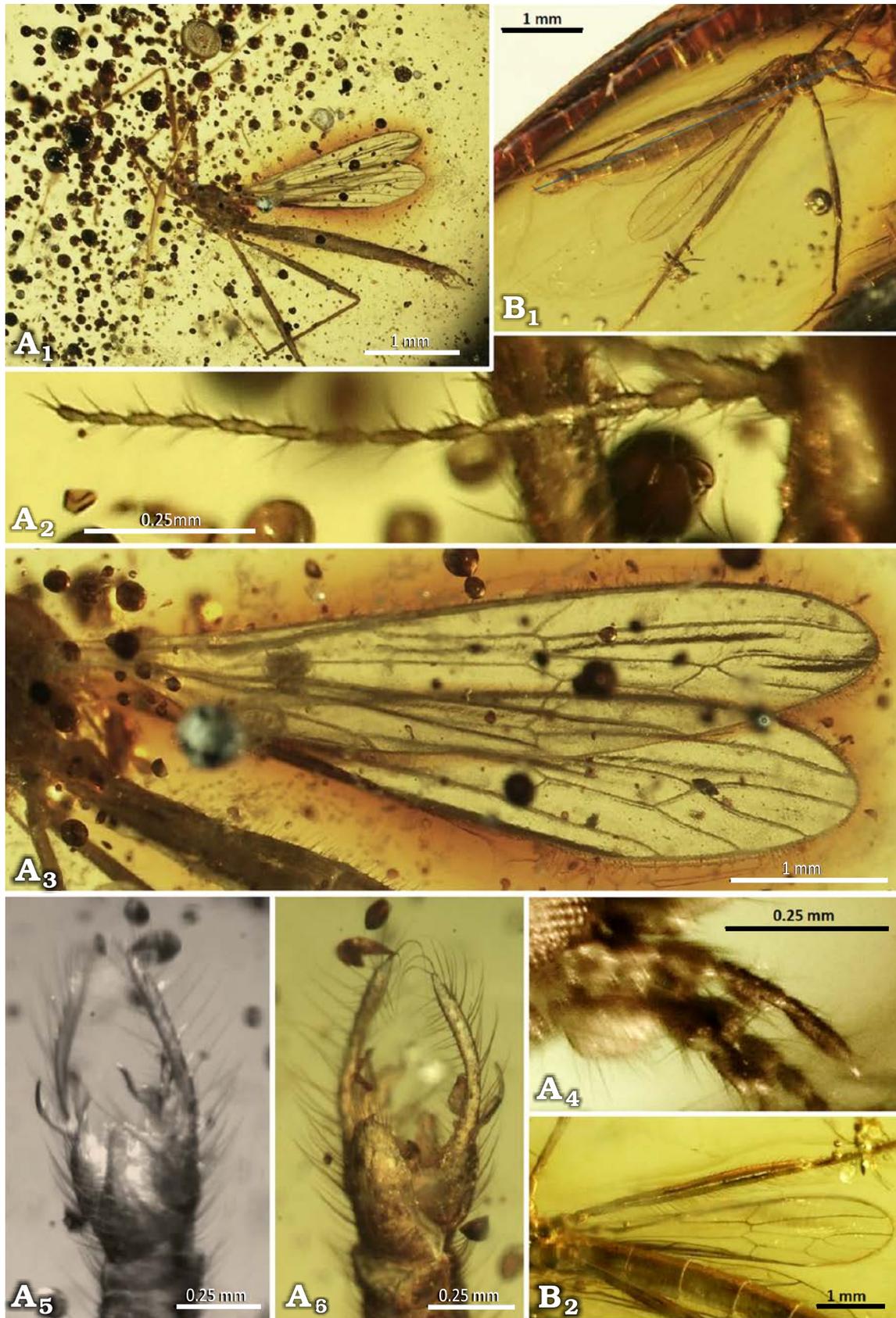


Fig. 4. Limoniid cranefly *Styryngomyia caribearia* sp. nov. from Dominican amber, Dominican Republic, Lower Miocene (Burdigalian). A. Holotype ISEA PAS MP/5259, male; body in lateral view (A₁), antenna (A₂), wing (A₃), palpus (A₄), hypopygium in latero-dorsal (A₅) and latero-ventral (A₆) views. B. Paratype AMNH 10937, male; body in latero-ventral view (B₁), wing (B₂).

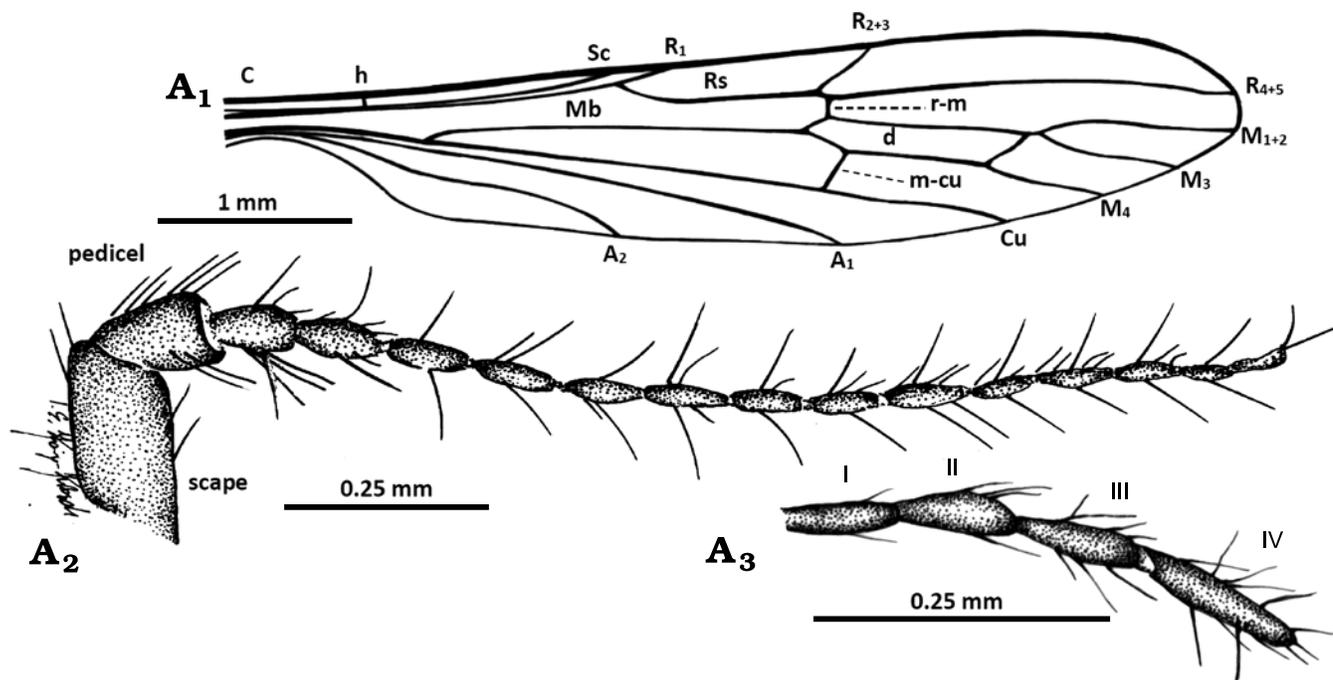


Fig. 5. Limoniid cranefly *Styringomyia caribeana* sp. nov. from Dominican amber, Dominican Republic, Lower Miocene (Burdigalian). Holotype ISEA PAS MP/5259, male; wing (A₁), antenna (A₂), and palpus (A₃). Abbreviations: A₁, A₂, anal veins; C, costal vein; Cu, cubital vein; d, discal cell; h, humeral vein; M₁₊₂–M₄, medial veins; Mb, medial-basal vein; m-cu, medial-cubital crossvein; R₁–R₅, radial veins; r-m, radial-medial crossvein; Rs, radial sector; Sc, subcostal vein; I–IV, palpomeres 1–4.

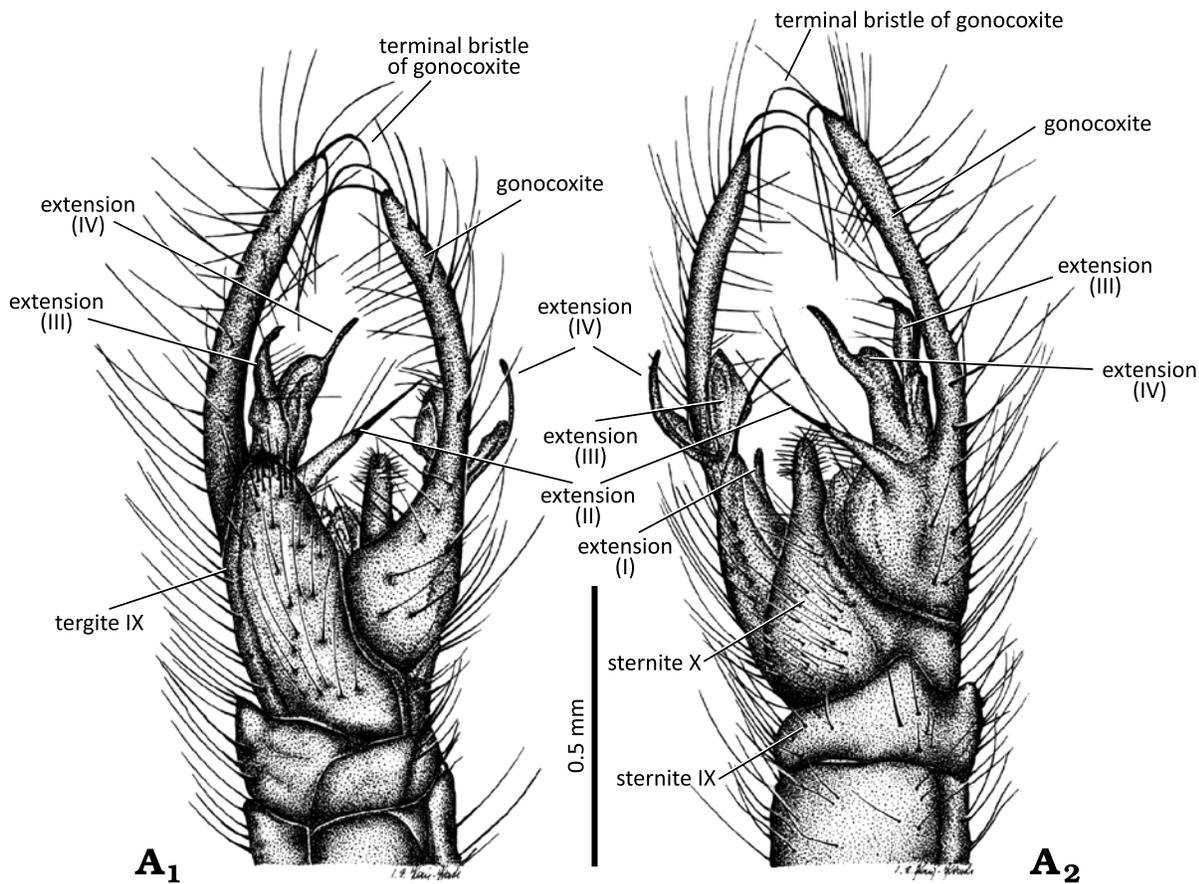


Fig. 6. Limoniid cranefly *Styringomyia caribeana* sp. nov. from Dominican amber, Dominican Republic, Lower Miocene (Burdigalian). Holotype ISEA PAS MP/5259, male; hypopygium in latero-ventral (A₁) and latero-dorsal (A₂) views.

Remarks.—*Styringomyia caribea* sp. nov. differs from the species described by Podenas and Poinar (1999, 2001), as both *S. dominicana* and *S. optiva* possess only one elongate terminal bristle (b) at the apex of the gonocoxite, whereas two such bristles are present in *S. caribea*. The hypopygium of *S. optiva* is relatively short and massive, and is characterized by a flattened intermediate arm (extension III) with an outward-pointing tip forming a right angle with the longitudinal axis of the gonostylus. The inner arm (extension IV) has a basal part broader than the apical one, is slightly sinusoidal, and its apical part forms an angle with the basal part, ending in an acute tip (Podenas and Poinar 2001). In *S. caribea*, the hypopygium is slender. The tip of extension III is bent inward, toward the inner part of the hypopygium, and is narrowed at the apex, strongly sinusoidal. Extension IV is characterized by a middle part wider than the apex, slightly sinusoidal, with the apical part forming an angle with the basal part, and ending in a sharp, strongly narrowed apex, which is distinctly shorter than in *S. optiva*. In *S. grimaldii* sp. nov., four apical extensions of the gonostylus are present, but the terminal bristle (b) at the apex of the gonocoxite is absent. In this species, extension I of the gonostylus is narrow and not very elongate, extension II is direct inward, toward the hypopygium, and ends with a short, triangular apical part bearing a thick, short spine at the tip, extension III is flattened with an outward-pointing tip forming a right angle with the longitudinal axis of the gonostylus, extension IV is short, narrowed at the middle, and ends with a very narrow, short, and strongly sclerotized tip. *Styringomyia caribea* is most similar to *S. caridadi* sp. nov. (see the comparison with *S. caridadi* above).

Geographic and stratigraphic range.—Dominican amber, Dominican Republic, Lower Miocene (Burdigalian).

Styringomyia grimaldii sp. nov.

Figs. 7, 8.

ZooBank LSID: urn:lsid:zoobank.org:act:6454CCE7-568B-4960-938A-AB06FF4958AE.

Etymology: Dedicated to the eminent scientist and entomologist David A. Grimaldi (AMNH).

Holotype: AMNH DR-8-73 (male), not well preserved male imago lacking head and thorax, but with preserved parts of palpi.

Type locality: Dominican amber, Dominican Republic.

Type horizon: Lower Miocene (Burdigalian).

Material.—Holotype only.

Diagnosis.—Last palpomere as long as penultimate one; wing without petiole, r-m short, almost completely reduced; d-cell elongate, 3.5× as long as wide; m-cu at 0.2× length from fork of Mb; hypopygium wide, as long as wide; basal part of gonocoxite massive, very short and wide, approximately 1.5× as long as wide, distal part of gonocoxite elongate and narrow 1.5× as long as its basal part; four apical extensions of gonostylus present, without terminal bristle (b) at the gonocoxite apex; extension I narrow, not very elongate; extension II

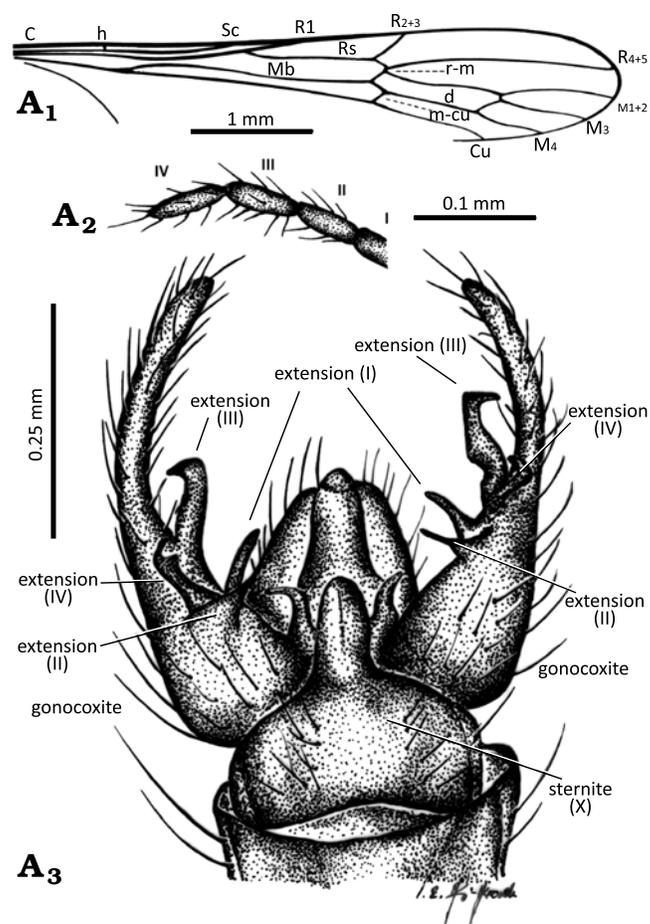


Fig. 7. Limoniid crane fly *Styringomyia grimaldii* sp. nov. from Dominican amber, Dominican Republic, Lower Miocene (Burdigalian). Holotype AMNH 11833, male; wing (A₁), palpus (A₂), hypopygium in dorsal view (A₃). Abbreviations: C, costal vein; Cu, cubital vein; d, discal cell; h, humeral vein; M₁₊₂–M₄, medial veins; Mb, medial-basal vein; m-cu, medial-cubital crossvein; R₁–R₅, radial veins; r-m, radial-medial crossvein; Rs, radial sector; Sc, subcostal vein; I–IV, palpomeres 1–4.

angled inward, with a short, triangular apical part bearing a thick and short spine at apex, extension III flattened, with an outward-pointing tip forming a right angle with longitudinal axis of gonostylus; extension IV short, narrowed in the middle, with a very narrow, short, strongly sclerotized tip; tergite IX elongate, 2× as long as wide, slightly rounded at the apex; sternite widened at the base, strongly tapering distally, forming a narrow tongue-shaped structure.

Description.—Body (Fig. 8A₁) pale brown, wings without color pattern, pterostigma absent.

Head: Palpomeres almost the same length, not very elongate (Fig. 7A₂).

Thorax: Wing (Figs. 7A₁, 8A₁, A₃) 5.0 mm long, 1.0 mm wide, approximately 4.5× as long as wide; Rs almost straight, slightly arched basally, elongate, shorter than R₄₊₅, 4× as long as R₂₊₃, R₁ ending at 0.3× the length of Rs; R₂ 2× as long as Rs; M₃ approximately 1.3× the length of d-cell; d-cell 1.11 mm long; tip of Cu just beyond the fork of M₃₊₄ on M₃ and M₄.

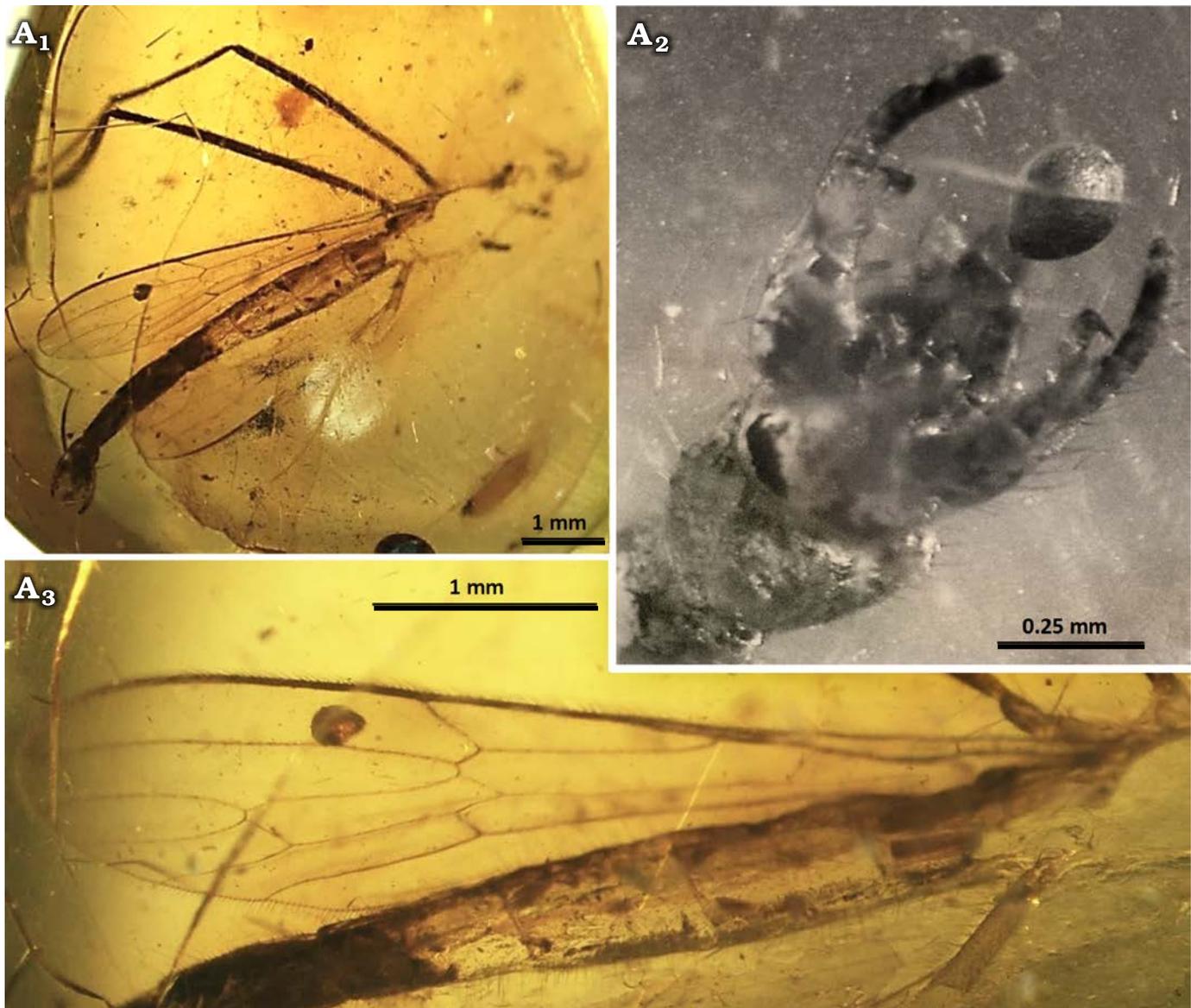


Fig. 8. Limoniid crane fly *Styringomyia grimaldii* sp. nov. from Dominican amber, Dominican Republic, Lower Miocene (Burdigalian). Holotype AMNH 11833, male; body in latero-ventral view (A₁), hypopygium in dorsal view (A₂), wing (A₃).

Abdomen (Fig. 7A₃, 8A₁, A₃): Hypopygium pale brown, 0.7 mm long, with a brighter distal part of gonocoxite (Figs. 7A₃, 8A₁, A₂) 0.5 mm long, massive, constitute approximately $0.2 \times$ the body length; basal part of gonocoxite massive, $1.5 \times$ as long as wide; aedeagus tubular, thick, massive, wider than gonostylus; interbases slightly elongate, thick, angled toward the external part of hypopygium.

Remarks.—*Styringomyia grimaldii* sp. nov. is characterized by the absence of a petiole in the wing venation, similar to *S. caridadi* sp. nov., in which the petiole is also absent. In other species of *Styringomyia* from Dominican amber, the petiole is present. In *S. grimaldii*, vein r-m is almost completely reduced, whereas in *S. caridadi* this

vein is well developed, approximately as long as the basal section of R₄₊₅. However, the most important differences are visible in the morphology of the hypopygium. The hypopygium of *S. grimaldii* is massive, with a wide and relatively short basal part of gonocoxites and only moderately elongate distal parts. In contrast, in other species of *Styringomyia* from Dominican amber, the hypopygium is slender and elongate, with narrow and elongate distal parts of the gonocoxites. The basal part of the gonocoxite of *S. grimaldii* is broadened, approximately $2 \times$ as long as wide; the distal part is not strongly elongate, only slightly longer than the basal part.

Geographic and stratigraphic range— Dominican amber, Dominican Republic, Lower Miocene (Burdigalian).

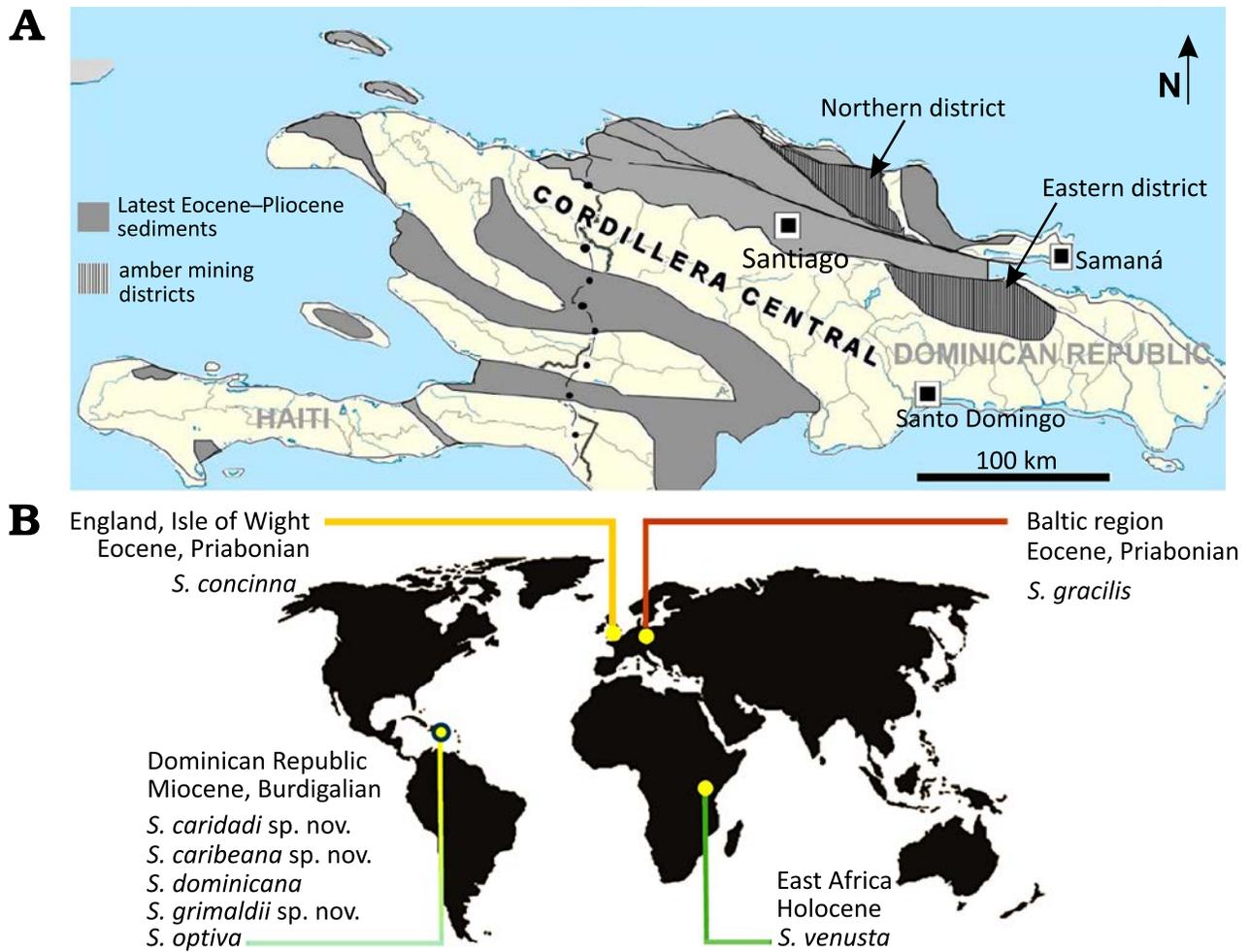


Fig. 9. A. Hispaniola map indicating actual amber mining districts in Dominican Republic (modified after Iturralde-Vinent and MacPhee 2019) with national and subnational borders according to https://commons.wikimedia.org/wiki/File:Hispaniola_location_map.svg). B. Localities where extinct species of *Styringomyia* have been found.

Results

Key to Miocene species of *Styringomyia*

- 1. Gonocoxite with apical bristle 2.
- Gonocoxite without apical bristle *S. grimaldii* sp. nov.
- 2. Gonocoxite with one apical bristle 3.
- Gonocoxite with two apical bristles 4.
- 3. Hypopygium slender, elongate; extension III flattened, with a slightly bent tip; inner arm of extension IV with a basal part broader than the apical part, straight; apical part elongate, with a sharp tip *S. dominicana* Podenas & Poinar, 1999
- Hypopygium rather broad, not very elongate; extension III flattened, with an outward-pointing tip forming a right angle with the longitudinal axis of the gonostylus; extension IV with a basal part broader than the apical part, slightly sinusoidal; apical part forming an almost right angle with the basal part, with an acute tip *S. optiva* Podenas & Poinar, 2001
- 4. Pedicel massive, bulbous; wing without petiole; d-cell

- 5.5 × as long as wide; basal section of R₅ elongate, as long as r-m; basal section of M₃ (from the fork of M₃₊₄ to the petiole) straight; tergite IX elongate, approximately 2 × as long as wide, truncate at apex; sternite X triangular, tapering towards the tip *S. caridadi* sp. nov.
- Pedicel elongate, cylindrical; wing with petiole; d-cell 7 × as long as wide; basal section of R₅ very short, 0.5 × the length of r-m; basal section of M₃ (from the fork of M₃₊₄ to the petiole) oblique; tergite IX elongate, approximately 2 × as long as wide, rounded at the apex, with a strongly sclerotized, small spine-like structure at the tip; sternite X triangular with a strongly tapered tip *S. caribeaana* sp. nov.

Discussion

The genus *Styringomyia* occupies a rather unique position within the family Limoniidae. Based on larval characteristics, it possesses a reduced head capsule compared to a more massive head capsule found in the lower Eriopterinae.

Oosterbroek and Theowald (1991) placed *Styringomyia* at the base of the so-called higher clade Eriopterinae [= Chioneinae] (Theischinger et al. 2018). Among modern representatives, the majority of species are found in the Oriental region (72 species) and Afrotropical region (55 species), with additional presence in the Australian and Oceanian regions (41 species). The genus is less diverse in the Neotropical and Palearctic regions each with only eight species. Although *Styringomyia* is sparsely represented in the fossil record, with only eight known species (including those described herein), the oldest dating back to the late Eocene, the body morphology of the Miocene representatives preserved in Dominican amber shows greater similarity to extant Australian species. Theischinger et al. (2018) identified three closely related species groups occurring in Australia: *S. bancrofti* group (five species), *S. terraereginae* group (two species), and *S. bipunctata* group (three species). The remaining five Australian species were not assigned to any of these groups. In the *S. bipunctata* group (*S. bipunctata* Theischinger & Billingham, 2018; *S. coronata* Theischinger & Billingham, 2018, and *S. williamsi* Theischinger & Billingham, 2018), male gonocoxites are evenly curved, almost conical, with the basal half noticeably expanded and a rather slender apical spine. The gonostyli consist of a single, slightly curved element that is subbasally expanded, bearing setae and short spines (Theischinger et al. 2018). Males of the *S. terraereginae* group (*S. terraereginae* Theischinger & Billingham, 2018, and *S. aterrima* Theischinger & Billingham, 2018) are characterized by long, slender gonocoxites bearing a longer spine at about midlength, a distinctly shorter apical spine, and gonostyli composed of three elements, including a whip-like one. The *S. bancrofti* group (*S. bancrofti* Edwards, 1914; *S. baroalba* Theischinger & Billingham, 2018; *S. collessi* Theischinger & Billingham, 2018, and *S. remex* Theischinger & Billingham, 2018) is characterized by conical gonocoxites with a broad basal lobe and a thick apical spine. Their gonostyli bear several comb-shaped elements (Theischinger et al. 2018). A narrow, slender hypopygium with very elongated gonocoxites is a feature observed in Miocene *Styringomyia* species. The gonostylus structures are positioned closer to the base of the gonocoxite than to its apex, similar to the condition in modern Australian species. Another distinctive feature of most extinct species is the presence of one or two very elongated, narrow structures at the apex of the gonocoxite, resembling the long, slender spines seen in some modern Australian taxa.

Craneflies of the genus *Styringomyia* currently inhabit tropical and subtropical climate zones. However, research on the modern fauna has shown that this genus is not represented on the island of Hispaniola (including the Dominican Republic) today (Oosterbroek 2025). It is quite surprising that the eight species found in the Neotropical region today (Alexander 1945a, b, 1946; Ribeiro 2003) are morphologically very different from those known from the Miocene, preserved in Dominican amber. Although representatives of the genus are rare in the fossil record, morphological com-

parison indicates a closer relationship between the extinct Miocene species from Dominican amber to the modern fauna of Australia, rather than the modern fauna of South America. Extant *Styringomyia* species from the Neotropical region, described and revised by Ribeiro (2003), are characterized by relatively broad and short gonocoxites, approximately the same size as the gonostyli. In contrast, the Miocene species from Dominican amber possess very elongate and narrow gonocoxites. Even in *S. grimaldii* sp. nov., which has a short and massive hypopygium, this structure is significantly more elongate than in species known from the modern Neotropical fauna. Of the 15 species currently known from Australia, as many as five (*S. aterrima*, *S. baroalba*, *S. bipunctata*, *S. coronata*, and *S. williamsi*), have very elongate and narrow gonocoxites, similar to those observed in species preserved in Dominican amber. Other Australian species, such as *S. collessi* and *S. remex*, also show some morphological similarities in the structures of the hypopygium. While their gonocoxites are as elongate, their shape resembles that found in the Miocene species. The two elongate bristles found at the apex of the gonocoxites in *S. caridadi* sp. nov. and *S. caribea* sp. nov. are likely homologous with the slender apical spine observed in the *S. bipunctata* group.

The evolution of this group of insects may have evolved a gradual reduction in the number of elongate bristles to a single, not very elongate spine at the apex of the gonocoxite, or even a complete loss of these structures. Over time, the shape of the gonocoxite likely evolved from a more elongate form, as seen in fossil representatives of the genus, to a shorter form, with the elements of the gonostylus shifted toward the apex of the gonocoxite. However, more fossil specimens and further research are needed to verify this hypothesis.

But, why has *Styringomyia* disappeared from the Caribbean? This question still remains unanswered, perhaps further research on the genus will clarify this issue.

Most species of this genus are currently found in the warmer regions of the world. Similarly, in the distant past, these insects most likely favored warm climatic conditions. This hypothesis is supported by the presence of their fossils resins deposits from present-day Central America and subfossil sites of Africa, as well as in Baltic amber (Fig. 9), dated to the Priabonian (Grimaldi and Ross 2017; Ross et al. 2024, in press).

Conclusions

Morphological analysis of fossil members of *Styringomyia* from Miocene Dominican amber indicates their closer relationship to the modern Australian fauna than to the modern Neotropical fauna. Key features, such as the strongly elongated and narrow gonocoxites and the presence of slender apical structures, show significant similarities to the morphology of some modern Australian species, particularly the *S. bipunctata* group.

The fossil record suggests that the original hypopygium

morphology in *Styringomyia* was characterized by more elongated gonocoxites and a more basal position of the gonostyle elements, whereas modern forms tend to shorten these structures and move them toward the apex of the gonocoxite. This may indicate directional evolutionary changes within the genus.

The absence of modern *Styringomyia* representatives in Dominican amber, despite their documented presence in the fossil record, suggests a regional extinction of the genus. The geographic distribution of both fossil and modern species indicates a preference for warm climates. Further research and the discovery of new fossil specimens are necessary to fully understand the evolutionary and biogeographic history of the genus *Styringomyia*.

Authors' contributions

KK, conceived and designed the study, obtaining material, lead and performed the data analysis, interpretations and analysis of the material, writing and corrections of the manuscript; IKK, conceived and designed the study, lead and performed the data analysis, interpretations and analysis of the material, environmental analysis, writing and corrections of the manuscript, graphics; AR, obtaining material, corrections of the manuscript; AS, writing and corrections of the manuscript; WK, conceived and designed the study, obtaining material, analysis, writing and corrections of the manuscript. All authors reviewed the manuscript.

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

Data availability: All data generated or analyzed during this study are included in this published article.

Acknowledgements

We would like to thank David A. Grimaldi (AMNH) for providing access to the material. This research was carried out as part of a project funded by the National Science Centre, Poland, Grant No. 2020/37/B/NZ8/03042. Funding: Open Access funding enabled and organized by Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Kraków, Poland.

Editor: Andrzej Kaim

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