Recent discoveries of new *Elephantomyia* (Diptera, Limoniidae) fossils in Baltic amber

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New data on the genus *Elephantomyia* (Diptera: Limoniidae) from Baltic amber are presented. A new subgenus *Hoffeinsonia* subgen. nov. is established with one new species: *Elephantomyia* (*Hoffeinsonia*) *prima* sp. nov. The new subgenus is characterized by a wing at most 2.5 × as long as it is wide without a darker pattern along the veins Sc and R1, elongate Sc, straight vein R1, sharp half of vein R2+3+4 sharply arched to the upper edge of the wing, short, wide, trapezoidal d-cell and oval pterostigma. The fossil subgenus *Hoffeinsonia* subgen. nov. shares features with the extant subgenera *Elephantomyodes* and *Elephantomyia*. One other extinct species of *Elephantomyia* was discovered and described herein as *E.* (s. str.) *christelae* sp. nov. Such features as a very elongate vein R2+3+4, 2.5 × as long as the Rs easily allowing this new species to be distinguished from the other fossil representatives of the genus *Elephantomyia*. The taxonomic decision on *Elephantomyia grata* as a species placed in nominative subgenus is provided. A list and key of fossil species of *Elephantomyia* are given. The morphological pattern of the genus is discussed in relation to the adaptation to a specific food spectrum, coevolution with Angiospermae of the representative genus *Helius* known since Cretaceous and closely related to this genus representatives of the much younger genus *Elephantomyia*.

The genus *Elephantomyia* Osten Sacken1, comprises over 140 extant species, which occur mainly in Neotropical and Afrotropical regions. In the Neotropics, the genus *Elephantomyia* is represented by 38 species, which belongs to three subgenera: the typical subgenus *Elephantomyia*, subgenus *Elephantomyina* Alexander2 (one species) and the subgenus *Xenoelephantomyia* Alexander3 (one species). In the Afrotropics, the genus *Elephantomyia* is represented by over 30 species, which are classified to only one subgenus *Elephantomyia*. The subgenus *Elephantomyodes* Alexander4 was recorded from Holarctic (only two species), from China /Hainan, Taiwan/, India /Tamil Nadu, Assam/, Malaysia /Borneo/, Indonesia /Java, Sumatra, Flores, Sulawesi/, Philippines, Thailand) (18 species) and Australian/Oceanian region (13 species)5.

From fossil record seven species of *Elephantomyia* are known, six of them are known to have come from Eocene Baltic amber and belong to nominative subgenus *Elephantomyia*6–8. We only know of one species of *Elephantomyia* from Miocene to this day unclassified to any subgenus—*Elephantomyia grata* Podenas & Poinar9 (Table 1; Fig. 1). None of the other three subgenera of *Elephantomyia: Elephantomyina*, *Elephantomyodes*, *Xenoelephantomyia* have so far been found in the fossil record.

Baltic amber forms the largest amber deposit in the world and is a relevant source for fossil insects. Diptera are largely dominant and diverse among animal inclusions in this kind of resin what may be related to the fact that the deposits of the Eocene Baltic amber were formed over a relatively long time and under various environmental conditions10.

The new materials under investigation made it possible to discover a representative of a new subgenus of *Elephantomyia* in the fossil material. This new, peculiar discovery from Baltic amber described herein, provides evidence of the existence of craneflies belonging to a new subgenus in the Eocene and this is the first case to confirm the existence of a subgenus other than nominative the *Elephantomyia* in the past.

**Results**

**Systematic palaeontology.** Order Diptera Linnaeus11.

Infraorder Tipulomorpha Rohdendorf12.

Family Limoniidae Speiser13.

Subfamily Limoniinae Speiser13.

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Genus *Elephantomyia* Osten Sacken\(^1\).

Type species: *Limnobiorhynchus canadensis* Westwood\(^4\), 684, sensu Osten Sacken\(^1\): 221; by original designation (= *westwoodi* Osten Sacken\(^5\): 109, misidentification).

*Elephantomyia* Osten Sacken\(^1\) subg. *Elephantomyia* Alexander, 1938 emend.

**Emended diagnosis** Wing at most 2.5× as long as wide without darker pattern along vein Sc and R\(_1\); pterostigma oval; tip of Sc before or at Mb bifurcation level, opposite crossvein m-cu; vein R\(_1\) slightly curved at the tip, vein R\(_{2+3+4}\) slightly arched to the upper edge of wing, the distance between veins R\(_{2+3+4}\) and R\(_4\) and between veins R\(_{2+3+4}\) and R\(_5\) comparable; d-cell almost rectangular; two anal veins well developed; gonostyles elongate,
approximately 1/3 the length of gonocoxite or longer, gonocoxites elongate but rather wide, approximately twice
their width or shorter.

**Elephantomyia (Elephantomyia) grata** Podenas & Poinar⁹,

Electphantomyia grata: Podenas & Poinar⁹; 867.

**Remark** The species *Elephantomyia grata* Podenas & Poinar⁹ described from Dominican amber has not been
classified into a subgenus so far. Based on species characteristics consistent with the diagnosis of the subgenus,
we decided to classify *E. grata* under the subgenus *Elephantomyia*. *E. grata* subgeneric placement is based on the
original description without examination of the type specimen.

*Elephantomyia (Elephantomyia) christelae* sp. nov. (Figs. 2, 3 and 4).

**Figure 2.** *Elephantomyia (s. str.) christelae* sp. nov. No. CCHH 874–2 (male), coll. Ch. & H. W. Hoffeins,
holotype, drawings: (A) head (ventral view); (B) antenna; (C) palpus; (D) the diagram illustrating the
relationship between the length of wing (w), rostrum (r) and abdomen (ab); (E) wing; (F) hypopygium
(dorsal view). Abbreviation: a—antenna; r—rostrum; ped—pedicel; scp—scape; I-IV—palpomeres I-IV; gx—
gonocoxite.
Diagnosis Antennae 14-segmented; rostrum shorter than wing, only slightly longer than 1/2 of wing, longer than abdomen; palpus longer than glossal lobes; R2+3+4 very elongate, 2.5 x as long as Rs; d-cell short and wide, 1.5 x as long as wide; m-cu just before half the length of d-cell; M3 2 x longer than d-cell; vein m-m very short, almost completely reduced; vein Rs relatively short, length of vein Rs arranges only about twice the length of the basal deflection of R5; shorter than R2+3+4.

Etymology The new species is dedicated to Christel Hoffeins from Hamburg, Germany, the amber collection owner and expert of the Baltic amber inclusions.

Material examined Holotype No. CCHH 874–2 (male), coll. Ch. & H. W. Hoffeins, the specimen housed in Senckenberg Deutsches Entomologisches Institut (SDEI) Müncheberg, Germany.

Horizon and locality The age of Baltic amber has been a matter of debate for many years9,16–23. But, the most current state of knowledge is that it is of Priabonian age17. This means it is between 38 and 34 million years old (based on pollen, spores and phytoplankton of the amber embedding layer, the Blue Earth). The age of Baltic amber has also been estimated to approximately 47–41 Ma, which is mainly based on a study by Ritzkowski24; however, the reliability of the methods used in his study have been questioned due to contaminations that can lead to older age estimations16,17. The age range of all Baltic amber bearing strata possibly cover 48 to 23 million years, and it is still debatable18–23.

Description Body (Fig. 3A): brown with dark distal part of abdomen darker than rest of body, body 3.28 mm long (without rostrum).

Head (Figs. 2A, 3A, 4B): 0.45 mm wide, 0.34 mm high; rostrum elongate 2.24 mm long, shorter than wing, terminate just behind half of wing, rostrum longer than abdomen (1.84 mm long) (Figs. 2D, 3A, 4B); antenna (Figs. 2A, B, 3A, B, 4B) small, 0.64 mm long, flagellar segments crowded, scape cylindrical, widened, pedicel wide, first flagellomere elongate, second flagellomere only slightly shorter than rest of flagellomeres, flagellomeres 1–8 with two elongate setae on each flagellomere; flagellomeres 9–12 with four elongate setae.

Palpus (Figs. 2C, 4A, B): longer than glossal lobes, 0.19 mm long, 4-segmented, last palpomeres short, other palpomeres elongate, third palpomere shorter than second. The small microtrichia on all segments well visible.

Wing (Figs. 2E, 3A, 4C): 3.52 mm long, 0.88 mm wide; pterostigma present, darkened, oval, brown; vein Sc elongate, ending opposite 3/4 the length of Rs; sc-r short, one time the distance from the tip of Sc; vein Rs slightly arcuated, R1 ending before half of the length of R2+3+4; r-t (R1) atrophy; d-cell 0.26 mm long, M3 0.61 mm long; A1 almost straight, A2 slightly curved at wing margin.
Hypopygium (Figs. 2F, 3A, C): 0.46 mm, gonocoxite approximately two times as long as wide with elongate and narrow, lobe-shaped interbase; male genitalia with lobe, outer gonostylus (branch II = clasper of gonostylus; ventral gonostylus) narrow, distinctly bifid at the end, the distal part slightly curved outside; inner gonostylus (branch I = lobe of gonostylus; dorsal gonostylus) slightly widened at base, directed inside of hypopygium.

Remarks

A well preserved holotype specimen, but only partially preserved legs.

Comparison

The species differ from all other known from fossil records due to the very short cross-vein m-m. Veins M1+2 and M3 in E. (E.) christelae sp. nov. is narrowly separated and the distance between veins M1+2/M3 is smaller than between veins M3/M4 while in other known fossil record species of Elephantomyia veins M1+2 and M3 are widely separated and the distance between veins M1+2/M3 and veins M3/M4 is comparable, cross-vein m-m is well developed. Moreover, this species is characterized by the occurrence of 15-segmented antenna while in E. (E.) baltica and E. (E.) brevipalpa antennae are 14-segmented. Palpus in E. (E.) christelae sp. nov. is elongate, longer than glossal lobes, while in E. (E.) brevipalpa palpus is very short, being less than half the length of the rostrum’s glossal lobes. Vein Rs in E. (E.) brevipalpa is as long as, or longer than vein R1+3+4, in contrast to E. (E.) christelae sp. nov. where Rs is distinctly shorter than R1+3+4. E. (E.) christelae sp. nov. differs also from the other species of Elephantomyia in the ratio between wing, rostrum, and abdomen length. In E. (E.) christelae sp. nov. rostrum is slightly longer than the abdomen, being longer than half wing length, but shorter than wing.

Hoffeinsonia subgen. nov.

Type species: Elephantomyia (Hoffeinsonia) prima subgen. et sp. nov.

Diagnosis Wing at most 2.5 × as long as wide without darker pattern along vein Sc and R1; pterostigma oval; vein Sc elongate, tip of Sc beyond Mb bifurcation level, opposite crossvein m-cu; vein R1 straight, basal half of vein R2+3+4 sharply arched to the upper edge of wing, veins R1+3+4, and R1, running closer together than veins R2+3+4 and R3; d-cell short, wide, trapezoidal; two anal veins well developed; gonostyles small, about 1/3 length of gonocoxite, gonocoxites elongate and rather narrow, longer than twice their width.

Etymology

The new subgenus is dedicated to Christel Hoffeins from Hamburg, Germany, the amber collection owner and expert of the Baltic amber inclusions.

Description As for species.

Comparison What occurs in Elephantomyina is a strong supernumerary cross-vein connecting vein R2+3+4 shortly before tip of latter, cross-vein r-m connecting with Rs a short distance before its fork 1, while in other subgenera of the genus Elephantomyia (including Hoffeinsonia subgen. nov.) the supernumerary cross-vein does not occur and cross-vein r-m connecting with Rs beyond of Rs. Moreover, as mentioned by Osten Sacken 25: “anal field of wing reduced in area, with a single vein”, while in three other known subgenera of Elephantomyia and Hoffeinsonia subgen. nov. two well developed anal veins are observed.

Only the hind leg with part of the tarsus of the specimen of Hoffeinsonia subgen. nov. is preserved, but is clearly visible that basal and middle part of femur and part of tibia are pale. This feature and others such as: vein R1 straight, basal half of vein R2+3+4 sharply arched to the upper edge of wing, veins R2+3+4 and R1 running closer together than veins R2+3+4 and R3, reduced palpi are similar to these which occur in subgenus Elephantomyodes.
The aforementioned features are well visible in recent representatives of the subgenus as *Elephantomyia* (*Elephantomyodes*) *tianmushana* Zhang, Li and Yang\(^{26}\), *Elephantomyia* (*Elephantomyodes*) *sophiarum* Ito\(^{27}\), *Elephantomyia* (*Elephantomyodes*) *angusticellula* Alexander\(^{28}\) or *Elephantomyia* (*Elephantomyodes*) *major major* Alexander\(^{4}\). Pterostigma in *Hoffeinsonia* subgen. nov. is distinctly oval, like in *Elephantomyia*. The wing of *Hoffeinsonia* subgen. nov. is wider than the wing of *Elephantomyodes* and arrange at most 2.5 × the length of its width, while the wing of *Elephantomyodes* 3.5x. Moreover, in *Elephantomyodes* along vein Sc and R1 occur darker pattern, in contrast to *Hoffeinsonia* subgen. nov.

*Elephantomyia* (*Hoffeinsonia*) *prima* subgen. et sp. nov. (Figs. 5, 6, and 7).

**Diagnosis** Antennae 15-segmented; rostrum shorter than wing, shorter than 1/2 of wing, shorter than abdomen; palpus shorter than glossal lobes; R\(_{3+4}\) 1.5 × as long as Rs; d-cell approximately 1.5 × as long as wide; m-cu

**Figure 5.** *Elephantomyia* (*Hoffeinsonia*) *prima* sp. nov. No. CCHH 874–1 (male), coll. Ch. & H. W. Hoffeins, holotype, drawings: (A) head, latero-ventral view; (B) enlarged view of apical part of rostrum; (C) gonocoxite and gonostyles; (D) antenna; (E) the diagram illustrating the relationship between the length of wing (w), rostrum (r) and abdomen (ab); (F) wing. Abbreviation: a—antenna; ped—pedicel; scp—scape; I–IV—palpomeres I–IV; gx—gonocoxite; oug—outer gonostylus; ing—inner gonostylus; p—palpus.
in half the length of d-cell; M3 1.5 × longer than d-cell; vein m-m well developed; length of vein Rs arranges only about five the length of the basal deflection of R5; R5 approximately as long as R2+3+4.

**Etymology.** The specific epithet is derived from „prima“ (Latin) = the first.

**Material examined.** Holotype No. CCHH 874–1 (male), coll. Ch. & H. W. Hoffeins, the specimen housed in Senckenberg Deutsches Entomologisches Institut (SDEI) Müncheberg, Germany.

**Horizon and locality** as for *E. (s.str.) christelae* sp. nov.

**Description** Body 3.61 mm long (Fig. 6A).

Head (Fig. 6B, C) width 0.42 mm, 0.38 mm high; rostrum 1.36 mm long, approximately as long as half the body length, shorter than half wing; length of antenna 0.72 mm (Fig. 5A); scape elongate, cylindrical, pedicel oval, wider than scape and other antennal segments, flagellomeres 1 and 2 only slightly elongate, longer than wide, flagellomeres 3–15 elongate, longer than twice of its width with very elongate setae, approximately twice

**Figure 6.** *Elephantomyia (Hoffeinsonia) prima* sp. nov. No. CCHH 874–1 (male), coll. Ch. & H. W. Hoffeins, holotype, photographs: (A) body, latero-dorsal view; (B) head, latero-ventral view; (C) apical part of rostrum with palpi visible; (D) hypopygium, lateral view; (E) wing.
as long as its width or longer; length of flagellomers: 1/0.08 mm; 2/0.06 mm; 15/0.04 mm; palpus very short, 0.13 mm long, shorter than glossal lobes.

Thorax (Fig. 6A): wing (Figs. 5B, 6A, E) longer than body, without colour pattern, 3.95 mm long, 1.10 mm wide; oval pterostigma brown, vein Sc elongate, tip of Sc beyond Mb bifurcation level, opposite crossvein m-cu; cross-vein sc-r one of its length from the tip of Sc, fork of Rb beyond half the length of wing towards the apex of wing; fork of Rs beyond fork of Mb level and opposite approximately 1/3 of d-cell length measured from fork of Mb; Rs 0.70 mm long; R2,3,4 approximately 1.6 × as long as Rs; cross-vein m-cu in half the length of d-cell; d-cell 0.42 mm long, wide, approximately 1.5 × as long as wide; length of M1 0.64 mm; tip of A1 beyond fork of Mb toward the apex of wing; macrotrichia on radial and medial veins occur, vein M3 with macrotrichia arranged close to each other at equal intervals; hind legs with pale parts of femur and tibia (Fig. 7A–C).

Abdomen (Fig. 6A) 2.04 mm long; hypopygium 0.37 mm long with lobe—short, small, comparable length gonostyles, outer gonostylus (branch II = clasper of gonostylus; dorsal gonostylus) narrow, tapered at the end, strongly sclerotized, inner gonostylus (branch II = lobe of gonostylus; dorsal gonostylus) widened at the base and in its middle, narrowed at the end (Fig. 6D), less sclerotized than the outer gonostylus.

Remarks Well preserved holotype specimen, but only partially preserved legs.

Key to fossil species of the genus Elephantomyia.

1. Rostrum longer than half wing length (Fig. 10A–H); tip of Sc before or at fork of Mb, before crossvein m-cu measured from the base of the wing; vein R1 at least slightly curved at the tip; vein R2,3,4 with a slight curve to the upper edge of wing, the distance between veins R2,3,4/R1 and veins R2,3,4/R5 comparable (Fig. 9A); gonostyles elongate, about 1/2 of the length of gonocoxite (Fig. 2F); .......................................................... 2.
   - Rostrum measures approximately 1/3 of wing length (Fig. 10I); tip of Sc far beyond fork of Mb measured from the base of the wing, opposite crossvein m-cu; vein R1 straight; basal half of vein R2,3,4 sharply arched to the upper edge of wing; veins R2,3,4 and R4 closer together than veins R2,3,4 and R3 (Fig. 9D); gonostyles small, about 1/3 length of gonocoxite (Fig. 5C); ............................................ E. (Hoffeinsonia) prima subgen et sp. nov

2. Veins M1+2 and M3 widely separated; the distance between veins M1+2/M3 and veins M3/M4 comparable; cross-vein m-m very well developed (Fig. 8A–H) ...................... 3.
   - Veins M1+2 and M3 narrowly separated; the distance between veins M1+2/M3 smaller than between veins M3/M4; cross-vein m-m very short (Figs. 2E, 8I) .......................... E. (s. str.) christelae sp. nov.

3. Wings longer than rostrum (Fig. 10A, C–I); relatively short vein Rs, the length of vein Rs at least three times of the basal deflection of R3, .................................................. 4.
   - Wings as long as rostrum (Fig. 10B); the length Rs only slightly longer than twice the length of the basal deflection of R3 (Fig. 8C) ......................................................... E. (s. str.) baltica Alexander

4. Palpus longer than the glossal lobes; antennae 15-segmented; Rs distinctly shorter than R2+3+4 .............. 5.
- Palpus shorter than one half of the glossal lobes of the rostrum; antennae 14-segmented; Rs as long as R2+3+4 or slightly longer (Fig. 8F) 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Figure 10. Relation between the length of wing (w), rostrum (r) and abdomen (ab) in different fossil species of *Elephantomyia*: (A) *Elephantomyia* (s. str.) grata, (B) *Elephantomyia* (s. str.) baltica, (C) *Elephantomyia* (s. str.) bozenae, (D) *Elephantomyia* (s. str.) brevipalpa, (E) *Elephantomyia* (s. str.) christelae sp. nov., (F) *Elephantomyia* (s. str.) irinae, (G) *Elephantomyia* (s. str.) longirostris, (H) *Elephantomyia* (s. str.) pulchella, (I) *Elephantomyia* (Hoffeinsonia) prima subgen. et sp. nov.

- …………………………………………...….. E. pulchella  
  - Rostrum elongate, as long or longer than abdomen, only slightly shorter than wing  
  - …………………………………………...….. E. (s. str.) pulchella (Loew, 1851) 
  - Wing approximately 1/3 longer than rostrum (Fig. 10H); cross-vein m-cu in 1/2 of d-cell length  
  - …………………………………………...….. E. (s. str.) longirostris Loew  

Discussion

Craneflies from the genus *Elephantomyia* to present were represented in the fossil record only by the subgenus *Elephantomyia*. The most well known species from the fossil record were described on the basis of inclusions in Eocene Baltic amber. We do not know the older representatives of the genus *Elephantomyia*. One species was described from a younger period (the Miocene) and to this day it has not been classified under any subgenus of the genus *Elephantomyia*. After careful analysis, it was possible to indicate herein that this species, like the other species described based on fossil material, belongs to the nominative subgenus *Elephantomyia*. So, of the four known subgenera of the genus *Elephantomyia*, only one is represented in the fossil record. The subgenus *Elephantomyia* is also the most diverse in modern fauna. There are over 100 species belonging to the subgenus *Elephantomyia* occurring in modern fauna. Subgenera like *Elephantomyina* and *Xenoelephantomyia* are represented by only single species.

The characteristic morphological features of the newly discovered specimens mentioned in this paper allows the indication and description of a new subgenus of *Elephantomyia*. The general features which characterize the genus *Elephantomyia* are: very elongate rostrum, sometimes longer than the body length, maxillary palpus four segmented, first palpomere reduced, atrophy of cross-vein r-r (R2) and comparatively short and wide gonocoxites with small gonostyles. The combination of features such as legs at least partially pale, these parts almost white, vein R1 is straight, basal half of vein R2+3+4 is sharply arched to the upper edge of wing, veins R3+4 and R5 are positioned closer together than veins R4 and R5 and pale brown oval pterostigma, wing without colour pattern distinguish the new subgenus from other subgenera within the genus (Fig. 8).

It is also worth noting that the fossil subgenus *Hoffeinsonia* subgen. nov. shares features with the extant subgenera *Elephantomyodes* [such as basal half of vein R2+3+4 sharply arched to the upper edge of wing, veins R2+3+4 and R5 running closer together than veins R2+3+4 and R5 and straight R5, reduced palpi, legs with very light (almost white) parts] and *Elephantomyia* (such us oval pterostigma and wing distinctly wider than in *Elephantomyodes*) (Fig. 9). These similarities can indicate a phylogenetic relationship of *Hoffeinsonia* subgen. nov. and *Elephantomyodes* or *Elephantomyia*. The colour patterns of legs are rather rare in craneflies belonging...
to subgenus Elephantomyia and are very variable among taxa, eg. Elephantomyia (s. str.) catarractes Gavryushin 2016 describes from Tanzania, Morogoro env., Uluguru Mts, Majiyanakwendo waterfall, characterized by the colour pattern of legs which are mostly brown with tips of femora conspicuously yellow. The relation between the length of wing, rostrum and abdomen of Elephantomyia (Hoffeinsonia) prima subgen. nov. is also different than in fossil representatives of Elephantomyia. The rostrum of Elephantomyia (Hoffeinsonia) prima subgen. et sp. nov. measures no more than 1/3 wing length, while in fossil Elephantomyia rostrum measures at least half wing length (Fig. 10).

Fossil records prove the existence of these insects as early as the Eocene. The discovery of the new subgenus sheds new light on the diversity of the genus Elephantomyia, the evolution of the Limoniidae and introduces important information that can be used in further research on the phylogenetic relationships of this group of insects.

The presence in Baltic amber of inclusions of flies of the genus Elephantomyia with a very elongate rostrum adapted to a specific food spectrum (most likely the nectar of Angiospermae flowers) can provide evidence that in "Baltic amber forests" were plants pollinated by these insects. This co-evolution of Angiospermae and Limoniinae began much earlier, in Cretaceous. From Cretaceous period are known species of genus Helius which are characterized by an elongate rostrum – flies adapted to feed on the nectar of Angiospermae flowers. This genus is closely related to Elephantomyia9,10.

It has been also proven that the Baltic amber flora comprises elements of both extant northern American and East Asian warm-temperature flora in "Baltic amber forests" and humid climate10. Recent species of subgenus Elephantomyia occur mainly in Neotropical and Afrotropical regions5,16 and are represented as an inclusions in Baltic amber while Elephantomyoides occur in Holarctic region. But, its absence in Baltic amber may be due to the fact that these insects were very rare in the Eocene, as in modern fauna9.

Material and methods
The study was based on four inclusions in Eocene Baltic amber from the collection of Christel and Hans Werner Hoffeins. The holotypes of new described species here are deposited in Senckenberg Deutsches Entomologisches Institut (SDEI) Müncheberg, Germany. The specimens were examined using a Nikon SMZ 1500 stereomicroscope equipped with a Nikon DS-F11 camera. The measurements were taken with NIS-Elements D 3.0 software. The length of head was measured as length of head capsule excluding rostrum. The length of the discal cell—measurements were given from its posterior edge to the point of connection of vein m-m with vein m₃ to the margin of wing. The length of hypopygium was measured from the posterior margin of tergite IX to the apex of gonocoxite. The measurements and the relationship between the length of rostrum, wing and abdomen were given only in case when relevant structures were not distorted. Drawings were made by tracing the specimens and the photographs. Drawings and photographs (Figs. 2, 3, 4, 5, and 6, graphics 8–10 partially) were made by Iwona Kania-Klosok. The map was built using the map Maps-For-Free (https://maps-for-free.com) and modified with the software programs Corel Draw and Corel Photopaint X7. The stratigraphic chart was used according to International Stratigraphic Chart, International Commission of Stratigraphy (v. 2021/05) https:// stratigraphy.org/ chart. The wing venation follows that of5,16, terminology applied to the male genitalia nomenclature, is in accordance1,2,3,4.
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Author contributions
I.K.-K. conceived and designed the study, lead and performed the data analysis, interpretations and writing, making photographs, drawings, graphical figures, analysis, writing and corrections of the manuscript. W.K. analysis and corrections of the manuscript. All authors reviewed manuscript.

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Competing interests
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