Minute and diverse in fossil sticky stuff: Tanytarsini (Diptera: Chironomidae) from early Eocene Indian Cambay amber

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We here present a pioneering systematic review of fossil dipterans of the tribe Tanytarsini (family Chironomidae) discovered in Indian amber from Cambay. The specimens examined belong to five species: *Gujaratomyia miripes*, ***Stempellina stebneri* sp. nov.**, ***Stempellinella pollex* sp. nov.**, ***Tanytarsus forfex* sp. nov.** and ***Tanytarsus ramus* sp. nov.**, which are described. All species belong to the oldest known Tanytarsini and come from the Cambay shale formation in Tadkeshwar, dated to the early Eocene (~54 Mya). Displaying unusual characters/structures of diagnostic and phylogenetic importance, the specimens studied are discussed against the background of the evolution and systematics of the oldest fossil (Eocene) and extant representatives in the tribe. An updated checklist and key to the identification of genera and species of Tanytarsini from Eocene amber is also provided. The spectral characteristics and physical properties of Cambay amber are similar to those of glessite resins, which are discussed in detail in order to substantiate the identity of the amber and the origin of the inclusions studied.

ADDITIONAL KEYWORDS: amber identification – Eocene – Fourier transform infrared spectroscopy – new species – non-biting midges – systematics.

INTRODUCTION

THE OLDEST CHIRONOMIDAE AND THE TANYTARSINI

The Chironomidae, commonly known as non-biting midges, are a large and diverse family of mostly aquatic dipterans. On the basis of a summary by Pape *et al.* (2011) and data published afterwards, the number of chironomid taxa is approaching 7500 species and 550 genera. This family is divided into 12 subfamilies, with the second largest, Chironominae, comprising three tribes: Chironomini, Pseudochironomini and Tanytarsini. The last is probably one of the most diverse,

but consists of minute midges. Extant Tanytarsini can be found worldwide, but some species are endemic to tropical or mountain areas. Adults can often be observed in huge swarms, which in humans can give rise to allergic symptoms that may develop into diseases of the respiratory system (Cranston *et al.*, 1981; Hirabayashi *et al.*, 1997; Giłka, 2009). Their larvae and pupae inhabit all types of freshwater bodies and, because they are often associated with a specific habitat, have proved to be useful indicators of extant, subfossil or fossil aquatic environments (e.g. Stebner *et al.*, 2017).

The oldest species of the family Chironomidae, *Aenne triassica* Krzemiński & Jarzembowski, 1999, comes from Upper Triassic deposits (~202 Mya; Krzemiński & Jarzembowski, 1999; Benton & Donoghue, 2007). It is followed by specimens preserved as Jurassic and Cretaceous rock impressions (e.g. Kalugina, 1980a, 1985, 1986, 1993; Zhang, 1991; Lukashevich & Przhiboro,

2011, 2015, 2018). Nonetheless, the vast majority of Cretaceous chironomids have been described on the basis of inclusions in Lebanese (~130 Mya; e.g. Brundin, 1976; Veltz *et al.*, 2007; Azar *et al.*, 2008), Wealden (UK) (~128 Mya; e.g. Jarzembowski *et al.*, 2008; Baranov *et al.*, 2019), Burmese (Myanmar) (~100 Mya; e.g. Baranov *et al.*, 2017; Giłka & Zakrzewska, 2017; Giłka *et al.*, 2019, 2020), Siberian (Russia) (~85 Mya; Kalugina, 1976, 1980b) and Canadian amber (~74 Mya; Boesel, 1937). However, the oldest known representatives of subfamily Chironominae and tribe Tanytarsini have been described only from Eocene resins; therefore, the tribe is considered relatively young. The majority of species have been found in Baltic amber (~40 Mya; Seredszus & Wichard, 2007; Giłka, 2010, 2011; Giłka *et al.*, 2013; Zakrzewska & Giłka, 2013, 2014, 2015a, b; Zakrzewska *et al.*, 2016), whereas a single species has been discovered in Chinese Fushun amber (~50–53 Mya; Giłka *et al.*, 2016). Another tanytarsine, *Gujaratomyia miripes* Giłka & Zakrzewska, 2018 [to date the only described non-biting midge from early Eocene Cambay amber (~54 Mya; Zakrzewska *et al.*, 2018)] was thus considered the oldest. Although a preliminary generic placement of several further Tanytarsini species from the same deposit has already been defined (Stebner *et al.*, 2017), herein they are formally designated and described for the first time.

CAMBAY AMBER: GEOLOGICAL CONTEXT

The Cambay rift basin, situated in Gujarat, one of the states of western India, is a narrow, elongated, intracratonic graben extending from Surat in the south to Sanchor in the north. The graben consists mainly of Mesozoic–Cenozoic rocks (Merh, 1995) covered by alluvial and fluvial sediments. Tectonically, it extends beyond Sanchor to the Barmer Basin of Rajasthan (Mathur *et al.*, 1968). The basin is flanked in the north-east by the Aravalli–Delhi Supergroup (fold belt), in the east by the Deccan Craton, and in the south-east and west by the Saurashtra Craton. The Cambay shale formation consists of sandstones, bentonitic and carbonaceous clays and lignite beds. The early Eocene subsurface lignite-bearing sequence that contains the amber is restricted to the lower clay bed. Among the most important localities with regard to the quantity of amber and abundance of inclusions are the Vastan and Tadkeshwar active opencast lignite mines, located in southern Cambay, ~30 km north-east of Surat (Rust *et al.*, 2010; Nadein & Perkovsky, 2019). The amber occurs in lignitic and mud-dominated sediments, which were deposited in a near-shore chenier plain system, where the sediment input was seasonal (e.g. McCann, 2010). On basis of research into Protista and mammalian fossils, and data from stable carbon and strontium isotopes, the age of the Cambay amber can be estimated at ~54 Mya (Sahni *et al.*, 2006; Garg *et al.*,

2008; Punekar & Saraswati, 2010; Clementz *et al.*, 2011; Smith *et al.*, 2016). It is thus much older than Eocene Baltic amber and slightly older than Chinese Fushun amber. The age of Cambay amber implies that the deposit was formed immediately after the Late Palaeocene Thermal Maximum and at the beginning of the Early Eocene Climatic Optimum (Zachos *et al.*, 2008). Cambay amber has been identified as an angiosperm dammar resin (Grimaldi *et al.*, 2013). Studies of amber forest composition also suggest that Dipterocarpaceae, which are a dominant element in the extant tropical forests in south-eastern Asia, were the source of the Indian Cambay amber deposits (e.g. Rust *et al.*, 2010).

MATERIAL AND METHODS

The specimens examined are adult males preserved in Cambay amber from the Tadkeshwar lignite mine. The amber was ground using a Buehler Phoenix Beta grinder and polished manually, so that the inclusion could be observed and illustrated as clearly as possible and its diagnostic structures studied. Owing to the sticky nature of amber, which makes polishing and preservation a challenge, several amber pieces were embedded in a plastic mass.

Measurements of specimens are in micrometres, except for the total length (in millimetres, rounded off to the first decimal place). The body length was measured from the antennal pedicel to the end of the gonostylus, and the wing from the arculus to the tip. Lengths of leg segments and palpomeres were rounded off to the nearest 5 and 1 μm, respectively. The hypopygium ratio (HR) was calculated to the first decimal place, and the antennal, leg and venarum ratios (AR, LR and VR) to the second digit after the decimal point. Morphological terminology and abbreviations follow Sæther (1980). Photographs were taken using a PZO Biolar SK14 microscope and Helicon Focus 6 image stacking software.

Wherever possible, Fourier transform infrared spectroscopy (FT-IR) spectra [attenuated total reflectance (ATR)] were obtained as support for the identity of the examined amber (for details, see Discussion: Cambay amber identity). A Nicolet iS10 FT-IR spectrometer was used for recording ATR (diamond crystal) FT-IR spectra. The resolution was 4 cm^{-1} and the number of scans was 16. The ATR spectra were subjected to advanced ATR correction. All spectra were baseline corrected, and spectral operations were performed using standard spectrophotometer software. Reference spectra of glessite samples of different geographical origin were recorded using a Mattson II FT-IR spectrometer (KBr pellet) of the same resolution at Gdańsk University of Technology, Faculty of Chemistry, Department of Chemistry and Technology of Functional Materials.

For comparison, transmittance spectra were converted to absorbance mode using spectrophotometer software. The spectra with reference curve numbers obtained from Cambay amber are registered and stored in the archives of the Laboratory of the International Amber Association (IAA), Gdańsk, Poland and in the Laboratory of Systematic Zoology at the Department of Invertebrate Zoology & Parasitology (LSZ DIZP), University of Gdańsk, Poland. The inclusions are part of the collection of the Birbal Sahni Institute of Palaeosciences (BSIP), Lucknow, India.

RESULTS

Eleven of the Tanytarsini individuals from the BSIP collection are preserved well enough to be presented here, including seven specimens designated as types for new taxa. They belong to the extinct genus *Gujaratomyia* (three males) and three extant genera: *Stempellina* Thienemann & Bause in Bause, 1913 (one male); *Stempellinella* Brundin, 1947 (two males) and *Tanytarsus* van der Wulp, 1874 (five males) (Table 1).

SYSTEMATIC PALAEONTOLOGY

FAMILY: CHIRONOMIDAE NEWMAN, 1834

SUBFAMILY: CHIRONOMINAE NEWMAN, 1834

TRIBE: TANYTARSINI ZAVŘEL, 1917

SUBTRIBE: TANYTARSINA ZAVŘEL, 1917

GUJARATOMYIA GIŁKA & ZAKRZEWSKA, 2018

Type species: Gujaratomyia miripes Giłka & Zakrzewska, 2018.

(FIGS 1A–F, 11A, B)

Material examined

Adult male, inventory no. BSIP Tad-610 (left: antenna, wing, foreleg, tarsi of mid- and hindlegs and tarsus of right foreleg damaged; Fig. 1A, B) preserved in an 8.5 mm × 4.5 mm × 3.5 mm piece of amber (early Eocene, ~54 Mya, Tadkeshwar mine, Gujarat state, India; IR spectrum no. 14258 IAA; Fig. 11A). Holotype and paratype, inventory no. *BSIP Tad-607 a* and b, syninclusions (see Zakrzewska *et al.*, 2018); IR spectrum no. 14259 IAA (Fig. 11B).

Diagnostic description (complemented)

The recently established genus *Gujaratomyia* was described on the basis of two adult males (including one specimen preserved in part) in a single chunk of amber from the Tadkeshwar mine. The currently examined specimen, obtained from the same source, is clearly conspecific with *G. miripes*, because it has the peculiar leg armature (Fig. 1C) and characters of the hypopygium (cf. Zakrzewska *et al.*, 2018), which are analysed here for the first time and described from the recommended dorsal view (Fig. 1F). The description is thus supplemented with the following characters (measurements of the holotype are in bold): eyes with slight dorsomedian extensions (Fig. 1D), but broadly separated by frons; length of palpomeres 2–5 (in micrometres): ~**30**, 92–**103**, 107–**117** and 101–**117**; wing length 785–**820** μm, VR_{Cu} 1.63–**1.65**; thorax chaetotaxy: Ac reaching antepronotum, Dc ultimate posterior seta in each row placed on distinct protuberance, Pa five on each side, biserial (three + two), placed on roundish protuberance, Scts ten, strong, as shown in Figure 1E.

Table 1. List of Tanytarsini from Cambay amber from the BSIP collection, after Stebner *et al.* (2017), adjusted

No.	Species	Sex	Number	Type	Figure
1.	*Gujaratomyia miripes* Giłka & Zakrzewska, 2018	♂	*BSIP Tad-607 a*	Holotype	1A*
2.	*Gujaratomyia miripes* Giłka & Zakrzewska, 2018	♂	BSIP Tad-607 b	Paratype	1A*
3	*Gujaratomyia miripes* Giłka & Zakrzewska, 2018	♂	BSIP Tad-610	Additional individual	1A
4.	**Tanytarsus forfex** Giłka & Zakrzewska **sp. nov.**	♂	*BSIP Tad-568 a*	Holotype	2A
5.	**Tanytarsus ramus** Giłka & Zakrzewska **sp. nov.**	♂	*BSIP Tad-521*	Holotype	4A
6.	*Tanytarsus* sp. 1	♂	BSIP Tad-533	Not designated	6A
7.	*Tanytarsus* sp. 2	♂	BSIP Tad-883 a	Not designated	6C
8.	*Tanytarsus* sp. 3	♂	BSIP Tad-884	Not designated	6E
9.	**Stempellina stebneri** Giłka & Zakrzewska **sp. nov.**	♂	*BSIP Tad-882*	Holotype	7A
10.	**Stempellinella pollex** Giłka & Zakrzewska **sp. nov.**	♂	*BSIP Tad-571 a*	Holotype	9A
11.	**Stempellinella pollex** Giłka & Zakrzewska **sp. nov.**	♂	BSIP Tad-546	Paratype	9B

The acronym AMNH has been replaced by BSIP owing to a change in repository for the material. *Zakrzewska *et al.* (2018).

Figure 1. *Gujaratomyia miripes*, adult male, BSIP Tad-610, early Eocene, ~54 Mya, Tadkeshwar mine, Gujarat, India. A, inclusion in amber. B, habitus. C, apical part of hindleg tibia. D, head. E, scutellum with strong setae. F, hypopygium in dorsal aspect.

Table 2. Leg segment lengths (in micrometres) and leg ratios of male *Gujaratomyia miripes*

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR
p_1	410–**445**	165–**180**	–	–	–	–	–	–
p_2	410–**460**	195 (**195**)	**505**–530	**205**–215	170 (**170**)	105–**115**	50–**60**	**2.59**–2.72
p_3	440–**445**	200–**220**	605	240	215	150	70	3.02

Measurements of the holotype are in bold (cf. Zakrzewska *et al.*, 2018).
Abbreviations: fe, femur; LR, leg ratio; p_1–p_3, pair of legs 1–3; ta_1–ta_5, tarsomeres 1–5; ti, tibia.

LR_3 high: 3.02. The measurements of leg segments and leg ratios are compiled with those taken from the holotype, as shown in Table 2.

TANYTARSUS VAN DER WULP, 1874

Type species: Tanytarsus signatus (van der Wulp, 1858).

TANYTARSUS FORFEX GIŁKA & ZAKRZEWSKA **SP. NOV.**

(FIGS 2A–D, 3A–C, 11C)

LSID:urn:lsid:zoobank.org:act:2DA56E07-BC10-4830-9C34-05B7C8978275

Type material
Holotype, inventory no. *BSIP Tad-568 a*: adult male (thorax deformed, wings deformed/missing, tarsi of all legs missing; Fig. 2A, B) preserved in a 4.5 mm × 3.5 mm × 2 mm piece of amber (early Eocene, ~54 Mya, Tadkeshwar mine, Gujarat state, India; IR spectrum no. 14260 IAA; Fig. 11C). Syninclusion: Chironomidae female (BSIP Tad-568 b).

Etymology
From Latin *forfex*, scissors, refering to its long, narrow, pointed gonostyli. Noun in apposition.

Diagnosis
Small species, total length ~1.2 mm. Eyes reniform, broadly separated by frons. AR only 0.30. Gonostylus distinctly longer than gonocoxite (HR ~0.6), slender. Anal tergite convex, semispherical, with median setae. Anal point broad but short, semicircular, with spinulae in shallow pit. Superior volsella stout, roundish. Digitus extending slightly beyond superior volsella. Stem of median volsella short, ~10 μm, bulbous, bearing slender falciform and setiform lamellae. Inferior volsella club shaped, extending slightly beyond base of gonostylus.

Description
Adult male (*N* = 1). Total length ~1.2 mm.

Head (*Fig. 2B, C*): Eyes bare, reniform, broadly separated by frons. Antenna with 13 clearly discernible flagellomeres, AR 0.30. Length of palpomeres 2–5 (in micrometres): 22, 52, 60 and 90.

Legs: Tibia of foreleg with single spur ~12 μm long. Tibial combs of mid- and hindlegs separated, teeth ≤ 14 μm long; one comb with spur ≤ 20 μm long, second comb bearing thin spur nearly two times longer (~35 μm), longer spur on hindleg distinctly curved (Fig. 2D).

Hypopygium (*Fig. 3A–C*): Gonostylus ~80 μm long, distinctly longer than gonocoxite (HR ~0.6), narrow, straight, apex pointed. Anal tergite convex in median area, semispherical, bearing several median setae and seven or eight posterolateral setae on each side of anal point. Anal point broad at base, short, semicircular, with two spinulae placed in shallow pit, anal point crests absent. Superior volsella stout, roundish, bearing three or four dorsal setae (setal tubercles) arranged in a row. Digitus with apex extending slightly beyond superior volsella. Stem of median volsella short (~10 μm), bulbous, bearing several slender falciform and setiform lamellae (Fig. 3C). Inferior volsella extending only slightly beyond base of gonostylus, club shaped, with several strong setae.

Remarks
Considering both extant and Eocene Tanytarsini, *Tanytarsus* is the most species-rich genus of the tribe. So far, six species have been described from the Eocene (Zakrzewska *et al.*, 2016), four of which have been placed in several systematic groups, i.e. the *Tanytarsus gregarius* group (including the *Tanytarsus lugens* group, previously treated separately), the *Tanytarsus mendax* and the *Tanytarsus serafini* group. However, several species have not been ascribed to any group owing to a set of characters indicating an unknown membership within *Tanytarsus* (*Tanytarsus crocota* Giłka, Zakrzewska & Krzemiński, 2016 and *Tanytarsus glaesarius* Giłka & Zakrzewska, 2015). This also pertains to *T. forfex* The long, narrow and pointed gonostyli, the short and semicircular anal point, the round superior volsella and the short bulbous median
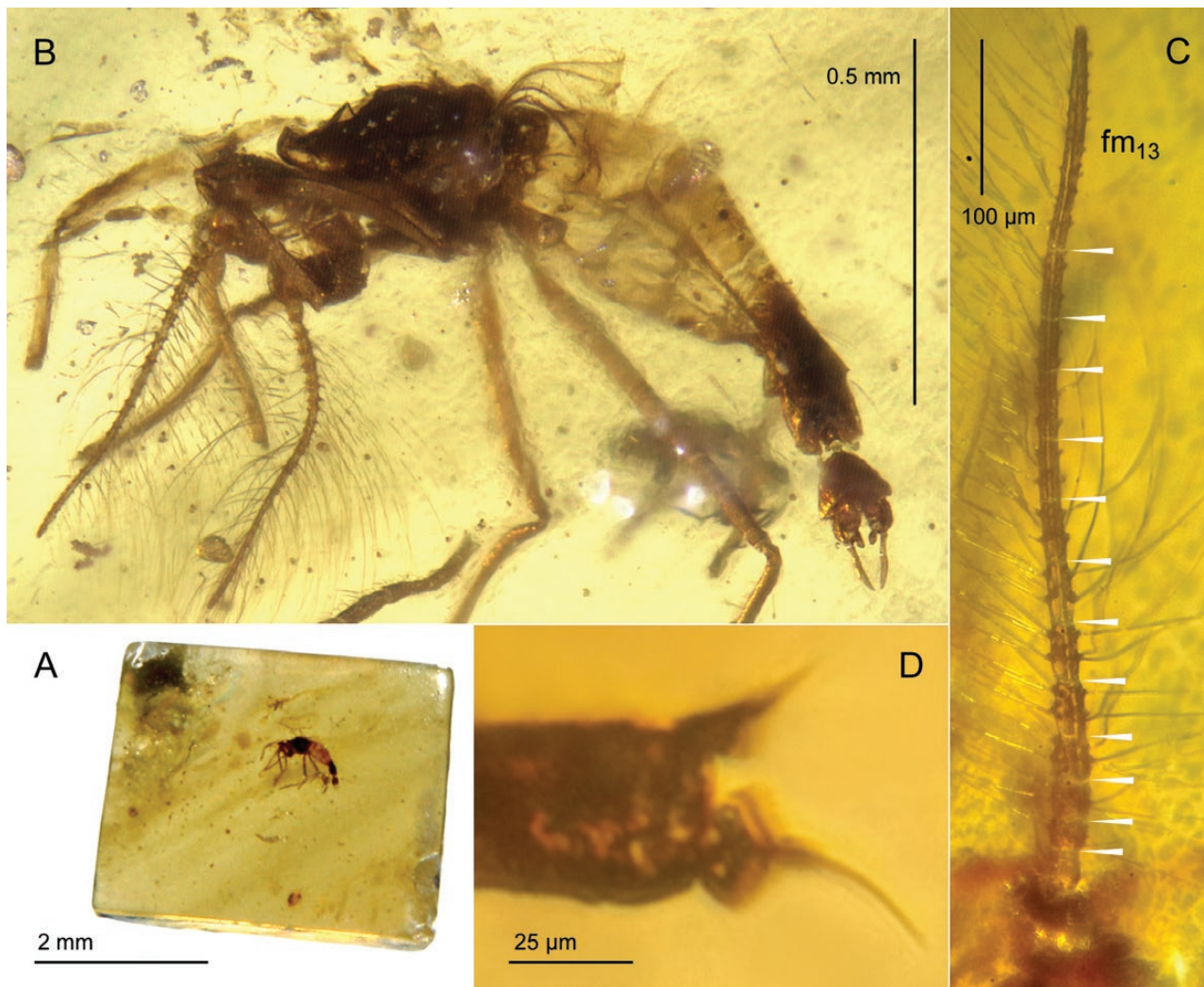
Figure 2. *Tanytarsus forfex*, adult male, *BSIP Tad-568 a*, early Eocene, ~54 Mya, Tadkeshwar mine, Gujarat, India. A, inclusion in amber. B, habitus. C, antenna (arrowheads indicate borders between flagellomeres fm$_{1-13}$). D, tibial combs and spurs of hindleg.

volsella found in *T. forfex* form a combination unknown from any species group within the genus. Nevertheless, the generic placement of *T. forfex* is legitimate based on several distinct characters, i.e. the bare eyes with small dorsomedian extensions, the 13 clearly discernible antennal flagellomeres, the vein R_{4+5} ending distal to M_{3+4} towards the wing apex, the gonostylus longer than the gonocoxite, and the presence of the anal point spinulae and the digitus (the combination typical of *Tanytarsus*).

TANYTARSUS RAMUS Giłka & Zakrzewska **SP. NOV.**

(Figs 4A–F, 5A–F, 11D)

LSID:urn:lsid:zoobank.org:act:D8802738-369F-4D19-823F-379C31FFA80B

Type material

Holotype, inventory no. *BSIP Tad-521*: adult male (tarsi of left foreleg and of both mid- and hindlegs missing; Fig. 4A, B) in a 7 mm × 5 mm × 2.5 mm piece of amber preserved in a cubicoid plastic mass (early Eocene, ~54 Mya, Tadkeshwar mine, Gujarat state, India; IR spectrum no. 14257 IAA, Fig. 11D).

Etymology

From Latin *ramus*, branch or twig, refering to the frail, simply branched median volsellae. Noun in apposition.

Diagnosis

Wing vein Sc extending well beyond RM; FCu placed well distal to RM; distance between ends of R_1–R_{2+3}
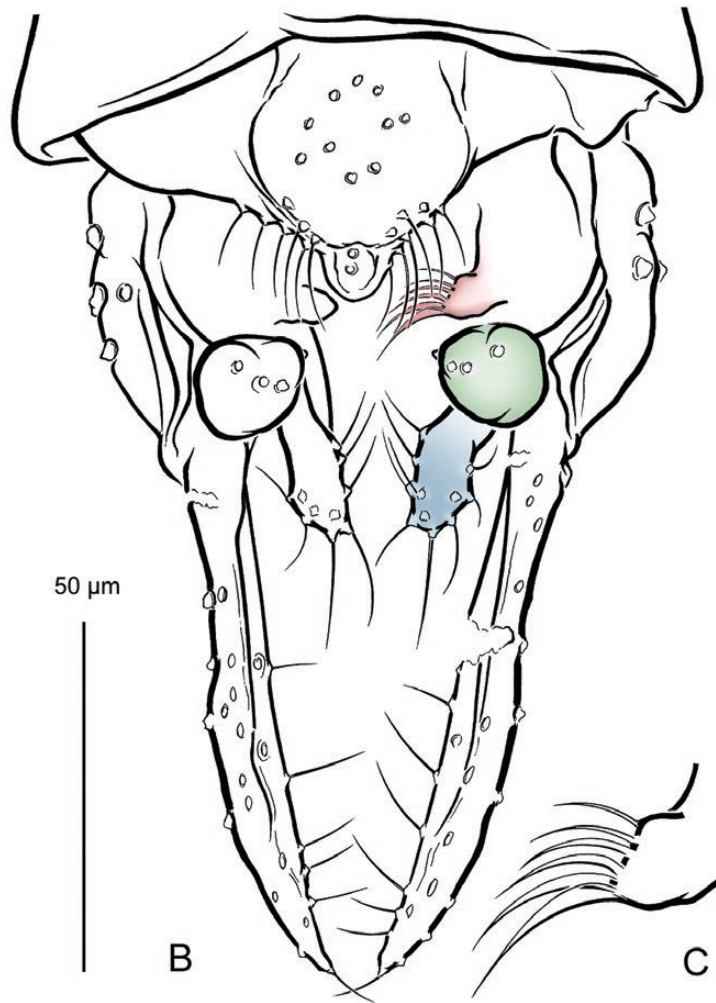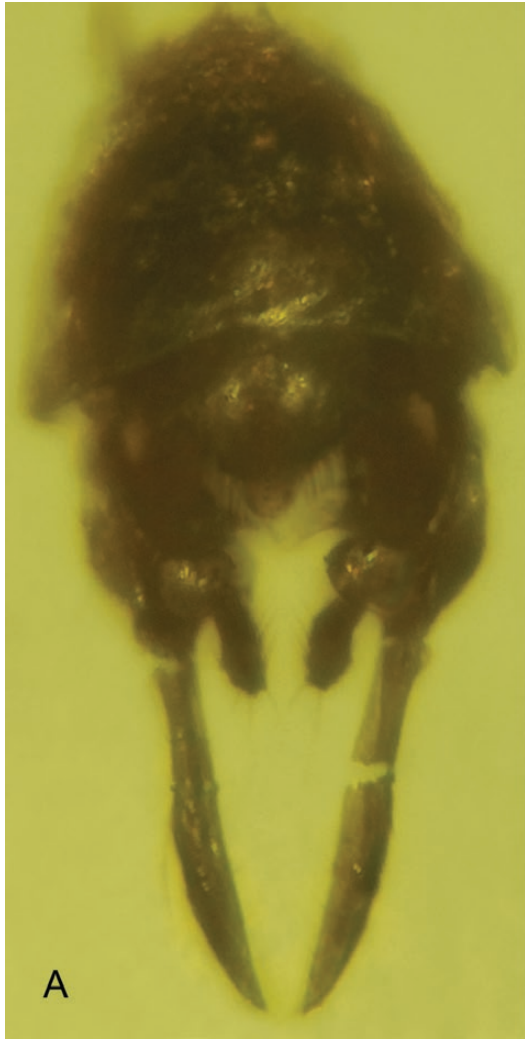
Figure 3. *Tanytarsus forfex*, adult male, *BSIP Tad-568 a*, early Eocene, ~54 Mya, Tadkeshwar mine, Gujarat, India. A, B, hypopygium in dorsal aspect. C, median volsella. Volsellae: green, superior; red, median; blue, inferior.

and R_{2+3}–R_{4+5} unequal, VR_C ~5. Tibial combs and spurs stout, combs fan shaped, only one comb with spur on mid-leg, each comb with spur on hindleg. Anal tergite with three spinulae in a row, placed in pit surrounded by crest-like ridges. Anal point slender, long, reaching apex of inferior volsella. Superior volsella pipe shaped. Stem of median volsella twig shaped, branched into two simple, slender lamellae. Inferior volsella parallel sided.

Description

Adult male (*N* = 1). Total length ~2.1 mm; wing length ~840 µm.

Head (*Fig. 4B*): Eyes bare, slightly produced in dorsomedian position. Frontal tubercles not observed. Antenna with 13 flagellomeres, AR unmeasurable, plume fully developed. Length of palpomeres 2–5 (in micrometres): ~25, 105, 105 and 169. At least 12 strong clypeals.

Thorax: Dc at least nine, Pa at least one, other thoracic setae unobservable.

Wing (*Fig. 4C*): Anal lobe relatively well developed, broadest at two-thirds of length, width 265 µm, length/width ratio 3.17. Sc extending well beyond RM. RM slightly oblique relative to M and R. R_1 and R_{2+3} arcuate in distal section. FCu placed well distal to RM; VR_{Cu} 1.35. Veins ending as follows (in order from base to tip): An, Sc, Cu_1, R_1, R_{2+3}, M_{3+4}, R_{4+5}, M_{1+2}; distance between ends of R_1–R_{2+3} and R_{2+3}–R_{4+5} unequal; VR_C ~5. Wing membrane covered with macrotrichia in distal half.

Legs: Tibia of foreleg with stout spur ~25 µm long. Tibial combs of mid leg fan shaped, teeth ≤ 25 µm
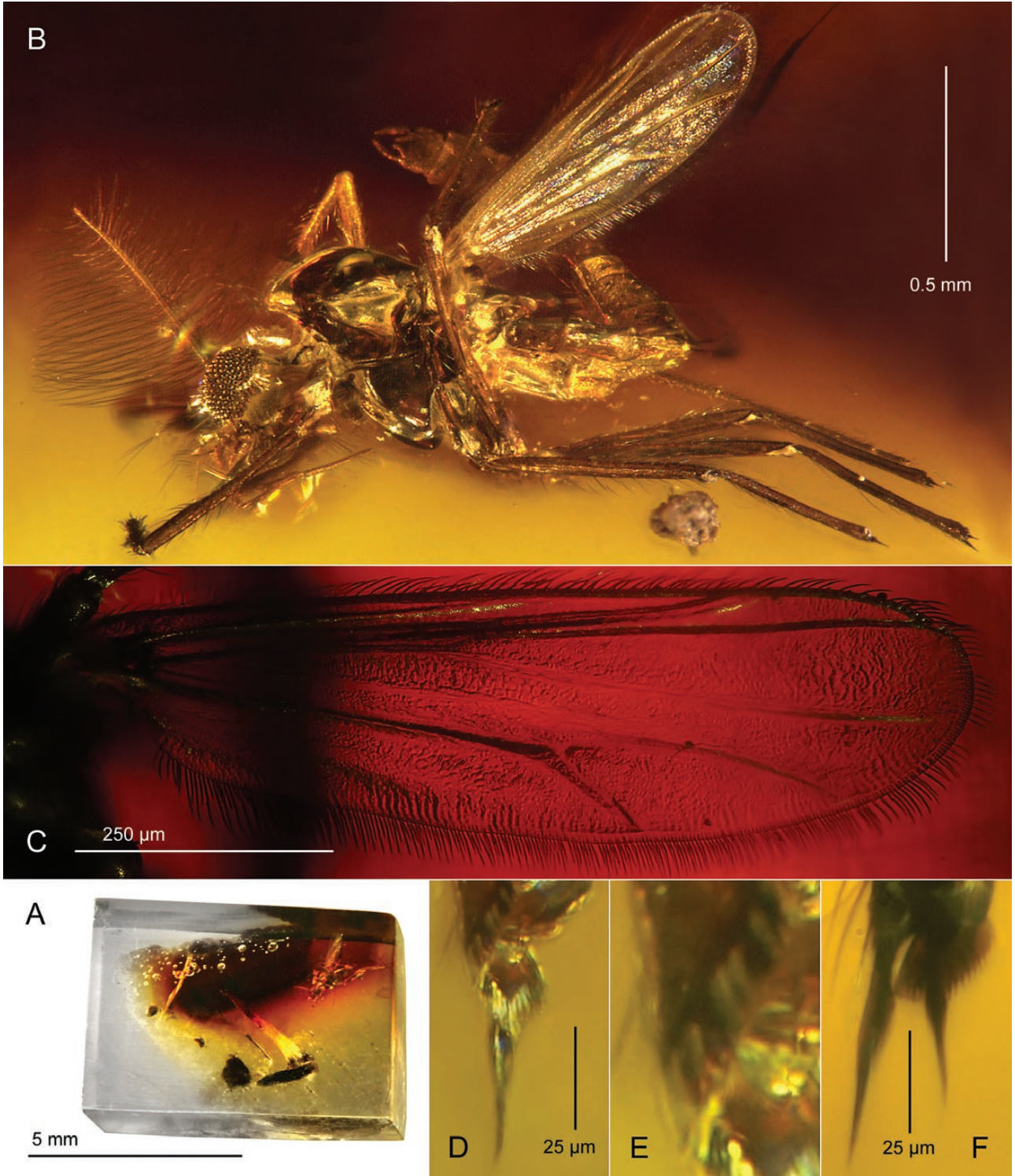
Figure 4. *Tanytarsus ramus*, adult male, *BSIP Tad-521*, early Eocene, ~54 Mya, Tadkeshwar mine, Gujarat, India. A, inclusion in amber. B, habitus. C, wing. D, tibial armature of mid-leg. E, spurless comb of mid-leg magnified approximately three times relative to D. F, tibial combs and spurs of hindleg.
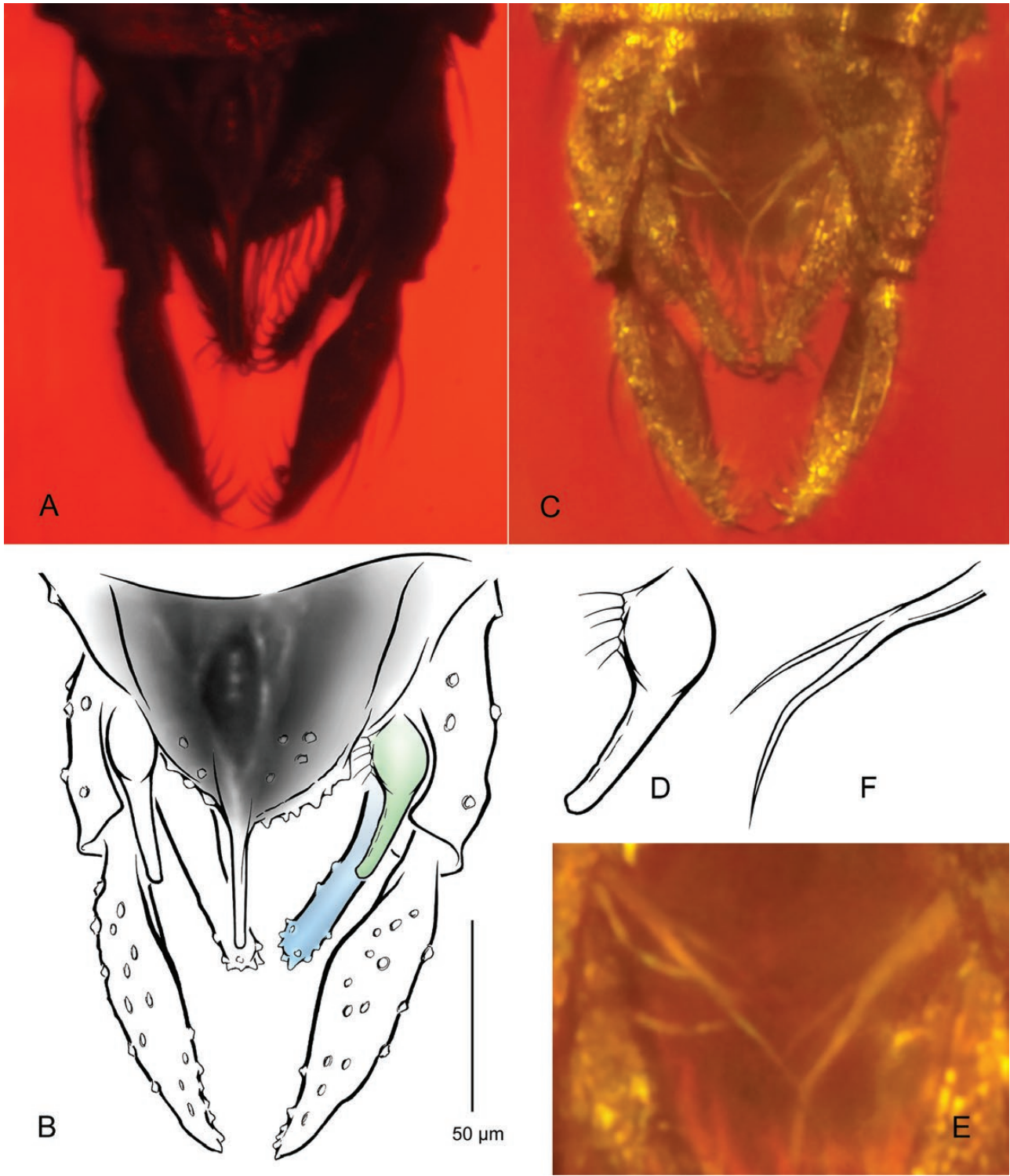
Figure 5. *Tanytarsus ramus*, adult male, *BSIP Tad-521*, early Eocene, ~54 Mya, Tadkeshwar mine, Gujarat, India. A–C, hypopygium in dorsal (A, B) and ventral (C) aspect. D, superior volsella. E, F, median volsella. Volsellae: green, superior; blue, inferior.

long, only one comb bearing slender spur ~55 µm long (Fig. 4D, E); combs of hindleg broadly separated, fan shaped; one comb broad, with teeth ≤ 25 µm long, bearing spur ~50 µm long; second comb slender, teeth ≤ 30 µm long, bearing spur ~60 µm long (Fig. 4F). For the leg segment lengths and leg ratios, see Table 3.

Hypopygium (*Fig. 5A–F*): Gonostylus slightly longer than gonocoxite, ~85 µm long, tapering towards pointed apex. Anal tergite semicircular, bearing three spinulae arranged in a row, placed in rounded, longitudinal pit, its crest-like ridges tapering towards base of anal point; several setae on each side. Anal point long, reaching apex of inferior volsella, slender, parallel sided with blunt tip; several strong posterolateral setae on each side (Fig. 5A, B). Superior volsella pipe shaped, with oval basal part, distinctly narrowed at mid-length, distal part elongate with apex blunt; several short setae at median margin of basal part (Fig. 5B, D). Digitus not observed. Stem of median volsella ~20 µm long, posteromedially directed, twig shaped, branched into two simple, slender lamellae (Fig. 5C, E, F). Inferior volsella reaching half the length of the gonostylus, nearly parallel sided, with distal half armed, bearing numerous stout setae.

Remarks

Tanytarsus ramus differs from all known species of the genus by a set of distinct characters as follows: the VR_C ratio is nearly five (Fig. 4C), the anal tergite has a couple of spinulae placed in a row in a large pit, and the anal point is slender and extraordinarily long (Fig. 5A, B); the pipe shaped superior volsella should be considered a key feature (Fig. 5B, D), whereas the digitus, typical of *Tanytarsus*, is not observed (probably absent). The most peculiar structure diagnostic of *T. ramus* is the hypopygial median volsella (Fig. 5E, F) of a shape perceived as a plesiomorphy (see Discussion: Evolution of the diagnostic structures).

TANYTARSUS SPP.

(FIG. 6A–F)

Material examined

Tanytarsus sp. 1, one adult male in an 8.5 mm × 6 mm × 3.5 mm piece of amber (inventory no. BSIP Tad-533; Fig. 6A, B); *Tanytarsus* sp. 2, one adult male in a 6.5 mm × 5 mm × 4 mm piece of amber (inventory no. BSIP Tad-883 a; Fig. 6C, D), syninclusion: Coleoptera (inventory no. BSIP Tad-883 b); *Tanytarsus* sp. 3, one adult male in a 6 mm × 3 mm × 1 mm piece of amber preserved in a cubicoid plastic mass (inventory no. BSIP Tad-884; Fig. 6E, F); Early Eocene, ~54 Mya, Tadkeshwar mine, Gujarat state, India.

Remarks

The above three specimens are ascribed to the genus *Tanytarsus* on the basis of the head, wing and hypopygium characters (cf. Stebner *et al.*, 2017). However, most of the diagnostic structures are weakly observable, deformed or insufficiently preserved to define the individuals definitively to species level. Nevertheless, these males differ distinctly from each other and from those designated as new species described in this paper, thus they most probably belong to another species. Therefore, with presumably five species, *Tanytarsus* is the most species-rich genus among the Cambay Tanytarsini. The specific diversity proportions within the tribe may thus be similar relative to the extant fauna: five *Tanytarsus*/ eight Tanytarsini in Cambay amber vs. ~360 *Tanytarsus*/~700 Tanytarsini extant species (Giłka W, Zakrzewska M, unpublished data).

SUBTRIBE: ZAVRELIINA SÆTHER, 1977

STEMPELLINA THIENEMANN & BAUSE, 1913

Type species: *Stempellina bausei* (Kieffer, 1911).

STEMPELLINA STEBNERI GIŁKA & ZAKRZEWSKA SP. NOV.

(FIGS 7A–D, 8A–D)

LSID:urn:lsid:zoobank.org:act:E7BFCFFA-2EC3-410A-904B-087B6D728E23

Type material

Holotype, inventory no. *BSIP Tad-882*: adult male (tarsi of both forelegs and tarsi of left mid- and hindlegs

Table 3. Leg segment lengths (in micrometres) and leg ratios of male *Tanytarsus ramus*

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR
p_1	605	305	715	305	215	160	80	2.34
p_2	585	430	–	–	–	–	–	–
p_3	630	460	–	–	–	–	–	–

Abbreviations: fe, femur; LR, leg ratio; p_1–p_3, pair of legs 1–3; ta_1–ta_5, tarsomeres 1–5; ti, tibia.
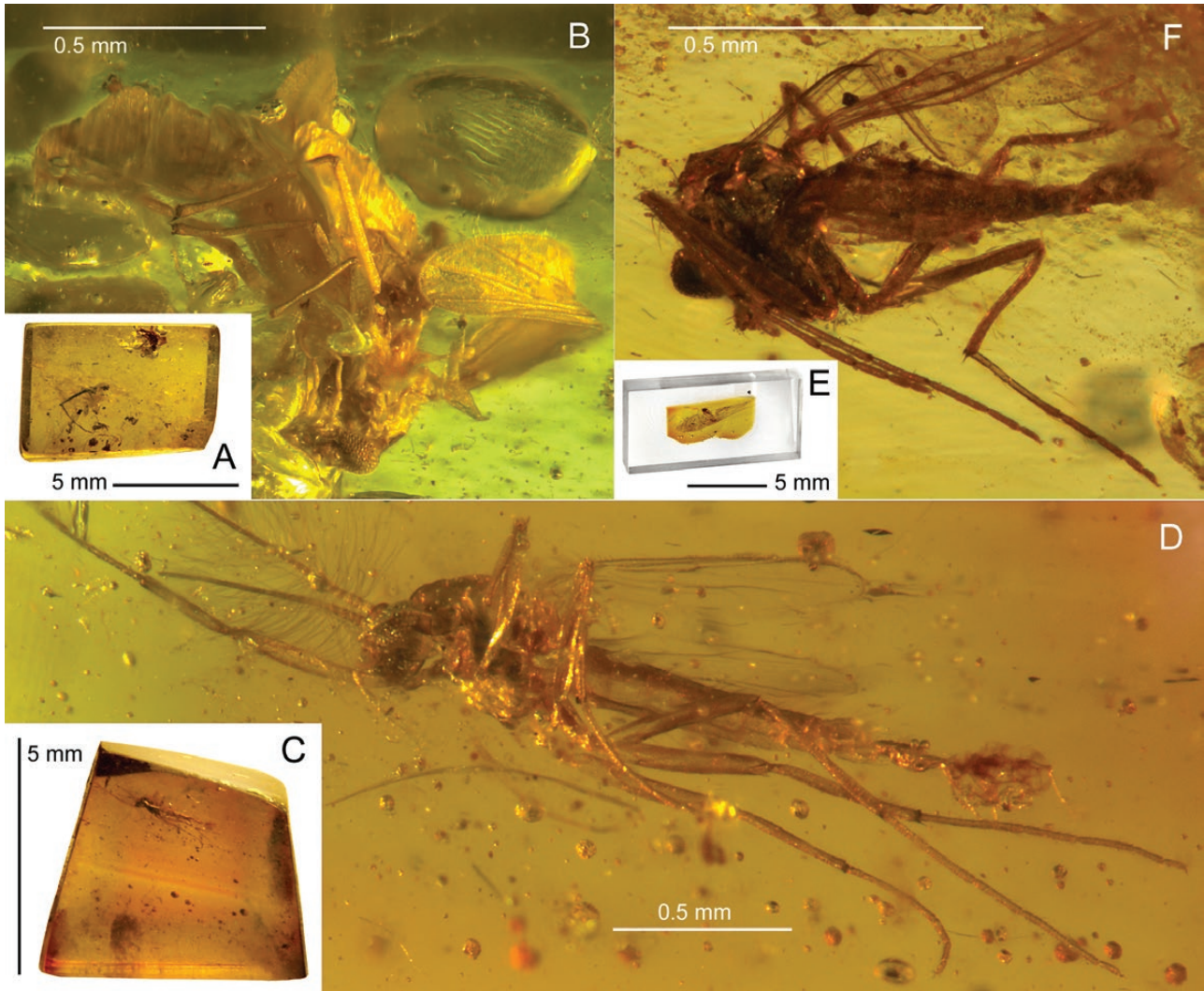
Figure 6. *Tanytarsus* spp., adult males, early Eocene, ~54 Mya, Tadkeshwar mine, Gujarat state, India. A, B, *Tanytarsus* sp. 1, BSIP Tad-533. C, D, *Tanytarsus* sp. 2, BSIP Tad-883 a. E, F, *Tanytarsus* sp. 3, BSIP Tad-884. A, C, E, inclusion in amber. B, D, F, habitus.

missing; left wing deformed, right wing separated; Fig. 7A, B) in a 7.5 mm × 4 mm × 3 mm piece of amber preserved in a cubicoid plastic mass (early Eocene, ~54 Mya, Tadkeshwar mine, Gujarat state, India).

Etymology

The specific epithet honours our colleague, Frauke Stebner (Bonn, Germany), commemorating her contribution to the study of fossil Diptera.

Diagnosis

Minute species, total length ~1 mm, wing length 615 µm. Antenna with 13 flagellomeres, 12 of which are readily discernible (flagellomeres 12–13 partly fused); AR exceptionally low. R_{4+5} ending proximally of M_{3+4} towards wing apex. LR of mid- and hindlegs relatively high (0.95 and 0.86, respectively). Gonostylus slender, bearing strong apical seta. Anal point long, tapering towards distinct narrow elongation, with a couple of equidistant spinulae placed between distinct crests. Superior volsella cylindrical, apically rounded. Digitus absent. Stem of median volsella slender, curved, with several setiform lamellae. Inferior volsella short, reaching slightly beyond base of gonostylus.

Description

Adult male (*N* = 1). Total length ~1 mm; wing length 615 µm.

Figure 7. *Stempellina stebneri*, adult male, *BSIP Tad-882*, early Eocene, ~54 Mya, Tadkeshwar mine, Gujarat, India. A, inclusion in amber. B, habitus. C, antenna (arrowheads indicate borders between flagellomeres fm_{1-13}; white arrowheads indicate borders between readily discernible flagellomeres; black arrowhead indicates incomplete fusion). D, wing.

Head (*Fig. 7B, C*): Eyes bare, reniform, widely separated by frons. Frontal tubercles not observed. Antenna with 13 flagellomeres, 12 of which are readily discernible, flagellomeres 12–13 partly fused; AR exceptionally low, 0.36 (when flagellum measured as 12-segmented), 0.24 (as 13-segmented). Length of palpomeres 3–5 (in micrometres): 36, 67 and 95. At least nine strong clypeals.
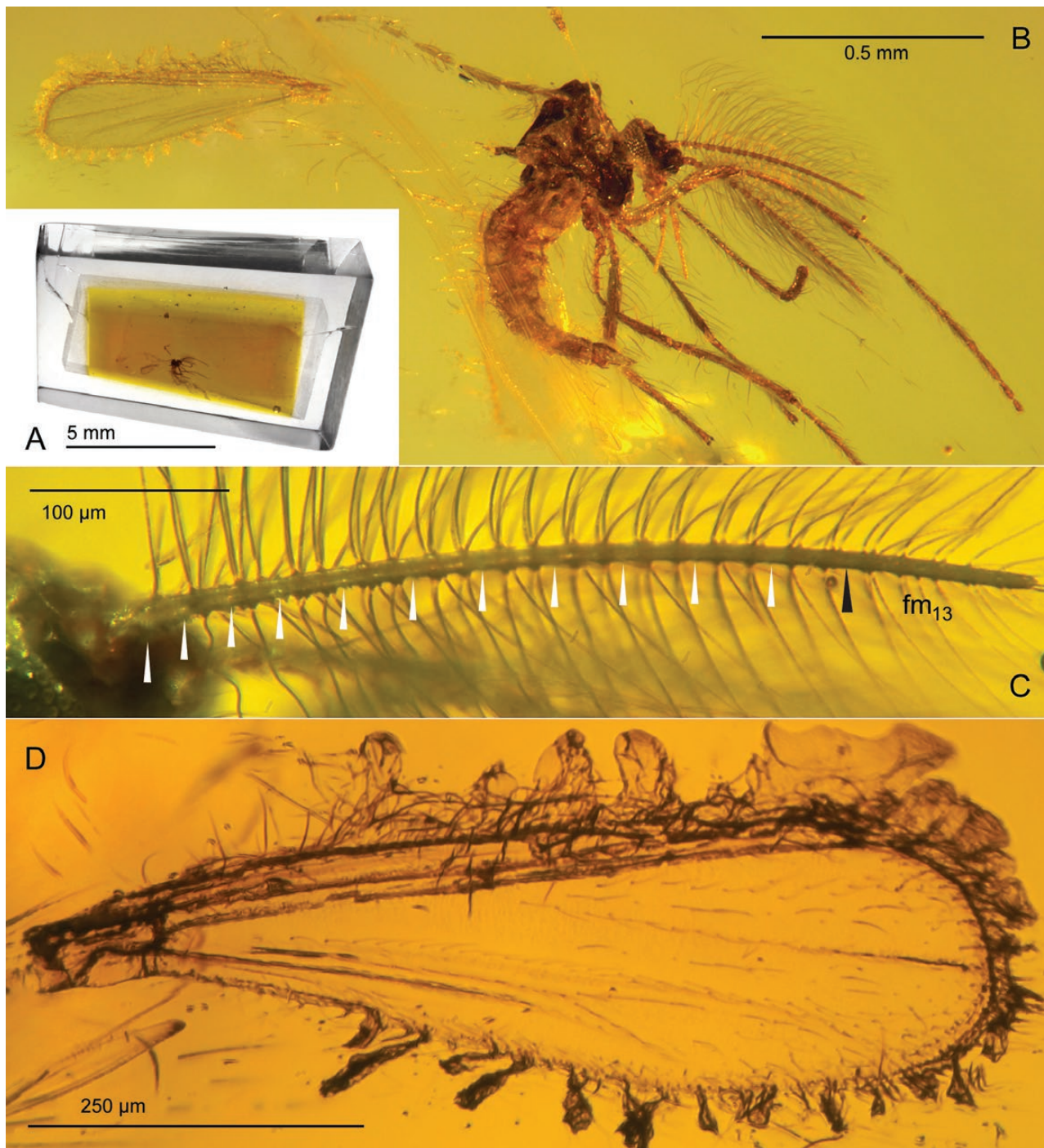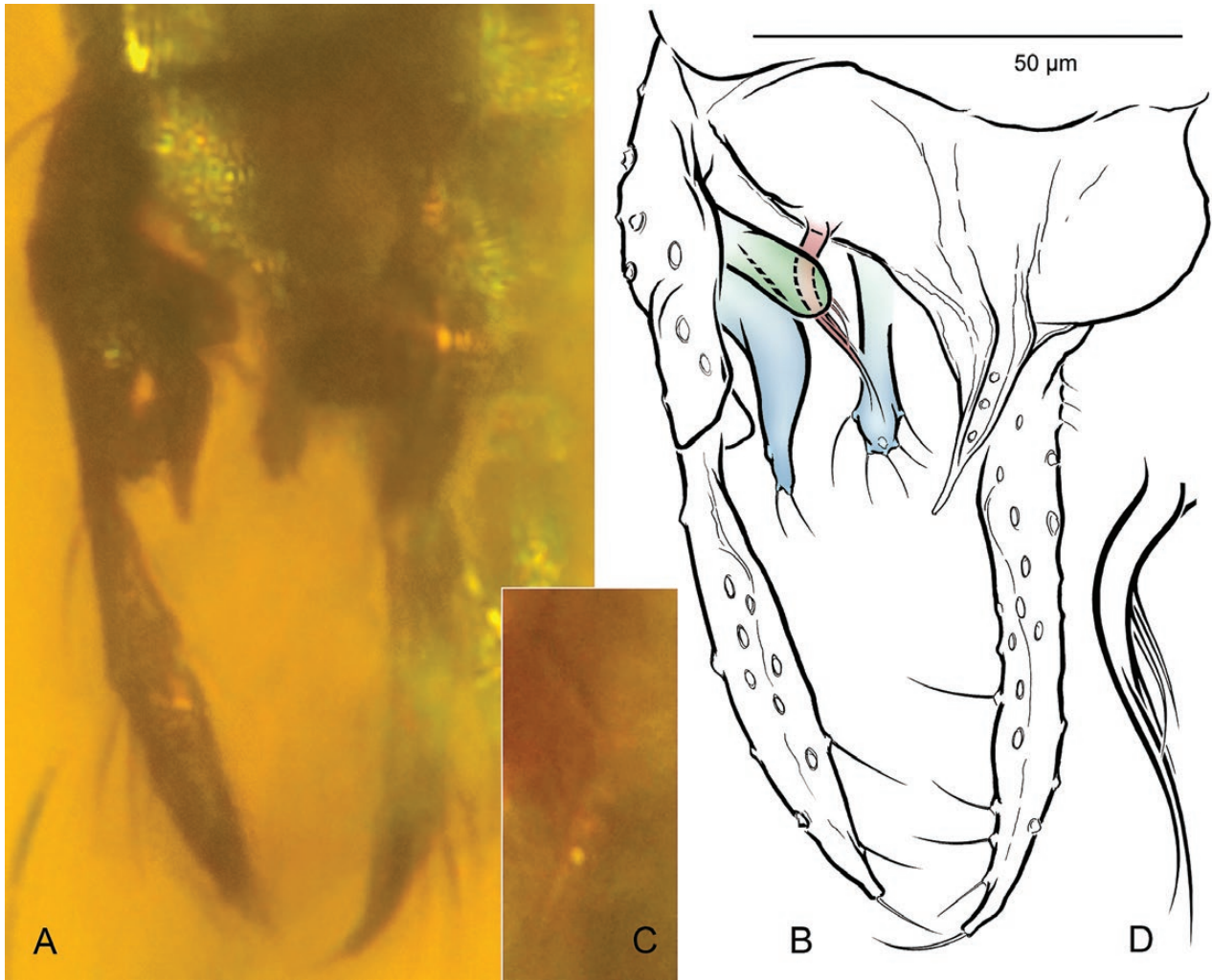
Figure 8. *Stempellina stebneri*, adult male, *BSIP Tad-882*, early Eocene, ~54 Mya, Tadkeshwar mine, Gujarat, India. A, B, hypopygium in dorsal aspect. C, anal point. D, median volsella magnified approximately two times relative to B. Volsellae: green, superior; red, median; blue, inferior.

Thorax: Damaged; chaetotaxy unobservable.

Wing (*Fig. 7D*): Spatulate, with anal lobe not developed, broadest at two-thirds of length, width 200 μm, length/width ratio 3.1. RM parallel relative to M and R. R_1 and R_{2+3} poorly visible. FCu placed distal to RM; VR_{Cu} 1.36. Veins ending as follows (in order from base to tip): Sc, An, Cu_1, R_1, R_{2+3}, R_{4+5}, M_{3+4} and M_{1+2}. Wing covered with dense macrotrichia in distal half, along whole length of Cu and its false vein placed above.

Legs: Tibia of foreleg with spur ~10 μm long. Tibial combs of mid- and hindlegs well separated, fan shaped, teeth ≤ 12 μm long; spurs of mid-leg unequal: first 16 μm, second 28 μm long; spurs of hindleg equal, 30 μm long. Sensilla chaetica on ta_1 of p_2 not observed.

Pulvilli absent. For leg segment lengths and leg ratios, see Table 4.

Hypopygium (*Fig. 8A–D*): Gonostylus ~65 μm long, distinctly longer than gonocoxite, slender, tapering towards slender, elongated apex bearing strong seta. Anal tergite semicircular. Anal point long, reaching beyond apex of inferior volsella, slender, tapering towards distinct narrow elongation, bearing three equidistant spinulae between distinct crests (Fig. 8A–C). Superior volsella elongated, cylindrical, with round apex (Fig. 8A, B). Digitus not observed. Stem of median volsella ~15 μm long, slender, curved, bearing several setiform lamellae; stem as long as apical lamella (Fig. 8A, B, D). Inferior volsella reaching slightly beyond base of gonostylus, simple, typical of the genus, as shown in Figure 8A, B.

Table 4. Leg segment lengths (in micrometres) and leg ratios of male *Stempellina stebneri*

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR
p_1	380	210	–	–	–	–	–	–
p_2	–	320	305	120	90	55	35	0.95
p_3	–	320	275	140	135	80	50	0.86

Abbreviations: fe, femur; LR, leg ratio; p_1–p_3, pair of legs 1–3; ta_1–ta_5, tarsomeres 1–5; ti, tibia.

Remarks

Stempellina is a relatively small genus with a worldwide distribution (Giłka, 2005). To date, nearly ten extant species have been described, as has a single extinct species found in Baltic amber: *Stempellina exigua* Seredszus & Wichard, 2007. *Stempellina stebneri* is thus the second fossil and the oldest representative of this genus. Both fossil species show a set of characters typical of the genus, i.e. the bare, widely separated reniform eyes, the wing vein R_{4+5} ending proximal to M_{3+4}, at least one spur on the mid- and hindleg tibiae ,and the slender gonostylus, longer than the gonocoxite (cf. Giłka, 2005). A character that clearly separates the two Eocene species is the shape of the hypopygial superior volsella: cylindrical in *Stempellina stebneri* (typical of extant representatives) but strongly elongated in *Stempellina exigua*. For a definition of the characters of phylogenetic importance see Discussion below.

STEMPELLINELLA BRUNDIN, 1947

Type species: Stempellinella saltuum (Goetghebuer, 1921).

STEMPELLINELLA POLLEX GIŁKA & ZAKRZEWSKA **SP. NOV.**

(FIGS 9A–G, 10A–C, 11E)

LSID:urn:lsid:zoobank.org:act:E8518084-C85E-4332-B009-CCFCD6EA2A9A

Type material

Holotype, inventory no. *BSIP Tad-571 a*: adult male (right mid- and hindlegs deformed, tarsi of both forelegs and left hindleg missing; thorax deformed, apex of left wing missing; Fig. 9A, C) preserved in a 4 mm × 3 mm × 2 mm piece of amber (Early Eocene, ~54 Mya, Tadkeshwar mine, Gujarat state, India; IR spectrum no. 14262 IAA; Fig. 11E). Syninclusion: Chironominae female (inventory no. BSIP Tad-571 b). Paratype, inventory no. BSIP Tad-546: adult male (tarsi of forelegs separated or missing, ultimate tarsomeres of hindlegs damaged; Fig. 9B) preserved in a 5.5 mm × 4.5 mm × 3 mm piece of amber (Early Eocene, ~54 Mya, Tadkeshwar mine, Gujarat state, India).

Etymology

From Latin, *pollex*, thumb, referring to the stout thumb shaped process of the hypopygial inferior volsella. Noun in apposition.

Diagnosis

Small species, total length slightly > 1 mm, wing length < 700 µm. Antenna with 13 flagellomeres, flagellomeres 12–13 partly fused. Sc ending far distal to RM; RM long, slightly oblique relative to M. Vein M_{3+4} ending immediately under R_{4+5}. Mid- and hindleg tibia with two separated combs, each comb bearing a spur. Gonostylus stout, shorter than gonocoxite. Anal point missile shaped. Superior volsella extensive, with slight incision on apex. Stem of median volsella short, bulbous, with falciform lamellae. Inferior volsella with stout process on median margin and with flattened lobe distally.

Description

Adult male (*N* = 2; measurements of the holotype are in bold). Total length ~**1.1**–1.2 mm, wing length **640**–690 µm.

Head (*Fig. 9D*): Eyes bare. Antenna with 13 flagellomeres, 12 of which are readily discernible, flagellomeres 12–13 partly fused; AR **0.61**–0.66 (when flagellum measured as 12-segmented), AR **0.46**–0.52 (as 13-segmented); plume fully developed. Length of palpomeres 3–5 (in micrometres): **35** (36), **50** (48) and **80** (80). Clypeus with at least ten setae.

Wing (*Fig. 9E–G*): Slender, with anal lobe weak, broadest at two-thirds of length, width **200**–215 µm, length/width ratio **3.20**–3.21. Sc ending far distal to RM, R_{2+3} fading distally (Fig. 9E). RM long, slightly oblique relative to M (Fig. 9F). FCu placed distinctly distal to RM; VR_{Cu} ~1.50. Veins ending as follows (in order from base to tip): An, Sc, Cu_1 and R_1, R_{4+5} and
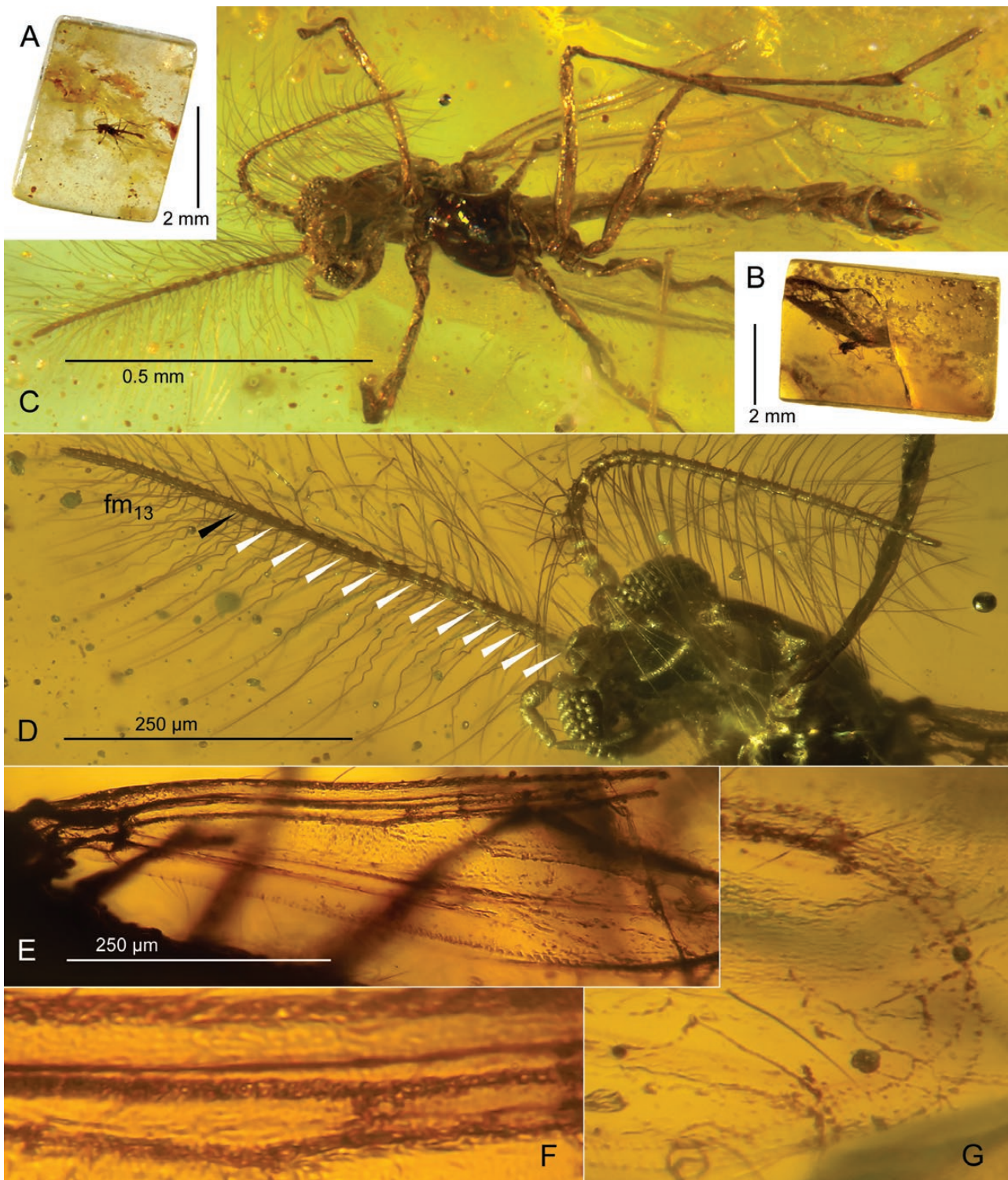
Figure 9. *Stempellinella pollex*, adult males: holotype *BSIP Tad-571 a* (A, C–G), paratype BSIP Tad-546 (B), early Eocene, ~54 Mya, Tadkeshwar mine, Gujarat, India. A, B, inclusions in amber pieces. C, habitus. D, head and antenna (arrowheads indicate borders between flagellomeres $fm_{1–13}$; white arrowheads indicate borders between readily discernible flagellomeres; black arrowhead indicates incomplete fusion; proximal flagellomere fm_1 hidden under pedicel). E–G, wing, with vein RM (F) and distal section (G) magnified.

Figure 10. *Stempellinella pollex*, adult male, *BSIP Tad-571 a*, early Eocene, ~54 Mya, Tadkeshwar mine, Gujarat, India. A, B, hypopygium in ventral aspect. C, median volsella and appendage of inferior volsella. Volsellae: green, superior; red, median; blue, inferior; purple, process of inferior volsella.

M_{3+4} and M_{1+2} (Fig. 9E, G). Wing membrane covered with macrotrichia on two-thirds distal part of wing at least.

Legs: Tibia of foreleg with spur ~15 µm long. Mid- and hindleg tibia with two separated combs, length of teeth ≤ 15 µm; each comb bearing spur ~20–25 µm long (mid-leg) and ~25–30 µm long (hindleg). Sensilla chaetica on ta_1 of p_2 not observed. Leg segments lengths and leg ratios are given in Table 5.

Hypopygium (*Fig. 10A–C*): Gonostylus short (~50 µm), shorter than gonocoxite, stout, with blunt apex bearing apical seta. Anal tergite subtriangular, with at least one posterolateral seta on each side of anal point. Anal point missile shaped, reaching posterior margins of superior volsellae. Superior volsella extensive, roundish, with slight incision on apex (Fig. 10A, B). Digitus not observed. Stem of median volsella short (~5 µm), bulbous, bearing three falciform lamellae (Fig. 10C). Inferior volsella reaching one-third of the length of gonostylus at most, its median margin

with anteromedially directed stout process ['wart' or 'digitus' according to Ekrem (2007)] (Fig. 10A–C), and with extensive flattened lobe distally.

Remarks

Stempellinella pollex is the fifth fossil species of the genus found in Eocene ambers, along with *Stempellinella bicorna* Seredszus & Wichard, 2007, *Stempellinella ivanovae* Giłka & Zakrzewska, 2014, *Stempellinella electra* Giłka & Zakrzewska, 2015 and *Stempellinella fibra* Giłka, Zakrzewska & Krzemiński, 2016 (Seredszus & Wichard, 2007; Zakrzewska & Giłka, 2014, 2015a; Zakrzewska *et al.*, 2016). All four previous species were described from amber deposits from the Baltic Sea region, thus *Stempellinella pollex* is the first representative of both the genus and subtribe Zavreliina described from Cambay amber. *Stempellinella pollex* displays an unusual structure of the hypopygium, sharing characters typical of the genus and ones unique to the species, which explains their homology relative to extant species (see
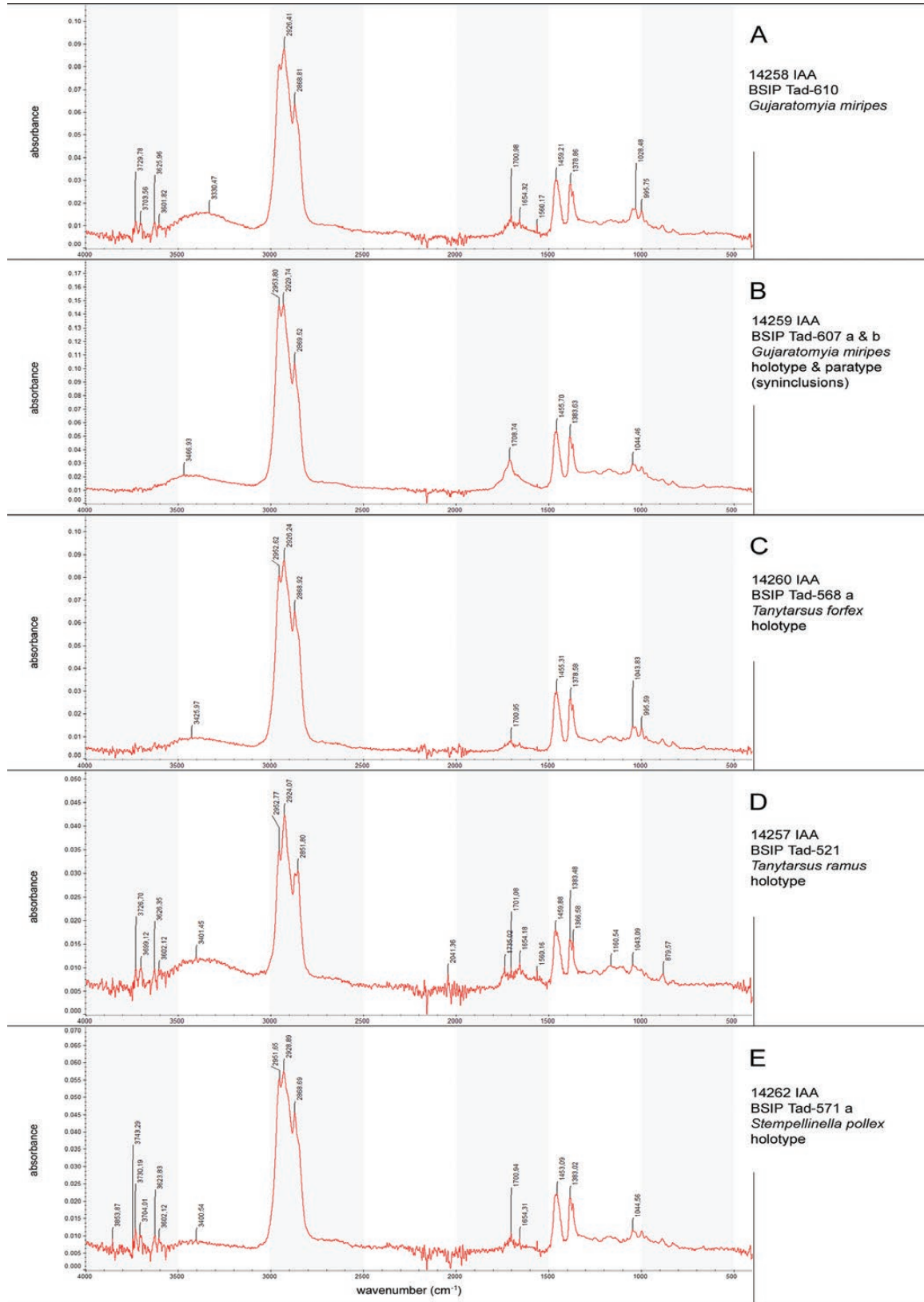
Figure 11. Fourier transform infrared spectroscopy (attenuated total reflectance) spectra obtained from Cambay amber chunks with the examined inclusions (early Eocene, ~54 Mya, Tadkeshwar mine, Gujarat, India).

Table 5. Leg segment lengths (in micrometres) and leg ratios of male *Stempellinella pollex*

	fe	ti	ta_1	ta_2	ta_3	ta_4	ta_5	LR
p_1	410	200	395	205	165	120	50	1.97
p_2	**360**–380	**280**–285	**175**	**70**–75	**55**–60	**40** (40)	**30**–35	**0.62**
p_3	**380**–400	**355**	210	105	–	–	–	–

Measurements of the holotype are in bold.
Abbreviations: fe, femur; LR, leg ratio; p_1–p_3, pair of legs 1–3; ta_1–ta_5, tarsomeres 1–5; ti, tibia.

Table 6. The position of the main peaks in Fourier transform infrared spectroscopy spectra of the Cambay resins investigated in this study and their proposed assignments

Functional group	14258 IAA	14259 IAA	14260 IAA	14257 IAA	14262 IAA
	Saturated C-H moieties				
ν C-H: methyl (-CH_3) and methylene (-CH_2-) groups	2953 (s)	2954 (s)	2953 (s)	2953 (s)	2952 (s)
	2926 (s)	2930 (s)	2926 (s)	2924 (s)	2929 (s)
	2869 (s)	2870 (s)	2869 (s)	2852 (s)	2869 (s)
δ C-H:	1463 (m)	1463 (m)	1463 (m)	1460 (m)	1458 (m)
$δ_{as}$ -CH_3,	1459 (m)	1455 (m)	1455 (m)	1453 (m)	1455 (m)
$δ_{sym}$ -CH_2-, observed as doublets					
δ C-H:	1379 (m)	1384 (m)	1379 (m)	1384;1377 (m)	1383 (m)
$δ_{sym}$ -CH_3 observed as doublets	1367 (m)	1367 (m)	1367 (m)	1366 (m)	1367 (m)
	Unsaturated C=C and C=C-H moieties				
ν =C-H	nd	nd	Nd	nd	nd
ν C=C	~1654 (w, b)	~1654 (w, b)	~1654 (w, b)	~1654 (w, b)	~1654 (w, b)
γ RHC=CH_2 (vinyl)	996 (m)	996 (m)	996 (m)	997 (m)	995 (m)
γ R_2C=CH_2 (vinylidene)	885, 879 (m)	884 (m)	885 (m)	879 (m)	884 (m)
	Oxygen-containing functional groups				
ν O-H (e.g. alcohols)	3370 (m, b)	3430 (m, b)	3400 (w, b)	3370 (m, b)	~3400 (w, b)
ν C=O (ketones and carb-oxylic acids)	1701 (w, b)	1709 (m, b)	1701 (w, b)	1701 (w, b)	1701 (w, b)
ν C-C(=O)-C* (aryl and mixed ketones)	1248 (w)	1254 (w)	1252 (w)	1254 (w)	1248 (w)
ν C-C(=O)-C* (saturated ke-tones)	1162 (w)	1176 (w)	1161 (w)	1160 (w)	1160 (w)
ν C-OH (alcohols) observed as doublet	1044, 1029 (m)	1045, 1031 (m)	1044, 1029 (m)	1043, 1028 (m)	1045, 1028 (m)

Vibrations: ν, stretching; δ, in-plane bending; γ, out-of-plane bending; as, asymmetric; sym, symmetric. Relative intensity: b, broad; m, medium; nd, not determined; s, strong; w, weak.
*Region of overlapping of bands of different functional groups, e.g. skeletal γ C-C vibrations of -CH-($CH_3)_2$ (1175–1140 cm^{-1}), > C-($CH_3)_2$ (1220–1190 cm^{-1}), -C-($CH_3)_3$ (1250–1200 cm^{-1}).

Discussion). The new species complies well with the amended generic diagnosis for extant *Stempellinella* Brundin, 1947 (Ekrem, 2007). The adult male has bare ovoid and broadly separated eyes (Fig. 9D), the wing vein R_{4+5} ending slightly distally to M_{3+4} (Fig. 9G), the broadened superior volsella, and the gonostylus shorter than the gonocoxite (Fig. 10A, B). On the other hand, the short and stout median volsella bearing simple lamellae (Fig. 10A–C) differs distinctly from the elongated one, typical of extant [with a sole exception of *Stempellinella reissi* Casas & Vilchez-Quero, 1991 (Ekrem, 2007)] as well as some Eocene *Stempellinella* (see the Key below). For an interpretation of the most important characters of *Stempellinella pollex* (the antennal flagellum and the process of the inferior volsella), see Discussion below.

The checklist covers nine genera (four extinct and five extant) and 26 Eocene species of the tribe Tanytarsini:

†*Archistempellina* Giłka & Zakrzewska, 2013

   †*Archistempellina bifurca* Giłka & Zakrzewska, 2013
   †*Archistempellina falcifera* Giłka & Zakrzewska, 2013
   †*Archistempellina perkovskyi* Giłka & Zakrzewska, 2014

†*Corneliola* Giłka & Zakrzewska, 2013

   †*Corneliola avia* Giłka & Zakrzewska, 2013

†*Eonandeva* Giłka & Zakrzewska, 2015

   †*Eonandeva helva* Giłka & Zakrzewska, 2015
   †*Eonandeva latistyla* Giłka & Zakrzewska, 2015

†*Gujaratomyia* Giłka & Zakrzewska, 2018

   †*Gujaratomyia miripes* Giłka & Zakrzewska, 2018

Nandeva Wiedenbrug, Reiss & Fittkau, 1998

   †*Nandeva pudens* Giłka, Zakrzewska, Baranov, Wang & Stebner, 2016

Rheotanytarsus Thienemann & Bause, 1913

   †*Rheotanytarsus alliciens* Giłka & Zakrzewska, 2013
   †*Rheotanytarsus hoffeinsorum* Giłka, Zakrzewska & Krzemiński, 2016

Stempellina Thienemann & Bause, 1913

   †*Stempellina exigua* Seredszus & Wichard, 2007
   †***Stempellina stebneri*** Giłka & Zakrzewska **sp. nov.**

Stempellinella Brundin, 1947

   †*Stempellinella bicorna* Seredszus & Wichard, 2007
   †*Stempellinella electra* Giłka & Zakrzewska, 2015
   †*Stempellinella fibra* Giłka, Zakrzewska & Krzemiński, 2016
   †*Stempellinella ivanovae* Giłka & Zakrzewska, 2014
   †***Stempellinella pollex*** Giłka & Zakrzewska **sp. nov.**

Tanytarsus van der Wulp, 1874

   †*Tanytarsus congregabilis* Giłka & Zakrzewska, 2013
   †*Tanytarsus crocota* Giłka, Zakrzewska & Krzemiński, 2016
   †*Tanytarsus fereci* Giłka, 2011
   †***Tanytarsus forfex*** Giłka & Zakrzewska **sp. nov.**
   †*Tanytarsus glaesarius* Giłka & Zakrzewska, 2015
   †*Tanytarsus protogregarius* Giłka & Zakrzewska, 2015
   †***Tanytarsus ramus*** Giłka & Zakrzewska **sp. nov**.
   †*Tanytarsus serafini* Giłka, 2010
   †*Tanytarsus szadziewskii* (Giłka & Zakrzewska, 2013)

   The only known fossil species of the genus *Nandeva* is also included. The phylogenetic position of *Nandeva* was analysed with respect to the sister genus *Eonandeva* (Zakrzewska & Giłka, 2015b; Giłka *et al.*, 2016). Both genera presumably hold a crucial position in the phylogeny of Tanytarsini and related tribes of subfamily Chironominae and form a common group dating back to the early Eocene at least. However, phylogenetic relationships between *Nandeva*, *Eonandeva* and other Tanytarsini remain an open question, especially in light of the ambiguous taxonomic status of *Nandeva*, hitherto postulated to be assigned to each

of the three Chironominae tribes (including Pseudochironomini and Chironomini). The most recent research (Cranston, 2019) presents *Nandeva* as a member of the tribe Tanytarsini and, possibly, subtribe Tanytarsina. However, the precise relationships of *Nandeva* in Tanytarsina still lack support, and analyses of the tempo of diversification based on a molecular clock suggest the position of a node connecting *Nandeva* with Tanytarsini in a time period ranging from the early Eocene to the earliest Oligocene (Cranston, 2019).

Recently, it was postulated that the genus *Caladomyia* should be treated as a junior synonym of *Tanytarsus* (Lin *et al.*, 2018). According to this concept, the only known fossil species, originally described in *Caladomyia*, is now given as *Tanytarsus szadziewskii* (Giłka & Zakrzewska in Zakrzewska & Giłka, 2013). More than 30 extant species previously ascribed to *Caladomyia* are widely distributed, mainly in the Southern Hemisphere, and belong to several species groups, at present all within *Tanytarsus* (Zakrzewska & Giłka, 2013; Lin *et al.*, 2018).

DISCUSSION

EVOLUTION OF DIAGNOSTIC STRUCTURES

Our study reveals an unexpectedly high diversity of Tanytarsini in amber from Cambay. These taxa, unknown until now and described here in detail, shed new light on the possible evolutionary trends of diagnostic structures and the systematics of this diversified tribe.

Antennal flagellum

Adult Tanytarsini males have a flagellum consisting of 13 segments at most, although the number may be lower: 12 (in *Stempellina*), ten (in the majority of genera of the subtribe Zavreliina) or six (in several brachypterous species), where the flagellomeres may be completely or partly fused. The number of flagellomeres is treated as a character in phylogenetic analyses (e.g. Sæther & Andersen, 1998; Sæther & Roque, 2004), where the fully segmented flagellum is a plesiomorphy, and the lower numbers imply more advanced states. Thus, we define the character state found in *Stempellina stebneri* (13 segments instead of 12 in extant species) as plesiomorphic (Fig. 7C) and, consequently, treat as fusion the trend whereby the number of flagellomeres in extant *Stempellina* tends to decrease. A similar tendency was observed in fossil species of the closely related genus *Stempellinella* (Fig. 9D; Zakrzewska & Giłka, 2014, 2015a; Zakrzewska *et al.*, 2016); see the diagnosis and description of *Stempellinella pollex* (above). It is worth noting that most species of Eocene Tanytarsini have a fully developed antenna with 13 flagellomeres (occasionally, with flagellomeres 12 and 13 partly fused).

Unusual legs and their function

In contrast to all known fossil and extant Tanytarsini, the tarsi of mid- and hindlegs in a *Gujaratomyia* male are disproportionately long, and the tibiae have peculiarly elongated lobes armed with long, filiform bristles (Fig. 1C; Zakrzewska *et al.*, 2018). These characters are interpreted as a gliding-enhancement adaptation similar to those found in the extant non-flying Tanytarsini (e.g. *Cladotanytarsus* Kieffer, 1921). This might enable the bearers to float on a water surface for a short time, but it seems hardly plausible that these structures would function in a similar manner on the ground. It might suggest that *Gujaratomyia* adults occurred in periodically or constantly flooded areas. *Gujaratomyia* and *Cladotanytarsus* were postulated as closely related genera within subtribe Tanytarsina (Zakrzewska *et al.*, 2018).

Hypopygial anal point

The character best separating *Stempellina stebneri* from all other described species in the genus is the anal point bearing a couple of spinulae placed equidistantly between distinct crests (Fig. 8B, C). This unique feature is not recorded in the majority of *Stempellina* except for one extant European species, *Stempellina tervolae* Giłka, 2005 (anal point elongated, with six to 20 fine, densely dispersed spinulae; Giłka, 2005) and at least one North American species as yet undescribed (J. E. Sublette, personal communication). The anal point spinulae are typical of both Tanytarsini subtribes (Tanytarsina and Zavreliina) also known from the Eocene. This feature is thus postulated to have been derived from an ancestor common to the two subtribes. Sæther (1977) and Sæther & Andersen (1998) analysed relationships between the genera of the subtribe Zavreliina, in which *Stempellina* and *Constempellina* Brundin, 1947 are clustered together and defined as a sister group to a clade consisting of *Friederia* Sæther & Andersen, 1998, *Neostempellina* Reiss, 1984, *Stempellinella* and *Zavrelia* Kieffer, 1913.

Median volsella (MVo)

In Tanytarsini, the median volsella is an appendage of the male gonocoxite, consisting of a stem that bears lamellae of highly diverse shapes (Sæther, 1980). The

UPDATED KEY TO THE IDENTIFICATION OF GENERA AND SPECIES OF THE TRIBE TANYTARSINI FROM EOCENE AMBERS

1. Hypopygium with gonostyli rigidly connected to gonocoxites, straight, directed posteriorly (Figs 1F, 2B, 3A, B, 5A–C, 8A, B, 10A, B) .... subfamily Chironominae 2

   Hypopygium with gonostyli movable, bent, directed posteromedially or medially ....
   ....other Chironomidae subfamilies (not keyed)

2. Wing vein RM parallel or slightly oblique relative to R and M, anal lobe weak or not developed, squama bare (Figs 4C, 7D, 9E, F) .... tribe Tanytarsini
   3

   Wing vein RM transverse relative to R and M, anal lobe well developed, squama with fringe of setae ....
   ....other Chironominae tribes (not keyed)

3. Tibiae of all legs much shorter than their femora; basitarsi of mid- and hindlegs extraordinarily long, much longer than their tibiae (LR > 1); mid- and hindleg tibiae with strongly elongated apical lobes, tapering to filiform apices; tibial combs and spurs absent (Fig. 1B, C; Zakrzewska *et al.*, 2018: figs 1, 2) .... *Gujaratomyia miripes* (India: Cambay)

   Tibiae and femora of mid- and hindlegs of similar length; basitarsi of mid- and hindlegs shorter than their tibiae (LR < 1); mid- and hindleg tibiae without elongated apical lobes; tibial combs and/or spurs present (Figs 2D, 4B, D–F, 6D, F, 7B, 9C) 4

4. Median volsella absent and superior volsella stout and/or strongly elongated (Zakrzewska & Giłka, 2015b: figs 2, 4; Giłka *et al.*, 2016: fig. 4) 5

   Median volsella present and/or superior volsella of another shape (Figs 3, 5, 8, 10) 7

5. Gonostylus without subapical lobe on median margin (Giłka *et al.*, 2016: fig. 4) ....
   .... *Nandeva pudens* (China: Fushun)

   Gonostylus with subapical lobe on median margin (Zakrzewska & Giłka, 2015b: figs 2, 4) *Eonandeva* … 6

6. Gonostylus slender, subapical lobe small; median setae absent; superior volsella cylindrical; inferior volsella with slightly enlarged apical part (Zakrzewska & Giłka, 2015b: fig. 2) ....
   .... *Eonandeva helva* (Baltic region: Gulf of Gdańsk)

   Gonostylus broad near apex, subapical lobe large; median setae present; superior volsella swollen in apical part; inferior volsella with distinctly enlarged head-like apical part (Zakrzewska & Giłka, 2015b: fig. 4) …
   .... *Eonandeva latistyla* (Baltic region: Gulf of Gdańsk)

7. Dorsomedian extensions of eyes developed (Giłka *et al.*, 2013: figs 2, 3, 6, 8; Zakrzewska & Giłka, 2015a: figs 5, 7), if not developed (Fig. 2B) then digitus present (Fig. 3A, B) and/or wing vein R_{4+5} ending distal to M_{3+4} towards wing apex (Fig. 4C; Giłka, 2010: plate 2; Giłka, 2011: fig. 2; Giłka *et al.*, 2013: figs 1, 2, 4, 6, 7; Zakrzewska & Giłka, 2013: fig. 1; Zakrzewska & Giłka, 2014: fig. 1; Zakrzewska & Giłka, 2015a: figs 5, 7; Zakrzewska *et al.*, 2016: fig. 4) 8

   Dorsomedian extension of eye not developed; eyes reniform (Fig. 7B; Zakrzewska & Giłka, 2015a: fig. 3; Zakrzewska *et al.*, 2016: fig. 7), digitus never present and wing vein R_{4+5} ending opposite to or proximal to M_{3+4} towards wing apex (Figs 7D, 9G; Zakrzewska & Giłka, 2014: fig. 3; Zakrzewska & Giłka, 2015a: fig. 3) 22

8. Superior volsella small, boomerang shaped or cylindrical; median volsella with two slender falciform lamellae (Giłka *et al.*, 2013: figs 1, 2; Zakrzewska & Giłka, 2014: fig. 2) .... *Archistempellina* 9

   Superior volsella solid, elongated and/or broadened, roundish, pipe shaped, bean shaped or reniform; median volsella never with two slender falciform lamellae (Figs 3, 5; Giłka, 2010: plate 2; Giłka, 2011: fig. 2; Giłka *et al.*, 2013: figs 4, 6, 7; Zakrzewska & Giłka, 2013: fig. 2; Zakrzewska & Giłka, 2015a: figs 6, 8; Zakrzewska *et al.*, 2016: figs 3, 5) 11

9. Anal tergite with semicircular posterolateral lobes covered with dense setae; superior volsella boomerang shaped, with triangular tip; stem of median volsella directed posteromedially, tip narrow (Zakrzewska & Giłka, 2014: fig. 2) .... *Archistempellina perkovskyi* (Baltic region: Gulf of Gdańsk, Rovno)

Anal tergite without semicircular posterolateral lobes covered with dense setae; superior volsella cylindrical, swollen in distal part; stem of median volsella directed medially, tip swollen (Giłka *et al.*, 2013: figs 1, 2) 10

10. Anal point acute, reaching beyond superior and median volsellae; stem of median volsella longer than its falciform lamellae (Giłka *et al.*, 2013: fig. 1) .... *Archistempellina bifurca* (Baltic region: Rovno)

Anal point with swollen roundish tip, reaching bases of median and inferior volsellae; stem of median volsella and its falciform lamellae of the same length (Giłka *et al.*, 2013: fig. 2) .... *Archistempellina falcifera* (Baltic region: Gulf of Gdańsk, Rovno)

11. Eyes hairy; gonostylus with strong spine-like apical bristle (Giłka *et al.*, 2013: fig. 4) .... *Corneliola avia* (Baltic region: Gulf of Gdańsk, Rovno)

Eyes bare; gonostylus with simple apical seta at most (Figs 3, 5; Giłka, 2010: plate 2; Giłka, 2011: fig. 2; Giłka *et al.*, 2013: figs 6, 7; Zakrzewska & Giłka, 2013: fig. 2; Zakrzewska & Giłka, 2015a: figs 6, 8; Zakrzewska *et al.*, 2016: figs 3, 5) 12

12. Superior volsella roundish with slightly projecting posterior part or reniform, anal point spinulae absent (Giłka *et al.*, 2013: fig. 6; Zakrzewska *et al.*, 2016: fig. 3) .... *Rheotanytarsus* … 13

Superior volsella usually more or less elongated, if roundish then spinulae present (Figs 3, 5; Zakrzewska *et al.*, 2016: fig. 5; Giłka, 2010: plate 2; Giłka *et al.*, 2013: fig. 7; Zakrzewska & Giłka, 2013: fig. 2; Zakrzewska & Giłka, 2015a: figs 6, 8) .... *Tanytarsus* 14

13. Anal point tapering to slender tip; superior volsella roundish; digitus present; stem of median volsella stout and short, simple, with pectinate or leaf shaped lamellae fused at bases (Giłka *et al.*, 2013: fig. 6) ....*Rheotanytarsus alliciens* (Baltic region: Rovno)

Anal point with swollen tip; superior volsella reniform; digitus absent; stem of median volsella bone shaped, with separated leaf shaped lamellae (Zakrzewska *et al.*, 2016: fig. 3).. .... *Rheotanytarsus hoffeinsorum* (Baltic region: Gulf of Gdańsk)

14. Distal portion of anal point with horizontally expanded lateral enlargements and small distal section between; posteriorly directed bar present (Zakrzewska & Giłka, 2013: fig. 2) .... *Tanytarsus szadziewskii* (Baltic region: Gulf of Gdańsk)

Distal portion of anal point without lateral enlargements, distal section or bar (Figs 3, 5; Giłka, 2010: plate 2; Giłka, 2011: fig. 2; Giłka *et al.*, 2013: fig. 7; Zakrzewska & Giłka, 2015a: figs 6, 8; Zakrzewska *et al.*, 2016: fig. 5) 15

15. Anal point long and slender; superior volsella pipe shaped; stem of median volsella twig shaped, branched into two simple lamellae (Fig. 5) .... *Tanytarsus ramus* (India: Cambay)

Anal point, superior volsella and median volsella never as above (Fig. 3; Giłka, 2010: plate 2; Giłka, 2011: fig. 2; Giłka *et al.*, 2013: fig. 7; Zakrzewska & Giłka, 2015a: figs 6, 8; Zakrzewska *et al.*, 2016: fig. 5) 16

16. Gonostyli nearly twice as long as gonocoxites; anal point broad but short, semicircular, with spinulae in shallow pit; superior volsella stout, roundish (Fig. 3) .... *Tanytarsus forfex* (India: Cambay)

Gonostyli slightly longer than or as long as gonocoxites; anal point never as above; superior volsella slightly elongated at least (Giłka, 2010: plate 2; Giłka *et al.*, 2013: fig. 7; Zakrzewska & Giłka, 2015a: figs 6, 8; Zakrzewska *et al.*, 2016: fig. 5) 17

17. Wing veins R and M short, nearly half as long as Cu, VR_{Cu} 1.70–1.82; stem of median volsella with setiform and slender subuliform lamellae (Giłka, 2010: plate 2) .... *Tanytarsus serafini* (Baltic region: Gulf of Gdańsk, Rovno)

Wing veins R and M long, VR_{Cu} 1.16–1.52. Stem of median volsella with arcuate, spindle shaped or leaf shaped (foliate) lamellae (Giłka, 2011: fig. 2; Giłka *et al.*, 2013: fig. 7; Zakrzewska & Giłka, 2015a: figs 6, 8; Zakrzewska *et al.*, 2016: fig. 5)..18

18. Digitus well developed, extending beyond superior volsella (Zakrzewska & Giłka, 2015a: fig. 6) .... *Tanytarsus GLAESARIUS* (Baltic region: Gulf of Gdańsk)

Digitus not observed 19

19. Ultimate palpomere with strong, stiff apical seta; anal tergite with longitudinal crest-like hump bearing median setae (Giłka, 2011: figs 1, 2) .... *Tanytarsus fereci* (Baltic region: Gulf of Gdańsk)

Ultimate palpomere without stiff apical seta; anal tergite without longitudinal hump, median setae absent (Giłka *et al.*, 2013: fig. 7; Zakrzewska & Giłka, 2015a: fig. 8; Zakrzewska *et al.*, 2016: fig. 5) 20

20. Gonostylus straight, with long seta on apex; superior volsella finger like, distinctly curved at mid-length and directed medially; median volsella sickle shaped, with slender arcuate lamellae (Zakrzewska *et al.*, 2016: fig. 5) .... *Tanytarsus crocota* (Baltic region: Gulf of Gdańsk)

Gonostylus curved at mid-length or boomerang like, with subapical tooth-like process at most; superior volsella bean shaped or with nipple-like apical extension, straight, directed posteromedially or posteriorly; median volsella never sickle shaped, bearing leaf shaped (foliate) lamellae (Giłka *et al.*, 2013: fig. 7; Zakrzewska & Giłka, 2015a: fig. 8; Zakrzewska *et al.*, 2016: fig. 6)...21

21. Stem of median volsella bulb shaped (Giłka *et al.*, 2013: fig. 7) .... *Tanytarsus congregabilis* (Baltic region: Rovno)

Stem of median volsella elongated, straight (Zakrzewska & Giłka, 2015a: fig. 8) .... *Tanytarsus PROTOGREGARIUS* (Baltic region: Gulf of Gdańsk)

22. Gonostylus distinctly longer than gonocoxite (Fig. 8; Seredszus & Wichard, 2007: fig. 18)   *Stempellina* … 23

Gonostylus shorter than or as long as gonocoxite (Fig. 10; Seredszus & Wichard, 2007: fig. 19; Zakrzewska & Giłka, 2014: fig. 4; Zakrzewska & Giłka, 2015a: fig. 4; Zakrzewska *et al.*, 2016: fig. 8) .... *Stempellinella* 24

23. Anal point spinulae absent; superior volsella twig shaped, strongly elongated: length/width ratio nearly ten (Seredszus & Wichard, 2007: fig. 18) .... *Stempellina exigua* (Baltic region: Gulf of Gdańsk)

Anal point spinulae present; superior volsella cylindrical, apically rounded, slightly elongated: length/width ratio nearly two (Fig. 8) .... *Stempellina stebneri* (India: Cambay)

24. Inferior volsella with stout process on median margin (Fig. 10) .... *Stempellinella pollex* (India: Cambay)

Inferior volsella without process on median margin 25

25. Gonostylus with apical nipple-like process; anal point with spinulae; superior volsella directed posteriorly; inferior volsella with beak-like protrusion (Zakrzewska & Giłka, 2014: fig. 4) .... *Stempellinella ivanovae* (Baltic region: Gulf of Gdańsk, Rovno)

Gonostylus without apical nipple-like process; anal point without spinulae; superior volsella directed medially; inferior volsella without beak-like protrusion (Seredszus & Wichard, 2007: fig. 19; Zakrzewska & Giłka, 2015a: fig. 4; Zakrzewska *et al.*, 2016: fig. 8) 26

26. Antennal flagellum consisting of ten flagellomeres; median volsella shorter than superior volsella (Seredszus & Wichard, 2007: fig. 19) .... *Stempellinella bicorna* (Baltic region: Gulf of Gdańsk)

Antennal flagellum consisting of 13 flagellomeres, flagellomeres 11–13 or 12–13 partly fused (Zakrzewska & Giłka, 2015a: fig. 3; Zakrzewska *et al.*, 2016: fig. 7); median volsella longer than superior volsella (Zakrzewska & Giłka, 2015a: fig. 4; Zakrzewska *et al.*, 2016: fig. 8) 27

27. Median volsella (stem + lamellae) distinctly shorter than gonostylus, bearing wide pectinate and foliate lamellae (Zakrzewska & Giłka, 2015a: fig. 4) .... *Stempellinella electra* (Baltic region: Gulf of Gdańsk)

Median volsella (stem + lamellae) and gonostylus of similar length, bearing slender foliate lamellae, single lamella with strongly elongated filiform tip (Zakrzewska *et al.*, 2016: fig. 8) .... *Stempellinella fibra* (Baltic region: Gulf of Gdańsk)

median volsellae, with a couple of exceptions (i.e. when reduced, cf. Ekrem & Reiss, 1999), are thus the most important diagnostic structures in Tanytarsini. In *T. ramus*, the MVo is simple, consisting of a twig shaped stem, branched into two lamellae (Fig. 5E, F). If we treat *T. ramus* as one of the oldest known tanytarsines, we then assume that this type of volsella might display one of the simplest/oldest types of MVo structure in Tanytarsini (plesiomorphy), comparable to that known from the extinct genus *Archistempellina* Giłka

& Zakrzewska, 2013 described from Baltic amber (cf. Giłka *et al.*, 2013; Zakrzewska & Giłka, 2014).

Process on the inferior volsella (IVo)

Interestingly, the thumb shaped process observed in *Stempellinella pollex* (Fig. 10B, C) is a unique form of a structure within Tanytarsini, both extinct and extant. We consider it to be a plesiomorphic state of a tiny process that persists only in three extant species: *Stempellinella ciliaris* (Goetghebuer, 1944), *Stempellinella saltuum* (Goetghebuer, 1921) and *Stempellinella sublettorum* Ekrem, 2007. We presume that this structure, called a microtrichose wart or digitus (Ekrem, 2007), which is minute (*Stempellinella ciliaris* and *Stempellinella saltuum*) or elongated but frail (*Stempellinella sublettorum*), has vanished in the majority of extant species.

CAMBAY AMBER IDENTITY

The staggering prices of amber containing animal inclusions, offered for sale worldwide, have paved the way for an extensive market of fakes (e.g. Eriksson & Poinar, 2015). A number of counterfeit amber-like materials are on sale, and true ambers are offered, mistakenly or intentionally, as having been mined from other, usually older geological deposits. This serious problem can also affect incorrectly dated specimens designated as types for new taxa. The archival storage of IR spectra obtained from amber with registered reference curve numbers is thus a procedure highly recommended for museum materials, especially for name-bearing inclusions, in order to support the validity of newly described taxa.

The FT-IR spectra of the Cambay amber chunks analysed in this study are shown in Figure 11. The spectral patterns are characteristic of fossil resins. The positions of the main peaks and proposed assignments are listed in Table 6. Comparison of these spectra with the literature data (Dutta *et al.*, 2009; Mallick *et al.*, 2009) for Cambay resins confirms their identity.

The position (~1700 cm^{-1}) and low relative intensity of the carbonyl group vibration band is characteristic of all spectra of the Cambay resins investigated here. In conjunction with certain physical properties, such as the sticky nature of the material, which makes it difficult to polish, this indicates that it is highly similar to the resins of the glessite (mineral name) group of different geographical origin and geological age. We thus compared our FT-IR spectra with the spectra of glessite from Germany (Bitterfeld, Goitzsche Mine, Eocene; Fig. 12A) (E. Wagner-Wysiecka & R. Wimmer, unpublished data) and Miocene ambers from Borneo (Fig. 12B) and Sumatra (Fig. 12C) (E.

Wagner-Wysiecka, unpublished data). The similarities in the spectral patterns are evident and consistent with published spectral data (Kosmowska-Ceranowicz & Vávra, 2015).

The main differences enabling one to identify and differentiate Cambay amber from the above glessite-type resins seem to be the νC-OH and γRHC=CH$_2$ vibration bands in the fingerprint region. The well-defined signals at ~1044 and ~1030 cm^{-1} in the spectra of Cambay resins, along with the band at ~996 cm^{-1}, form a unique 'doublet-like' pattern not observed in the reference material. Analysis of the chemical composition of Cambay resins using Pyrolysis-gas chromatogrphy–mass spectrometry revealed, among other things, the presence of cadalene-type sesquiterpenoids, which are said to be characteristic of Dipterocarpaceae resins (Mallick *et al.*, 2009). Gas chromatogrphy–mass spectrometry analysis of Bitterfeld glessite samples suggests Burseraceae as the botanical source of glessite (Yamamoto *et al.*, 2006). The similarity of Burseraceae and Dipterocarpaceae resins was also confirmed by comparison of the IR spectra of contemporary resins of these families (Kosmowska-Ceranowicz, 2012). All these facts confirm that the investigated Cambay amber belongs to the II Class of resins (Anderson *et al.*, 1992) and can be referred to Eocene glessite from Cambay, by analogy to other resins of the same class of different geographical origin and age. The use of mineralogical names for fossil resins should prevent confusion when discussing resins of different geographical origin, but with the same properties (class) (cf. Vávra, 2009).

CONCLUSION

Chironomidae are the most abundant Diptera inclusions in Cambay amber, as in the majority of Eocene amber deposits worldwide. Five subfamilies have been identified to date: Chironominae, Orthocladiinae, Podonominae, Prodiamesinae and Tanypodinae (Stebner *et al.*, 2017). The first mentioned seems to have been the most common during the formation of early Eocene Cambay amber (Stebner *et al.*, 2017), although this subfamily, including the tribe Tanytarsini, has not been recorded before the Cenozoic (Zakrzewska *et al.*, 2018). Eocene Tanytarsini, the oldest within the tribe, can thus be considered a highly diverse group, as represented by ten genera and 26 species described, including four genera and five species recorded from one of the oldest known sources: Cambay amber. The Tanytarsini studied here display unknown structures of diagnostic and phylogenetic importance that are discussed in relationship to extant representatives of the tribe. Cambay amber exhibits some significant
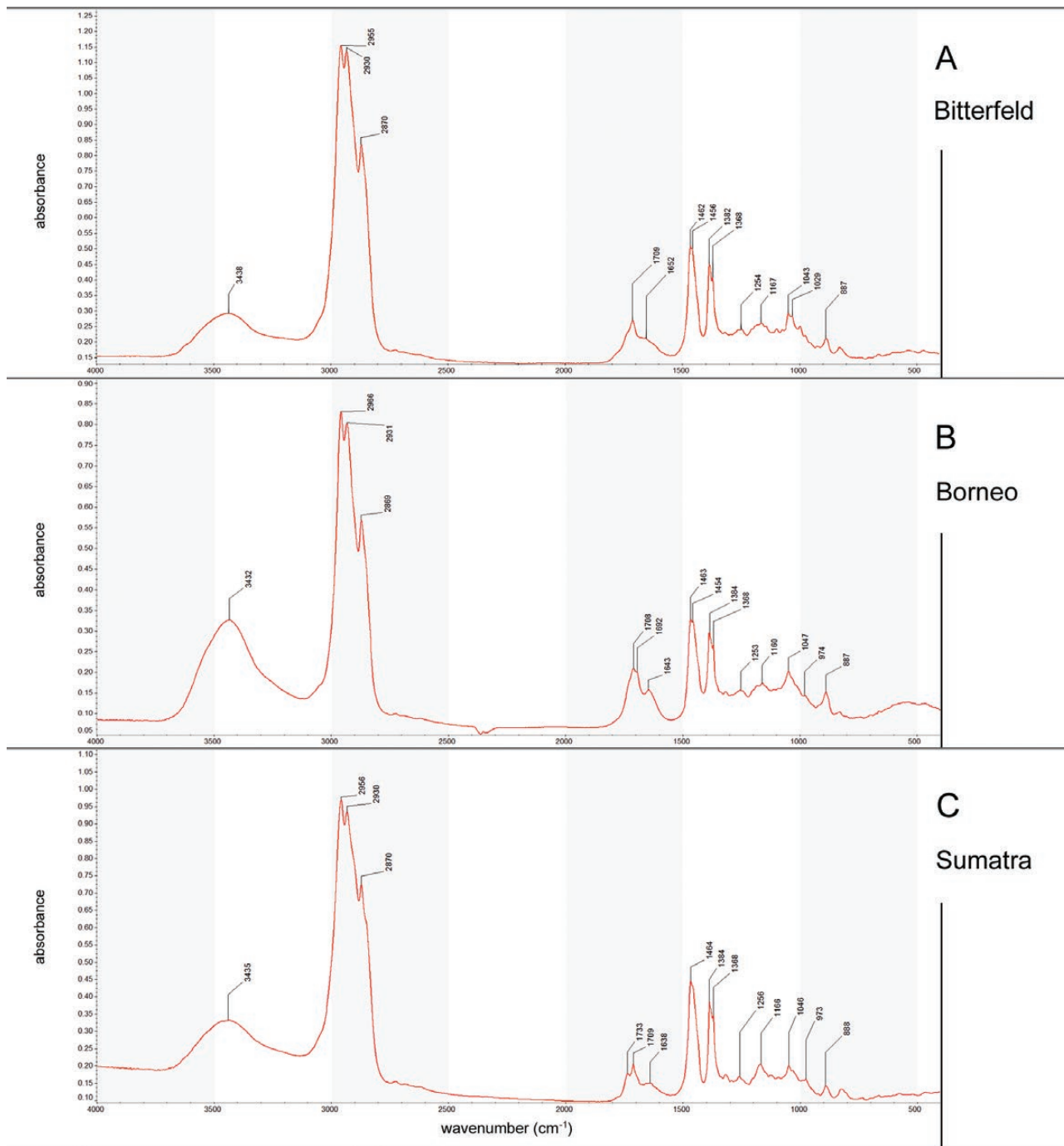
Figure 12. Comparison of Fourier transform infrared spectroscopy spectra (KBr pellet) of Bitterfeld glessite (A), glessite from Borneo (B) and a sample from Sumatra (C). A, Wagner-Wysiecka E. & Wimmer R. (unpublished data). B, C, Wagner-Wysiecka E. (unpublished data).

similarities in physical properties and FT-IR spectral pattern to the glessite group of resins, but it was found that well-defined bands in the fingerprint region can be diagnostic for its unequivocal identification.

ACKNOWLEDGEMENTS

REFERENCES

Anderson KB, **Winans RE**, **Botto RE. 1992.** The nature and fate of natural resins in the geosphere—II. Identification, classification and nomenclature of resinites. *Organic Geochemistry* **18:** 829–841.

Azar D, **Veltz I**, **Nel A. 2008**. Mandibulate chironomids: primitive or derived? (Diptera: Chironomidae). *Systematic Entomology* **33:** 688–699.

Baranov V, **Giłka W**, **Zakrzewska M**, **Jarzembowski E. 2019**. New non-biting midges (Diptera: Chironomidae) from Lower Cretaceous Wealden amber of the Isle of Wight (UK). *Cretaceous Research* **95:** 138–145.

Baranov V, **Góral T**, **Ross A. 2017**. A new genus of Buchonomyiinae (Diptera, Chironomidae) from Upper Cretaceous Burmese amber, with the phylogeny of the subfamily revisited. *Cretaceous Research* **79:** 146–152.

Benton MJ, **Donoghue PC. 2007.** Paleontological evidence to date the tree of life. *Molecular Biology and Evolution* **24:** 26–53.

Boesel MW. 1937. Diptera, Chironomidae. In: Carpenter FM, Folsom JW, Essig EO, Kinsey AC, Brues CT, Boesel MW, Ewing HE, eds. *Insects and arachnids from Canadian amber. University of Toronto Studies, Geology Series* **40:** 44–55.

Brundin L. 1976. A Neocomian chironomid and Podonominae Aphroteniinae (Diptera) in the light of phylogenetics and biogeography. *Zoologica Scripta* **5:** 139–160.

Clementz M, **Bajpai S**, **Ravikant V**, **Thewissen JGM**, **Saravanan N**, **Singh IB**, **Prasad V. 2011**. Early Eocene warming events and the timing of terrestrial faunal exchange between India and Asia. *Geology* **39:** 15–18.

Cranston PS, **Gad El Rab MO**, **Kay AB. 1981.** Chironomid midges as a cause of allergy in the Sudan. *Transactions of the Royal Society of Tropical Medicine and Hygiene* **75:** 1–4.

Cranston PS. 2019. An enigmatic Chironomidae (Diptera): first larval description for *Nandeva* Wiedenbrug, Reiss and Fittkau and evidence for phylogenetic position in Tanytarsini. *Chironomus Journal of Chironomidae Research* **32:** 25–32.

Dutta S, **Mallick M**, **Bertram N**, **Greenwood PF**, **Mathews RP. 2009.** Terpenoid composition and class of Tertiary resins from India. *International Journal of Coal Geology* **80:** 44–50.

Ekrem T. 2007. A taxonomic revision of the genus *Stempellinella* (Diptera: Chironomidae). *Journal of Natural History* **41:** 1367–1465.

Ekrem T, **Reiss F. 1999.** Two new *Tanytarsus* species (Diptera: Chironomidae) from Brazil, with reduced median volsella. *Aquatic Insects* **21:** 205–213.

Eriksson ME, **Poinar GO Jr. 2015.** Fake it till you make it—the uncanny art of forging amber. *Geology Today* **31:** 21–27.

Garg R, **Ateequzzaman K**, **Prasad V**, **Tripathi SKM**, **Singh IB**, **Jauhri AK**, **Bajpai S. 2008.** Age-diagnostic dinoflagellate cysts from the lignite-bearing sediments of the Vastan lignite mine, Surat District, Gujarat, western India. *Journal of the Palaeontological Society of India* **53:** 99–105.

Giłka W. 2005. A systematic review of European *Stempellina* Thienemann *et* Bause (Diptera: Chironomidae) with description of a new species from Fennoscandia. *Annales Zoologici* **55:** 413–419.

Giłka W. 2009. Order Diptera, family Chironomidae, tribe Tanytarsini. In: Sheikh Tahnoon Bin Zayed Al Nahyan HH (patron), Van Harten A, eds. *Arthropod fauna of the United Arab Emirates*, **Vo. 2**. Abu Dhabi: Dar Al Ummah Printing, Publishing, Distribution & Advertising, 667–682.

Giłka W. 2010. A new species group in the genus *Tanytarsus* van der Wulp (Diptera: Chironomidae) based on a fossil record from Baltic amber. *Acta Geologica Sinica (English Edition)* **84:** 714–719.

Giłka W. 2011. A new fossil *Tanytarsus* from Eocene Baltic amber, with notes on systematics of the genus (Diptera: Chironomidae). *Zootaxa* **3069:** 63–68.

Giłka W, **Makarchenko EA**, **Pankowski MK**, **Zakrzewska M. 2019.** *Myanmaro primus* gen. *et* sp. nov., the first orthoclad (Diptera: Chironomidae) from Cretaceous Burmese amber. *Zootaxa* **4565:** 61–70.

Giłka W, **Zakrzewska M. 2017.** A new species of the subfamily Buchonomyiinae (Diptera: Chironomidae) from Cretaceous Burmese amber. *Dipteron* **33:** 26–33.

Giłka W, **Zakrzewska M**, **Baranov V**, **Wang B**, **Stebner F. 2016.** The first fossil record of *Nandeva* Wiedenbrug, Reiss *et* Fittkau (Diptera: Chironomidae) in early Eocene Fushun amber from China. *Alcheringa: An Australasian Journal of Palaeontology* **40:** 390–397.

Giłka W, **Zakrzewska M**, **Dominiak P**, **Urbanek A. 2013.** 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). *Zootaxa* **3736:** 569–586.

Giłka W, **Zakrzewska M**, **Makarchenko EA. 2020.** *Burmochlus* gen. nov., the first Cretaceous member of the *Archaeochlus* cluster (Diptera: Chironomidae: Podonominae). *Cretaceous Research* **106:** 104261.

Grimaldi DA, **Engel MS**, **Singh H. 2013.** Bugs in the biogeography: Leptosaldinae (Heteroptera: Leptopodidae) in amber from the Miocene of Hispaniola and Eocene of India. *Journal of the Kansas Entomological Society* **86:** 226–243.

Hirabayashi K, **Kubo K**, **Yamaguchi S**, **Fujimoto K**, **Murakami G**, **Nasu Y. 1997.** Studies of bronchial asthma induced by chironomid midges (Diptera) around a hypereutrophic lake in Japan. *Allergy* **52:** 188–195.

Jarzembowski EA, **Azar D**, **Nel AN. 2008.** A new chironomid (Insecta: Diptera) from Wealden amber (Lower Cretaceous) of the Isle of Wight (UK). *Geologica Acta: an International Earth Science Journal* **6:** 285–291.

Kalugina NS. 1976. Non-biting midges of the subfamily Diamesinae (Diptera, Chironomidae) from the Upper Cretaceous of Taimyr. *Paleontological Journal* **1:** 78–83 [in Russian].

Kalugina NS. 1980a. Chaoboridae and Chironomidae from the Lower Cretaceous deposits of Manlay. In: Kalugina NS, ed. Early Cretaceous Lake Manlay. *Transactions of the Joint Soviet-Mongolian Palaeontological Expedition* **13:** 61–64 [in Russian].

Kalugina NS. 1980b. Cretaceous Aphroteniinae from north Siberia (Diptera, Chironomidae), *Electrokejia brundini* gen. nov., sp. nov. *Acta Universitatis Carolinae Biologica* **1978:** 89–93.

Kalugina NS. 1985. Infraorder Culicomorpha. In: Kalugina NS, Kovalev VG, eds. *Dipteran insects of the Jurassic of Siberia*. Moscow: USSR Academy of Sciences, 63–113 [in Russian].

Kalugina NS. 1986. Muscida (Diptera). Infraorders Tipulomorpha and Culicomorpha. In: Rasnitsyn AP, ed. Insects in the Early Cretaceous ecosystems of the west Mongolia. *Transactions of the Joint Soviet-Mongolian Palaeontological Expedition* **28:** 112–125 [in Russian].

Kalugina NS. 1993. Chaoborids and midges from the Mesozoic of eastern Transbaikalia (Diptera: Chaoboridae and Chironomidae). In: Ponomarenko AG, ed. Mesozoic insects and ostracods from Asia. *Trudy Paleontologicheskogo Instituta Rossijskoj Akademii Nauk* **252:** 117–139 [in Russian].

Kosmowska-Ceranowicz B. 2012. *Amber in Poland and in the World*. Warsaw: Warsaw University Press, 104.

Kosmowska-Ceranowicz B, **Vávra N. 2015.** *Atlas. Infrared spectra of the world's resins. Holotype characteristics*. Warsaw: Museum of the Earth, Polish Academy of Sciences, 40–49.

Krzemiński W, **Jarzembowski E. 1999.** *Aenne triassica* sp.n., the oldest representatives of the family Chironomidae (Insecta: Diptera). *Polish Journal of Entomology* **68:** 445–449.

Lin X, **Stur E**, **Ekrem T. 2018.** Molecular phylogeny and temporal diversification of *Tanytarsus* van der Wulp (Diptera: Chironomidae) support generic synonymies, a new classification and centre of origin. *Systematic Entomology* **43:** 659–677.

Lukashevich ED, **Przhiboro AA. 2011.** New Chironomidae (Diptera) with elongate proboscises from the Late Jurassic of Mongolia. *ZooKeys* **130:** 307–322.

Lukashevich ED, **Przhiboro AA. 2015.** A new tribe of Diamesinae (Diptera: Chironomidae) from the Lower Cretaceous of Mongolia. *Cretaceous Research* **52:** 562–569.

Lukashevich ED, **Przhiboro AA. 2018.** A new genus of Chironomidae (Insecta: Diptera) from the Lower Cretaceous of Mongolia. *Paleontological Journal* **52:** 1401–1407.

Mallick M, **Dutta S**, **Greenwood PF**, **Bertram N. 2009.** Pyrolytic and spectroscopic studies of Eocene resin from Vastan lignite Mine, Cambay basin, western India. *Journal of the Geological Society of India* **74:** 16–22.

Mathur LP, **Rao KLN**, **Chaube AN. 1968.** Tectonic framework of Cambay basin, India. *Oil and Natural Gas Commission Bulletin* **5:** 7–28.

McCann T. 2010. Chenier plain sedimentation in the Palaeogene-age lignite-rich successions of the Surat area, Gujarat, western India [Chenier-Plain-Sedimentation in den paläogenen braunkohlereichen Einheiten von Surat, Gujarat, West-Indien]. *Zeitschrift der Deutschen Gesellschaft für Geowissenschaften* **161:** 335–351.

Merh SS. 1995. *Geology of Gujarat*. Bangalore: Geological Society of India, 222.

Nadein KS, **Perkovsky EE. 2019.** Small and common: the oldest tropical Chrysomelidae (Insecta: Coleoptera) from the lower Eocene Cambay amber of India. *Alcheringa: An Australasian Journal of Palaeontology*. doi:10.1080/03115518.2019.1622780

Pape T, **Blagoderov V**, **Mostovski MB. 2011.** Order Diptera Linnaeus, 1758. In: Zhang ZQ, ed. Animal biodiversity: an outline of higher-level classification and survey of taxonomic richness. *Zootaxa* **3148:** 222–229.

Punekar J, **Saraswati PK. 2010.** Age of the Vastan lignite in context of some oldest Cenozoic fossil mammals from India. *Journal of Geological Society of India* **76:** 49–72.

Rust J, **Singh H**, **Rana RS**, **McCann T**, **Singh L**, **Anderson K**, **Sarkar N**, **Nascimbene PC**, **Stebner F**, **Thomas JC**, **Solórzano Kraemer M**, **Williams CJ**, **Engel MS**, **Sahni A**, **Grimaldi D. 2010.** Biogeographic and evolutionary implications of a diverse paleobiota in amber from the early Eocene of India. *Proceedings of the National Academy of Sciences of the United States of America* **107:** 18360–18365.

Sæther OA. 1977. Female genitalia in Chironomidae and other Nematocera: morphology, phylogenies, keys. *Bulletin of Fisheries Research Board of Canada* **197:** 1–209.

Sæther OA. 1980. Glossary of chironomid morphology terminology (Diptera: Chironomidae). *Entomologica Scandinavica Supplement* **14:** 1–51.

Sæther OA, **Andersen T. 1998.** *Friederia*, a new Afrotropical tanytarsine genus (Diptera: Chironomidae). *Entomologica Scandinavica* **29:** 29–37.

Sæther OA, **Roque FO. 2004.** New Neotropical species of *Nandeva* (Diptera: Chironomidae), with a phylogeny of the Tanytarsini. *Tijdschrift voor Entomologie* **147:** 63–80.

Sahni A, **Saraswati PK**, **Rana RS**, **Kumar K**, **Singh H**, **Alimohammadian H**, **Sahni N**, **Rose KD**, **Singh L**, **Smith T. 2006.** Temporal constraints and depositional palaeoenvironments of the Vastan lignite sequence, Gujarat: analogy for the Cambay Shale hydrocarbon source rock. *Indian Journal of Petroleum Geology* **15:** 1–20.

Seredszus F, **Wichard W. 2007.** Fossil chironomids (Insecta, Diptera) in Baltic amber. *Palaeontographica Abteilung A: Paläozoologie – Stratigraphie* **279:** 49–91.

Smith T, **Kumar K**, **Rana RS**, **Folie A**, **Solé F**, **Noiret C**, **Steeman T**, **Sahni A**, **Rose K. 2016.** New early Eocene vertebrate assemblage from western India reveals a mixed

fauna of European and Gondwana affinities. *Geoscience Frontiers* **7:** 969–1001.

Stebner F, **Baranov V**, **Zakrzewska M**, **Singh H**, **Giłka W. 2017.** The Chironomidae diversity based on records from early Eocene Cambay amber, India, with implications on habitats of fossil Diptera. *Palaeogeography, Palaeoclimatology, Palaeoecology* **475:** 154–161.

Vávra N. 2009. Amber, fossil resins, and copal – contributions to the terminology of fossil plant resins. *Denisia* **26:** 213–222.

Veltz I, **Nel A**, **Azar D. 2007.** New chironomid flies in Early Cretaceous Lebanese amber (Diptera: Chironomidae). *African Invertebrates* **48:** 169–191.

Yamamoto S, **Otto A**, **Krumbiegel G**, **Simoneit BR. 2006.** The natural product biomarkers in succinite, glessite and stantienite ambers from Bitterfeld, Germany. *Review of Palaeobotany and Palynology* **140:** 27–49.

Zachos JC, **Dickens GR**, **Zeebe RE. 2008.** An early Cenozoic perspective on greenhouse warming and carbon-cycle dynamics. *Nature* **451:** 279–283.

Zakrzewska M, **Giłka W. 2013.** In the Eocene, the extant genus *Caladomyia* occured in the Palaearctic (Diptera: Chironomidae: Tanytarsini). *Polish Journal of Entomology* **82:** 397–403.

Zakrzewska M, **Giłka W. 2014.** The oldest known chironomids of the tribe Tanytarsini (Diptera: Chironomidae) indicate plesiomorphic character states. *Geobios* **47:** 335–343.

Zakrzewska M, **Giłka W. 2015a.** The Tanytarsini (Diptera: Chironomidae) in the collection of the Museum of Amber Inclusions, University of Gdańsk. *Zootaxa* **3946:** 347–360.

Zakrzewska M, **Giłka W. 2015b.** *Eonandeva* gen. nov., a new distinctive genus from Eocene Baltic amber (Diptera: Chironomidae). *Zootaxa* **4044:** 577–584.

Zakrzewska M, **Krzemiński W**, **Giłka W. 2016.** Towards the diversity of non-biting midges of the tribe Tanytarsini from Eocene Baltic amber (Diptera: Chironomidae). *Palaeontologia Electronica* **19.2.18A:** 1–21.

Zakrzewska M, **Stebner F**, **Puchalski M**, **Singh H**, **Giłka W. 2018.** A peculiar leg structure in the first non-biting midge described from Cambay amber, India (Diptera: Chironomidae). *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **107:** 255–261.

Zhang JF. 1991. New genera and new species of Chironomidae (Diptera, Insecta) from Late Jurassic of China. *Acta Palaeontologica Sinica* **30:** 556–569 [in Chinese, with English summary].