A peculiar leg structure in the first non-biting midge described from Cambay amber, India (Diptera: Chironomidae)

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ABSTRACT: We present the first specific record of a chironomid of the tribe Tanytarsini from early Eocene Cambay amber, India (54 Ma). The oldest known extinct tanytarsine genus, *Gujaratomyia* Giłka & Zakrzewska, gen. nov., is described on the basis of adult males of *G. miripes* Giłka & Zakrzewska, sp. nov. The species displays an unusual leg structure with unique leg ratios and tibial armature. The combination of the head and genital apparatus characters supports the hypothesis that *Gujaratomyia* and *Cladotanytarsus* are members of a common group within the subtribe Tanytarsina.

KEY WORDS: early Eocene, fossils, functional anatomy, new genus, Tanytarsini, taxonomy.

Today, Chironomidae have a worldwide distribution, with more than 7,000 species (Pape *et al.* 2011). This family also has a rich fossil record, with the oldest finding, *Aenne triassica* Krzemiński & Jarzembowski, 1999 dating back to the Upper Triassic (~202 Ma; Benton & Donoghue 2007). Non-biting midges are commonly recorded in ambers of various origin: from the Cretaceous (e.g., in Lebanese amber; Veltz *et al.* 2007), through the Eocene (e.g., in Sakhalin amber; Baranov *et al.* 2015) to the Miocene (e.g., in Amazonian amber; Antoine *et al.* 2006). The vast majority of species of the chironomid tribe Tanytarsini have so far been described from extensively examined Baltic amber (~43–48 Ma; Seredszus & Wichard 2007; Giłka 2010, 2011a; Giłka *et al.* 2013; Zakrzewska & Giłka 2013, 2014, 2015a, b; Zakrzewska *et al.* 2016), whereas the oldest known member of this tribe is *Nandeva pudens* Giłka, Zakrzewska, Baranov, Wang & Stebner, 2016, found in Chinese Fushun amber (~50–53 Ma; e.g., Wang *et al.* 2014); however, this fossil belongs to the genus that is presumably either a member of the Tanytarsini or is defined as the tribe's sister group (Giłka *et al.* 2016).

Cambay amber is found in several active opencast lignite mines located in the state of Gujarat, India, about 30 km northeast of Surat. 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). Cambay amber has been dated to the early Eocene (54 Ma; *cf.* Smith *et al.* 2016, Stebner *et al.* 2017a); it is thus contemporaneous with Fushun amber from China and slightly older than amber from the Baltic region. Furthermore, Cambay amber was formed at a time of expanding modern diversity, at the beginning of the Early Eocene Climatic Optimum (EECO) and just after the Late Palaeocene Thermal Maximum (LPTM) (e.g., Zachos *et al.* 2008).

As in many other amber deposits, Chironomidae are the most common dipteran inclusions in Cambay amber, in which five subfamilies have been found so far. With nearly 50 % of all chironomids recorded, Chironominae (including the tribe Tanytarsini) is the most abundant, followed by Orthocladiinae, Tanypodinae, Podonominae and Prodiamesinae. The Tanytarsini is represented by three extant genera: *Stempellina* Thienemann & Bause in Bause, 1913; *Stempellinella* Brundin, 1947; and *Tanytarsus* van der Wulp, 1874 (Stebner *et al.* 2017b); however, no specific description has been published so far. Therefore, a species of an unknown extinct genus presented below is the first tanytarsine and non-biting midge described from early Eocene Cambay amber.

1. Material and methods

The specimens examined are adult male chironomids preserved in early Eocene Cambay amber from India (54 Ma), derived from the Tadkeshwar lignite mine. The inclusions are part of the collection of the Birbal Sahni Institute of Palaeosciences (BSIP), Lucknow, India. The amber was ground using a Buehler Phoenix Beta grinding machine and polished manually. Measurements of specimens are in micrometres, except for the total length (in millimetres, rounded off to the first decimal digit). 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 μm and 1 μm, respectively. The antennal, leg and venarum ratios (AR, LR, VR) were calculated to the second decimal place. The morphological terminology and abbreviations follow Sæther (1980). The photographs were taken using the microscope PZO Biolar SK14 and Helicon Focus 6 image stacking software.
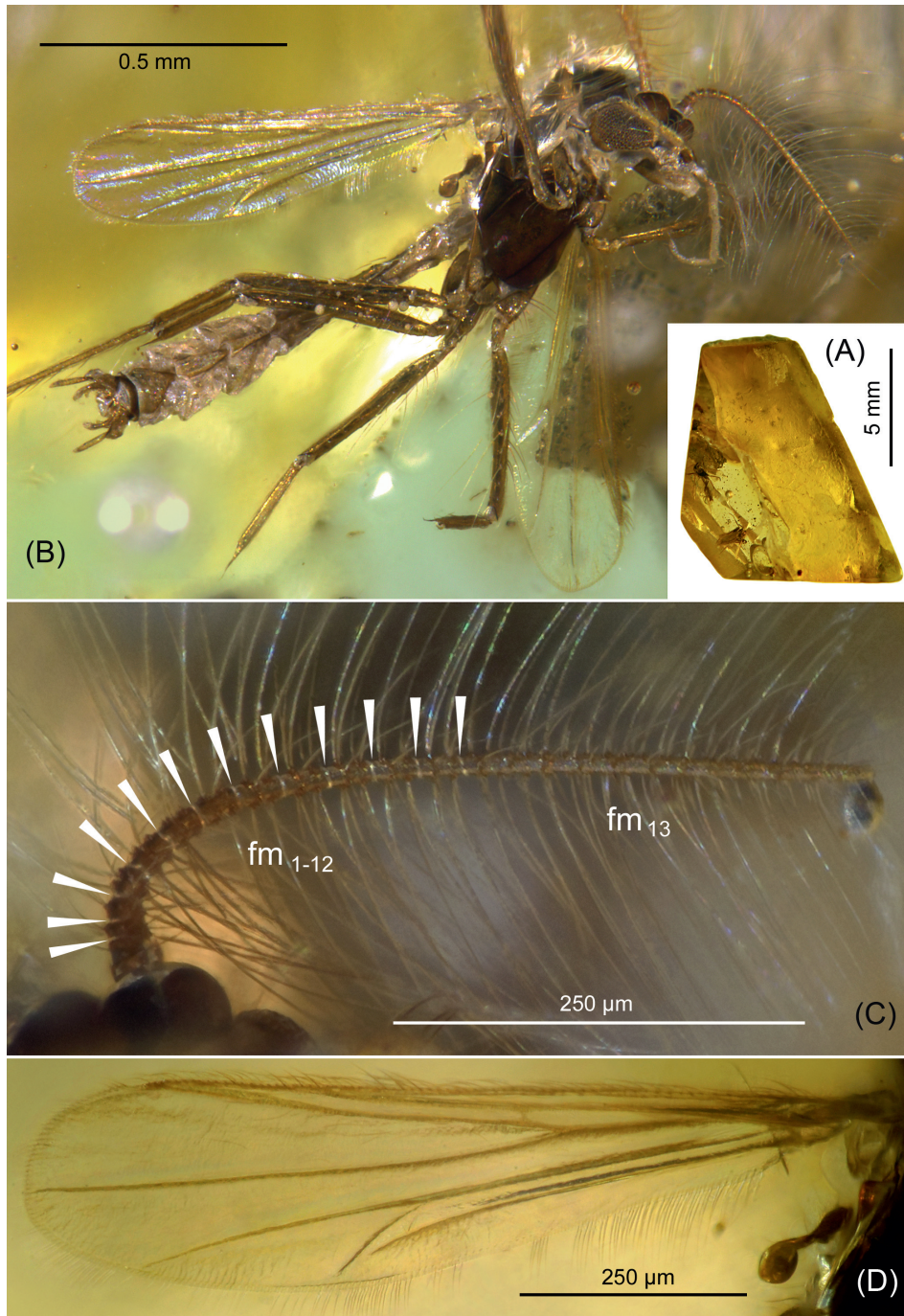
Figure 1 *Gujaratomyia miripes* gen. *et* sp. nov., adult male, holotype, BSIP Tad-607 a, early Eocene, 54 Ma, Tadkeshwar mine, Gujarat, India: (A) inclusion in amber; (B) habitus; (C) antenna (arrows indicate borders between flagellomeres, fm$_{1-13}$); (D) wing.

2. Systematics

Family Chironomidae Newman, 1834
Subfamily Chironominae Newman, 1834
Tribe Tanytarsini Zavřel, 1917
Subtribe(?) Tanytarsina Zavřel, 1917
Gujaratomyia Giłka & Zakrzewska, gen. nov.

Type species. *Gujaratomyia miripes* Giłka & Zakrzewska, sp. nov. (by present designation and monotypy).

Etymology. After Gujarat, the state in Western India, where the Cambay amber deposits are located.

Diagnosis. Eyes bare, reniform. Antenna with 13 flagellomeres. Tibiae of all legs similarly short, much shorter than their femora; tarsus of mid leg extraordinarily long, with basitarsus much longer than tibia. Fore leg tibia with pair of stout apical bristles; mid and hind leg tibia with strongly elongated apical lobe, evenly tapering to bristle-like distal part, with apex bent, filiform. Gonostylus longer than gonocoxite; digitus absent; stem of median volsella short, apically branched into several lamellae.

Gujaratomyia miripes Giłka & Zakrzewska, sp. nov.

Holotype. Adult male (tarsi of left mid and both fore and hind legs missing) preserved in $10 \times 6 \times 2.5$ mm piece of amber (early Eocene, 54 Ma, Tadkeshwar mine, Gujarat State, India; BSIP Tad-607 a; Fig. 1A).

Paratype. Adult male, incomplete specimen (only distal part of abdomen, including hypopygium, preserved) as syninclusion

Figure 2 *Gujaratomyia miripes* gen. *et* sp. nov., adult male, holotype, BSIP Tad-607 a, early Eocene, 54 Ma, Tadkeshwar mine, Gujarat, India: (A) mid and hind leg (fe = femur; ti = tibia; ta$_{1-5}$ = tarsomeres 1–5 of mid leg; arrows indicate borders between leg segments); (B–E) tibiae and tibial armature of fore (B) and hind leg (C–E).

with the holotype (BSIP Tad-607 b). Other syninclusion: Chironominae, one female (BSIP Tad-607 c).

Etymology. The specific epithet is referred to the unusual leg structure described below.

Diagnosis. As for the genus.

Description. Adult male. Total length $c.1.5$ mm; wing length $c.820$ μm.

Head (Fig. 1B, C). Eyes bare, reniform, without dorsomedian extensions. Frontal tubercles conical, $c.20$ μm long. Antenna with 13 well discernible flagellomeres, AR 0.77, plume fully developed (Fig. 1C). Length of palpomeres 2–5: $c.30$ μm, 103 μm, 117 μm, 117 μm (ultimate palpomere slightly deformed). At least 16 clypeals.

Thorax chaetotaxy. Ac at least 16, Dc at least 12, Pa at least 3, Scts at least 8.

Wing (Fig. 1D). Slender, broadest at two-thirds of length, width: 220 μm, length/width ratio 3.73. Sc and R$_{2+3}$ not observed. RM as parallel continuation of R$_{4+5}$, slightly oblique relative to M. An long, ending well distally of cubital fork. FCu placed distinctly distally of RM, VR$_{Cu}$ $c.1.65$. Veins ending as follows (in order from base to tip): An, Cu$_1$, R$_1$, M$_{3+4}$ and R$_{4+5}$, M$_{1+2}$. Anal lobe weak. Squama bare. Wing, including membrane covered with macrotrichia in distal half at least.

Legs (Figs 1B, 2A–E). Coxae of mid and hind legs bearing several strong bristles (Fig. 1B). Tibiae of all legs similarly short, much shorter than their femora; tarsus of mid leg (the only preserved in the specimen examined) extraordinarily long, with basitarsus much longer than tibia (Fig. 2A); for length of leg segments and leg ratios see Table 1. Fore leg tibia armed with pair of stout apical bristles $c.140–180$ μm long

Table 1 Leg segment lengths (μm) and leg ratios of male *Gujaratomyia miripes* gen. *et* sp. nov. Abbreviations: p_1–p_3 = legs of pair 1–3; fe = femur; ti = tibia; ta_1–ta_5 = tarsomeres 1–5; LR = leg ratio.

	fe	ti	ta$_1$	ta$_2$	ta$_3$	ta$_4$	ta$_5$	LR
p$_1$	445	180	–	–	–	–	–	–
p$_2$	460	195	505	205	170	115	60	2.59
p$_3$	445	220	–	–	–	–	–	–

(Fig. 2B). Mid and hind leg tibia with strongly elongated apical lobe, evenly tapering to bristle-like distal part, apex bent, filiform; each lobe bearing pair of subapical setae; length of whole structure *c.*75 μm (Fig. 2C–E). Sensilla chaetica on ta_1 of p_2 not observed. Pulvilli absent.

Hypopygium (Fig. 3). Gonostylus 85 μm long, longer than gonocoxite, straight, with several long setae on apex. Anal tergite semicircular, with dense setae surrounding base of anal point. Anal point long, tapering to bevelled apex with small subapical pit (Fig. 3A, B), upturned in lateral view (Fig. 3C). Superior volsella stout, parallel-sided in proximal part, oblique relative to main body axis, with distal part slightly swollen and medially directed, bearing three long setae placed on distinct protuberances on median margin (Fig. 3A–E). Digitus absent. Stem of median volsella straight and short (*c.*12 μm), apically branched into one short and three longer lamellae (Fig. 3D, F, G). Inferior volsella arcuate, with enlarged apical part armed with dense setae.

3. Discussion

3.1. Systematic position of *Gujaratomyia*

Several unique characters of the legs and hypopygium have not been found in any extant/fossil chironomid and support our concept of erecting the new genus *Gujaratomyia* (see diagnosis). The slender wing with the reduced anal lobe, the RM vein placed as a parallel continuation of R_{4+5}, the bare squama and the membrane covered with macrotrichia (Fig. 1D) form a set of characters typical of the Tanytarsini and testify to the position of *Gujaratomyia* within this tribe (*cf.* Giłka *et al.* 2016). Although the subtribal placement of the new genus remains open, a combination of characters (the reniform eyes without dorsomedian extensions; the antenna with 13 flagellomeres (Fig. 1C); and, above all, the stem of the hypopygial median volsella branched apically into lamellae (Fig. 3F, G)) suggests that *Gujaratomyia* and *Cladotanytarsus* Kieffer, 1921a may be members of a common group within the subtribe Tanytarsina. Apart from the characters listed in the diagnosis and defined as apomorphies for *Gujaratomyia* (see also below), these two genera differ from each other in the absence/ presence of the hypopygial digitus and in the gonocoxite– gonostylus length proportions.

3.2. Legs in the adult male of *Gujaratomyia*

3.2.1. Length proportions.
In adult males of the Chironomidae, the fore legs are the longest and the mid legs the shortest, since the five-segmented tarsus of the fore leg is elongated the farthest, whereas the tarsomeres of the mid leg are the shortest. The rule of mid leg tarsomeres being strongly shortened applies, in particular, to species that are flightless or have only limited flying ability (Sæther 1971; Giłka 2011b, c) (see below). In the Tanytarsini, the leg ratios $LR_{1–3}$, calculated as the ratio of the length of the basitarsus to that of the tibia of the same leg, are as follows: $LR_1 > 1$, $LR_2 < 1$, $LR_3 < 1$. In all the Tanytarsini, as in many chironomids, the fore leg femur is much longer than the tibia ($fe_1 \gg ti_1$), whereas the femora and tibiae of the mid and hind legs are approximately of the same length ($fe_2 \approx ti_2$, $fe_3 \approx ti_3$). The male of *Gujaratomyia* examined here diverges distinctly from these rules: the tarsomeres of the mid leg (especially the basitarsus) are strongly elongated and LR_2 is more than 2.5. Interestingly, the femora of the mid and hind legs are more than twice the length of the tibiae ($fe_2 \gg ti_2$, $fe_3 \gg ti_3$), the proportions being much the same as those of the fore leg (Figs 1B, 2A; Table 1). The total length of the mid legs in male *Gujaratomyia* (unfortunately, the only one preserved intact in the specimens examined) is also relatively high, when compared with that in males of Eocene species of a similar body and wing lengths (Table 2; *cf.* Zakrzewska & Giłka 2015a, b).

The strong elongation of the legs may be an expression of adaptations to non-typical mode of life and/or habitat, known in, for example, the related subfamily Orthocladiinae. The brachypterous *Bryophaenocladius chrissichuckorum* Epler, 2012, known from its ground mating behaviour, has long but stocky legs (Epler 2012). The fully-winged *Troglocladius hajdi* Andersen, Baranov & Hagenlund, 2016 (*in* Anderson *et al.* 2016), found in Croatian caves, features exceptionally long legs, the proportions of which (including the LR ratios), however, being within the range diagnostic for the subfamily; such legs, called "feelers", are considered to be a part of a well-developed sensory system and an adaptation to live in caves (Andersen *et al.* 2016). The leg and/or wing structure observed in the Orthocladiinae is not, however, fully comparable with those observed in *Gujaratomyia*, and cannot underpin a hypothesis of adaptations to a similar mode of life and/or habitat (see below).

In contrast to the long-legged chironomids, strongly shortened mid legs are observed in some of the Tanytarsini, for example *Corynocera* Zetterstedt, 1838, *Thienemanniola* Kieffer, 1921b and *Tanytarsus tika* (Tourenq, 1975), in whose legs all the segments of the mid leg, and the tarsus in particular, are strongly shortened; nevertheless, the $LR_2 < 1$, typical of the tribe, has been retained (Lehmann 1973; Cranston 1980). The first two genera include brachypterous species, lacking the ability to fly; on the other hand, the non-typical leg length proportions in the winged male of *T. tika* are most likely an adaptation to being able to additionally inhabit the surface of the water or the ground. A parallel adaptation in the Tanytarsini mentioned above is the naked wing membrane, devoid of macrotrichia (*cf.* Cranston 1980). It is worth reiterating, however, that neither the rule of strong mid leg shortening, nor that of a reduced naked-wing membrane, applies to the male *Gujaratomyia miripes*.

3.2.2. Tibial armature.
The tibiae of Tanytarsini imagines are armed with spurs and combs, the structure of which is a key generic character (*i.a.* Giłka 2011b). The tibia of the fore leg usually has a single spur but no combs. The anomaly of a double spur or comb occurring on the fore leg is known from both extant and fossil Tanytarsini (*cf.* Giłka & Paasivirta 2008; Giłka *et al.* 2013; Zakrzewska & Giłka 2015a), whereas the presence of one or more stout bristles in place of the fore leg tibial spur is a diagnostic character recorded above all in fossil species of the genera *Archistempellina* Giłka & Zakrzewska, 2013, *Corneliola* Giłka & Zakrzewska, 2013 and *Tanytarsus* van der Wulp, 1874 (*cf.* Giłka 2010; Giłka *et al.* 2013; Zakrzewska *et al.* 2016). This character appears also in *Gujaratomyia* (Fig. 2B).

The tibiae of the mid and hind legs of Tanytarsini are usually armed with two combs, consisting of teeth arranged in the shape of a fan. The combs may be separate or may form a uniform crown; only rarely they are absent (Giłka 2011b). There are usually two spurs on the mid and hind tibiae – one on each
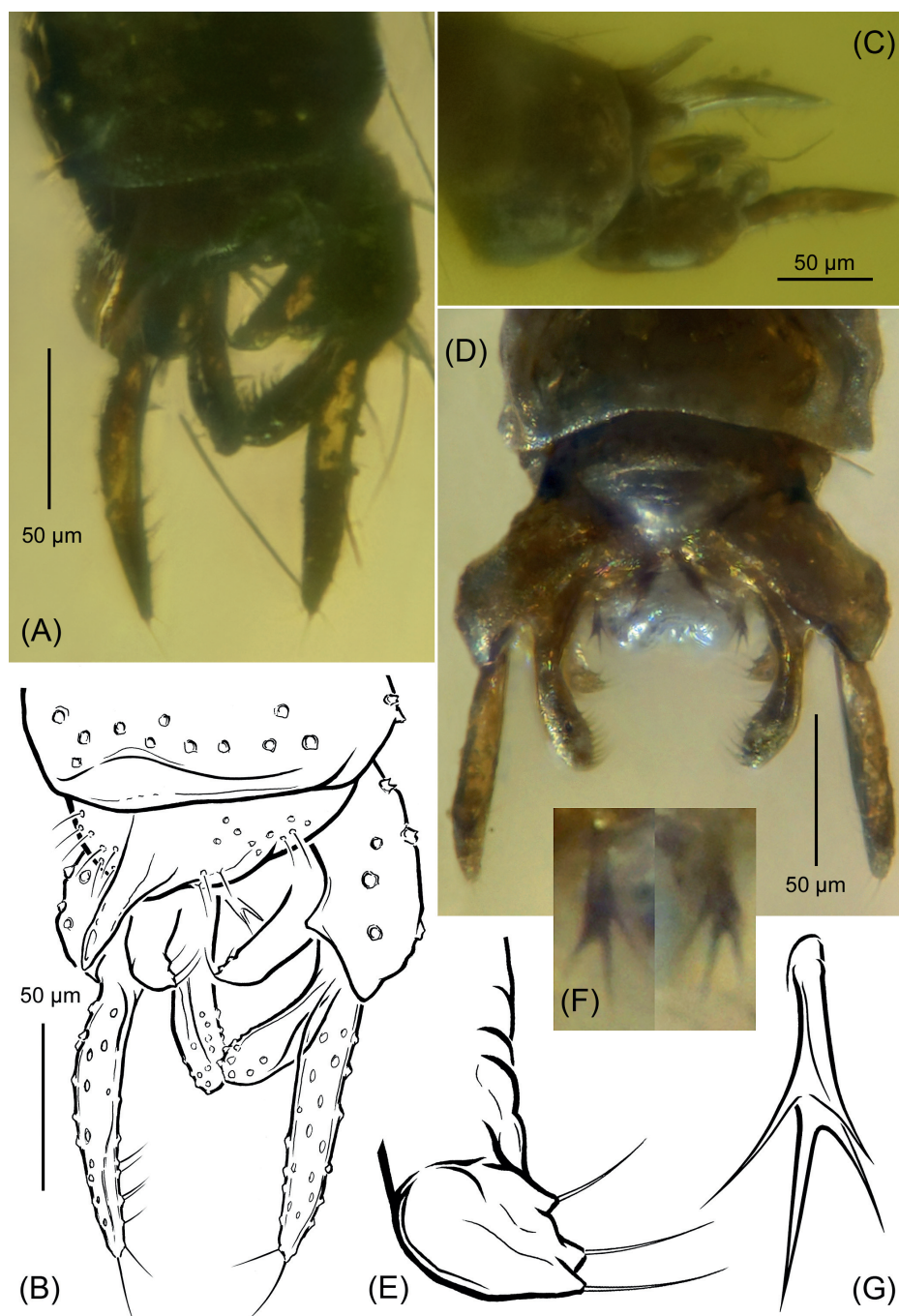
Figure 3 *Gujaratomyia miripes* gen. *et* sp. nov., adult male, early Eocene, 54 Ma, Tadkeshwar mine, Gujarat, India: (A–C) paratype, BSIP Tad-607 b, hypopygium and its structures in dorsal (A–B) and lateral (C) aspects. (D–G) holotype, BSIP Tad-607 a, hypopygium and its structures in ventral aspect: (E) superior volsella, magnified *ca.* 6 times relative to (D); (F) median volsella, magnified *ca.* 3 times relative to (D); (G) median volsella, magnified *ca.* 6 times relative to (D).

comb. They can be completely absent, or be present only on one of the two combs; sometimes they have a unique structure (Giłka 2011b, c). In contrast to most Tanytarsini, combs and spurs do not occur in *Gujaratomyia*. In the male of this genus, the tibiae bear strongly elongated apical lobes tapering to a bristle-like distal part with a filiform apex (Fig. 2C–E). Somewhat similar structures, but never as these observed in *Gujaratomyia*, occur in some Tanytarsini lacking the (or with a limited) ability to fly, or showing a ground/water mating behaviour. Relatively small tibial lobes or pads can be observed in *Cladotanytarsus* in the subgenus *Lenziella* Kieffer, 1922. However, the mid and hind legs in *Lenziella* are stocky, and the apical lobes of the tibiae are armed with dense setae, exceptionally with a single stout apical bristle (Giłka 2011c, fig. 8C).

Nevertheless, all these are typical setae/bristles arising from tubercles, and are apparently not homologous with the bristle-like structures found in *Gujaratomyia*. *Tanytarsus tika* shows setose pads (Cranston 1980), similar to those found in *Lenziella*. The monotypic *Thienemanniola* also bears extensions on its mid and hind tibiae, along with a brush composed of the long setae, but their spurs are short, stout and strongly bent apically – similar to those known from *Corynocera* (Lehmann 1973). However, the structures mentioned above, observed in the extant Tanytarsini, differ distinctly from those found in *Gujaratomyia*, the oldest extinct genus of this tribe.

3.2.3. Function. Despite the distinct leg structure suggestive of non-typical mode of life in the adult male of *Gujaratomyia miripes*, we see no reason to contend that the species' imago

Table 2 Lengths of mid leg (µm), body (mm) and wing (µm) of male *Gujaratomyia miripes* gen. *et* sp. nov. and several comparable Eocene species of the tribe Tanytarsini.

Species	body (mm)	wing (µm)	mid leg (µm)	LR$_2$
Gujaratomyia miripes sp. nov.	**1.5**	**820**	**1710**	**2.59**
Eonandeva latistyla Giłka & Zakrzewska, 2015[b]	1.7	810	1515	0.66
Stempellinella electra Giłka & Zakrzewska, 2015[a]	1.5	890	1400	0.66
Tanytarsus glaesarius Giłka & Zakrzewska, 2015[a]	1.2	820	1235	0.72

[a]*in* Zakrzewska & Giłka 2015a; [b]*in* Zakrzewska & Giłka 2015b

was limited in its flying ability, or occurred in a habitat not typical of the Chironomidae. Our opinion is based on the observation that: (1) the wing of *Gujaratomyia* is fully developed, and its membrane is covered by macrotrichia, a character typical of the flying Chironomidae; (2) the long and slender legs featured by *Gujaratomyia* are characteristic of flying species, as opposed to shortened and/or stout legs (and also palps and antennae) shown by brachypterous species; (3) *Gujaratomyia* lacks other characters typical of the chironomids with non-typical behaviour/habitat (e.g., caves) – *Gujaratomyia* has well-developed eyes, palps and antennae bearing fully plumose flagellum. We interpret the elongated legs in *Gujaratomyia* as a gliding-enhancement adaptation; enhancement of in-flight stimulus reception cannot be ruled out, either (*cf.* Andersen *et al.* 2016). The non-typical tibial structures of *Gujaratomyia* most likely reflect adaptations somewhat similar to those found in the non-flying Tanytarsini, and may adapt the bearers to short-term presence on the water surface. However, it seems hardly plausible that they would function similarly on the ground surface.

In conclusion, we interpret the leg ratios and the tibial structures found in *Gujaratomyia miripes* as unique characters (these can be perceived as autapomorphies until the genus remains monotypic), which – in combination with the reniform broadly separated eyes, fully plumose 13-segmented antennal flagellum and several diagnostic hypopygial features – form a set not known from any other non-biting midge, and justify erection of the new genus.

3.3. Biogeography

Today, India harbours many endemic taxa, especially in the Western Ghats area (Myers *et al.* 2000). In this context, Indian amber inclusions have proven to provide an important contribution to the discussion about India's complex geological history and the processes that shaped India's modern flora and fauna (summarised in Rust *et al.* 2010). It has been shown that Indian amber inclusions show worldwide connections, whereas only minimal evidence for faunal isolation has been reported so far (Engel *et al.* 2011, 2013; Grimaldi & Singh 2012; Grimaldi *et al.* 2013a, b; Rust *et al.* 2010). Various biogeographic patterns of the Indian amber inclusions have been observed within the order Diptera (Rust *et al.* 2010; Stebner *et al.* 2017a, c). At this stage of research, taxa that are endemic to the Indian subcontinent appear to be rather rare, and have been reported so far only from the families Keroplatidae (*Vastaplatyura electrica* Solórzano, Kraemer & Evenhuis, 2008) and Psychodidae (*Phlebotoiella eoindianensis* Solórzano, Kraemer & Wagner, 2009). *Gujaratomyia* gen. nov. now adds further evidence for the presence of endemic elements in Eocene India. The genus seems to be restricted to the Indian subcontinent, since neither fossil nor recent relatives are known from elsewhere. It must be considered, however, that the Tanytarsini are probably a rather young group, with the oldest members known from the early Eocene's Fushun amber (Giłka *et al.* 2016) and, as reported herein, from early Eocene Indian amber; a fact which doubtless has substantial implications for biogeographic patterns. In conclusion, many more studies on the Indian amber inclu-

sions and their distributional patterns are needed to get a more complete picture of the origins and ranges of fossil as well as modern Indian insect faunas.

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