

## Non-biting midges of the tribe Tanytarsini in Eocene amber from the Rovno region (Ukraine): a pioneer systematic study with notes on the phylogeny (Diptera: Chironomidae)

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### Abstract

The first detailed systematic study on the tanytarsine chironomids recorded in the Eocene amber from the Rovno region (Ukraine) revealed seven new taxa. *Archistempellina* gen. nov., represented by *A. bifurca* sp. nov. (type for the genus, male) and *A. falcifera* sp. nov. (male), displays characters similar to those found in *Stempellina* Thienemann et Bause, and is recognized as one of probable basal lineages in the subtribe Stempellinina Shilova. *Corneliola* gen. nov., represented by *C. avia* sp. nov. (male, female), combines features known from several genera of the tribe Tanytarsini, and tentatively is regarded as the closest relative of *Constempellina* Brundin. *Rheotanytarsus alliciens* sp. nov. (male), featuring a long hypopygial digitus, is considered to be the oldest species of the genus. *Tanytarsus congregabilis* sp. nov. (male) is the first known Eocene representative of the *lugens* systematic species group. A complemented description of the male of *Tanytarsus serafini* Gilka is provided as well.

**Key words:** Diptera, Chironomidae, Tanytarsini, new taxa, systematics, phylogeny, Eocene, amber

### Introduction

The tribe Tanytarsini belongs to the relatively young subfamily Chironominae unknown before the Cenozoic except the unspecified record by Kalugina (1974). Representatives of the subfamily account for 23.7% of chironomid inclusions in the French amber of Oise (early Eocene, ~53 Ma), but no Tanytarsini have been reported from these resins (Doitteau & Nel 2007). The oldest known Tanytarsini are thus inclusions found in Baltic amber (Seredszus & Wichard 2007; Gilka 2010, 2011b). However, their advanced diversity in the middle Eocene indicates an earlier origin and may suggest them to have appeared before ~45–40 Ma.

Published data on the Eocene Tanytarsini are scarce. Detailed descriptions concern only four species of the genera *Stempellina* Thienemann et Bause, *Stempellinella* Brundin and *Tanytarsus* van der Wulp (Seredszus & Wichard 2007; Gilka 2010, 2011b). Analyses of diagnostic characters found in these taxa clearly indicate their advanced speciation. They are represented by genera of the two subtribes: the Stempellinina Shilova and the Tanytarsina Zavřel, among which two species of *Tanytarsus* are classified in separate systematic groups: the extinct *serafini*, and the *mendax* group, represented by numerous extant species (op. cit).

The specimens examined in the present study are inclusions collected from deposits distributed north of Rovno (Ukraine), in the Pripyat River basin; outside Ukraine, the deposits are found also in Belarus and in south-eastern Poland (Perkovsky *et al.* 2003). The Rovno amber chironomids were first reported recently (Zelentsov *et al.* 2012); they were identified only to the genus level and did not include the Tanytarsini. So far, there have been several attempts at determining the age of the Rovno amber deposits; however, well-documented studies indicate that the Rovno, Gulf of Gdańsk, and Bitterfeld (Germany) amber deposits were formed synchronously (*cf.* Sontag & Szadziewski 2011). Our systematic study comprises detailed descriptions of two new genera and five new species which are thus considered to be the oldest Tanytarsini.

## Materials and methods

The amber was cut into small pieces, ground and polished manually, as described recently by Gilka (2010). Measurements are in  $\mu\text{m}$  except the total length (in mm, rounded off to the first decimal place); the body was measured from the antennal pedicel to the end of the gonostylus/cercus, the wing from the arculus to the tip; lengths of leg segments and palpomeres were rounded off to the nearest 5 and 1  $\mu\text{m}$ , respectively; the antennal, leg and venarum ratios (AR, LR, VR, respectively) were calculated to the second decimal place. Wherever possible, the morphological terminology and abbreviations follow Sæther (1980). Illustrations were prepared using the technique of Gilka (2008); selected photographs were taken using the Nomarski DIC. The type material is deposited in the collection of the I.I. Schmalhausen Institute of Zoology (SIZ), National Academy of Sciences of Ukraine, Kiev.

## Systematics

### Family: Chironomidae Newman, 1834

#### Subfamily: Chironominae Newman, 1834

#### Tribe: Tanytarsini Zavřel, 1917

#### *Archistempellina* Gilka et Zakrzewska, gen. nov.

Type species: *Archistempellina bifurca* Gilka et Zakrzewska, sp. nov. (by present designation).

Other species: *Archistempellina falcifera* Gilka et Zakrzewska, sp. nov.

**Derivatio nominis.** We believe that the genus represents one of basal lineages of the subtribe Stempellinina.

**Diagnosis.** Eyes bare, with fully developed dorsomedian extensions. Antenna with 13 flagellomeres. Antepronotum relatively well developed. Tuber on scutum absent. Wing veins  $R_{2+3}$  and/or  $R_1$  arcuate, RM slightly oblique relative to R,  $R_{4+5}$  ending distal to apex of  $M_{3+4}$ , anal lobe weak. Tibia of mid leg with single comb bearing spur; tibia of hind leg with two well separated combs, one comb with spur. Gonostylus longer than gonocoxite, with apical seta. Anal tergite with median setae. Anal point slender, styliform, without spinulae and crests, upturned in lateral view with tip bent down. Superior volsella extraordinarily small, cylindrical, with rounded apex. Digitus absent. Stem of median volsella about the size and shape of superior volsella, bearing two slender falciform lamellae. Inferior volsella with enlarged head-like apical half, armed with stout curved setae.

**Remarks.** Several distinct characters found in the two species described below have not been found in any extant/fossil taxon and support our concept of erecting the new genus *Archistempellina*. These are: the shape of the hypopygial superior and median volsellae, and the combination of characters/structure of eye, antenna and wing.

We presume that the simple superior volsella found in *Archistempellina* (Figs 1J, 2I) and *Stempellina* is derived from a slender-type superior volsella, similar to that known from the Chironomini. This character probably indicates plesiomorphy in the Tanytarsini, as clearly different from those more sophisticated shapes known from other genera of the tribe. A tendency to reduction of the superior volsella (apomorphy) is displayed by both *Archistempellina* and *Stempellina*, in particular when the extremely small superior volsella in *Archistempellina* is taken into account, or when the long slender-type superior volsella known from the Eocene *Stempellina exigua* Seredszus et Wicha and the much shorter cylindrical/conical superior volsellae of extant *Stempellina* are compared (*cf.* Gilka 2005, Seredszus & Wicha 2007). We believe that a similar trend to reduction was appearing in both these genera, but in the Eocene it was much more advanced in *Archistempellina*.

The structure of the median volsella found in *Archistempellina* is here proposed to be treated as a prior generic character. The short stem bearing the two slender lamellae, as in Figs 1K and 2J (setiform lamellae absent), possibly show one of the simplest types of structure among the Tanytarsini. The median volsella of a similar shape is known from *Stempellina tervolae* Gilka, but the stem is much shorter, and armed with setiform and leaf-shaped lamellae (Gilka 2005).

*Archistempellina* display also a set of characters considered as less advanced among the Tanytarsini (plesiomorphies), which clearly separate the new genus from *Stempellina* and from most of the genera of the subtribe Stempellinina, but are typical for the Tanytarsina. These are, respectively: the wing vein  $R_{4+5}$  ending distal to apex of  $M_{3+4}$ , the fully developed dorsomedian extension of the eye, and the antenna with 13 well discernible flagellomeres. We consider this combination as an indication that *Archistempellina* is one of probable basal lineages in the subtribe Stempellinina; however, we do not ascribe *Archistempellina* to any subtribe definitely until a complex parsimony analysis is performed (Gilka & Zakrzewska, in prep.).

***Archistempellina bifurca* Gilka et Zakrzewska, sp. nov.**

**Type material.** Holotype. Adult male (tarsus of left fore leg and right mid leg missing) in 8 x 6 x 4 mm piece of amber (SIZ K-26075, Fig. 1A).

**Derivatio nominis.** From Latin, meaning ‘forked’, in reference to the shape of the hypopygial median volsella armed with two slender lamellae.

**Diagnosis.** Tibia of fore leg with small spur; femur of mid leg longer than femur of hind leg. Anal point tapering to pointed apex, reaching over superior and median volsellae and over half length of inferior volsella. Superior volsella very small, cylindrical. Stem of median volsella longer than its falciform lamellae.

**Description. Adult male** ( $n = 1$ ). Total length 2.7 mm; wing length c. 1400  $\mu\text{m}$ .

*Head* (Fig. 1B–D). Eyes bare, with well developed dorsomedian extensions. Frontal tubercles not observed. Antenna with 13 well discernible flagellomeres, AR 1.12–1.15, plume fully developed (Fig. 1C, D). Palps slightly asymmetrical, length of palpomeres 2–5 ( $\mu\text{m}$ ): 48, 123, 147, 205–245. Clypeals unobservable.

*Thorax* (Fig. 1B). Antepronotum relatively well developed, scutum not overreaching antepronotum. Tuberle on scutum absent. Most of setae unobservable, at least 8 scutellars.

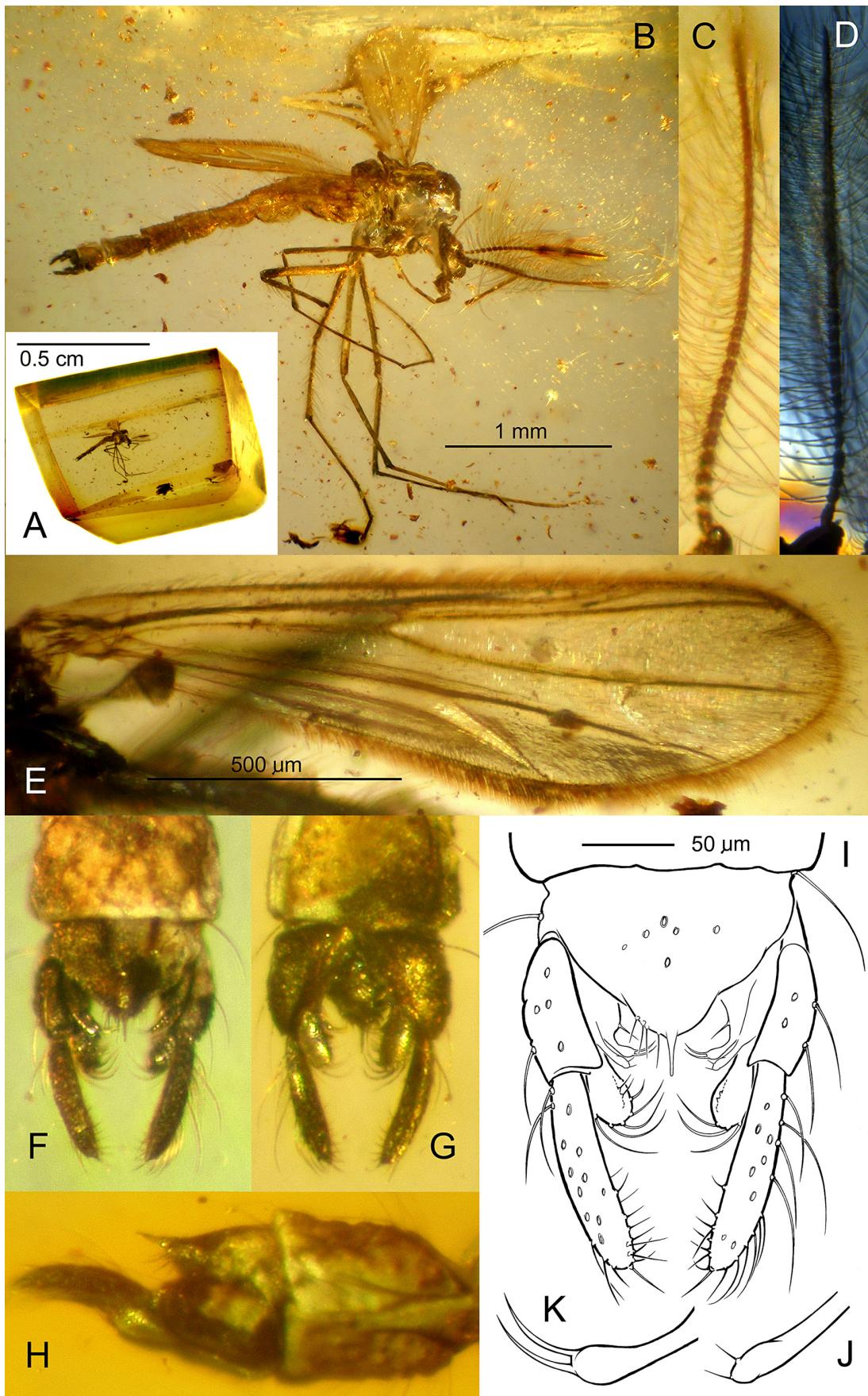
*Wing* (Fig. 1E). Slender, with anal lobe weak, broadest at 2/3 length, width: 387  $\mu\text{m}$ , length/width ratio 3.62. RM slightly oblique relative to R. Sc unobservable.  $R_1$  and  $R_{2+3}$  arcuate. FCu placed distally of RM;  $VR_{Cu}$  1.25. Veins ending as follows (in order from base to tip): An,  $Cu_1$ ,  $R_1$ ,  $R_{2+3}$ ,  $M_{3+4}$ ,  $R_{4+5}$ ,  $M_{1+2}$ ; distances between ends of  $R_1$ – $R_{2+3}$  and  $R_{2+3}$ – $R_{4+5}$  unequal ( $VR_C$  c. 4); An reaching FCu at least. Wing membrane covered with dense macrotrichia in distal half.

*Legs.* Tibia of fore leg with small spur, c. 10  $\mu\text{m}$  long. Single tibial comb of mid leg fan-shaped, teeth up to 20  $\mu\text{m}$  long, with single slender c. 40–45  $\mu\text{m}$  long spur; combs of hind leg broadly separated, fan-shaped, one comb broad (composed of c. 15 teeth) up to 20  $\mu\text{m}$  long, without spur, second comb narrow, teeth up to 25  $\mu\text{m}$  long, bearing c. 50  $\mu\text{m}$  long spur. Sensilla chaetica on  $ta_1$  of  $p_2$  not observed. Pulvilli absent. For length of leg segments and leg ratios see Table 1.

**TABLE 1.** Leg segment lengths ( $\mu\text{m}$ ) and leg ratios of male *Archistempellina bifurca* sp. nov.

	fe	ti	$ta_1$	$ta_2$	$ta_3$	$ta_4$	$ta_5$	LR
$P_1$	585	395–410	760	-	-	255	85	1.85
$P_2$	685	560	400	195	140	90	60	0.71
$P_3$	645	595	520	285	240	140	80	0.87

*Hypopygium* (Fig. 1F–K). Gonostylus cylindrical, straight, c. 115  $\mu\text{m}$  long, distinctly longer than gonocoxite, with strong apical seta. Anal tergite subtriangular, bearing several strong median setae. Anal point slender, styliform, tapering to pointed apex, without spinulae and crests, bearing at least 4 posterolateral setae on each side; anal point reaching over superior and median volsellae and over half length of inferior volsella; upturned in lateral view with tip bent down (Fig. 1F–J). Superior volsella extraordinarily small, cylindrical, slightly swollen in distal part, bearing at least 2 setae at rounded apex (Fig. 1J). Digitus absent. Stem of median volsella about the size and shape of superior volsella, c. 20  $\mu\text{m}$  long, slightly curved, medially directed, bearing 2 slender falciform lamellae; stem distinctly longer than lamellae (Fig. 1K). Inferior volsella reaching 1/3 length of gonostylus at most, club-shaped, with distinctly enlarged head-like apical half, armed with several stout curved setae.



**FIGURE 1.** *Archistempellina bifurca* sp. nov., male. A—holotype (inclusion); B—habitus; C, D—antenna (D—photographed using Nomarski DIC); E—wing; F–K—hypopygium: F, I—dorsal aspect; G—ventral aspect; H—lateral aspect; J—superior volsella; K—median volsella (J, K—magnified three times relative to hypopygium drawn).

**Remarks.** The best diagnostic characters that allow the separation of *Archistempellina bifurca* and *A. falcifera* are the shape of the anal point, the arrangement/position of the anal point apex in relation to the hypopygial volsellae (*cf.* Fig. 1F, G, I and Fig. 2E, G, H), and the lamellae/stem length proportions in median volsellae (*cf.* Fig. 1K and 2J).

***Archistempellina falcifera* Gilka et Zakrzewska, sp. nov.**

**Type material.** Holotype. Adult male (tarsus of left mid leg and both hind legs missing) in 13 x 7 x 7 mm piece of amber (SIZ K-8884, Fig. 2A; syninclusion: undeterminable chironomid female).

**Derivatio nominis.** From Latin, meaning ‘bearing sickles’, in reference to the bifid falciform hypopygial median volsellae.

**Diagnosis.** Tibia of fore leg with strong subapical bristles, spur absent; femur of mid leg longer than femur of hind leg. Anal point with swollen roundish tip, reaching bases of median and inferior volsellae. Superior volsella very small, cylindrical. Stem of median volsella and its falciform lamellae of the same length.

**Description. Adult male** (n = 1). Total length 3.5 mm; wing length c. 1610 µm.

**Head** (Fig. 2B, C). Eyes bare, with well developed dorsomedian extensions. Frontal tubercles not observed. Antenna with 13 well discernible flagellomeres, AR 1.26, plume fully developed (Fig. 2C). Length of palpomeres 3–5 (µm): 156, 163, 277. Long clypeals present but uncountable in lateral position.

**Thorax** (Fig. 2B). Antepronotum relatively well developed, scutum not overreaching antepronotum. Tuber on scutum absent. Ac at least 12, Dc at least 14 on each side, Pa 3 on each side, Scts at least 7.

**Wing** (Fig. 2D). Slender, with anal lobe weak, broadest at 2/3 length, width: 406 µm, length/width ratio 3.97. RM slightly oblique relative to R. Ends of Sc and R<sub>2+3</sub> fading, not visible; R<sub>1</sub> arcuate. FCu placed distally of RM; VR<sub>Cu</sub> 1.25. Veins ending as follows (in order from base to tip): An, Cu<sub>1</sub>, R<sub>1</sub>, M<sub>3+4</sub>, R<sub>4+5</sub>, M<sub>1+2</sub>. An fading in distal part, reaching FCu at most. Wing macrotrichia unobservable.

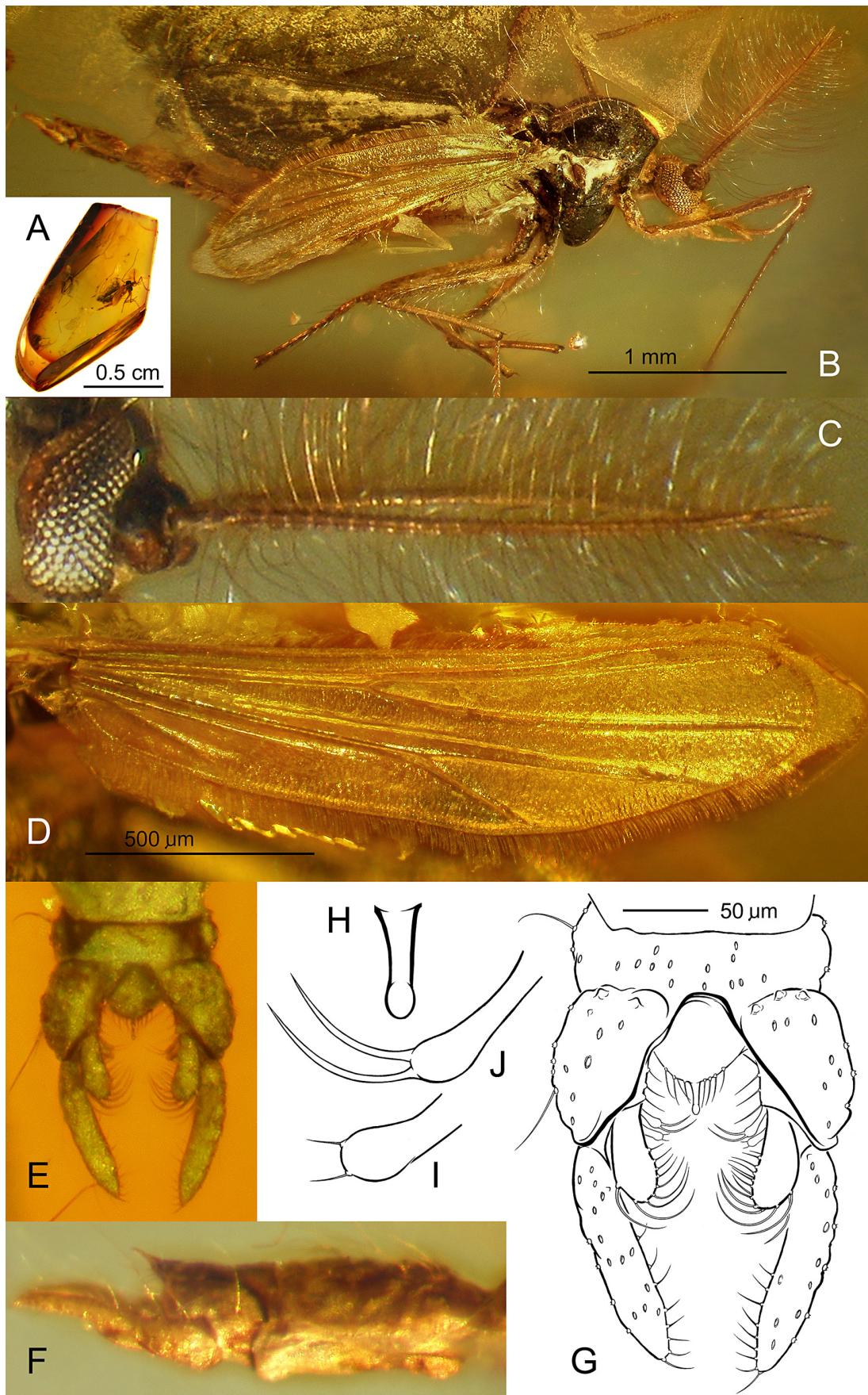
**Legs.** Tibia of fore leg with 4 strong subapical bristles, spur absent. Single tibial comb of mid leg fan-shaped, teeth up to 20 µm long, with single slender c. 30–40 µm long spur; combs of hind leg broadly separated, fan-shaped, one comb broad, teeth up to 12–16 µm long, without spur, second comb narrow, teeth up to 20 µm long, bearing 50–55 µm long spur. Sensilla chaetica on ta<sub>1</sub> of p<sub>2</sub> not observed. Pulvilli absent. For length of leg segments and leg ratios see Table 2.

**TABLE 2.** Leg segment lengths (µm) and leg ratios of male *Archistempellina falcifera* sp. nov.

	fe	ti	ta <sub>1</sub>	ta <sub>2</sub>	ta <sub>3</sub>	ta <sub>4</sub>	ta <sub>5</sub>	LR
P <sub>1</sub>	-	500	960	480	400	305	120	1.92
P <sub>2</sub>	825	630–645 slightly asymmetric	460	-	-	-	-	0.71
P <sub>3</sub>	780	750	-	-	-	-	-	-

**Hypopygium** (Fig. 2E–J). Gonostylus cylindrical, straight, tapering to conical apex, c. 135 µm long, much longer than gonocoxite, with apical seta. Anal tergite subtriangular. Anal point slender, styliform, with swollen roundish tip, without spinulae and crests, bearing at least 4 posterolateral setae on each side; anal point reaching bases of median and inferior volsellae; upturned in lateral view with tip bent down (Fig. 2E–H). Superior volsella very small, cylindrical, slightly swollen in distal part, bearing at least 2 setae at rounded apex (Fig. 2I). Digitus absent. Stem of median volsella about the size and shape of superior volsella, c. 20 µm long, slightly curved, medially directed, bearing 2 slender falciform lamellae; stem and lamellae of the same length (Fig. 2J). Inferior volsella reaching 1/3 length of gonostylus at most, club-shaped, with distinctly enlarged head-like apical half, armed with several stout and strongly curved setae.

**Remarks.** Apart from the characters listed in the diagnoses, *Archistempellina falcifera* and *A. bifurca* differ from each other in their general dimensions and colouration; however, in amber inclusions, the latter feature cannot be used with any certainty.



**FIGURE 2.** *Archistempellina falcifera* sp. nov., male. **A**—holotype (inclusion); **B**—habitus; **C**—antenna; **D**—wing; **E–J**—hypopygium; **E, G**—ventral aspect; **F**—lateral aspect; **H**—anal point; **I**—superior volsella, **J**—median volsella (**H–J**—magnified c. three times relative to hypopygium drawn).

## *Corneliola* Gilka et Zakrzewska, gen. nov.

Type species: *Corneliola avia* Gilka et Zakrzewska, sp. nov. (by present designation and monotypy).

**Derivatio nominis.** The senior author dedicates the name to his recently deceased grandmother, Kornelia.

**Diagnosis.** Eyes hairy, with well developed dorsomedian extensions. Male antenna with 9–10 flagellomeres, distal flagellomeres separated in part or fused; female antenna with 6 clearly separated flagellomeres. Antepronotum well developed; tubercle on scutum absent. Wing spatulate, with anal lobe not developed, covered with dense macrotrichia except basal part; RM parallel or slightly oblique relative to R,  $R_{4+5}$  ending distal to apex of  $M_{3+4}$ . Tibial combs of mid and hind legs separated, each comb with spur or with short spoor-like tooth. Gonostylus longer than gonocoxite, with strong spine-like apical bristle. Anal point without spinulae and crests. Superior volsella slender, somewhat conical, swollen in proximal part, with distinct digitiform extension. Digitus absent. Median volsella with well developed stem and long setiform and spindle-shaped lamellae.

**Remarks.** *Corneliola* displays an extraordinary set of structures, including the strong spine-like bristle on the apex of the gonostylus (Fig. 4D, E), a unique character here. The peculiarity of this new genus is expressed also by the following character combination: the hairy eyes with a long dorsomedian extension resemble *Afrozavrelia* Harrison (Stempellinina); the male antenna with less than 13 flagellomeres fits diagnoses of several genera of the tribe (most of the Stempellinina); the female antenna with 6 flagellomeres is known from *Rheotanytarsus* Thienemann et Bause (Tanytarsina); the spatulate wing with a strongly reduced anal lobe is similar to those known from *Stempellinella* Brundin or *Zavrelia* Kieffer (Stempellinina); the shape of the anal point (Fig. 4B, D, F) resembles that found in several *Paratanytarsus* Thienemann et Bause or *Cladotanytarsus* Kieffer (Tanytarsina), but has no crests and/or spinulae; the slender superior volsella with the swollen proximal part is similar to that known from *Constempellina* Brundin (Stempellinina), and the lack of digitus is characteristic of species or species groups of different genera in the tribe (most of the Stempellinina, but also the Tanytarsina). When a complemented character set based on that used for the Tanytarsini (e.g. Sæther & Andersen 1998, Ekrem & Saether 2000, Sæther & Roque 2004) is analysed, *Corneliola* and *Constempellina* are the closest genera, and *Corneliola* is treated as a member of the subtribe Stempellinina (we believe this is probable) on the background of the Tanytarsina (outgroup). However, the subtribal placement of the new genus must remain open until the set of published data on the oldest Tanytarsini becomes more complete (Giłka & Zakrzewska, in prep.).

## *Corneliola avia* Gilka et Zakrzewska, sp. nov.

**Type material.** Holotype. Adult male, complete specimen preserved in 10 x 8 x 2 mm piece of amber (SIZ K-7240, Fig. 3A). Paratypes. Adult male (tarsus of right fore leg missing) in 8 x 7 x 6 mm piece of amber (SIZ K-25833, Fig. 3B; syninclusions: Acari, 2 specimens); adult male (tarsus of right fore leg missing) and female (tarsi of all left legs and right mid leg missing), syninclusions preserved in 20 x 19 x 9 mm piece of amber (SIZ K-6973, Fig. 3C; other syninclusions: Collembola, 3 specimens).

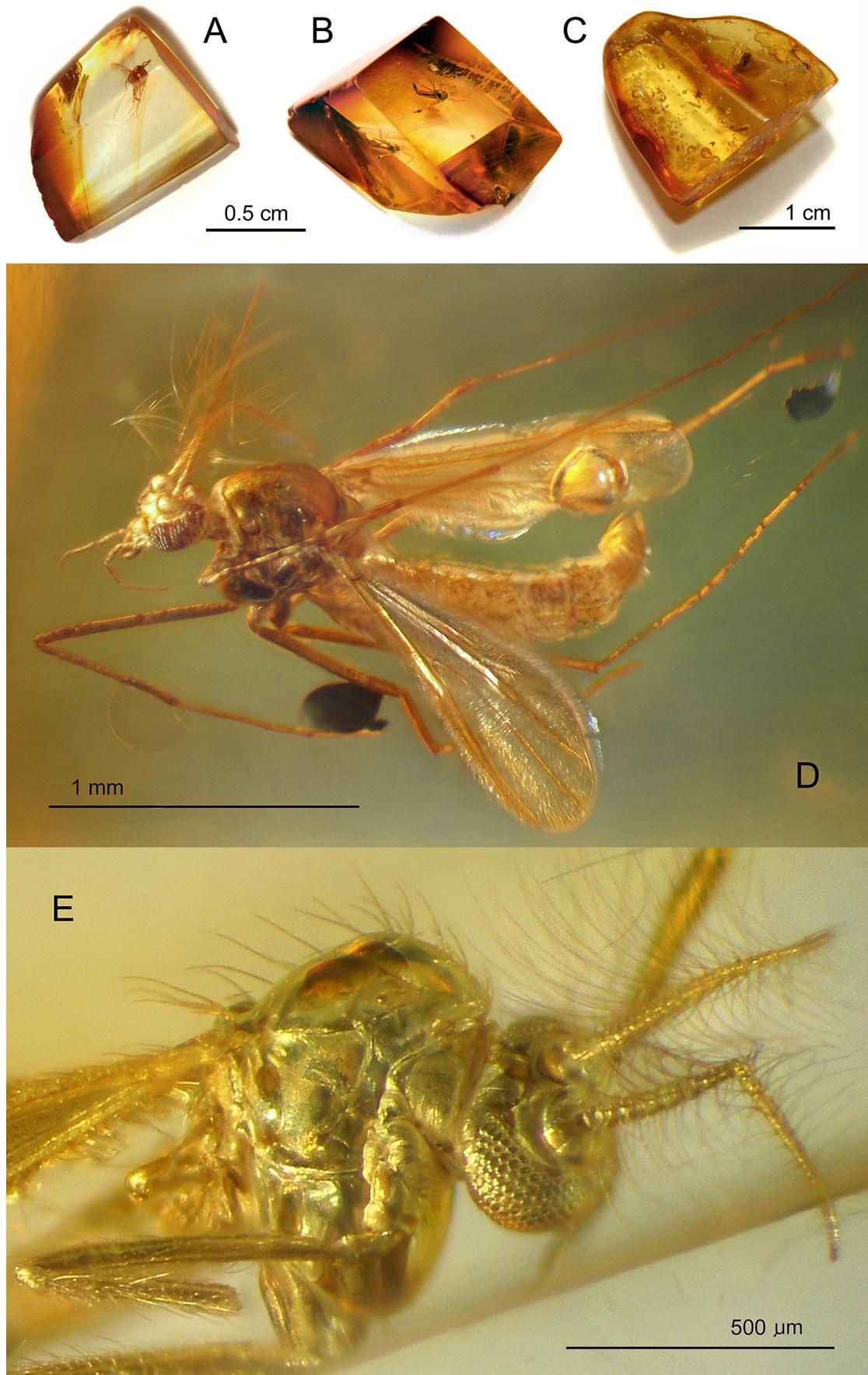
**Derivatio nominis.** From Latin, meaning ‘grandmother’.

**Diagnosis.** As for the genus.

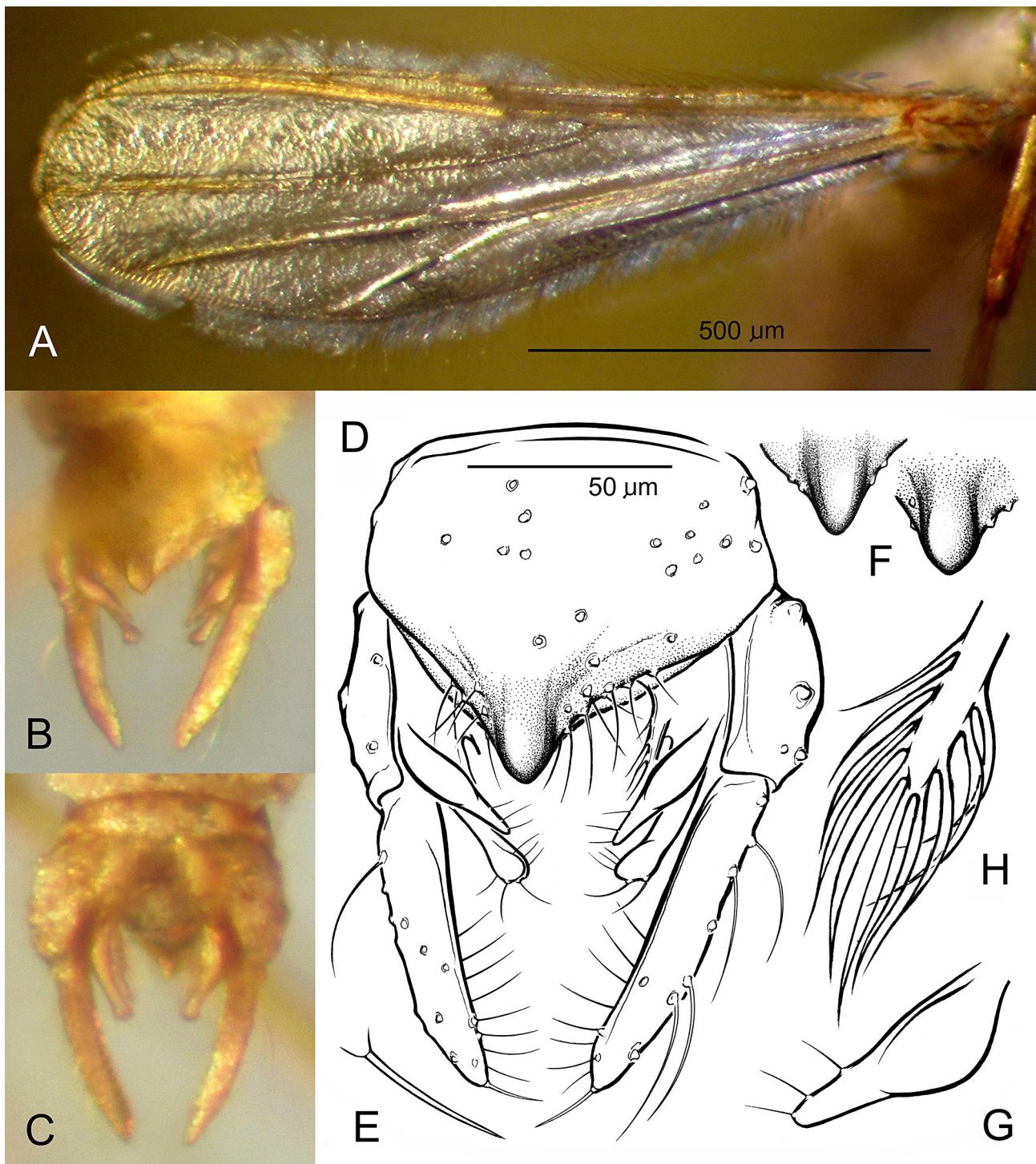
**Description. Adult male** ( $n = 3$ ). Total length 1.70–2.2 mm; wing length 850–1165  $\mu\text{m}$ .

**Head** (Fig. 3D, E). Eyes hairy, with microtrichia between ommatidial lenses distinctly longer than height of lens (visible in transmitted light); well developed dorsomedian extensions of eyes gradually narrowing from 5–6 facets at base to 2–3 facets medially, apex rounded, reaching frons; frontal lobes convex, distinctly divided by sagittal suture, without tubercles. Antennal flagellum composed of 9–10 discernible segments, flagellomeres 9–11 or 12 (apparently less than 13, according to distribution of setae) separated in part or completely fused, AR c. 1.3 when flagellum measured as 9-segmented; plume fully developed. Length of palpomeres 2–5 ( $\mu\text{m}$ ): 32, 68–88, 72–88, 133–149. Clypeals present but impossible to count, their tubercles weak.

**Thorax** (Fig. 3D, E). Antepronotum relatively well developed, scutum not overreaching antepronotum. Tubercle on scutum absent. Setae strong, complete in one specimen examined. Ac 14; Dc 6 on each side; Pa 1; at least 5–6 strong scutellars.



**FIGURE 3.** *Corneliola avia* sp. nov. A–C—type series: A—holotype, male; B—paratype, male; C—paratypes, male and female (syninclusions); D—male, habitus (holotype); E—thorax and head of male with 11/12-segmented antennal flagellum.



**FIGURE 4.** *Corneliola avia* sp. nov., male. A—wing; B–H—hypopygium: B, D—dorsal aspect, C—ventral aspect; E—apical bristle of gonostylius; F—anal point (variation); G—superior volsella; H—median volsella (E, G, H—magnified twice relative to hypopygium drawn).

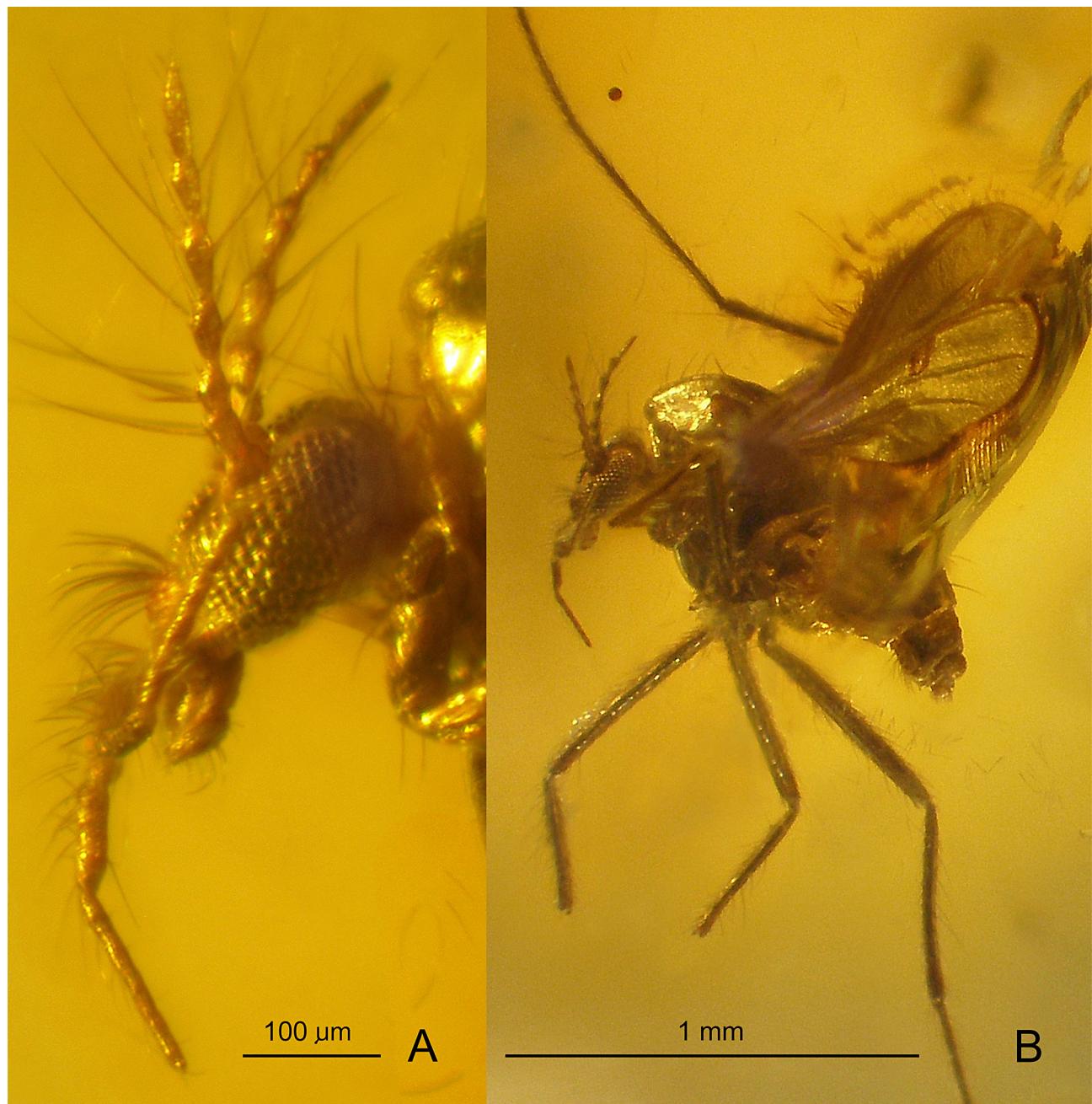
**Wing** (Fig. 4A). Spatulate, with anal lobe not developed, broadest at 2/3 length, width: 283–362 µm, length/width ratio 3.00–3.22, apex widely rounded. RM parallel or slightly oblique relative to R. FCu placed distally of RM; VR<sub>Cu</sub> 1.35–1.38. Veins ending as follows (from base to tip): An, Sc, Cu<sub>1</sub>, R<sub>1</sub>, R<sub>2+3</sub>, M<sub>3+4</sub>, R<sub>4+5</sub>, M<sub>1+2</sub>; ends of R<sub>1</sub>, R<sub>2+3</sub>, R<sub>4+5</sub> equidistant (VR<sub>C</sub> 1.0). Distal section of Cu<sub>1</sub> sinuous. Wing membrane covered with dense macrotrichia except basal part.

**Legs.** Tibia of fore leg with 2–3 strong subapical bristles (length: 110–120 µm), spur absent, at most vestigial dentiform process on apex. Tibial combs of mid leg small, teeth up to 10 µm long, one comb with single slender c.

20 µm long spur, second comb with slightly elongated spur-like tooth; combs of hind leg broadly separated, fan-shaped, teeth c. 12 µm long, each comb with slender spur c. twice the length of the longest tooth. Sensilla chaetica on  $ta_1$  of  $p_2$  not observed. Pulvilli absent. For length of leg segments and leg ratios see Table 3.

**TABLE 3.** Leg segment lengths (µm) and leg ratios of male *Corneliola avia* sp. nov.

	fe	ti	$ta_1$	$ta_2$	$ta_3$	$ta_4$	$ta_5$	LR
P <sub>1</sub>	500–560	260–340	550–720	300–400	240–310	180–240	80–95	1.76–2.31
P <sub>2</sub>	475–590	380–490	270–365	125–165	105–125	70–90	50–60	0.70–0.87
P <sub>3</sub>	515–590	455–580	365–455	185–255	165–215	105–135	50–65	0.74–0.81



**FIGURE 5.** *Corneliola avia* sp. nov., female. A—head with 6-segmented antennal flagellum, B—habitus.

*Hypopygium* (Fig. 4B–H). Gonostylus cylindrical, straight or slightly curved, slender, 70–100 µm long, much longer than gonocoxite, with strong spine-like apical bristle (Fig. 4D, E). Anal tergite semicircular, bearing several

strong median setae. Anal point short, triangular or somewhat lanceolate, apex blunt, spinulae and crests absent (Fig. 4D, F), bearing 6–8 posterolateral setae on each side. Superior volsella slender, conical, slightly swollen in proximal part, with distinct digitiform extension, apex blunt; 3 setae placed on anteromedian margin (Fig. 4D, G). Digitus absent. Stem of median volsella c. 20–25 µm long, straight, posteriorly directed, bearing setiform and slender spindle-shaped lamellae (Fig. 4H). Inferior volsella reaching half length of gonostylus at most, narrowed in mid length and slightly bent medially, swollen, head-like apical part, armed with several stout curved setae (Fig. 4D).

**Adult female** (n = 1). Total length c. 1.2 mm; wing length 630 µm.

*Head* (Fig. 5A). Eyes hairy, as in male. Frontal tubercles absent. Antenna with 6 clearly separated flagellomeres: 35, 34, 50, 53, 39, 67 µm long. Palps similar to those found in male; length of palpomeres 3–5 (µm): 84, 82, 145. Clypeus with 12 setae.

*Thorax* (Fig. 5A, B). Antepronotum relatively well developed, but slightly weaker than in male. Tuberle on scutum absent. Setae strong, but poorly countable in the specimen examined. Ac at least 6, Dc at least 6 on one side, Pa and Scts unobservable.

*Wing* (Fig. 5B). As in male, with usual sexual differences. Width: 270 µm, length/width ratio: 2.33.

*Legs*. Tibial spurs and combs as in male. For length of leg segments and leg ratios see Table 4.

*Genitalia*. Cercus 24 µm long, 38 µm high (in lateral view). Other diagnostic structures of genitalia unobservable.

**TABLE 4.** Leg segment lengths (µm) and leg ratios of female *Corneliola avia* sp. nov.

	fe	ti	ta <sub>1</sub>	ta <sub>2</sub>	ta <sub>3</sub>	ta <sub>4</sub>	ta <sub>5</sub>	LR
P <sub>1</sub>	440	305	585	315	255	195	85	1.92
P <sub>2</sub>	510	375	-	-	-	-	-	-
P <sub>3</sub>	520	460	350	185	175	95	60	0.76

### Genus: *Rheotanytarsus* Thienemann et Bause, 1913

#### *Rheotanytarsus alliciens* Gilka et Zakrzewska, sp. nov.

**Type material.** Holotype. Adult male (distal flagellomeres, palpi and tarsi missing or broken and separated) preserved in 12 x 7 x 2 mm piece of amber (SIZ 155, Fig. 6A; syninclusion: Acari, 1 specimen).

**Derivatio nominis.** From Latin, meaning ‘interesting, engaging’. This is the oldest *Rheotanytarsus*, known from male with a fully-developed hypopygial digitus.

**Diagnosis.** Tibial combs of mid and hind legs with short spurs at most twice the length of the comb. Gonostylus distinctly narrowed in distal half, much longer than gonocoxite. Anal point long, triangular, tapering to slender pointed apex, bearing two long crests; spinulae absent. Superior volsella roundish, with slightly projecting posterior part. Digitus long, distinctly extending beyond superior volsella. Stem of median volsella stout and short, with several pectinate or leaf-shaped lamellae fused at bases.

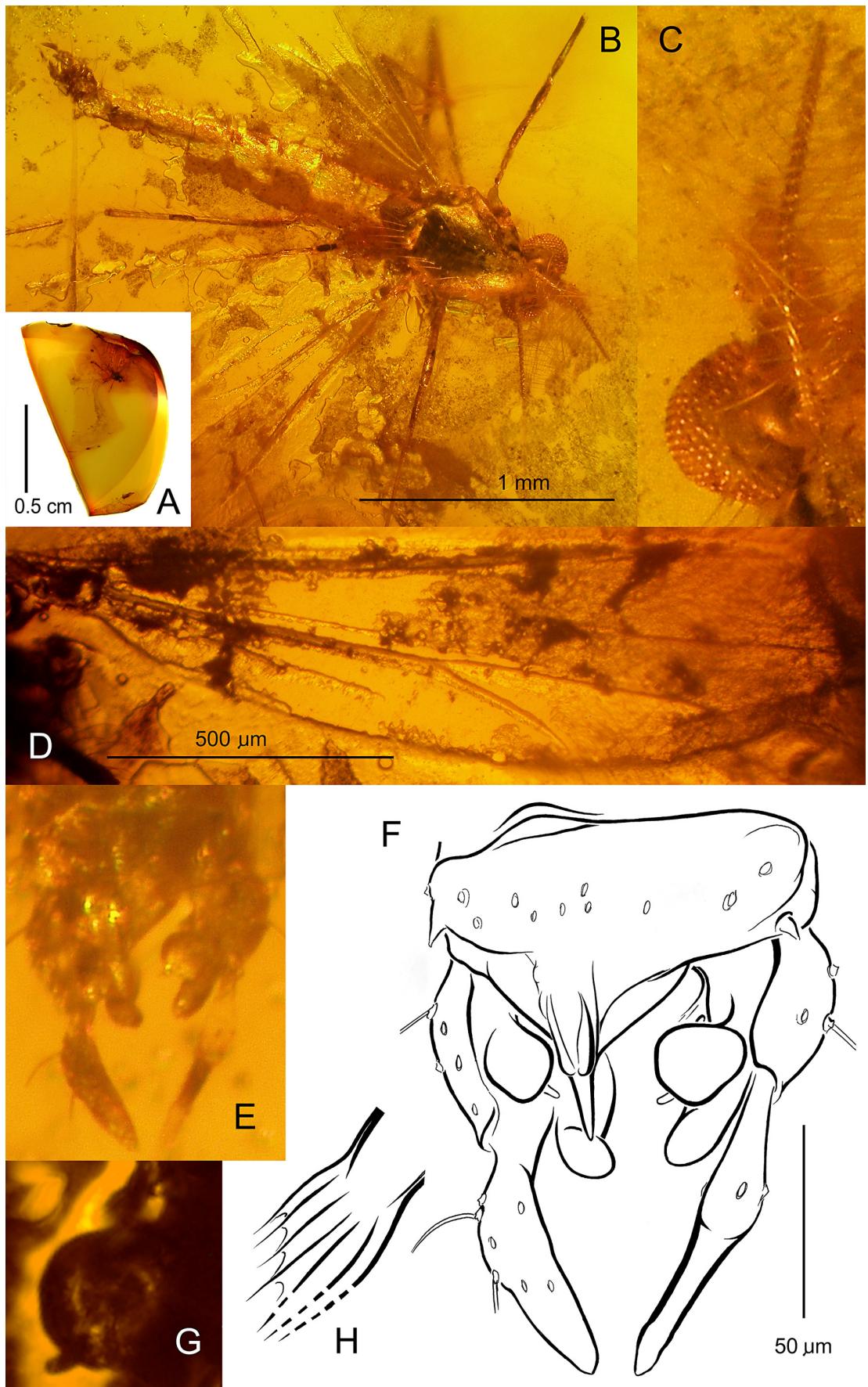
**Description. Adult male** (n = 1). Total length 2.3 mm; wing length 1315 µm.

*Head* (Fig. 6B, C). Eyes bare, with dorsomedian extensions. Frontal tubercles not observed. Antenna with 13 flagellomeres. Clypeals unobservable.

*Thorax* (Fig. 6B). At least several acrostichals present; Dc at least 7 on each side, Pa 2 on each side, Scts at least 5.

*Wing* (Fig. 6D). Slender, with anal lobe weak, broadest at 2/3 length, width: 380 µm, length/width ratio 3.46. Venation observable only in part. FCu placed distally of RM; VR<sub>Cu</sub> non-measurable. Visible veins ending as follows (in order from base to tip): An, Cu<sub>1</sub>, M<sub>3+4</sub>, R<sub>4+5</sub>, M<sub>1+2</sub>. Wing macrotrichia unobservable.

*Legs*. Apices of fore leg tibiae poorly preserved. Tibial combs of mid and hind legs with short spurs at most twice the length of the comb. Sensilla chaetica on ta<sub>1</sub> of p<sub>2</sub> not observed. Pulvilli not observed (distal tarsomeres missing or poorly preserved). For length of leg segments and leg ratios see Table 5.



**FIGURE 6.** *Rheotanytarsus alliciens* sp. nov., male. A—holotype (inclusion); B—habitus; C—head with antenna; D – wing; E–H—hypopygium: E, F—dorsal aspect; G—superior volsella, digitus and median volsella; H—median volsella (magnified c. three times relative to hypopygium drawn).

**TABLE 5.** Leg segment lengths ( $\mu\text{m}$ ) and leg ratios of male *Rheotanytarsus alliciens* sp. nov.

	fe	ti	ta <sub>1</sub>	ta <sub>2</sub>	ta <sub>3</sub>	ta <sub>4</sub>	ta <sub>5</sub>	LR
P <sub>1</sub>	-	305–310	-	-	-	-	-	-
P <sub>2</sub>	-	-	-	-	-	-	-	-
P <sub>3</sub>	670	595–605	380–400	255	195	110	-	0.64–0.66

*Hypopygium* (Fig. 6E–H). Gonostylus cylindrical, slightly curved, distinctly narrowed in distal half, c. 90  $\mu\text{m}$  long, much longer than gonocoxite. Anal point long, triangular, wide at base, tapering to slender pointed apex, bearing two long crests, spinulae absent, posterolateral setae not observed (Fig. 6E, F). Superior volsella roundish, with slightly projecting posterior part; digitus long, distinctly extending beyond superior volsella (Fig. 6E–G). Stem of median volsella stout but short, c. 5  $\mu\text{m}$ , with several pectinate or leaf-shaped lamellae fused at bases (Fig. 6G, H). Inferior volsella reaching 1/3 length of gonostylus, somewhat S-shaped, with slightly swollen head-like apex (Fig. 6E, F).

**Remarks.** Adult males of *Rheotanytarsus* are distinguishable by the long and usually distally narrowed gonostylus and by the elongate anal tergite point and its crests. Their lamellae are more or less fused into a plate on the stem of the median volsella. They are also known to lack the digitus. In rare cases, the lamellae are separate or fused only at their bases, and the digitus is vestigial and only exceptionally fully developed (Kyerematen & Sæther 2000, Gilka 2011a, Moubayed-Breil *et al.* 2012). We recognize that the fusion of the lamellae and the formation of the plate, as well as the reduction of the digitus are distinct trends in *Rheotanytarsus*; in contrast, the lack of the plate and the presence of the digitus indicate plesiomorphy as displayed by *R. alliciens* (Fig. 6E–H) and few extant *Rheotanytarsus* (op. cit.). The adult male of *R. alliciens* is peculiar in the shape of its superior volsella which is roundish, but has the slight posterior projection typical of *Rheotanytarsus* (Fig. 6F, G).

#### Genus: *Tanytarsus* van der Wulp, 1874

##### *Tanytarsus congregabilis* Gilka et Zakrzewska, sp. nov.

**Type material.** Holotype. Adult male (tarsus of left fore leg missing, tarsi of hind legs broken and separated). Paratypes. Adult male (left hind leg and wings poorly observable); adult male (tarsi of all legs missing and/or unobservable, distal abdominal segments missing). Three syninclusions preserved in 15 x 10 x 4 mm piece of amber (SIZ K-8855, Fig. 7A).

**Derivatio nominis.** From Latin, meaning ‘gregarious’. We presume that the specimens examined were trapped in resin during swarming.

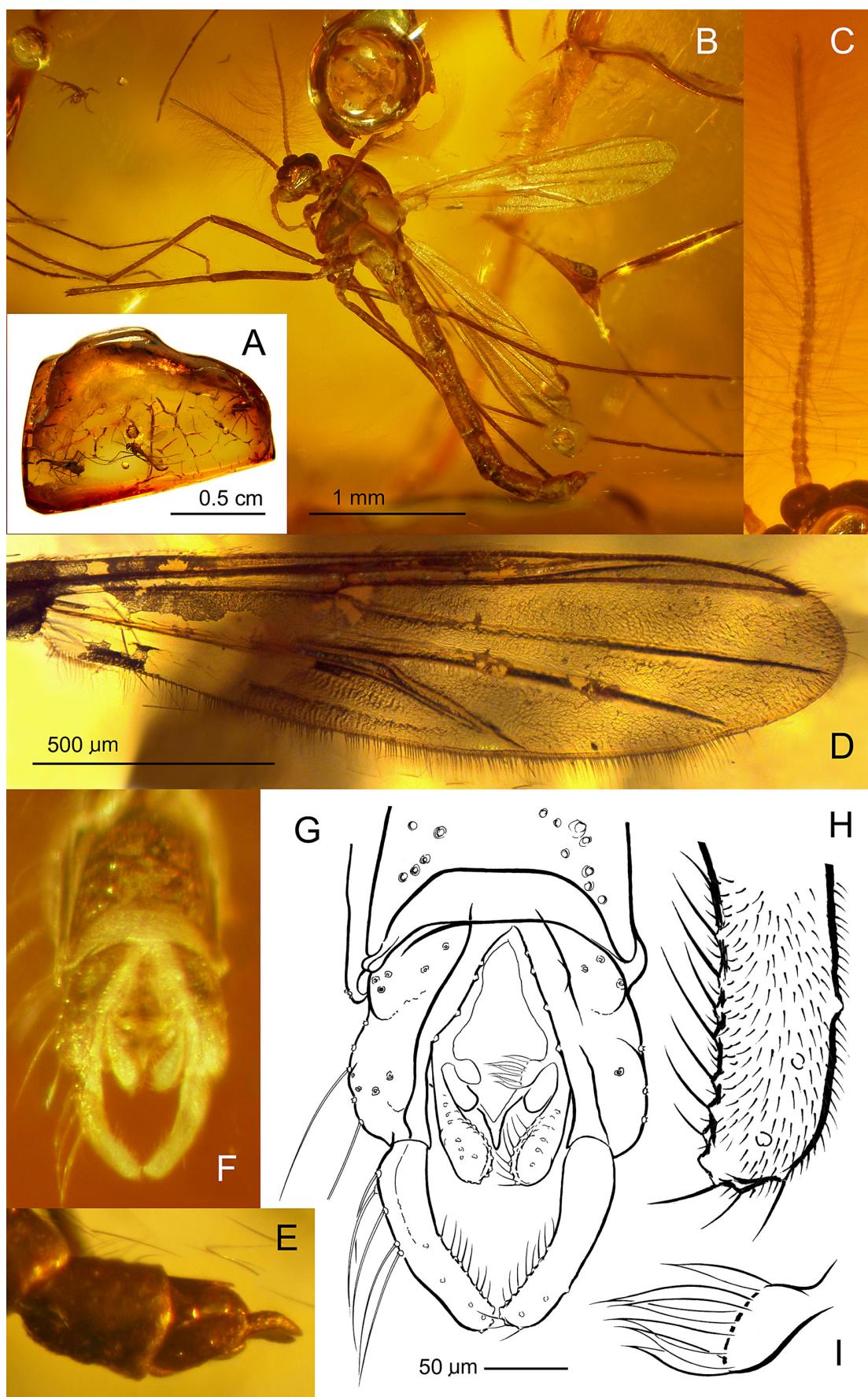
**Diagnosis.** Femur of mid leg longer than femur of hind leg. Gonostylus stout, slightly curved at mid length, as long as gonocoxite, in distal half with several setae placed at median margin and directed anteriorly. Median setae on anal tergite absent. Anal point triangular, tapering to blunt apex; in lateral aspect visible as straight prolongation of anal tergite, with tip bent down. Superior volsella stout, bean-shaped, with broadly rounded apex, directed posteromedially. Stem of median volsella bulb-shaped, with slender leaf-shaped lamellae. Inferior volsella robust, club-shaped.

**Description. Adult male** (n = 1–3). Total length 2.7–3.2 mm; wing length 1620–1680  $\mu\text{m}$ .

*Head* (Fig. 7B, C). Eyes bare, with dorsomedian extensions. Frontal tubercles not observed. Antenna with 13 well discernible flagellomeres, AR 1.05–1.07, plume fully developed (Fig. 7C). Length of palpomeres 2–5 ( $\mu\text{m}$ ): 45–48, 112–141, 97–141, 179–193. Clypeals present but uncountable in lateral position.

*Thorax* (Fig. 7B). Ac at least 8, Dc 5 on each side, Pa 3 on each side, Scts unobservable.

*Wing* (Fig. 7D). Ellipse-shaped, with weak anal lobe, broadest at 2/3 length, width: 410–430  $\mu\text{m}$ , length/width ratio 3.77–4.10. FCu placed distally of RM; VR<sub>Cu</sub> 1.16–1.18. Veins ending as in most extant *Tanytarsus* (from base to tip): An, Sc, Cu<sub>1</sub>, R<sub>1</sub>, R<sub>2+3</sub>, M<sub>3+4</sub>, R<sub>4+5</sub>, M<sub>1+2</sub>; ends of R<sub>1</sub>, R<sub>2+3</sub>, R<sub>4+5</sub> equidistant (VR<sub>C</sub> 1.0). Wing membrane densely covered with macrotrichia in distal part of r<sub>4+5</sub>, m<sub>1+2</sub>, and at posterior margin of wing. Proximal section of Cu<sub>1</sub> slightly deflected.



**FIGURE 7.** *Tanytarsus congregabilis* sp. nov., male. **A**—type series: holotype and two paratypes (syninclusions); **B**—habitus (holotype); **C**—antenna; **D**—wing; **E–I**—hypopygium: **E**—lateral aspect; **F, G**—ventral aspect; **H**—distal part of gonostyles; **I**—median volsella (**H, I**—magnified three times relative to hypopygium drawn).

**Legs.** Tibia of fore leg with single, 32–37 µm long spur (single comb composed of 6 teeth up to 15 µm long observed in one specimen is recognized as artefact). Tibial combs of mid and hind legs separated, fan-shaped, teeth up to 15 µm long (mid leg) and c. 15–20 µm long (hind leg); each comb with slender spur, 20–30 µm long (mid leg) and 40–48 µm long (hind leg). Sensilla chaetica on  $ta_1$  of  $p_2$  not observed. For lengths of leg segments and leg ratios see Table 6.

**TABLE 6.** Leg segment lengths (µm) and leg ratios of male *Tanytarsus congregabilis* sp. nov.

	fe	ti	$ta_1$	$ta_2$	$ta_3$	$ta_4$	$ta_5$	LR
$P_1$	715–805	590–660	775–795	460–510	365–415	280–285	115–125	1.28–1.34
$P_2$	765–780	720–780	425–460	245–290	180–215	110–140	75–90	0.55–0.60
$P_3$	700–715	910–915	515–555	335–365	260–290	150–170	90–110	0.57–0.61

**Hypopygium** (Fig. 7E–I). Gonostylus stout, slightly curved at mid length, boomerang-like, c. 115–125 µm, as long as gonocoxite, in distal half with several setae placed at median margin and directed anteriorly (Fig. 7F–H). Median setae on anal tergite absent. Anal point triangular, tapering to blunt apex; in lateral aspect visible as straight prolongation of anal tergite, tip bent down (Fig. 7E); spinulae, crests and posterolateral setae unobservable from ventral/lateral side. Superior volsella stout, bean-shaped, with broadly rounded apex, directed posteromedially. Digitus not observed (Fig. 7F, G). Stem of median volsella c. 25 µm long, bulb-shaped, with 5–6 slender leaf-shaped lamellae (Fig. 7I). Inferior volsella reaching 1/3 length of gonostylus at most, robust, club-shaped, armed with several stout curved setae (Fig. 7F, G).

**Remarks.** The structure of male hypopygium of *Tanytarsus congregabilis* suggests inclusion in the *lugens* species group. *T. congregabilis* fits the group diagnosis (Reiss & Fittkau 1971, Gilka & Paasivirta 2007) and displays the following character combination: gonostylus stout; median setae on anal tergite absent; superior volsella bean-shaped, with broadly rounded apex, directed posteromedially; digitus not observed; stem of median volsella bulb-shaped, bearing leaf-shaped lamellae (Fig. 7E–I). Unfortunately, the specimens examined are positioned such as to render observation of the dorsal aspect of hypopygium impossible, but the shape of the anal point in lateral view is similar to that known from *Tanytarsus bathophilus* Kieffer (Reiss & Fittkau 1971, fig. 36a). The peculiar, boomerang-shaped gonostylus is the best character for rapid identification of the species (Fig. 7F–H).

The large size (the largest among the known Eocene Tanytarsini) of adult *Tanytarsus congregabilis* males are also consistent with the *lugens* group diagnosis, although *T. congregabilis* is one of the smallest representatives of the group. We observed a similar pattern in other families of dipterans of the suborder Nematocera which, in the Baltic amber, are represented by specimens smaller than those belonging to related extant taxa (cf. Szadziewski 1988). The nature of the resin trap, enclosing primarily small insects, does not seem to particularly affect the Tanytarsini, as neither the fossil nor extant representatives of the tribe are larger than 6 mm. Our hypothesis gains an additional support from the fact that the three *T. congregabilis* specimens examined in this study are syninclusions in an amber chunk slightly larger than 0.5 cm<sup>3</sup>.

### *Tanytarsus serafini* Gilka, 2010

*Tanytarsus serafini* Gilka, 2010: 715.

**Material examined.** Adult male (tarsi of fore legs separated) preserved in 14 x 13 x 3/5 mm piece of amber (SIZ K-8193, Fig. 8A, B; syninclusions: Formicidae, 1 specimen; Acari, 2 specimens).

**Additions to original description. Adult male** ( $n=1$ ) (Fig. 8B). Total length c. 2.2 mm. AR 0.61. Palpomeres slightly asymmetric,  $Pm_{3-5}$ : 97–100, 88–96, 185 µm long (proximal palpomeres unobservable). Eight thoracic dorsocentral setae on left side. Wings slightly asymmetric, 1180–1210 µm long, 350 µm wide, length/width ratio 3.37–3.46;  $VR_{Cu}$  1.76–1.82. Tibia of fore leg with 1 or 2 strong subapical bristles (length: 179–208 µm), spurs absent.  $LR_1$  2.05;  $ta_4/ta_5 = 3.26$  ( $p_1$ ) and 2.77 ( $p_3$ );  $ta_3$  and  $ta_4$  of mid leg of equal length. Gonostylus c. 100 µm long. Stem of median volsella c. 55 µm long.



**FIGURE 8.** *Tanytarsus serafini* Gilka, 2010, male. A—*inclusion*, B—*habitus*.

**Remarks.** *Tanytarsus serafini* has been known so far from amber collected in the Gulf of Gdańsk (Gilka 2010), and is at present recorded in the Rovno region. Our preliminary data indicate the species to be one of the most frequent tanytarsines in the Eocene Baltic amber (Gilka & Zakrzewska, in prep.), and confirm the hypothesis that resins from Rovno and Gulf of Gdańsk were forming synchronously.

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