Subfamily Limoniinae Speiser, 1909 (Diptera, Limoniidae) from Baltic Amber (Eocene): The Genus Elephantomyia Osten Sacken, 1860

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Abstract
A revision of the genus Elephantomyia Osten Sacken (Diptera: Limoniidae) from Baltic amber (Eocene) is presented. Four species—E. baltica Alexander, E. brevipalpa Loew, E. longirostris Loew, and E. pulchella Loew—are redescribed and documented with photographs and drawings. In addition, two new species of the genus are described: Elephantomyia bozenae sp. nov., and Elephantomyia irinae sp. nov. All these fossil species are placed within the subgenus Elephantomyia. A key to the extinct species of Elephantomyia is provided, and the genus’ ecological pattern and evolutionary aspects are discussed.

Introduction
The subfamily Limoniinae [1] of the most diverse dipteran family Limoniidae [1] comprises over 30 genera [2], of which 13 are well represented in the fossil record, including the genus Elephantomyia [3].

There are more than 130 extant species ascribed to the genus Elephantomyia, distributed across four subgenera: Elephantomyia (Elephantomyia) [3], Elephantomyia (Elephantomyina) [4], Elephantomyia (Elephantomyodes) [5], and Elephantomyia (Xenelephantomyia) [6], [2]. These extant representatives of Diptera [7], occur mainly in Neotropical and Afrotropical regions [2]. In the Neotropics, the genus is represented by three subgenera, with 40 species belong to the typical subgenus, and one representative each of the subgenera E. (Elephantomyina) [4], and E. (Xenelephantomyia) [6]. A similar number of species are reported from the Afrotropics, but all 37 species belong to a single subgenus: E. (Elephantomyina) [4]. In the Oriental, Australian, and Oceanian regions, E. (Elephantomyodes) [5] is the most species rich subgenus, although representatives of the typical subgenus are also found in all three regions.

Fossil representatives of the genus Elephantomyia are known from amber inclusions, mainly from Eocene Baltic amber, but none were assigned to a subgenus. Four species of Elephantomyia are known from the Baltic amber: E. baltica [8], E. brevipalpa [9], E. longirostris [9], and E. pulchella [9]. Three of these taxa—E. brevipalpa [9], E. longirostris [9], and E. pulchella [9]—were originally described as species of Toxorhina by Loew [10]. Osten Sacken [3] initially
placed Loew’s fossils within the genus Limnobiorhynchus, but later [11] considered all of them part of his genus Elephantomyia. Although Scudder [12] claimed Toxorhina was a valid genus containing Loew’s fossil species and a single recent species, thereby rejecting their placement within Elephantomyia, a later revision [13] again ascribed these species to the genus Elephantomyia (Table 1). Handlirsch [14] listed Loew’s species within the genus Toxorhina, but listed the Osten Sacken [3] and Meunier [13] combinations as synonyms. Evenhuis [15] listed all Loew’s species in the genus Elephantomyia.

In addition to the species from Baltic amber, two species are also known from the Miocene Dominican amber: Elephantomyia grata [16], and an individual not identified to species level [17].

The discovery of a new Elephantomyia specimens from Baltic amber has allowed the description of two new extinct species within this genus. Further, this new research, which incorporates both previously known and new fossil materials, has enabled the revision of all Elephantomyia species from Baltic amber, and placement of these taxa into the subgenus Elephantomyia.

Materials and Methods
Specimens

The study herein is based on material from the collections: Institute of Systematic and Evolution of Animals, Polish Academy of Sciences (ISEA PAS) (15 specimens); Museum of the Earth, Polish Academy of Sciences, Warsaw (MEPAS) (1 specimen); University of Göttingen (GMUG)

Table 1. List of species of the genus Elephantomyia from Baltic amber known so far and revised herein.

| Subgenus | Species      | The number of specimen | Material examined | Sex     | Collection        |
|----------|--------------|------------------------|------------------|---------|-------------------|
| Elephantomyia | E. baltica  | 282                    | Holotype         | male    | (GMUG)            |
|          | E. bozenae sp. nov. | MP/3338         | Holotype         | male    | (ISEA PAS)        |
|          | E. brevipalpa | MB.J.337           | Holotype         | male    | Coll. Berendt (NHMB) |
|          |              | MP/3323            | add. mat.      | female  | (ISEA PAS)        |
|          |              | 161                 | add. mat.      | male    | Coll. Kutscher (GMUG) |
|          | E. irinae sp. nov. | MP/3324          | Holotype         | male    | (ISEA PAS)        |
|          |              | MP/3330            | add. mat.      | male    | (ISEA PAS)        |
|          |              | MP/3331            | add. mat.      | male    | (ISEA PAS)        |
|          |              | MP/3337            | add. mat.      | male    | (ISEA PAS)        |
|          |              | 250                 | add. mat.      | male    | Coll. Künow (GMUG) |
|          | E. longirostris | MB.J.338           | Holotype         | male    | Coll. Berendt (NHMB) |
|          |              | 1089–6              | add. mat.      | male    | Coll. Ch. and H. W. Hoffeins |
|          |              | MP/1627             | add. mat.      | female  | (ISEA PAS)        |
|          |              | MP/3319             | add. mat.      | male    | (ISEA PAS)        |
|          |              | MP/3322             | add. mat.      | male    | (ISEA PAS)        |
|          |              | MP/3325             | add. mat.      | male    | (ISEA PAS)        |
|          |              | MP/3328             | add. mat.      | male    | (ISEA PAS)        |
|          |              | MP/3329             | add. mat.      | male    | (ISEA PAS)        |
|          |              | MP/3333             | add. mat.      | male    | (ISEA PAS)        |
|          |              | MP/3334             | add. mat.      | male    | (ISEA PAS)        |
|          | E. pulchella | 19946                | add. mat.      | male    | (ME PAS)          |
|          |              | MB.J.336            | Holotype         | male    | Coll. Berendt (NHMB) |
|          |              | 1195–5              | add. mat.      | male    | Coll. Ch. and H. W. Hoffeins |
|          |              | MP/3336             | add. mat.      | male    | (ISEA PAS)        |

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(1 specimen), Coll. Künow (GMUG) (1 specimen), Coll. Kutscher (GMUG) (1 specimen), Coll. Berendt, Natural History Museum Humboldt University, Berlin (NHMB) (3 specimens) and private collection of Christel and Hans Werner Hoffeins (2 specimens). Of the new species described herein, holotypes obtained from the Hoffeins’ collection will be deposited in Senckenberg Deutsches Entomologisches Institut (SDEI), Müncheberg, Germany.

**Nomenclature**

The wing venation nomenclature is after Krzemiński [18], terminology for the male genitalia follows that of Ribeiro and Amorim [19], the terms “outer gonostylus” and “inner gonostylus” equal the terms “clasper of gonostylus” (branch II) and “lobe of gonostylus” (branch I) proposed by Ribeiro [20].

**Imaging**

The specimens were studied using a Nikon SMZ 1500 stereomicroscope equipped with a Nikon DS-Fi1 camera. Drawings were produced using both specimens and photographs.

**Measurements**

All measurements were taken with NIS-Elements D 3.0 software. The length of discal cell was measured from its basal edge to the point of connection of vein m-m with vein M3. The length of M3 is given from the wing margin to the point of connection of vein m-m with vein M3. The relations of rostrum, wing, and abdomen length are only given in those cases where the structures are not distorted. Chresonymy is used according to open nomenclature rules proposed by Matthews [21] and Bengtson [22] for the names of fossil taxa.

**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 online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix “http://zoobank.org/”. The LSID for this publication is: urn:lsid:zoobank.org:pub:546335C5-B194-4221-9F68-F20A3E8E2588. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: PubMed Central, LOCKSS [author to insert any additional repositories].

**Systematic palaeontology**

Order: Diptera Linnaeus, 1758  
Family: Limoniidae Speiser, 1909  
Subfamily: Limoniinae Speiser, 1909

**Genus:** *Elephantomyia* Osten Sacken, 1860  
**Type species.** *Limnobiorhynchus canadensis* [23]: 684, *sensu* [3]: 221; by original designation [*Elephantomyia westwoodi* [11]: 109, misidentification].
Subgenus: *Elephantomyia* Osten Sacken, 1860

**Type species.** *Limnobiorhynchus canadensis* [23]: 684, *sensu* [3]: 221; by original designation [= *Elephantomyia westwoodi* [11]: 109, misidentification).

**Key to species of the genus Elephantomyia Osten Sacken, 1860 from Baltic amber**

1. Wings longer than rostrum; relatively short vein Rs, the length of Rs at least three times of the length of the basal section of R₅ ................................................................. 2.
   2. Wings as long as rostrum; length Rs only slightly longer than twice the length of the basal section of R₅ ........................................................................................................................................ 2.
      3. Palpus elongate, 4-segmented, much longer than the glossal lobes; antennae 15-segmented; Rs distinctly shorter than R₂₃₄₊ ........................... 3.
      4. Palpus shorter than half the length of the rostrum’s glossal lobes; antennae 14-segmented; Rs as long as, or slightly longer than R₂₃₄₊ ...................................................... E. (E.) *brevipalpa*
      5. D-cell distinctly elongate, narrow, approximately twice as long as wide; vein M₁ as long as d-cell ................................................................. E. (E.) *bozenae* sp. nov.
      6. D-cell wide, length approximately 1.5 times width; vein M₃ 1.5 times longer than d-cell ... 4.
      7. Rostrum not very elongate, shorter than abdomen, distinctly shorter than wing, only slightly longer than half wing length ........................................... E. (E.) *irinae* sp. nov.
      8. Rostrum elongate, as long as or longer than abdomen, only slightly shorter than wing length .............................................................................................. 5.
      9. Wing approximately 1.3 times rostrum length; cross-vein m-cu at half of d-cell length ........................................................................................................ E. (E.) *pulchella*
      10. Rostrum very elongate, wing approximately 1.2 times the rostrum length; cross-vein m-cu just after the fork of Mb into M₁+2 and M₃+₄ .................................................. E. (E.) *longirostris*

*Elephantomyia* (*Elephantomyia*) *baltica* Alexander, 1931

v* 1931 *Elephantomyia baltica* Alexander, p. 88.
1994 *Elephantomyia baltica* Alexander, 1931: 58 [sic!]: Evenhuis, p. 69.

**Material examined.** Holotype: No. 282 (male), Coll. University of Göttingen (GMUG).

**Diagnostic characters**

*E. (E.) baltica* clearly differs from the other Baltic amber species of the genus *Elephantomyia* in its relatively short Rs vein. The length of vein Rs is only slightly longer than twice the length of the basal section of R₅, in other species of this genus, the length of Rs is at least three times that of the basal section of R₅. *E. (E.) baltica* also differs distinctly in the ratio between the wing, rostrum, and abdomen lengths: in *E. (E.) baltica*, the wing is as long as the rostrum, whereas in other species, the wing is distinctly longer than the rostrum. In *E. (E.) baltica*, the rostrum is longer than abdomen, whereas in *E. (E.) brevipalpa*, *E. (E.) irinae* sp. nov., and *E. (E.) pulchella*, the rostrum is shorter than, or as long as, the abdomen. Additionally, vein Rs in *E. (E.) baltica* is shorter than R₂₃₄₊, in contrast to *E. (E.) brevipalpa*, where Rs is as long as or longer than R₂₃₄₊. Moreover, *E. (E.) baltica* has an elongate palpus, much like the other Baltic amber
species of the genus *Elephantomyia*, whereas the palpus in *E. (E.) brevipalpa* is very short, being less than half the length of the rostrum’s glossal lobes. In *E. (E.) baltica*, cross-vein m-cu is situated just after the fork of Mb into M1+2 and M3+4, whereas in *E. (E.) pulchella*, m-cu is situated at exactly half the length of the d-cell.

**Redescription**

**Body:** brown, 9.5 mm long (without rostrum).

**Head:** rostrum elongate, 8.5 mm long, as long as the wing, longer than abdomen (Fig. 1D), antenna (Fig. 1A) small; scape cylindrical; pedicel widened; basal flagellar segments short and crowded; last segments elongate, cylindrical, with two elongated setae on each flagellomere; palpus (Fig. 1B) elongate, 4-segmented, last segment short, other segments elongate and cylindrical; system of small microtrichia visible on all segments.

**Wing** (Fig. 1C): 8.5 mm long; pterostigma present, not darkened, oval, pale brown; vein Sc moderate length, ending opposite two-thirds Rs length; sc-r short, twice the distance from Sc tip; vein Rs gently arcuate, only slightly longer than twice length of basal section of R5, shorter than the length of R2+3+4; R1 ending approximately two-fifths length of R2+3+4; r-r (R2) atrophied; M3 one and half times longer than d-cell; cross-vein m-cu before d-cell mid-length, just after of fork of Mb; A1 and A2 almost straight.

**Leg:** tibial spurs not visible.

**Hypopygium:** not clearly visible.

**Ovipositor:** only male specimens known.

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**Fig 1.** *Elephantomyia (E.) baltica* [8], No. 282 (male), holotype: A. antenna; B. apical part of rostrum with maxillary palps; C. wing venation; D. relation between the wing (w), rostrum (r), and abdomen (ab) lengths. Abbreviations: clyp—clypeus, lbl—labellum, mxp—maxillary palps, ped—pedicel, scp—scape.

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Remarks. The specimen is well preserved, but the number of segments of antenna is probably 14, but the flagellomeres are very crowded and the boundaries between individual flagellomeres is not clear.

Elephantomyia (Elephantomyia) bozenae sp. nov. urn:lsid:zoobank.org:act:47F3BA11-F251–4BA2–8BE1–A85DEA1D0754

Material examined. Holotype: No. MP/3338 (male), Coll. Institute of Systematic and Evolution of Animals, Polish Academy of Sciences (ISEA PAS).

Etymology. The specific name is dedicated to the eminent biologist Bożena Szala, MSc.

Diagnosis

E. (E.) bozenae sp. nov. is characterized by its elongate and narrow d-cell, which is approximately twice as long as wide; in E. (E.) baltica, E. (E.) irinae sp. nov., E. (E.) longirostris, and E. (E.) pulchella, the d-cell is shorter, being approximately 1.5 times longer than wide. In E. (E.) bozenae sp. nov., vein M₃ is almost the same length as the d-cell, whereas M₃ is longer than the d-cell in E. (E.) baltica, E. (E.) irinae sp. nov., E. (E.) longirostris, and E. (E.) pulchella sp. nov. Moreover, E. (E.) bozenae sp. nov. differs from other Baltic amber Elephantomyia species in the ratio of wing, rostrum, and abdomen lengths. In E. (E.) bozenae sp. nov., the rostrum is shorter than the wing, being slightly longer than half wing length, and longer than the abdomen. In contrast to E. (E.) pulchella, where m-cu is situated at exactly half of d-cell length, in E. (E.) bozenae sp. nov., m-cu is just before of half d-cell length. In E. (E.) bozenae sp. nov., Rs length is at least three times that of the basal section of R₅, whereas in E. (E.) baltica the wing is as long as the rostrum, vein Rs is relatively short, and the length of vein Rs is only about twice the length of the basal section of R₂. In E. (E.) bozenae sp. nov., Rs is shorter than R₂+₃+₄, which contrasts to E. (E.) brevipalpa, where Rs is as long as R₂+₃+₄ or longer. Moreover, the palpus in E. (E.) bozenae sp. nov. is elongate, unlike E. (E.) brevipalpa, where the palpus is very short, being shorter than half the length of the rostrum’s glossal lobes.

Description

Body: brown, distal part of abdomen darker than rest of body, body 3.16 mm long (without rostrum).

Head: rostrum elongate, 2.14 mm long, shorter than wing, ending just after half wing length, rostrum longer than abdomen (Fig. 2C). Antenna (Figs. 2A, 3D) small, 0.53 mm long, 15-segmented, flagellar segments crowded; scape cylindrical, widened; pedicel wide; first flagellomere elongate; second flagellomere very short, crowded with first flagellomere; flagellomeres 5–15 elongate; the last one flagellomere widened at apex; antennae with two elongated setae on each segment of antennae; palpus (Figs. 2B, 3B) elongate, 0.20 mm long, 4-segmented, the last segment short, other segments elongate. System of small microtrichia clearly visible on all segments.

Wing (Figs. 2E, 3A): 3.56 mm long, 0.86 mm wide; pterostigma present, not darkened, oval, pale brown; vein Sc elongate, ending opposite five-sixths Rs length; sc-r short, twice the distance from Sc tip; Rs slightly arcuate, at least three times basal section of Rs, shorter than length of R₂+₃+₄; R₁ ending approximately half length of R₂+₃+₄; r-r (R₂) atrophied; M₃ almost equal to d-cell length; cross-vein m-cu just before of d-cell mid-length; A₁ almost straight, A₂ slightly waved.

Leg: tibial spurs not visible.

Hypopygium (Figs. 2D, 3C): 0.37 mm, gonocoxite as in other Elephantomyia species, approximately twice as long as wide, with elongate, narrow, lobe-shaped interbase; outer
gonostylus narrow, distinctly bifid at end, distal part curved externally; inner gonostylus slightly widened, strongly narrowed in apical part; directed into hypopygium.

Ovipositor: only male specimens known.

Elephantomyia (Elephantomyia) brevipalpa (Loew, 1851)

1850 Toxorhina brevipalpa Loew, p. 37. (nomen nudum).
* 1851 Toxorhina brevipalpa Loew, p. 400.
1860 (1859) Limnobiorhynchus [brevipalpa] Osten Sacken, p. 221.
Material examined. Holotype: No. MB.J., 337 (male), Coll. Berendt (NHMB); No. MP/3323 (female), Institute of Systematic and Evolution of Animals, Polish Academy of Sciences (ISEA PAS); No. 161 (male), Coll. Kutscher, University of Göttingen (GMUG).

Fig 3. Morphology of Elephantomyia (E.) bozenae sp. nov., No. MP/3338, holotype: A. body, latero-ventral view; B. maxillary palpi; C. hypopygium, ventral view; D. head, ventral view. Abbreviations: clyp—clypeus, lbl—labellum, gx—gonocoxite, ing—inner gonostylus, oug—outer gonostylus, intb—interbase, st IX—sternite IX, I–IV—maxillary palps segments.

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Diagnostic characters

*E. (E.) brevipalpa* differs distinctly from other Baltic amber species of this genus in the characteristic morphology of its palpus. In *E. (E.) brevipalpa*, the palpus is very short, being less than half the length of the rostrum’s glossal lobes, whereas in other species, the palpus is relatively long. *E. (E.) brevipalpa* also differs from the other species redescribed and described here in the ratio between wing, rostrum, and abdomen lengths. In *E. (E.) brevipalpa*, the rostrum is shorter than the wing, being only slightly longer than half wing length, and shorter than abdomen. Moreover, in *E. (E.) brevipalpa*, vein Rs is as long as, or longer than, vein R_{2+3+4}, in contrast to other species of this genus where Rs is distinctly shorter than R_{2+3+4}. In *E. (E.) brevipalpa* Rs is more than three times the basal section of R_{5}; in comparison, *E. (E.) baltica* has a relatively short Rs, only about twice the length of the basal section of R_{5}. Cross-vein m-cu in *E. (E.) brevipalpa* is situated just after the fork of Mb into M_{1+2} and M_{3+4}, whereas in *E. (E.) pulchella*, vein m-cu is half d-cell length. In *E. (E.) brevipalpa*, the d-cell is comparatively short and wide, being approximately one and half longer than wide, unlike *E. (E.) bozenae* sp. nov., where the d-cell is elongate and narrow, twice as long as wide. Moreover, vein M_{3} in *E. (E.) brevipalpa* is approximately one and half times longer than the d-cell, whereas in *E. (E.) bozenae* sp. nov., M_{3} is almost the same length as the d-cell.

Redescription

Body: brown, 5.1 mm long (without rostrum) (female).

Head: rostrum elongate, 2.86 mm long (male), 2.86 mm long (female), shorter than wing, ending just longer than half wing length, longer than abdomen (male) (Figs. 4C, 5A). Antenna (Fig. 4A) relatively short, 14-segmented; scape elongated; pedicel widened; first flagellar segment widened; second flagellomere short; first flagellomeres crowded; flagellar segments 3–6 cylindrical and short; the last six segments cylindrical and elongate, with elongate setae that are much longer than the length of flagellomeres bearing them; flagellomeres 1–5 without elongate setae; flagellomeres 6–7 with three setae, not very elongate, shorter than segments bearing them; flagellomeres 8–11 with very elongate setae, much longer than segments bearing them; the last flagellomere with four very elongate setae; palpus (Figs. 4B, D, 5B, C) very short in both male and female, less than one half the length of rostrum’s glossal lobes; the last segment short, penultimate segment elongate and cylindrical.

Wing (Figs. 4F, 5A, E): 4.68 mm long, 1.18 wide (female); pterostigma present, not darkened, oval, pale brown; vein Sc moderate length, ending after half Rs length; sc-r short, twice distance from Sc tip; Rs slightly arcuate, at least three times length of R_{5} basal section, almost as long as, or longer than, R_{2+3+4}; R_{1} short, ending approximately one-third length of R_{2+3+4}; pterostigma base just after of Sc tip and before the bifurcation of Rs into R_{1}, R_{2+3+4}, and R_{5} (female); r-r (R_{2}) atrophied; M_{1} approximately one and half times longer than d-cell; cross-vein m-cu just before d-cell mid-length; A_{1} almost straight, A_{2} slightly waved.

Leg: tibial spurs presented.

Hypopygium (Figs. 4E, 5D): 0.4 mm long, gonocoxite as in other species of the genus, approximately twice as long as wide, with elongate, narrow, lobe-shaped interbase; outer gonostylus narrow, not forked at the end, inner gonostylus widened in half of length, strongly narrowed in final one-third of its length; outer and inner gonostyles directed internally; aedeagus elongate.

Ovipositor (Fig. 5F): 1.09 mm long, tergite 9 narrow; tergite 10 large, hypogynial valves and cerci narrow, almost equal in length.

Remarks. In contrast to other Baltic amber species of *Elephantomyia*, the pterostigma base in *E. brevipalpa* is distinctly shifted towards the base of wing, being just distal to the tip of Sc
and proximal of the bifurcation of Rs into R₁, R₂+3+4, and R₅ (Fig. 6A–C). However, this feature is only noted in the female wing, as details of the male wing are not observable due to poor preservation.

*Elephantomyia* (*Elephantomyia*) *irinae* sp. nov. urn:lsid:zoobank.org:act:4540675A-AE8A-4766-B0D9–958BDAE0FF6E8

**Material examined.** Holotype: No. MP/3324 (male). Additional material: No. MP/3330 (male), MP/3331 (male), No. MP/3337 (male), Coll. Institute of Systematic and Evolution of Animals, Polish Academy of Sciences (ISEA PAS); No. 250 (male), Coll. Künow, University of Göttingen (GMUG).
**Etymology**. The specific name is dedicated to the eminent palaeontologist Dr. Irina D. Sukatsheva.

**Diagnosis**

*E. (E.) irinae* sp. nov. differs from *E. (E.) longirostris*, *E. (E.) pulchella*, *E. (E.) bozenae* sp. nov., and *E. (E.) baltica* in the ratio of rostrum and wing lengths. In *E. (E.) irinae* sp. nov., the rostrum is distinctly shorter than wing, ending just after half wing length; in *E. (E.) baltica*, the rostrum is as long as the wing, whereas in *E. (E.) longirostris*, the wing is only one-fifth longer than the rostrum, and in *E. (E.) pulchella* the wing is one-third longer than the rostrum. In contrast to *E. bozenae* sp. nov., where the rostrum is longer than the abdomen, the rostrum in *E.
(E.) irinae sp. nov. is distinctly shorter than the abdomen. From E. (E.) brevipalpa, E. (E.) irinae sp. nov. differs in the length of palpus: where in E. irinae (E.) sp. nov. the palpus is elongate, in E. (E.) brevipalpa the palpus is very short, less than half the length of the rostrum’s glossal lobes. Moreover, in E. (E.) irinae sp. nov., the length of Rs is at least three times that of the basal section of R5, whereas in E. (E.) baltica, Rs is only about twice the length of the basal section of R5. Vein Rs in E. (E.) irinae sp. nov. is shorter than R2+3+4, in contrast to E. (E.) brevipalpa, where it is as long as, or longer than, R2+3+4. Cross-vein m-cu in E. (E.) irinae sp. nov. is situated after the fork of Mb into M1+2 and M3+4, but before half d-cell length; this is different from E. (E.) pulchella, where vein m-cu is situated at half d-cell length. In E. (E.) irinae sp. nov., the d-cell is rather short and wide, being one and half times as long as wide, whereas in E. (E.) bozenae sp. nov., the d-cell is elongate and narrow, and twice as long as wide. Moreover, vein M1 in E. (E.) irinae sp. nov. is approximately one and half times longer than the d-cell, but in E. (E.) bozenae sp. nov., M1 is almost the same length as the d-cell.

Description

Body: dark, 9.5 mm long (without rostrum).

Head: rostrum not very elongate, 2.41–2.82 mm long, only slightly longer than half wing length, shorter than abdomen (Fig. 7B). Antenna (Fig. 7A) 15-segmented, small; scape elongated, cylindrical; pedicel widened; first flagellar segment elongate; second flagellar segment short; flagellomeres 5–15 elongate, crowded; flagellomeres 2–14 with three elongate setae; the last flagellomere with four elongate setae; setae on flagellomeres much longer than length of segments bearing them; palpus (Fig. 7C) elongate, 0.31–0.35 mm long, 4-segmented, the last segment short, other segments elongate and cylindrical.

Wing (Figs. 7E, 8A, C): 3.49–8.5 mm long, 1.05–1.37 wide; pterostigma present, not darkened, oval, pale brown; vein Sc moderate length, ending opposite three-quarters Rs length; sc–r short, twice distance from Sc tip; vein Rs gently arcuate, Rs at least three times length of R5.
basal section, shorter than half length of R2+3+4; R1 ending approximately half length of R2+3+4; r-r (R2) atrophied; M3 approximately one and half longer than d-cell; cross-vein m-cu before d-cell mid-length, about one-fourth its length beyond fork of Mb; A1 and A2 almost straight.

Leg: tibial spurs invisible.

Hypopygium (Figs. 7D, 8B): 0.55 mm, gonocoxite as in other species of the genus, approximately twice as long as wide, with elongate, narrow, lobe-shaped interbase; outer gonostylus narrow, distal part curved externally; inner gonostylus widened, directed into hypopygium; aedeagus elongate.

Ovipositor: only male specimens known.
Elephantomyia (Elephantomyia) longirostris (Loew, 1851)

1850 Toxorhina longirostris Loew, p. 37 (nomen nudum).
1851 Toxorhina longirostris Loew, p. 400.
1860 (1859) Limnobiorhynchus [longirostris] Osten Sacken, p. 221.
1869 Elephantomyia [longirostris] Osten Sacken, p. 106.
1894 Elephantomyia longirostris Osten Sacken [sic!] (Toxorhina): Scudder: 180.
1906 Elephantomyia longirostris (Loew, 1851): Meunier, pp. 365–366.
1907 Toxorhina longirostris Handlirsch, p. 991.
1931 Elephantomyia longirostris (Loew, 1851): Alexander, p. 90.
1994 Elephantomyia longirostris Evenhuis, p. 69.

Material examined. Holotype: No. MB.J. 338 (male), Coll. Berendt (NHMB); No. 1089–6 (male), Coll. Ch. and H. Hoffeins; No. MP/1627 (female); No. MP/3319 (male), No. MP/3322 (male), No. MP/3325 (male), No. MP/3328 (male), No. MP/3329 (male), No. MP/3333 (male), No. MP/3334 (male), Coll. Institute of Systematic and Evolution of Animals, Polish Academy of Sciences (ISEA PAS); No. 19946 (male), Coll. Museum of the Earth, Polish Academy of Sciences, Warsaw (MEPAS).

Diagnostic characters

E. (E.) longirostris differs from other Baltic amber species of this genus in its very elongate rostrum, which is longer than the abdomen, and almost as long as the body length, being only
one-fifth shorter than wing length. In *E. (E.) baltica*, the rostrum is longer than the abdomen and is equal in length to the wing; in *E. (E.) bozenae* nov. and *E. (E.) brevipalpa*, the rostrum is longer than the abdomen but ends only slightly distal of half wing length; in *E. (E.) iriniae* sp. nov., the rostrum is shorter than the abdomen; and in *E. (E.) pulchella* the rostrum is one-third shorter than the wing, whereas in *E. (E.) iriniae* sp. nov., the rostrum ends just distal of half wing length. Although in *E. (E.) baltica* the length of vein Rs is only about twice the length of the basal section of Rs, in *E. (E.) longirostris* Rs is at least three times the length of the basal section of Rs. In *E. (E.) longirostris* sp. nov. vein Rs is shorter than Rs2+3+4, which contrasts to *E. (E.) brevipalpa*, where Rs is as long as, or longer than, Rs2+3+4. Moreover, *E. (E.) longirostris* differs from *E. (E.) brevipalpa* in palpus morphology: in *E. (E.) longirostris*, the palpus is elongate, whereas in *E. (E.) brevipalpa* the palpus is very short, being shorter than half the length of the rostrum’s glossal lobes. Cross-vein m-cu in *E. (E.) longirostris* is positioned shortly after of the fork of Mb into M1+2 and M3+4, different from in *E. (E.) pulchella*, where m-cu is at exactly half d-cell length. In *E. (E.) longirostris*, the d-cell is comparatively short and wide, being approximately one half and times longer than, whereas in *E. (E.) bozenae* sp. nov., the d-cell is elongate and narrow, being twice as long as wide. Moreover, vein M3 in *E. (E.) longirostris* is one and half times longer than the d-cell, but in *E. (E.) bozenae* sp. nov. M3 is almost the same length as the d-cell.

**Redescription**

**Body:** brown with elongate rostrum, 3.00–4.91 mm long (without rostrum).

**Head:** rostrum 2.66–4.20 mm long, approximately equal to body length, longer than abdomen length, only one-fifth shorter than wing (Fig. 9C). Antenna (Figs. 9A, 10A) relatively short, 0.80–1.11 mm, 15-segmented; flagellar segments crowded; scape elongate; pedicel wide; flagellomeres 2–15 elongate; first flagellomere very short, crowded with previous segments; final segments elongate, narrowed at apex; antennae with four elongate setae on each flagellomere; setae much longer than length of segments bearing them; palpus (Fig. 9B) elongate, 4-segmented, final segment short, other segments elongate and cylindrical, system of small microtrichia clearly visible on all segments.

**Wing** (Figs. 9E, 10B, D): 4.23–8.5 mm long, 1.04–1.41 mm wide; pterostigma present, not darkened, oval, pale brown; vein Sc moderate length, ending after half Rs length; sc-r short, at end of Sc; vein Rs arcuate, at least three times length of basal section of Rs, shorter than length of Rs2+3+4; R1 ending at approximately half length of Rs2+3+4; r-r (R2) atrophied; M3 approximately 1.5 times longer than d-cell length; cross-vein m-cu situated just after fork of Mb into M1+2 and M3+4; A1 almost straight, A2 slightly waved.

**Leg:** tibial spurs present.

**Hypopygium** (Figs. 9D, 10C): 0.50 mm, gonocoxite as in other species, approximately twice as long as wide, with elongate, narrow, lobe-shaped interbase; outer gonostylus narrow, distinctly bifid at end, distal part curved externally; inner gonostylus widened for basal half of its length, strongly narrowed in distal third, directed into hypopygium; aedeagus elongate.

**Remarks.** The specimens No. K5100Z4080 (GMUG) and No. 87 (GMUG), reported as *E. longirostris* by Alexander [8], lack sufficient features to allow them to be clearly placed within this species. In these specimens, the rostrum is not very elongate, being about half of the wing length or shorter, and is shorter than, or as long as, the abdomen. Further study of these specimens is necessary to clarify their taxonomic status.
Elephantomyia (Elephantomyia) pulchella (Loew, 1851)

1850 Toxorhina pulchella Loew, p. 37 (nomen nudum).
  * 1851 Toxorhina pulchella Loew, p. 400.
1860 (1859) Limnobiorhynchus [pulchella] Osten Sacken, p. 221.
1869 Elephantomyia [pulchella] Osten Sacken, p. 106.
1894 Elephantomyia pulchella Osten Sacken [sic!] (Toxorhina): Scudder, p. 180.
1906 Elephantomyia pulchella (Loew, 1851): Meunier, p. 365.
1907 Toxorhina pulchella Handlirsch, p. 991.
1931 Elephantomyia pulchella (Loew, 1851): Alexander, p. 91.
1994 Elephantomyia pulchella Loew, 1851: Evenhuis, p. 69.

Material examined. Holotype: No. MB.], 336 (male), Coll. Berendt (NHMB); No. 1195–5 (male), Coll. Ch. and H. W. Hoffeins; No. MP/3336 (male) Institute of Systematic and Evolution of Animals, Polish Academy of Sciences (ISEA PAS).

Fig 9. Elephantomyia (E.) longirostris [9], No. 1089–6 (male): A, antenna; B. apical part of rostrum with maxillary palps; C. relation between wing (w), rostrum (r), and abdomen (ab) lengths; D. hypopygium; E. wing venation. Abbreviations as in Fig. 2.

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Diagnostic characters

*E. (E.) pulchella* differs from all other species of the genus *Elephantomyia* known from the Baltic amber in the position of cross-vein m-cu, which in this species is located at exactly half d-cell length, whereas in other species of this genus, this cross-vein is situated just after the fork of Mb into M_{1+2} and M_{3+4} or just before the d-cell mid-length. *E. (E.) pulchella* also differs from the other fossil *Elephantomyia* species in the ratio of wing, rostrum, and abdomen length. In *E. (E.) pulchella*, the rostrum is one-third shorter than the wing, but is the same length, or slightly longer than, the abdomen. Moreover, in *E. (E.) pulchella* the length of Rs is at least three times that of the basal section of R_5, whereas in *E. (E.) baltica*, vein Rs is relatively short, being only about twice the length of the basal section of R_5. Additionally, Rs in *E. (E.) pulchella* is shorter than R_{2+3+4}, in contrast to *E. (E.) brevipalpa* where Rs is as long as, or longer than, R_{2+3+4}. Moreover, the palpus is elongate in *E. (E.) pulchella*, much like other fossil species of the
genus *Elephantomyia*, which differs from *E. (E.) brevipalpa*, where the palpus is very short, being less than half the length of the rostrum’s glossal lobes. In *E. (E.) pulchella*, the d-cell is comparatively short and wide, being approximately one and half times longer than wide; in *E. (E.) bozenae* sp. nov., the d-cell is elongate and narrow at twice as long as wide. Moreover, vein *M₃* in *E. (E.) pulchella* is approximately one and half times longer than the d-cell, whereas *M₃* is almost the same length as d-cell in *E. (E.) bozenae* sp. nov.

**Redescription**

Body: brown, 3.42–3.63 mm long (without rostrum).

![Redescription Diagram](image-url)
Head (Figs. 12C, 13B): head width 0.36–0.52 mm; rostrum elongate, 2.22–2.77 mm long, as long as or slightly longer than abdomen, one-third shorter than wing (Fig. 11C). Antenna (Figs. 11A, 12C, 13A, B) relatively short, 0.70–0.74 mm long, 15-segmented; flagellar segments crowded; scape elongate, cylindrical; pedicel wide; first flagellomere elongate, widened; second flagellomere short, widened, crowded with flagellomere 1; flagellomeres 3–6 short and widened; flagellomeres 7–15 elongate, cylindrical; final segments elongate, narrowed at apex; flagellomeres 1–5 with two elongate setae; flagellomeres 6–9 with three elongate setae; flagellomeres 10–13 with four elongate setae; elongate setae much longer than length of segments bearing them; palpus (Fig. 11B) elongate, 0.46 mm long, 4-segmented, final segment short, other segments elongate and cylindrical; system of small microtrichia clearly visible on all segments.

Fig 12. Morphology of *Elephantomyia* (*E.*) *pulchella* [9], No. 1195–5 (male): A. body, latero-ventral view; B. wing venation; C. head, dorsal view; D. apex of wing.

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Wing (Figs. 11E, 12A, B, D): 3.8–4.50 mm long, 1.06 mm wide; pterostigma present, oval, pale brown; vein Sc moderate length, ending distal of half Rs length; sc-r short, at end of Sc; vein Rs distinctly arcuate, at least three times length of basal section of R5, shorter than length of R2+3+4; R1 ending at approximately half length of R2+3+4; r-r (R5) atrophied; M3 approximately one and half times longer than d-cell; cross-vein m-cu at exactly half d-cell length; A1 almost straight, A2 slightly waved.

Leg: tibial spurs present.

Hypopygium (Figs. 11D, 13C): 0.53 mm, gonocoxite as in other species, approximately twice as long as wide; interbase elongate and narrow, lobe-shaped; outer gonostylus narrow, bifid at end, distal part curved externally; inner gonostylus widened for basal half of its length, strongly narrowed for distal third of length; directed into hypopygium; aedeagus elongate.

Ovipositor: only male specimens known.

Discussion

According to recent data, the first representatives of the genus *Elephantomyia* appeared in the Eocene, ~100 million years after the earliest representatives of the closely related genus *Helius*.
All of species of Elephantomyia known from Baltic amber can be placed within the nominative subgenus Elephantomyia, presently the most species-rich extant subgenus which is distributed worldwide. The other three extant subgenera—Elephantomyina, Elephantomyodes, and Xenoelephantomyia—are not presently represented in the fossil record, and are also rare in the extant fauna. Of these three subgenera, Elephantomyina is particularly rare, occur only in Ecuador and Peru, whereas Xenoelephantomyia is reported solely from Peru. These two subgenera each contain a single species: Elephantomyia (Elephantomyina) supernumeraria [26] and Elephantomyia (Xenoelephantomyia) penai [6]. The final subgenus, Elephantomyodes, is distributed in the Oriental, Australian, and Oceanian regions, and is represented by 32 extant species (Fig. 14). The fossil representatives of Elephantomyia known from the Baltic amber can be clearly placed within the subgenus Elephantomyia, and differ from species of the other subgenera particularly in regards to wing venation. In Elephantomyina, a strong supernumerary cross-vein connecting R2+3+4 and R5 occurs shortly before the tip of the latter, and r-m connects with Rs a short distance before its fork; in addition, the tibial spurs are absent in this subgenus [4]. Elephantomyodes differs from nominative subgenus in the lack of tibial spurs and the details of wing venation, particularly in having Rs in alignment with the basal section of R4+5 and R2+3, arising almost perpendicularly from the end of the sector [5]. In contrast to Elephantomyia, subgenus Xenoelephantomyia is characterised by a reduced anal field, with a single anal vein. Differences in the wing length to rostrum ratio are clearly observable among fossil representatives of the subgenus Elephantomyia known from the Baltic amber: In E. baltica, the rostrum is equal to the wing in length, whereas the rostrum is only slightly shorter than the wing in E. longirostris (1/7 shorter than the wing) or E. pulchella (1/3 shorter than the wing). Elephantomyia differs from the closely related genus Helius [27], [28] in the development of a poorly elongated rostrum, always shorter than half body length. In both E. brevipalpa
and *E. irinæ* sp. nov. we can observe that the rostrum is only slightly longer than half the wing length; these proportions can also be correlated to the length of abdomen, as in *E. brevipalpa* and *E. irinæ* sp. nov. the rostrum is distinctly shorter than the abdomen, whereas in other representatives of this genus the rostrum is always longer than, or equal to, the abdomen length.

The elongate rostrum is also seen in the Cretaceous species *Helius ewa* [25], which can be considered closely related to *Elephantomyia*. Therefore, it could be assumed that this feature of an elongate rostrum appeared much earlier than the earliest *Elephantomyia* crane-flies [25], [28]. The development of such a structure has been related to feeding behaviour, as elongate, nectar-feeding mouthparts occur among many groups of dipterans, including the Limoniidae. In modern dipterans, the exploitation of the great variety of flower types and angiosperm taxa is permitted through a unique repertoire of sensory cues, in conjunction with modified mouthparts, and the presence of frequently large to holoptic compound eyes with stereoscopic, and probably colour, vision in advanced forms [29]. Therefore, it could be hypothesized that the appearance of the elongate rostrum in *Elephantomyia* and related forms reflected the diversification of flowers of various floral types, including the plesiomorphic ANITA-grade [30] which began to offer various floral rewards for pollination (brood sites, starchy food bodies, nectar, pollen, and heat as a resource). The diversification of *Elephantomyia* would have been promoted by further diversification and specialization of floral arrangements, their scent production, size, shape, colour, thermogenesis presence, insect rewards, and overall specialization [29]. These co-evolutionary processes probably took place during the late Cretaceous and early Palaeogene, when floral structures became more variable and elaborate, nectar was anatomically deployed in various positions within the flower, and the more ingenious pollination mechanisms developed [29], [31], [32]. However, knowledge of the biology and diversity of the extant species of *Elephantomyia*, and of all Limoniidae, is presently insufficient to provide detailed analyses of this idea.

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**Author Contributions**

Conceived and designed the experiments: IK. Performed the experiments: IK. Analyzed the data: IK. Contributed reagents/materials/analysis tools: IK. Wrote the paper: IK. Photographs, drawings: IK.
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