1 Introduction

Nowadays, the family Tipulidae are represented by over 4000 fossil and extant species that are generally classified in three subfamilies: Ctenophorinae Kertész, 1902, Dolichopezinae Kertész, 1902 and Tipulinae Latreille, 1802. The majority of representatives of the family belong to the genus *Tipula* Linnaeus, 1758, in which 40 subgenera are distinguished, including a total of ca. 2450 extant species (Oosterbroek, 2019). Hitherto, 18 species from Baltic amber belonging to the Tipulinae were described (Loew, 1850; Meunier, 1899, 1906, 1917; Alexander, 1931; see Table 1). They were classified in two genera: a single species in *Maekistocera* Wiedemann, 1821b and 17 species in *Tipula*, of which 16 were not referred to any subgenus (Table 1).

From the Late Jurassic of Germany, Krzemiński and Ansorge (1995) described the genus *Tipunia*, which was recognized as the oldest genus belonging to the Tipulidae (De Jong, 2014; Lukashevich and Ribeiro (2018). Two more species of *Tipunia* known from the Mongolian Jurassic (Lukashevich, 2009) and one from the Early Cretaceous (Jarzembowski, 1991) were later described. The oldest representatives of the genus *Tipula* are known from the Paleocene, only from the Für Formation of Denmark (Freiwald, 1990; Krzemiński, 2001). From younger geological periods the species of *Tipula* were described by Presl (1822), Unger (1841), Heer (1849, 1861), Novák (1877), Omboni (1886), Scudder (1890, 1894), Meunier (1899, 1906, 1915, 1917), Cockerell (1909, 1910, 1915, 1917, 1921), Handlirsch (1910), Cockerell and Haines (1921), Handlirsch (1910), Cockerell and Haines (1921), Henriksen (1922), Alexander (1931, 1938), Piton (1934), Statz (1934, 1944), Théobald (1937), Zeuner (1938), Melander (1949), Lewis (1969, 1973), Wighton (1980), Brown (1985), Zhang (1989), Zhang et al. (1994), Krzemiński (2000), Byers (2011), Engel and Gross (2012), Kania and Nel (2013), and Kania et al. (2018). The majority of these species were described from two-dimensional compressions that do not offer any possibility of three-dimensional examination of the material and show much less structural detail than the inclusions in fossil resins.

In this paper, we aim to clarify the taxonomy of the Tipulidae and describe two new subgenera and new species of the genus *Tipula* from Eocene Baltic amber.

2 Geological Setting

The age of the Baltic amber is estimated as Eocene, Lutetian–Priabonian, as suggested by Grimaldi and Ross (2017).

3 Material and Methods

The study is based on material (two inclusions) in Baltic amber from the collections of G.C. Berendt, Natural History Museum Humboldt University, Berlin (NHMB) and the collection of Christel and Hans Werner Hoffeins. The holotype of the new species described herein was donated by Christel and Hans Werner Hoffeins to the
Table 1 Species list of the family Tipulidae from Baltic amber (after Evenhuis, 1996)

<table>
<thead>
<tr>
<th>Genus</th>
<th>Subgenus</th>
<th>Species</th>
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<tbody>
<tr>
<td>Maekistocera</td>
<td>Electrotipula Alexander, 1931</td>
<td>pinetorum Alexander, 1931</td>
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<tr>
<td>Tipula</td>
<td>Unplaced to subgenus</td>
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<td>Tipula</td>
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Carl Berendt, the original owner of the collection of Baltic amber from which the holotype originates.

Material examined: Holotype No. MB.J. 259 (♂), Coll. Berendt, Natural History Museum Humboldt University, Berlin (NHMB). Eocene.

Description: Body (Fig. 2a) 7.10 mm long; brown with dark brown hypopygium and head; head and thorax combined 2.74 mm long.

Head (Figs. 2a–b): 1.21 mm wide, 0.75 mm high; antenna (Figs. 1a, 2a–b, 3b–c) 13-segmented, about 4.83 mm long, scape cylindrical and elongate, with short but comparatively numerous setae, pedicel short and wide, wider than long; first flagellomere elongated, cylindrical, a fraction longer than the next one, not extended basally, and without ring of verticils at base; flagellomeres 2–10 dilated in basal part, base with five very long (0.28–0.40 mm) verticils arranged in a ring, sometimes longer than segments bearing them, last flagellomere very short and tiny, much shorter than penultimate one (flagellomeres length in mm: 1.059, 2: 0.40, 3: 0.42, 4: 0.39, 5: 0.44, 6: 0.42, 7: 0.41, 8: 0.36, 9: 0.39, 10: 0.35, 11: 0.30, 12: 0.26, 13: 0.10). Maxillary palp (Figs. 1b, 3a) five segmented, three basal segments almost equal in length (third palpomere 0.25 mm; fourth palpomere 0.28 mm), last palpomere very elongated, longer than all other palpomeres together (1.03 mm long).

Thorax (Fig. 2a): wing (Figs. 1c, 2a, 4a–c) 7.86 mm long, 2.13 mm wide; pterostigma present, ovale, pale brown; Sc relatively short, ends well before fork of Rs; R_{1} ends just before fork of R_{2+3+4}; R_{3} equal to R_{2+3+4}; R_{4} is about 1.3 × as long as R_{2+3+4}; R_{5} slightly sinuate, more than 3 × as long as R_{3}, almost 2 × as long as R_{5} and R_{3} × as long as R_{2+3+4}; cross-vein r+r (R_{5}) connecting R_{1} and R_{3}; cross-vein m-cu connected with M_{3+4} before its fork; d-cell small, 1/3 longer than petiole of cell m_{1}; twice longer than wide; M_{1} twice as long as petiole of cell m_{1}; M_{3} strongly waved, twice as long as d-cell; cross-vein m-cu long, equal in length to Rs, touches M_{3+4} before its fork; cell m_{4} markedly narrowed at 2/3 of its length, its posterior margin about 1/2 narrower than posterior margin of cell m_{3}; A_{1} and A_{2} almost straight, A_{3} rather short.

Legs (Figs. 4d–g) with massive and elongated tibial spurs, tibial spurs formula: 1: 2: 2; last tarsomere with a

4 Systematic Paleontology

Order Diptera Linnaeus, 1758
Infraorder Tipulomorpha Rohdendorf, 1961
Family Tipulidae Latreille, 1802
Subfamily Tipulinae Latreille, 1802
Genus Tipula Linnaeus, 1758

Subgenus: Succinica subgen. n.
LSID: urn:lsid:zoobank.org:act:BCB6B6E5-2779-4678-BC00-6F8A498D4898

Etyymology: The species name is derived from Latin "succinum"—amber. Gender: feminine.

Diagnosis: Sc ends opposite basal 1/3 of Rs; Rs about as long as m-cu; m-cu located clearly before fork of vein M_{3+4}; d-cell long and narrow; gonocoxite almost 1/4 longer than its largest width in lateral view; sternite IX longer than its largest width in lateral view; outer gonostylus wide at it base, narrowing in 2/3 of its length, resembling a distorted triangle; inner gonostylus only partly visible.

Diagnosis: As for the subgenus.

Etyymology: The specific name is given to honor Georg Carl Berendt, the original owner of the collection of Baltic amber from which the holotype originates.

Material examined: Holotype No. MB.J. 259 (♂), Coll. Berendt, Natural History Museum Humboldt University, Berlin (NHMB). Eocene.

Description: Body (Fig. 2a) 7.10 mm long; brown with dark brown hypopygium and head; head and thorax combined 2.74 mm long.

Head (Figs. 2a–b): 1.21 mm wide, 0.75 mm high; antenna (Figs. 1a, 2a–b, 3b–c) 13-segmented, about 4.83 mm long, scape cylindrical and elongate, with short but comparatively numerous setae, pedicel short and wide, wider than long; first flagellomere elongated, cylindrical, a fraction longer than the next one, not extended basally, and without ring of verticils at base; flagellomeres 2–10 dilated in basal part, base with five very long (0.28–0.40 mm) verticils arranged in a ring, sometimes longer than segments bearing them, last flagellomere very short and tiny, much shorter than penultimate one (flagellomeres length in mm: 1.059, 2: 0.40, 3: 0.42, 4: 0.39, 5: 0.44, 6: 0.42, 7: 0.41, 8: 0.36, 9: 0.39, 10: 0.35, 11: 0.30, 12: 0.26, 13: 0.10). Maxillary palp (Figs. 1b, 3a) five segmented, three basal segments almost equal in length (third palpomere 0.25 mm; fourth palpomere 0.28 mm), last palpomere very elongated, longer than all other palpomeres together (1.03 mm long).

Thorax (Fig. 2a): wing (Figs. 1c, 2a, 4a–c) 7.86 mm long, 2.13 mm wide; pterostigma present, ovale, pale brown; Sc relatively short, ends well before fork of Rs; R_{1} ends just before fork of R_{2+3+4}; R_{3} equal to R_{2+3+4}; R_{4} is about 1.3 × as long as R_{2+3+4}; R_{5} slightly sinuate, more than 3 × as long as R_{3}, almost 2 × as long as R_{5} and R_{3} × as long as R_{2+3+4}; cross-vein r+r (R_{5}) connecting R_{1} and R_{3}; cross-vein m-cu connected with M_{3+4} before its fork; d-cell small, 1/3 longer than petiole of cell m_{1}; twice longer than wide; M_{1} twice as long as petiole of cell m_{1}; M_{3} strongly waved, twice as long as d-cell; cross-vein m-cu long, equal in length to Rs, touches M_{3+4} before its fork; cell m_{4} markedly narrowed at 2/3 of its length, its posterior margin about 1/2 narrower than posterior margin of cell m_{3}; A_{1} and A_{2} almost straight, A_{3} rather short.

Legs (Figs. 4d–g) with massive and elongated tibial spurs, tibial spurs formula: 1: 2: 2; last tarsomere with a
pair of large, single-toothed claws (Figs. 4e–g).

Abdomen: hypopygium (Figs. 1d, 2a, 4h): 0.51 mm long (the distance between posterior margin of tergite VIII and tip of ventral extension of gonocoxite), short and stocky; tergite VIII narrow, appearing narrowed in the dorsal part; tergite IX wide, clearly indented on the dorsal part, posterior extension of tergite IX single, wide and triangular in lateral view (Figs. 1d, e); sternite VIII wide, clearly visible; sternite IX with a bunch of strong and long bristles; gonocoxite wide, almost rectangular, in lateral view 1.25 × longer than its largest width, on the ventral side with a brush of strong bristles; outer gonostylus wide, almost rectangular, in lateral view 1.25 × longer than its largest width, on the ventral side with a brush of strong bristles; inner gonostylus only partly visible.

Comparison: The structures of the male terminalia of the new species to some extent resemble those of *Tipula major* Meunier, 1906 and *Tipula media* Meunier, 1906, also from Baltic amber. Tergite IX in these three species carries a single medial extension. It is slightly upcurved in *major*, straight in *media* and *berendti* sp. n. Sternite IX carries a bunch of long and strong setae in *major* and *berendti* sp. n., but only a single slender spine in *media*. The gonocoxite is posteroventrally provided with densely set short setae in *major* and *berendti* sp. n., whereas there are hardly any setae in this area in *media*. The outer
Fig. 4. *Tipula (Succinica) berendti* sp. n., No. MB.J. 259, coll. Berendt (NHMB); holotype (♂).
(a) wing; (b) enlarged view of distal half of wing; (c) termination of vein Sc; (d) tibial spurs; (e–g) last tarsomere; (e) latero-dorsal view; (f) ventral view; (g) dorsal view; (h) male terminalia, lateral view. Abbreviations: TS—tibial spurs.
 gonostylus is large in \textit{major} and \textit{berendti} sp. n.; it is smaller and dorsally produced into a spine in \textit{media}.

The three species share a relatively short Sc that ends well before the fork of Rs. The d-cell is rather small and narrow. Medial veins are rather long, and M\textsubscript{3} is slightly sinusous in \textit{major} and \textit{berendti}, whereas it is relatively straight in \textit{media}. The crossvein m-cu touches the fork of M\textsubscript{3+4} in \textit{major}, and reaches M\textsubscript{3+4} before its fork in \textit{berendti} sp. n. and \textit{media}.

\textbf{Subgenus: Gedanica subgen. n.}


\textbf{Diagnosis:} Sc ends before half length of Rs; Rs almost \textit{1.3 ×} as long as m-cu; m-cu situated in the fork of M\textsubscript{3+4}; d-cell short and pentagonal; length of gonocoxite equal to its width in lateral view, posterovertrally with large, expanded lobe; no bristles on sternite IX; outer gonostylus wide and short, on the edges reinforced with two lobes and an acute process in the lower posterior part; inner gonostylus elongate club-shaped, with long extension near its posterior base.

Type species: \textit{Tipula (Gedanica) adamowiczi} sp. n., Baltic amber.

\textbf{Tipula (Gedanica) adamowiczi} sp. n.

\textbf{Diagnosis:} As for the subgenus.

\textbf{Material examined:} Holotype No. MAIG 5945 (♂), Coll. Museum of Amber Inclusions, University of Gdańsk (MAIG), donated by Christel and Hans Werner Hoffeins (Hamburg). Eocene.

\textbf{Description:} Body (Fig. 7a) 11.44 mm long; pale brown.

\textbf{Head} (Figs. 7a, d): 1.44 mm wide; antenna (Figs. 5a, 7c–e) 13-segmented, about 5.08 mm long, scape cylindrical and elongated; pedicel short and wide, wider than long, pot-shaped; flagellomeres elongated cylindrical, becoming more slender to the apex of antenna, not extended in basal part; first flagellomeres elongated and cylindrical, slightly longer than the next one, first and second flagellomeres with robust verticils but not longer than segment bearing them, on the others flagellomeres verticils longer; last flagellomere very short and tiny, about 0.7 as long as the penultimate one (length of flagellomeres in mm: 1: 0.58, 2: 0.50, 3: 0.46, 4: 0.38, 5: 0.44, 6: 0.38, 7: 0.36, 8: 0.41, 9: 0.34, 10: 0.35, 11: 0.48, 12: 0.27, 13: 0.13). Maxillary palp elongated (Fig. 5b), length of third palpomere 0.35 mm, fourth palpomere 0.34 mm, last palpomere 0.99 mm, approximately as long as 0.3 palpomeres combined, with few not very long setae at apex.

\textbf{Thorax} (Fig. 7a): wing (Figs. 5c, 7a, 8a–b) 11.61 mm long, 3.30 mm wide; pterostigma present, oval, pale-brown; Sc ends into R\textsubscript{i} before half the length of Rs; R\textsubscript{i} ends beyond fork of R\textsubscript{2+3+4}; R\textsubscript{3} almost \textit{2 ×} as long as R\textsubscript{2+3+4}; Rs is about \textit{2.5 ×} as long as R\textsubscript{2+3+4}, R\textsubscript{4} almost straight and twice as long as R\textsubscript{i}, slightly longer than Rs and almost \textit{3 ×} as long as R\textsubscript{2+3+4}; cross-vein r-r (R\textsubscript{2})
connecting R₁ and R₃; d-cell small, wide and 1.3 × its width; M₁ 1.5 × length of d-cell and more than twice longer than petiole of cell m₁; cross-vein m-cu long, 0.7 × of Rs, touching fork of M₃+₄; M₃ gently arched; cell m₁ wide at the base and evenly tapering to margin of wing; posterior margin of cell m₁ 1/3 wider than posterior margin of cell m₄; posterior margin of cell m₁ equal to posterior margin of cell m₂; A₁ and A₂ almost straight, slightly curved at tip.

Abdomen: hypopygium (Figs. 6a–e, 9): 1.59 mm long (the distance between posterior margin of tergite VIII and tip of ventral extension of gonocoxite), comparatively massive, tergite VII wide in the dorsal part; sternite VII very wide; tergite VIII rather short, sternite VIII ventrally much wider than in dorsal part; tergite IX transverse, medially provided with pair of short downcurved, acute extensions; sternite IX not visible; gonocoxite almost square in lateral view, robust, posteroventrally with large, oval and wide lobe; outer gonostylus wide and short, on the edges reinforced with two lobes and an acute process in the lower posterior part; inner gonostylus elongated, club-shaped, with a long extension near its posterior base.

Comparison: At first glance the new species superficially resembles *Tipula falco* (Alexander, 1931) from Baltic amber in some details of the male terminalia. Most remarkable in the new species is the huge median extension on the ventral side of the gonocoxites. In *falco* it is broad, flattened and tongue-like, whereas in *adamowiczi* sp. n. the sides of the extension are dorsally curved. The placement of the ventral extension differs in both species: it is located rather anteriorly in *falco*, and placed at the posteroventral margin of the gonocoxites in *adamowiczi*. Tergite IX has a single median extension, which appears as a downcurved, chitinized acute structure in *falco*...
(suggesting the species epithet), whereas tergite IX in *adamowiczi* carries a pair of slender and short median extensions. Tergite IX and sternite IX in *falco* are fused into a ring, whereas they are separated in *adamowiczi* sp. n. Also, the position of the inner and outer gonostyles differ in both species: they are placed rather low on the gonocoxite in *falco*, and high on the gonocoxite in *adamowiczi* sp. n. In addition, the wing venation shows differences in both species: Sc is rather short in *falco* in comparison with that of *adamowiczi* sp. n.; the d-cell is rather narrow in *falco*, whereas it is broadly pentagonal in *adamowiczi* sp. n.; and M₃ is sinuous in *falco* and more evenly curved in *adamowiczi*.

It thus seems that both species are not closely related, despite the shared presence of a remarkable median extension of the gonocoxites.

5 Discussion

The study of Baltic amber material of the genus *Tipula* poses special problems. Classification of extant Tipulidae relies heavily on morphological details of the male hypopygium, such as the shape of the posterior margin of

Fig. 8. *Tipula (Gedanica) adamowiczi* sp. n., No. MAIG 5945, holotype (♂).
(a) Wing; (b) enlarged view of distal half of wing.

Fig. 9. *Tipula (Gedanica) adamowiczi* sp. n., No. MAIG 5945, holotype (♂), hypopygium, lateral view.

Fig. 10. Map of the World with fossil localities of the genus *Tipula* marked.
tergite IX and the shape of the inner and outer gonostyles. Unfortunately, these structures and especially the important inner gonostyles are very rarely entirely visible and, as a result, proper classification of new material becomes difficult. Another drawback is the unsatisfactory subgeneric classification of the extant genus *Tipula*. Many of the current subgenera lack a robust foundation and thus the subgeneric classification is badly in need of revision. Consequently, fossil species are often hard to match with existing subgeneric taxa. Non-genitalic features like the build of the antennae, details of legs, and especially the wing venation might be helpful in suggesting affinities, but details of the male terminalia remain the single most informative set of characters to properly classify species. More recently, available techniques like micro-CT scans can be used profitably to investigate these structures in amber fossils in more detail.

6 Conclusion

Currently, the very numerous family Tipulidae (Diptera) has been known in fossil material since the Upper Jurassic (ca. 150 Ma). However, due to their large size, their representatives are rarely found in fossil resins. Therefore, each specimen found is extremely valuable for understanding the evolutionary past of this group of insects. Most of the knowledge on the evolution of this family is based on the analysis of specimens preserved in sedimentary rocks. Unfortunately, in this type of fossil material, the analysis of male copulatory apparatus, which is often the basis of species classification, is imprecise or even impossible due to the state of preservation. The two new species described herein are an excellent bridge between recent specimens and those preserved in sedimentary rocks, and thus complement the current knowledge on the evolution of the family.

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We would like to thank Christel and Hans Werner Hoffeins (Hamburg) for making their specimen available for our study. We would like to acknowledge the editors and two anonymous reviewers for valuable comments and corrections. This project was supported in part by an ISEA PAS grant (no. 6085/E-47/M/2017), supervised by Kornelia Skibińska. The authors declare no conflict of interest.

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