2-24-2022

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A journal of world insect systematics

INSECTA MUNDI

0919

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Robert E. Woodruff Festschrift Contribution
Date of issue: February 24, 2022

Center for Systematic Entomology, Inc., Gainesville, FL

Szadziewski R, Grogan WL Jr., Sontag E, Bojarski B. 2022. A new genus of predatory midge in the *Monohelea* complex from Eocene Baltic amber (Diptera: Ceratopogonidae). Insecta Mundi 0919: 1–9.

Published on February 24, 2022 by
Center for Systematic Entomology, Inc.
P.O. Box 141874
Gainesville, FL 32614-1874 USA
http://centerforsystematicentomology.org/

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Printed copies (ISSN 0749-6737) annually deposited in libraries

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Electronic copies (Online ISSN 1942-1354) in PDF format

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0919: 1–9 **INSECTA MUNDI** 2022

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Abstract. *Monogedania*, a new fossil monotypic genus of predatory midge (Diptera: Ceratopogonidae) is described from Eocene Baltic amber and its position within the *Monohelea* complex is discussed. We discovered that the membranous portion of the aedeagus is extended in *Monogedania clunipes* (Loew), **new combination**, which suggests that the aedeagus of some extinct predatory midges can be penis-like. The Eocene *Monohelea baltica* Szadziewski, is transferred to the genus *Schizohelea* Kieffer, **new combination**, and, the previously unknown female is described, and key characters are included in color photographs of its entire habitus, head, distal hind tarsomeres and claws.

Key words. Ceratopogoninae, Ceratopogonini, aedeagus.

ZooBank registration. urn:lsid:zoobank.org:pub:1E20AF94-52FE-48D0-B46B-280C81E3DCC2

Introduction

The *Monohelea* complex is a world-wide group of predatory midges that includes six genera in the tribe Ceratopogonini (Wirth and Grogan 1988). Their larvae are aquatic or semiaquatic in mainly small bodies of water and prey on aquatic larvae of a variety of insects. Adult females in this tribe are predators of mostly small nematocerous flies. This complex includes 232 extant species (Borkent and Dominiak 2020). Biting midges of this complex are rare in ambers worldwide (Szadziewski 2018). There are only two named species in the genus *Monohelea* Kieffer from Eocene Baltic amber (Szadziewski 1988). However, an enigmatic specimen of the genus *Austrohelea* Wirth and Grogan (sex unknown, no description or illustration) was reported by Schmidt et al. (2018) from Oligocene/Miocene amber of New Zealand; and a species from Eocene Australian (Anglesea) amber of an undetermined genus (Peñalver et al. 2021) may belong to this complex. It is worth noting that in Upper Cretaceous Canadian and Siberian ambers there are species in the fossil genus *Peronehelea* Borkent (Borkent 1995), that resemble species in the *Monohelea* complex. Females of *Peronehelea* have enlarged hind legs and hind claws, however, males in this genus have abdominal tergite 9 with distinct apicolateral processes which are absent or greatly reduced in males of the *Monohelea* complex. Females of *Peronehelea* have enlarged hind legs and hind claws, however, males in this genus have abdominal tergite 9 with distinct apicolateral processes which are absent or greatly reduced in males of the Monohelea complex (Szadziewski 1996). Two species from Eocene Baltic amber assigned to *Monohelea* by Szadziewski (1988) do not entirely resemble any of the genera in the revised *Monohelea* complex proposed by Wirth and Grogan (1988). Herein, we transfer these two extinct species from *Monohelea*, to *Schizohelea* Kieffer (Kieffer 1917), and, the new genus *Monogedania*, that we describe and illustrate.

We dedicate this article to the late Robert (Bob) Woodruff who generously supported our earlier studies of extant and fossil New World biting midges. Six workers of these small flies published the five patronyms below in recognition of Dr. Woodruff's support of their studies:

Atrichopogon (*Psilokempia*) *woodruffi* Spinelli, Marino and Huerta 2015: 58 (extant; Dominican Republic).
Bezzia (*Bezzia*) *woodruffi* Spinelli and Wirth 1989: 120. (extant; Jamaica).
Brachypogon (Brachypogon) *woodruffi* Spinelli and Grogan 1998: 72 (extant; Dominican Republic).
Culicoides woodruffi Spinelli and Huerta 2015: 133 (extant; Mexico).
Forcipomyia (*Lasiohelea*) *woodruffi* Szadziewski and Grogan 1998: 272 (fossil; Dominican amber).

Materials and Methods

All specimens examined are from the Museum of Amber Inclusions, University of Gdańsk, Poland (MAIG): Inv. No 4, 1 female; 1002, 1 female; 1003, 1 female; 1430, 1 male; 2150, 1 male; 2084, 1 male and 1 female; 2085, 1 female; 2109, 1 female; 2154, 1 male; 2528, 1 male; 2763, 1 female; 3387, 1 female; 3391, 1 male; 3706, 1 male; 3784, 1 male; 3917, 2 females; 4498, 1 male; 4608, 1 male; 4678, 1 male and 1 female in copula; 5515, 1 male; 5539, 1 male and 1 female in copula; 5576, 1 male; 5587, 2 females; 5621, 1 male; 5636, 1 female; 6694, 1 male. Photographs were taken with a LAS Montage multi-focus camera attached to a Leica DM6000 compound microscope. Morphological terms and their abbreviations are those by Wirth and Grogan (1988) and Szadziewski (1988).

Systematics

Subfamily CERATOPOGONINAE

Tribe CERATOPOGONINI

Monogedania Szadziewski, Grogan, Sontag and Bojarski, new genus

Type species. *Ceratopogon clunipes* Loew, 1850, by present designation.

Diagnosis. Moderately large predatory biting midges with wing lengths 1.1–1.5 mm. Palpus 5-segmented; segment 3 without sensory pit. Thorax convex; males with more dense elongate setae than females. Wing membrane with only apical macrotrichiae. Legs unarmed; foreleg, midleg slender, hind leg with greatly enlarged femur, tibia and tarsomeres 1–3; tarsomeres 4 cylindrical; male hind tarsomere 5 extremely slender with small equal-sized claws on all legs, female hind tarsomere 5 with greatly elongate single claw with a very short basal barb. Aedeagus entire, arch-like, with two sub-median apical, and one median ventral projections.

Etymology. The generic name, *Monogedania*, is a combination of *Monohelea,* a genus of extant predatory midges, and *Gedanum*, the Latin name of Gdańsk, Poland; this name is feminine.

Monogedania clunipes (Loew), new combination

Ceratopogon clunipes Loew 1850: 30 (male; Baltic amber); Meunier 1904: 234 (male; Baltic amber).
Monohelea clunipes: Szadziewski 1988: 127 (combination; male, female; Baltic amber); Szadziewski 1993: 631 (female redescribed; Baltic amber of Bitterfeld, Germany); Sontag and Szadziewski 2011: 790 (new record; Baltic amber from Rovno, Ukraine).
Monohelea sp. A: Szadziewski 1988: 131 (male; Baltic amber).

Fig. 1–3G–H

Description. Female (Fig. 1B). Body length 1.6–2.3 mm; wing length 1.1–1.5 mm. Proximal flagellomeres cylindrical. Proboscis relatively long, palpus 5-segmented, segment 3 slender without sensory pit. Scutellum with more than 10 long marginal setae. Foreleg, midleg slender, hind leg greatly swollen. Claws of foreleg,

Figure 1. *Monogedania clunipes* (Loew, 1850). **A)** Male, from collection of Artur Michalski. **B)** Female, MAIG 2109.

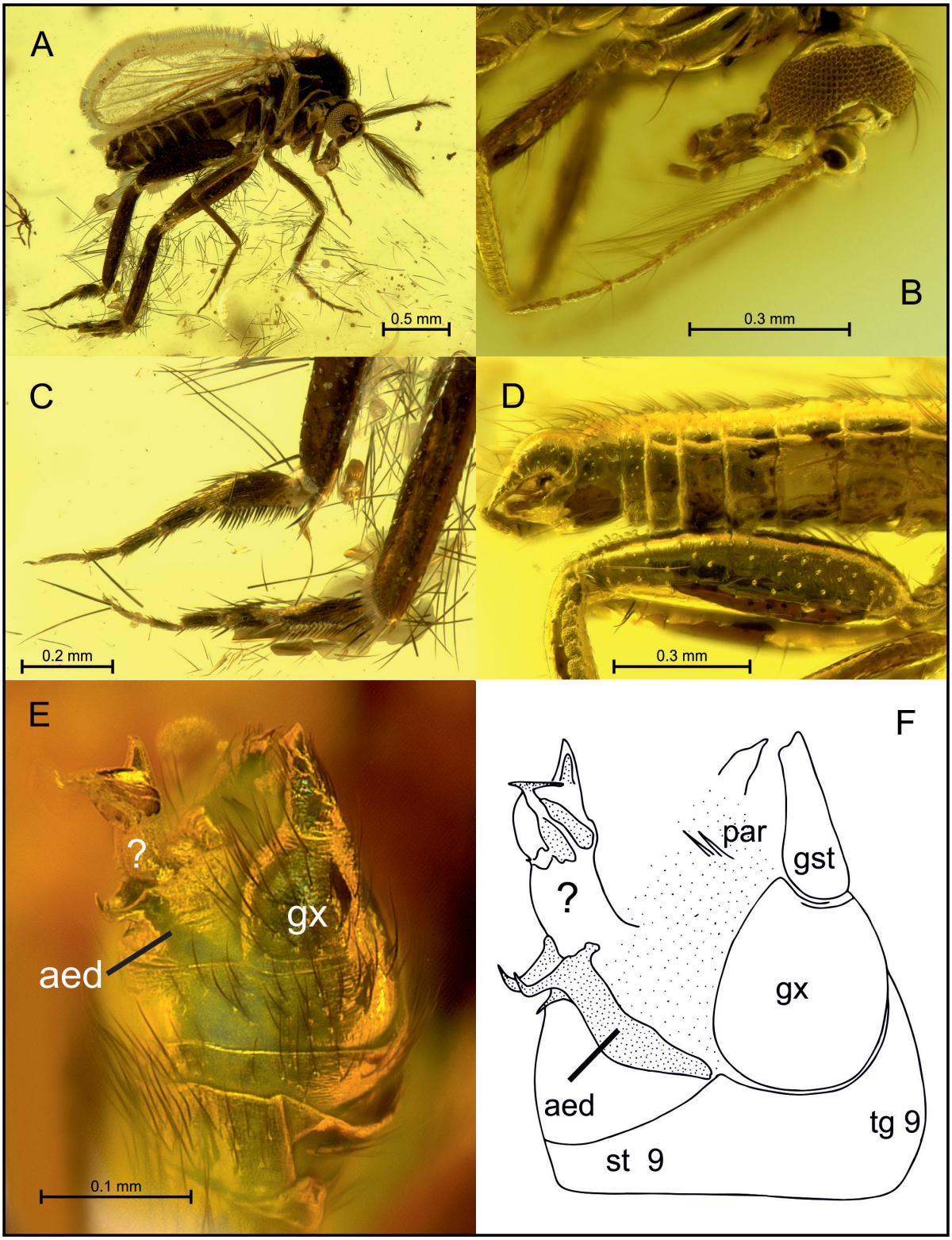

Figure 2. Male of *Monogedania clunipes*. **A)** Lateral aspect, MAIG 6010. **B)** Head and antenna, MAIG 5621. **C)** Hind tarsi, MAIG 6010. **D)** Abdomen with inverted genitalia, MAIG 5621. **E–F)** Lateral views of genitalia, photograph (E), illustration (F), MAIG 6694. Abbreviations: aed–aedeagus, gst–gonostylus, gx–gonocoxite, par–parameres, st 9–sternite 9, tg 9–tergite 9, ?–penis.

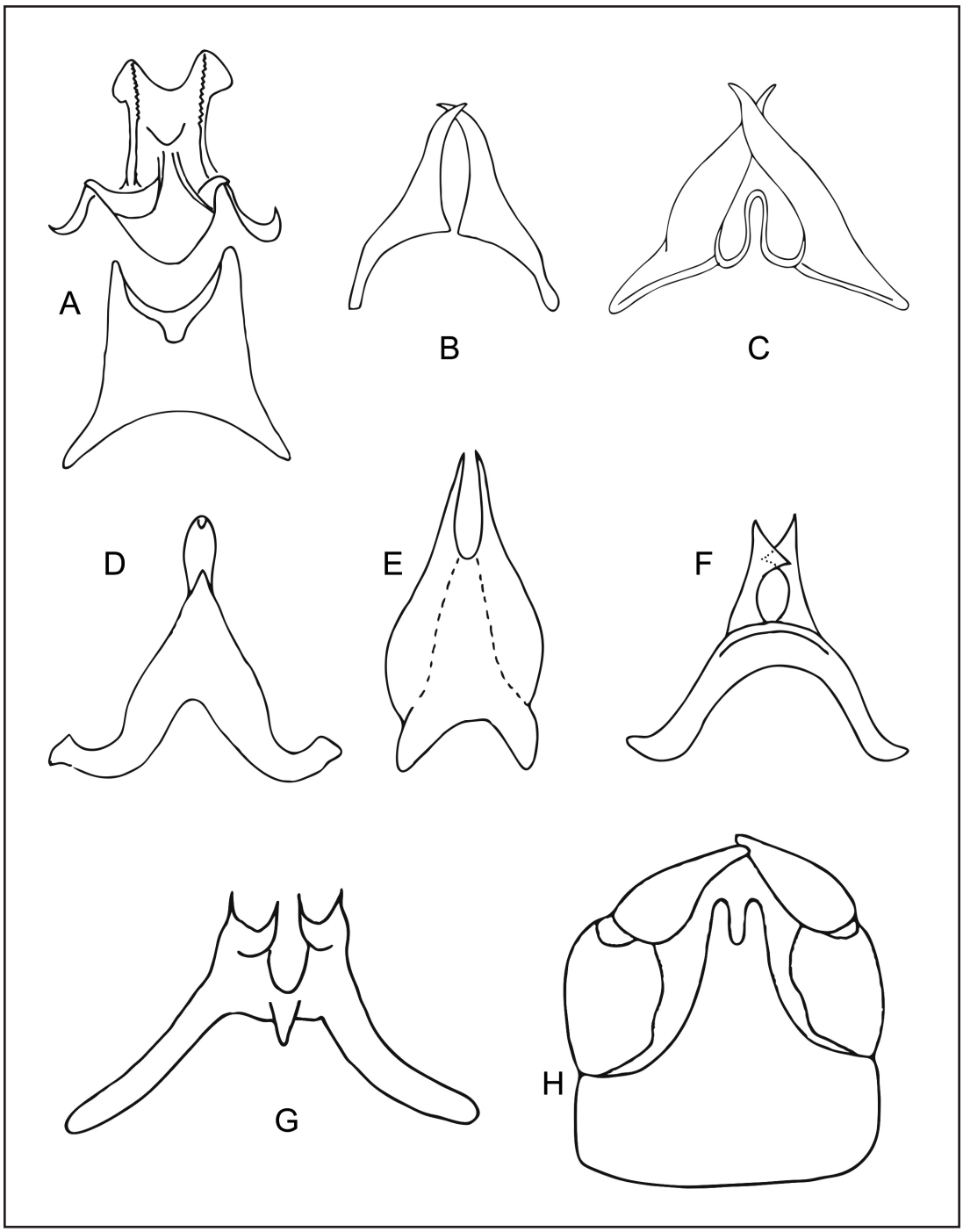

Figure 3. Male genitalia of genera in the *Monohelea* complex. **A)** Aedeagus of *Allohelea israelensis* Szadziewski and Alwin-Kownacka, 2016 in Alwin-Kownacka et al. (2016), redrawn from Alwin-Kownacka et al. (2016). **B)** Aedeagus of *Isthmohelea disjuncta* Ingram and Macfie, 1931, redrawn from Wirth and Grogan (1988). **C)** Aedeagus of *Monohelea mediterranea* Szadziewski et al., 2020, redrawn and modified from Szadziewski et al. (2020). **D)** Aedeagus of *Austrohelea shannoni* (Wirth and Blanton, 1972), redrawn and modified from Ronderos et al. (2017). **E)** Aedeagus of *Downeshelea stonei* (Wirth, 1953), redrawn from Wirth and Grogan (1988). **F)** Aedeagus of *Schizohelea leucopeza* (Meigen, 1804), extant male from Norway, coll. MAIG. **G)** Aedeagus of *Monogedania clunipes* (Loew, 1850), MAIG 3391. **H)** Dorsal aspect of male genitalia of *Monogedania clunipes* (Loew, 1850), redrawn from Szadziewski (1988).

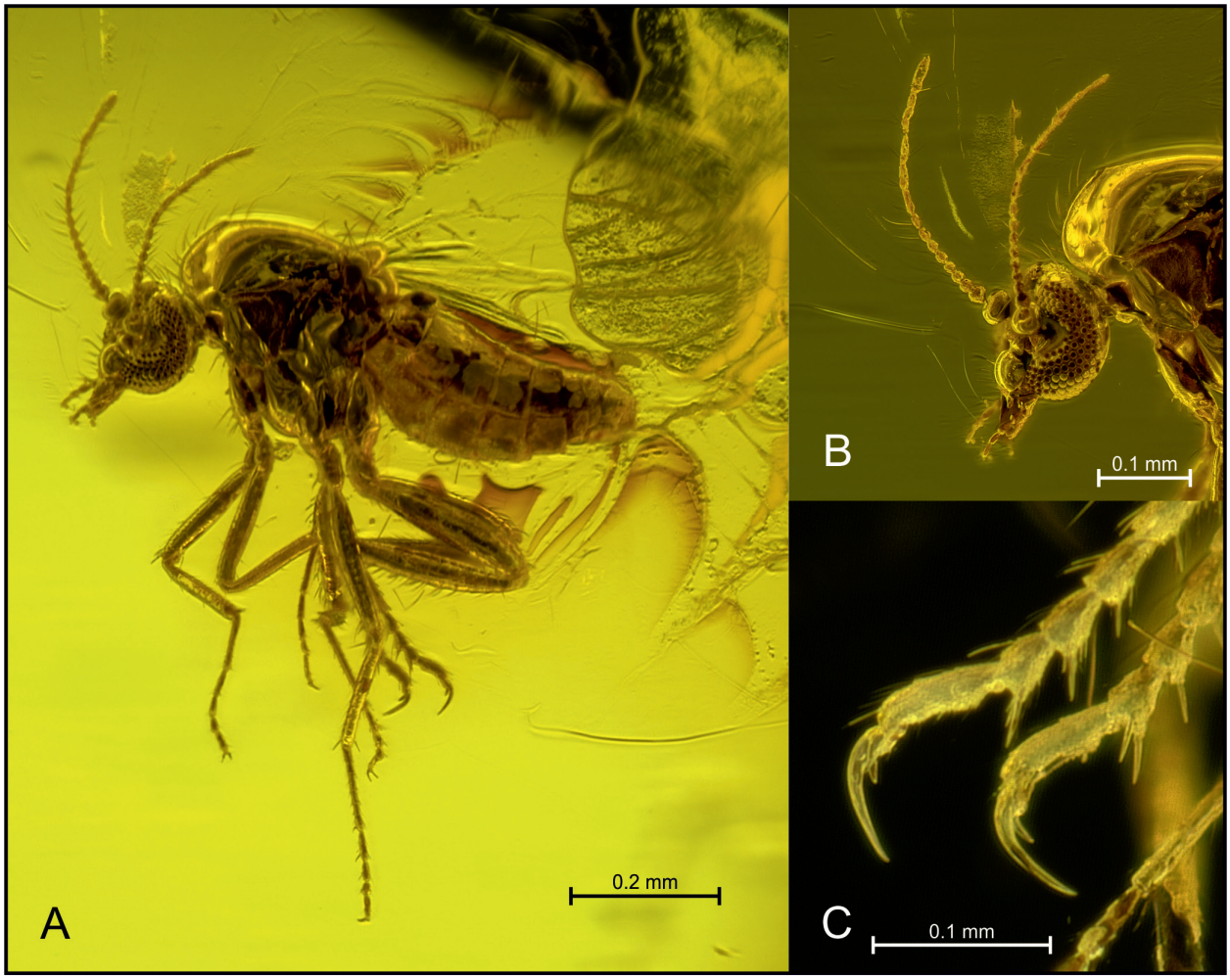

Figure 4. *Schizohelea baltica* (Szadziewski, 1988), comb. nov., female MAIG 5624. **A)** Total habitus. **B)** Head. **C)** Distal tarsomeres and claws of hind legs.

midleg short, equal-sized, with basal inner tooth. Hind leg with single very long claw (longer than tarsomere 5), with a short basal inner tooth. Wing with both first radial cells well developed, apex with macrotrichia. Seminal capsules not visible. **Male** (Fig. 1A, 2, 3G–H)**.** With more dense elongate setae than in female. Body length 1.82 mm; wing length 1.3–1.4 mm. Flagellar plume well developed (Fig. 2A–B). Scutum with numerous, stout setae (Fig. 1A, 2A). Foreleg, midleg slender; hind leg with greatly swollen femur, tibia and tarsomeres 1–3; femora, tibiae with numerous stout setae; hind tibial comb with very stout spines; hind tarsomere 1 moderately short, swollen, with a single row of stout palisade setae (Fig. 2C); tarsomeres 4 elongate, cylindrical; tarsomeres 5 greatly elongate, very slender. Claws small, simple, equal sized on all legs. Wing with macrotrichia on apex. Genitalia stout, short, inverted 180° (Fig. 2D–F). Sternite 9 with distinct caudomedian excavation. Tergite 9 tapering abruptly distally to narrow bilobed apex (Fig. 3H). Gonocoxite short, stout. Gonostylus narrowly triangular, broad at base, gradually tapering distally to blunt apex. Aedeagus (Fig. 2E–F, 3G) entire with distinct broad basal arch; with two sub-medial caudally directed projections, one median ventrally directed spine-like projection (Fig. 2E–F, 3G).

Discussion. This new genus is distinct in having males with dense coarse thoracic setae, a greatly enlarged hind tarsomere 1, extremely slender tarsomeres 5, and an entire aedeagus that is arch-like. In the genera included in the *Monohelea* complex by Wirth and Grogan (1988), males have a greatly modified ventral plate traditionally

called the aedeagus (Fig. 3A–H). However, in Ceratopogonidae and other genera of Culicomorpha, the true aedeagus with a gonopore is membranous and located above the sclerotized ventral plate (Sinclair et al. 2007).

The aedeagus (ventral plate) is composed of a proximal and distal piece in *Allohelea* (Fig. 3A); composed of two lateral pieces with a basal loop in *Monohelea* (Fig. 3C); it lacks a basal loop in *Isthmohelea* (Fig. 3B); it is single, plate-shaped with two sub-median projections in *Downeshelea* (Fig. 3E); it is single, arch shaped, with a single apical median projection in *Austrohelea* (Fig. 3D); it is single, arch shaped with two apical sub-median projections in *Schizohelea* (Fig. 3F), and, in the new genus *Monogedania* (Fig. 3G). Apparently, *Monogedania* is most similar to *Schizohelea* in having a similarly shaped arch-like aedeagus with two apical sub-median projections (Fig. 3F). However, these two genera differ by seven other characters in Table 1.

Monohelea baltica Szadziewski (1988: 130) described from males in Eocene Baltic amber with an entire aedeagus, and relatively slender hind legs armed with short equal-sized claws that we herein assign to the Holarctic genus *Schizohelea*, as previously suggested by Szadziewski (1988). The single female MAIG 5624 now determined as *Schizohelea baltica* (Fig. 4) confirms the new generic position of this species which was originally described from males. This female is very small (wing length 0.67 mm), like males; the wing membrane lacks macrotrichia; tarsomeres 4 are subcylindrical, hind leg tarsomere 5 with ventral basal swelling and hind claw single with long basal tooth (Fig. 4C). The wing membrane without macrotrichia and ventral swelling at the base of female tarsomere 5 are unique characters of the genus *Schizohelea* (Table 1).

Table 1. Comparison of genera in the *Monohelea* complex.

Characters	*Monohelea*	*Downeshelea*	*Allohelea*	*Isthmohelea*	*Schizohelea*	*Austrohelea*	*Monogedania*
1. Palpal segment 3 with sensory pit	+	+	+	–	–	–	–
2. Female fore, mid claws long, curved, with basal inner & outer teeth	+	+	–	–	–	–	–
3. Female fore, mid claws short, bent basally, straight distally, with basal inner & outer teeth	–	–	+	–	–	–	–
4. Female fore, mid claws short, curved, with basal inner teeth	–	–	–	+	+	–	+
5. Female fore, mid claws short, curved, without basal inner teeth	–	–	–	–	–	+	–
6. Female hind claw single without basal tooth	+	+	–	–	–	–	–
7. Female hind claw with short basal tooth	–	–	+	–	–	+	+
8. Female hind claw with long basal tooth	–	–	–	+	+	–	–
9. Male hind claws short, of normal size	+	+	–	+	+	+	+
10. Male hind claws enlarged, with basal tooth	–	–	+	–	–	–	–
11. Female fore, mid tarsomeres 5 swollen baso-ventrally	+	+	–	–	–	–	–
12. Female hind tarsomere 5 swollen baso-ventrally	–	–	–	–	+	–	–
13. Female fore, mid tarsomeres 5 slender	–	–	+	+	–	+	+
14. Tarsomeres 4 of fore, mid legs cylindrical	+	+	+	+	+	–	+
15. Tarsomeres 4 of fore, mid legs cordiform	–	–	–	–	–	+	–
16. Tarsomere 4 of hind leg elongate	+	+	+	–	+	+	+
17. Tarsomere 4 of hind leg short	–	–	–	+	–	–	–
18. Male tarsomere 1 of hind leg swollen	–	–	–	–	–	–	+
19. Male tarsomere 5 of hind leg slender, elongate	–	–	–	–	–	–	+
20. Wing membrane with distal macrotrichia	+	+	+	+	–	+	+
21. Scutellum with numerous very long setae	–	–	–	–	–	–	+
22. Tergite 9 of male genitalia narrow distally	–	–	–	–	+	–	+
23. Aedeagus with 2 lateral sections	+	–	–	+	–	–	–
24. Aedeagus with proximal and distal sections	–	–	+	–	–	–	–
25. Aedeagus entire	–	+	–	–	+	+	+

The *Monohelea* complex now includes 232 extant and two fossil species assigned to the following seven genera:

Allohelea Kieffer, 1917, worldwide, 62 extant species (Borkent and Dominiak 2020).

Austrohelea Wirth and Grogan, 1988, nine extant species from Argentina, Chile, Australia and New Zealand. Schmidt et al. (2018) reported an enigmatic specimen of the genus *Austrohelea* (sex unknown, no description or illustration) from Oligocene/Miocene amber of New Zealand.

Downeshelea Wirth and Grogan, 1988, worldwide, 60 extant species (Santarém et al. 2019; Borkent and Dominiak 2020).

Isthmohelea Ingram and Macfie, 1931, one extant species from Chile.

Monogedania Szadziewski, Grogan, Sontag and Bojarski, **new genus**, one Baltic amber fossil species.

Monohelea Kieffer, 1917, worldwide, 94 extant species.

Schizohelea Kieffer, 1917, Holarctic, six extant species, one fossil species in Eocene Baltic amber (*S. baltica* (Szadziewski, 1988), **new combination**).

In the material examined, one male of *Monogedania clunipes* has an extended membranous portion of the aedeagus that resembles a penis (Fig. 2E–F). However, in all other biting midges, sperm is transferred by spermatophores, but, their membranous aedeagi with a genital pore is not eversible (Sinclair et al. 2007). We suggest that this is an exceptional case within flies that produce spermatophores when the aedeagus is everted. However, an alternative explanation is possible, as it may be an artefact of fossilization wherein the distal tube of the male genital tract was unnaturally everted in liquid amber.

Acknowledgements

We are much indebted to the amber inclusion collector, Artur Michalski, Wrocław, Poland, for his generosity and photograph of a male *Monogedania clunipes* in Fig. 1A. We also thank Art Borkent, Salmon Arm, British Columbia, Canada for his comments on the everted aedeagus of this new fossil genus. We are especially grateful to Art Borkent and Gustavo Spinelli for their reviews of an earlier version of the manuscript. This research was supported by the National Science Centre of Poland under Grant No. 2020/37/B/NZ8/03042.

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Received January 13, 2022; accepted January 19, 2022.
Review editor Oliver Keller.