Biting midges (*Diptera*, *Ceratopogonidae*) from Miocene Saxonian amber

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Abstract. The biting midges found in Saxonian amber, collected from coals near Bitterfeld, Germany, are described, keyed and interpreted. This Miocene amber (dated at 22 million years), includes 37 species in 14 genera, with 22 of these are new: Culicoides subgedanensis, Brachypogon miocaenicus, Ceratopogon bitterfeldi, C. kotejai, C. miocaenicus, C. subeminens, C. succinicolus, Chimaerohelea miocaenica, Eohelea fossicola, E. miocaenea, Fossihelea miocaenica, Stilobezzia kutscheri, S. saxonica, S. succinea, Palpomyia erikae, Forcipomyia subgedanensis, F. unculiformis, F. miocaenica, F. tuberculosa, F. bifidicola, F. succinicola, and Dasyhelea miocaenica. The fossil genus Meunierohelea SZADZIEWSKI from Europe is recognized as a junior synonym of the recent genus Chimaerohelea DEBENHAM known only from Australia. A neotype is designated for Ceratopogon alpheus HEYDEN, and two new synonyms are proposed for fossil species. A numerical analysis comparing Saxonian amber with older Baltic amber indicates evolutionary stasis for almost 33% of the species in Saxonian amber over a minimum of 15 million years. Overall, the relative percentages of ceratopogonid genera that make up the fauna have not changed significantly during this period.

Key words: Diptera, Ceratopogonidae, fossils, Miocene, Saxonian amber.

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I. INTRODUCTION

Saxonian amber is found in Lower Miocene layers of coal in the Bitterfeld district near Halle (Saale), Germany. It is suggested that an extinct conifer *Cupressospermum saxonicum* MAI has contributed to the formation of this fossil resin. Its absolute age is about 22 million years (BARTHEL & HETZER 1982).

Amber of Bitterfeld contains many insect inclusions with *Diptera* making up 75% of the total fauna (SCHUMANN & WENDT 1989). The *Ceratopogonidae* are common in this amber as in other Tertiary fossil resins, and their state of preservation is very good. Despite this, only two species have been previously recorded, i.e. *Eohelea sinuosa* (SZADZIEWSKI 1988) and *Ceratopogon forcipiformis* (SCHUMANN & WENDT 1989) in Saxonian amber.

This paper is devoted mainly to the description of the biting midges fauna preserved in Saxonian amber and its relations to the older and well known Baltic amber fauna (SZADZIEWSKI 1988).

I am much indebted to Mr. Manfred KUTSCHER of Sassnitz (Germany) who sent me inclusions from his private collection and to Dr. Erika PIETRZENIUK of Museum für Naturkunde der Humboldt Universität, Berlin, who kindly arranged the loan of biting midges. I wish to express my deepest thanks to Professor William L. GROGAN, Jr., of Salisbury State University, Maryland, U.S.A., for reviewing the manuscript and help with English, as well as to Dr. Art BORKENT of Salmon Arm, British Columbia, Canada, for reviewing and commenting on the manuscript.

II. MATERIALS AND METHODS

This study is based on the examination of 218 biting midges in 191 amber pieces from the Museum für Naturkunde, Paläontologisches Museum, Invalidenstrasse 43, 1040 Berlin (abbreviated MBI) and 118 inclusions in 107 amber pieces from the private collection of Mr. Manfred KUTSCHER, Dorfstr. 10, 2355 Sassnitz, Germany (abbreviated K). The latter collection will be deposited in Museum für Naturkunde der Humboldt Universität at a future date.

The Bitterfeld amber, like Baltic amber, is a succinite and contains succinic acids which decompose insect pigments or "chemical colours" of wings and other parts of the body. Consequently, colour is not considered as a diagnostic character in this study.

Biting midges were prepared for entomological studies as previously described by SZADZIEWSKI (1988). Morphological terms, abbreviations for structures, keys, and diagnoses of subfamilies, tribes, genera, as well as a summary of our knowledge of fossils is also provided by SZADZIEWSKI (l.c.).

III. SYSTEMATICS

Arrangement of the genera and species

Subfamily Ceratopogoninae
Tribe Culicoidini
Culicoides LATREILLE

- 1. C. ceranowiczi SZADZIEWSKI
- 2. C. speciosus (MEUNIER)
- 3. C. subgedanensis sp. n.

Tribe Ceratopogonini

Brachypogon KIEFFER

Subgenus Brachypogon KIEFFER

4. B. miocaenicus sp. n.

Subgenus Isohelea KIEFFER

5. B. prominulus (MEUNIER)

Ceratopogon MEIGEN

- 6. C. bitterfeldi sp. n.
- 7. C. forcipiformis MEUNIER
- 8. C. hennigi SZADZIEWSKI
- 9. C. kotejai sp. n.
- 10. C. miocaenicus sp. n.
- 11. C. subeminens sp. n.
- 12. C. succinicolus sp. n.

Chimaerohelea DEBENHAM

- 13. Ch. miocaenica sp. n.
- 14. Ch. nielseni (SZADZIEWSKI)

Eohelea PETRUNKEVITCH

- 15. E. fossicola sp. n.
- 16. E. miocaenea sp. n.
- 17. E. sinuosa (MEUNIER)

Fossihelea SZADZIEWSKI

- 18. F. miocaenica sp. n.
- 19. F. sp. A

Mantohelea SZADZIEWSKI

20. M. gedanica SZADZIEWSKI

Monohelea KIEFFER

21. M. clunipes (LOEW)

Nannohelea GROGAN & WIRTH

22. N. sp. indet.

Serromyia MEIGEN

- 23. S. alphea (HEYDEN)
- 24. S. spinigera (LOEW)

Stilobezzia KIEFFER

- 25. S. falcata (MEUNIER)
- 26. S. kutscheri sp. n.
- 27. S. saxonica sp. n.
- 28. S. succinea sp. n.

Tribe Palpomyiini
Palpomyia MEIGEN

29. P. erikae sp. n.

Subfamily Forcipomyiinae Forcipomyia MEIGEN Subgenus Forcipomyia MEIGEN

- 30. F. gedanicola SZADZIEWSKI
- 31. F. subgedanicola sp. n.
- 32. F. unculiformis sp. n.

Subgenus Euprojoannisia BRÈTHES

- 33. F. miocaenica sp. n.
- 34. F. tuberculosa sp. n.

Subgenus Trichohelea GOETGHEBUER

- 35. F. bifidicola sp. n.
- 36. F. succinicola sp. n.

Subfamily Dasyheleinae Dasyhelea KIEFFER

37. D. miocaenica sp. n.

Subfamily Ceratopogoninae NEWMAN, 1834

Tribe Culicoidini Kieffer, 1911 Genus Culicoides Latreille, 1809

The *Culicoides* in Saxonian amber makes up 20.2% of the total fauna, as compared to 17.8% in Baltic amber. I was able to identify three well recognizable species, two of which are known from older Baltic amber, i. e. *C. ceranowiczi*, and *C. speciosus*. The key below does not include 12 species of the genus described by STATZ (1944) on the basis of compression fossils discovered in the brown coal of Rott (Germany). The age of these fossils is the same as those in Saxonian amber and may therefore include the same species. Unfortunately it is impossible to adequately compare such compression fossils, generally devoid of diagnostic characters, with either well preserved specimens in ambers or with extant material.

Culicoides indetermined 36 (20 of, 16 ∞).

MBI-7-2, 1 \circ ; 8-35, 1 \circ ; 8-38, 1 \circ ; 8-39, 1 \circ ; 8-43, 1 \circ ; 8-54, 1 \circ (+*Dolichopodidae* 1); 8-55, 1 \circ ; 8-64, 1 \circ ; 8-69, 1 \circ 1 \circ (+*Chironomidae* 3 \circ); 8-95, 1 \circ ; 8-99, 1 \circ ; 8-110, 1 \circ ; 8-112, 1 \circ ; 8-114, 1 \circ ; 8-118, 1 \circ ; 8-121, 1 \circ (+ *Sciaridae* 1 \circ); 8-124, 1 \circ ; 8-131, 1 \circ ; 8-137, 1 \circ ; 8-138, 1 \circ ; 8-142, 1 \circ ; 8-159, 1 \circ ; 8-160, 1 \circ ; 10-2, 1 \circ ; 11-4, 1 \circ 1 \circ ; 11-6, 1 \circ (+ *Chironomidae* 1 \circ 1 \circ).

K-5, 1 σ ; K-11, 1 σ ; K-24, 1 σ 1 \circ (+ Chironomidae 8 σ 1 \circ); K-53, 1 σ ; K-56.b, 1 σ (at 56.a Ceratopogon forcipiformis 1 σ); K-93, 1 σ (+ Ceratopogon indet. 1 \circ); K-107, 1 \circ .

Key to named Culicoides from Baltic and Saxonian amber

Males

1 Addangus more or less V shared condemnation assistant sized
1. Aedeagus more or less Y-shaped, caudomedian projection single
- Aedeagus with 2 or 3 distinct apical projections
2. Gonostylus sinuous, somewhat S-shaped
Gonostylus not sinuous, C-shaped
3. Basal arch of aedeagus low. Apicolateral process of tergite IX slender, cylindrical
Basal arch of aedeagus high. Apicolateral process of tergite IX broad, triangular
C. subgedanensis sp. n.
4. Apicolateral process of tergite IX blunt. Tip of paramere with fringe of spicules
- Apicolateral process of tergite IX pointed. Tip of paramere simple
5. Apicolateral process of tergite IX very short. Basal radial cell without macrotrichia
- Apicolateral process of tergite IX long. Basal radial cell with macrotrichia
6. Apicolateral process of tergite IX broad C. dasyheleiformis SZADZIEWSKI (Baltic amber)
- Apicolateral process of tergite IX slender
C. speciosus (MEUNIER) (Baltic and Saxonian amber)
7. Paramere short. Caudomedian margin of tergite IX extending beyond tip of apicolateral
process
Paramere long. Caudomedian margin of tergite IX not extending beyond tip of apicolateral
process8
8. Aedeagus with 3 long apical projections C. eoselficus SZADZIEWSKI (Baltic amber)
Aedeagus with 2 long apical projections
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(Danie and Bakenan amoor)

1. Culicoides ceranowiczi SZADZIEWSKI, 1988

Fig. 1

C. ceranowiczi SZADZIEWSKI, 1988: 45 (Baltic amber).

Material examined. MBI 8-165, 1 c.

N~o~t~e . The specimen is somewhat larger than those from Baltic amber. Wing length 1.06~ mm. Flagellum length $690~\mu m,~AR~0.92.$ Other features including the highly characteristic male genitalia (Fig. 1) as in specimens from Baltic amber.

2. Culicoides speciosus (MEUNIER, 1904)

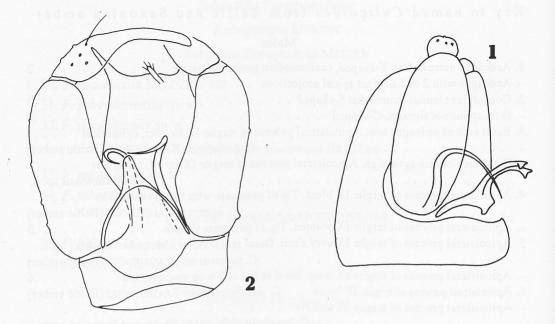
Fig. 2

Ceratopogon speciosus MEUNIER, 1904: 229 (Baltic amber).

Culicoides speciosus: SZADZIEWSKI 1988: 33 (Baltic amber).

Material examined: 30 (28 σ, 2 φ). MBI 8-75, 4 σ; 8-79, 7 σ (+ Chironomidae 1 φ); 8-100, 1 σ;8-107, 1 σ; 8-111, 3 σ; 8-115, 1 σ; 8-122, 1 σ; 8-136, 1 σ; 8-139, 2 σ; 8-158, 1 σ; 8-167, 1 σ; 10-11, 1 σ; 11-2, 1 φ. K-12, 1 σ; K-25, 1 σ; K-29, 2 σ; K-39, 1 φ.

Note. The name Culicoides speciosus likely represents a species complex. The shape of the male genitalia (Fig. 2) is similar to many recent species which are separated by



Figs. 1 - 2. Male genitalia of Culicoides. 1 - C. ceranowiczi SZADZIEWSKI, MBI-8-165; 2 - C. speciosus (MEUNIER), MBI-8-139a.

details of wing pattern, distribution of sensilla coeloconica, and subtle differences in the male genitalia. In the fossil material these characters are either not visible or not preserved.

3. Culicoides subgedanensis sp. n. Figs. 3 - 5

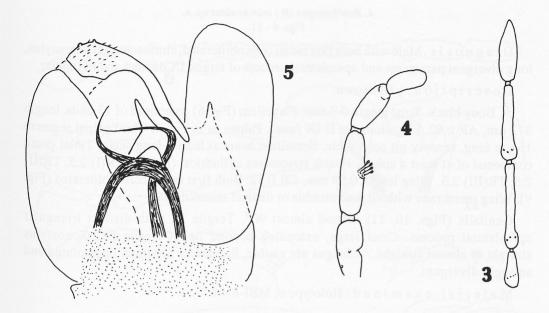
D i a g n o s i s . Male with sinuous gonostylus, broad triangular process of tergite IX and a high basal arch on the aedeagus. In addition the basal radial cell is covered with macrotrichia.

Description. q. Unknown.

 σ . Body blackish brown. Total length 1.6 mm. Flagellum length 816 $\mu m,~AR~0.83.$ Sensilla coeloconica not visible. Flagellomere X 2.2 times shorter than flagellomere XI (Fig. 3). Proboscis long. Palpus slender (Fig. 4). Third palpal segment cylindrical, length 64 $\mu m,$ sensory pit shallow, barely visible. Legs slender. Tibial comb composed of 5 spines. TR(I) 1.8, TR(III) 1.9. Wing length 1.25 mm, CR 0.56. Membrane including basal radial cell covered with macrotrichia.

Genitalia (Fig. 5). Sternite IX barely visible. Gonocoxite normal. Gonostylus sinuous or S-shaped. Aedeagus Y-shaped, with high basal arch and short, blunt apical projection. Parameres long and slender, gradually tapering to strongly recurved tips.

Material examined: Holotype o, MBI-8-157.



Figs. 3 - 5. Culicoides subgedanensis sp. n. male, MBI-8-157. 3 - distal four flagellomeres, 4 - palpus, 5 - genitalia.

Tribe Ceratopogonini NEWMAN, 1834

Ceratopogonini sensu WIRTH & GROGAN (1988) combines the genera previously assigned to the tribes Ceratopogonini and Stilobezziini.

Genus Brachypogon KIEFFER, 1899

Subgenus Brachypogon KIEFFER, 1899.

Brachypogon (B.) indetermined.

K-46, 1 o; K-57a, b, 2 o.

Key to species of Brachypogon (B.) from Baltic and Saxonian amber

Males

1. First radial cell well developed		B. eocenicus SZADZIEWSKI (Baltic amber)
Both radial cells obliterated		
2. Antenna with 10 flagellomeres		B. gedanicus SZADZIEWSKI (Baltic amber)
Antenna with 13 flagellomeres		
3. Gonostylus slender and strongly curved .		B. balticus SZADZIEWSKI (Baltic amber)
Gonostylus basally swollen nearly straight		R miocaenicus sp. n

4. Brachypogon (B.) miocaenicus sp. n. Figs. 6 - 11

D i a g n o s i s . Male with both first radial cells obliterated, almost straight gonostylus, long divergent parameres and apicolateral process of tergite IX distinct and triangular.

Description. Q Unknown.

 σ . Body black. Total length 0.7 mm. Flagellum (Fig. 6) composed of 13 units, length 372 μm , AR 0.82. Flagellomeres II-IX fused. Palpus as in Fig. 7. Third palpal segment 16 μm long, sensory pit not visible. Scutellum bears at least 4 long setae. Tibial comb composed of at least 4 spines. Fourth tarsomeres cylindrical (Fig. 8). TR(I) 2.5, TR(II) 2.8, TR(III) 2.3. Wing length 0.59 mm, CR 0.52. Both first radial cells obliterated (Fig. 9). Wing membrane without macrotrichia or distinct microtrichia.

Genitalia (Figs. 10, 11) rotated almost 90°. Tergite IX with distinct triangular apicolateral process. Cerci large, extending beyond tip of tergite IX. Gonostylus straight or almost straight. Aedeagus not visible. Parameres separate, tips pointed and strongly divergent.

Material examined: Holotype of, MBI-8-44.

Subgenus Isohelea KIEFFER, 1917

Brachypogon (Isohelea) indetermined. K-38, 1 o.

Key to named species of the subgenus Isohelea from Baltic and Saxonian amber

Males

- 1. Antenna with 11 flagellomeres . . B.(I.) prominulus (MEUNIER)(Baltic and Saxonian amber)
- 2. Gonostylus with enlarged and bilobed tip . .B.(I.) henningseni SZADZIEWSKI (Baltic amber)
- -. Gonostylus with blunt and simple tip B.(I.) polonicus SZADZIEWSKI (Baltic amber)

5. Brachypogon (I.) prominulus (MEUNIER, 1904)

 $Ceratopogon\ prominulus\ MEUNIER,\ 1904:\ 228\ (Baltic\ amber).$

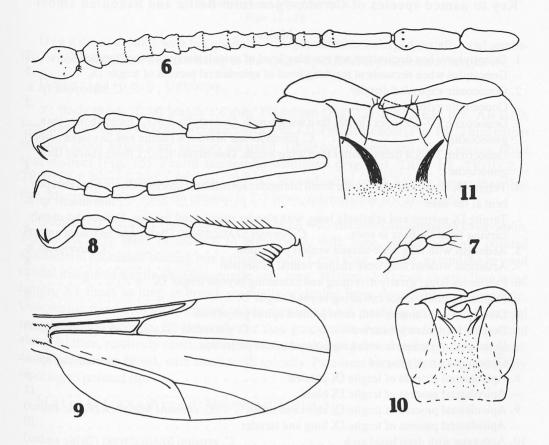
 ${\it Brachypogon\ prominulus:}\ SZADZIEWSKI\ 1988:83\ (Baltic\ amber).$

Material examined: K-17, 1 φ ; K-35, 1 φ (+ Forcipomyia indet., 1 φ); K-54, 1 φ ; K-85, 1 φ .

Genus Ceratopogon MEIGEN, 1803

In the material examined 36 males and 60 females have been recorded. Amongst the seven species determined, *C. forcipiformis*, and *C. hennigi* are previously known from Baltic amber while five are described as new.

Ceratopogon indetermined: 72 (13 od, 59 ∞)



Figs. 6 - 11. Brachypogon (B.) miocaenicus sp. n., male, MBI-8-44. 6 – flagellum, 7 – palpus, 8 – tarsi of fore, middle and hind leg, 9 – wing, 10, 11 – genitalia.

MBI-7-3, 1 \circ ; 8-7, 1 \circ ; 8-9, 1 \circ ; 8-12, 1 \circ (+*Chironomidae* 1 \circ , *Sciaridae*, 1 \circ); 8-13, 14, 15, each with 1 \circ ; 8-16, 1 \circ (+*Phoridae* 2); 8-17, 18, 19, 20, 21, each with 1 \circ ; 8-22, 1 \circ (+*Chironomidae* 1 \circ); 8-23 to 25 each with 1 \circ ; 8-26, 1 \circ (+*Chironomidae* 1 \circ); 8-27 to 30 each with 1 \circ ; 8-31, 2 \circ ; 8-36, 37, 40, 41, 45, 46, 50, 51, 57, 59, 60, 66 to 68, 102, 141, each with 1 \circ ; 8-144, 1 \circ ; 9-5, 1 \circ 1 \circ ; 9-6, 1 \circ ; 10-7, 1 \circ ; 10-9, 1 \circ ; 11-7, 1 \circ .

K-10, 1 \circ ; K-18, 1 \circ 1 \circ ; K-31, 1 \circ ; K-45, 1 \circ ; K-47, 1 \circ ; K-51, 1 \circ ; K-59, 1 \circ 1 \circ ; K-71, 1 \circ ; K-72, 1 \circ ; K-73, 1 \circ ; K-74, 1 \circ ; K-75, 1 \circ ; K-78, 1 \circ ; K-83, 1 \circ ; K-89, 1 \circ ; K-90, 1 \circ ; K-92, 1 \circ ; K-93, 1 \circ (+Culicoides 1 \circ); K-97, 1 \circ (+Formicidae 1); K-100, 1 \circ ; K-102, 1 \circ (+Chironomidae 1 \circ); K-106, 1 \circ .

Key to named species of Ceratopogon from Baltic and Saxonian amber

Males

	Gonostylus when decumbent not reaching level of apicolateral process of tergite IX
	Gonostylus when decumbent reaching level of apicolateral process of tergite IX
	Gonocoxite expanded distally
	Gonocoxite cylindrical
3.	Gonocoxite 1.7-2.7 times shorter than wing length. Gonostylus 2.5-3.5 times shorter than
	gonocoxite
	Gonocoxite 3.2-3.4 times shorter than wing length. Gonostylus 1.7-2.1 times shorter than
	gonocoxite
4.	Tergite IX broad and short, with broad triangular apicolateral process. Gonostylus abruptly
	bent at the base
	Tergite IX narrow and relatively long, with slender apicolateral process. Gonostylus evenly
	curving from the base to apex C. hennigi SZADZIEWSKI (Baltic and Saxonian amber)
5.	Aedeagus with long beak-shaped ventral projection
	Aedeagus without long beak-shaped ventral projection
	Parameres large, greatly diverging and extending beyond tergite IX
	Parameres smaller, not extending beyond tergite IX
	Distal part of paramere with short pointed apical projection.
	Gonostylus somewhat curved
- .	Distal part of paramere with long pointed apical projection.
	Gonostylus greatly curved
8.	Apicolateral process of tergite IX pointed
	Apicolateral process of tergite IX blunt
	Apicolateral process of tergite IX short and broad C. eminens MEUNIER (Baltic amber)
	Apicolateral process of tergite IX long and slender
	Aedeagus with deep basal arch
	Aedeagus with low basal arch
	Gonostylus 2.0-2.2 times shorter than gonocoxite
	Gonostylus 1.0-1.5 times shorter than gonocoxite
12.	Gonostylus abruptly bent near the base
	Gonostylus evenly curved throughout its length
13.	Paramere with twisted tip. Gonostylus as long as gonocoxite
_	Paramere without twisted tip. Gonostylus shorter than gonocoxite
	Tip of aedeagus distinctly forked
	Tip of aedeagus not forked
	Aedeagus with 2 pairs of dorsal projections. Gonocoxite 5.8 times shorter than wing length.
	Apicolateral process of tergite IX short
	Aedeagus without dorsal projections. Gonocoxite 6.7-6.8 times shorter than wing length.
	Apicolateral process of tergite IX long C. margaritae SZADZIEWSKI (Baltic amber)
16	Gonocoxite 5.7 times shorter than the wing
10.	
	Gonocoxite 3.6-4.1 times shorter than the wing
	Gonocoxite 3.6-4.1 times shorter than the wing
	C. Fuzkowsku SZADZIEWSKI (Dallic allicel)

6. Ceratopogon bitterfeldi sp. n. Figs. 12 - 19

D i a g n o s i s. Male with big genitalia with gonocoxites enlarged distally, and gonostyli, when decumbent not extending to the tips of apicolateral processes of tergite IX.

Description. Q. Unknown.

 $^{\circ}$. Body black. Total length 1.6 mm. Flagellum (Fig. 12); length 612 μm, AR 0.89. First flagellomere with sensilla coeloconica (Fig.13). Palpus slender (Fig. 14). Third palpal segment about 30 μm long, sensory pit small. Tibial comb composed of 7-8 spines; tibial spur distinct (Fig. 15). Fourth tarsomeres cordiform (Fig. 16). TR(I) 1.8, TR(II) 2.1, TR(III) 2.1. Wing length 1.03 mm, CR 0.62. Second radial cell 1.3 times longer than first one. Macrotrichia at wing tip present in 2-3 rows, microtrichia not discernible.

Genitalia (Figs. 18, 19) rotated 90° . Sternite IX with shallow caudomedian excavation. Tergite IX very short in relation to gonocoxite, with long, slender, evenly pointed apicolateral processes bearing one subapical seta. Cerci long, slender, extending beyond caudal margin of tergite IX. Gonocoxite very long, $360~\mu m$, 2.9 times shorter than wing length, 3.1 times as long as broad, gradually widening from slender base to broad tip. Gonostylus slender, slightly curved, when decumbent not reaching level of apicolateral process, length $172~\mu m$, 2.1 times shorter than gonocoxite. Aedeagus lightly sclerotized along midline, relatively short, tips of ventral projections pointed and slightly divergent; dorsal projections broad, with small teeth apically. Paramere slender and long, gradually tapering to pointed tip.

Material examined: Holotype of, MBI-8-3.

7. Ceratopogon forcipiformis MEUNIER, 1904 Figs. 20 - 22

Ceratopogon forcipiformis MEUNIER, 1904: 235 (Baltic amber); SZADZIEWSKI 1988: 57 (Baltic amber); SCHUMANN & WENDT 1989: 41 (Saxonian amber).

Material examined: (11 o)

MBI-8-4, 2 σ ; 8-5, 1 σ ; 8-8, 2 (+Chironomidae 1 σ); 8-73, 1 σ ; 8-168, 1 σ ; 10-5, 1 σ ; K-26, 1 σ ; K-56 a, 1 σ ; K-64, 1 σ .

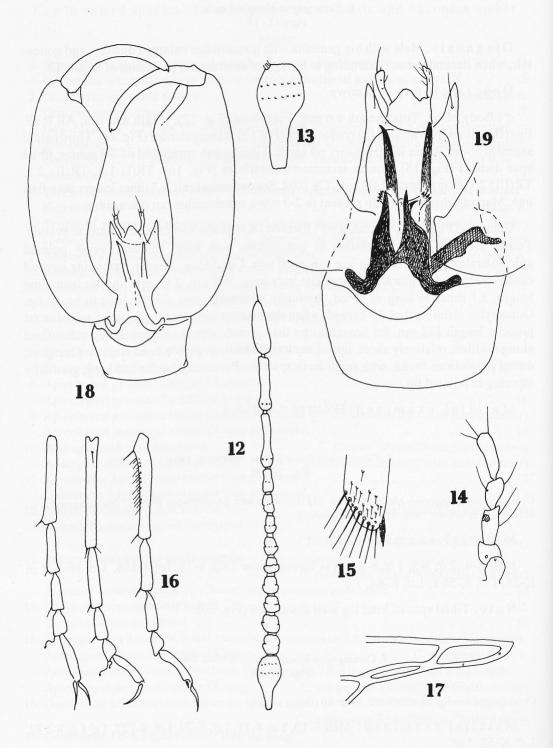
Note. Tibial spur of hind leg well developed (Fig. 20).

8. Ceratopogon hennigi SZADZIEWSKI, 1988 Figs. 23 - 24

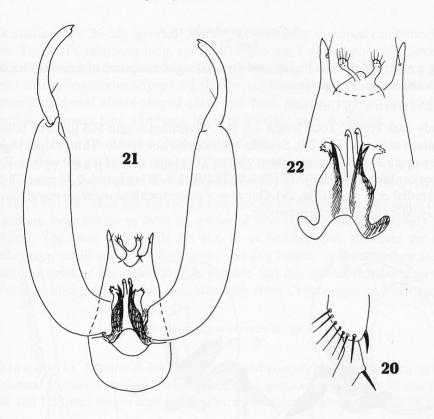
Ceratopogon hennigi SZADZIEWSKI, 1988: 60 (Baltic amber).

Material examined: MBI 8-10, 1 o; 8-11, 1 o; 8-70, 1 o; 8-127, 1 o 1 o; 8-132, 1 o; K-52, 1 o.

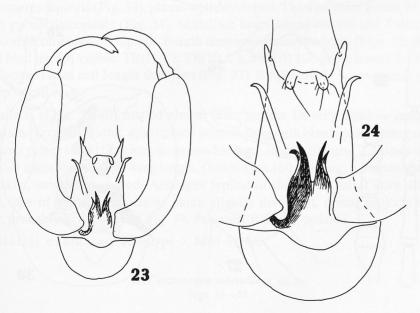
Note. Tibial spur of hind leg well developed.



Figs. 12 - 19. *Ceratopogon bitterfeldi* sp. n., male, MBI-8-3. 12 - flagellum, 13 - first flagellomere, 14 - palpus, 15 - tip of hind tibia, 16 - tarsi of fore, middle and hind leg, 17 - first radial cells, 18, 19 - genitalia.



Figs. 20 - 22. Ceratopogon forcipiformis MEUNIER, male. 20 – tibial comb and tibial spur of hind leg (K-56a); 21 – genitalia, 22 – aedeagus, parameres and tergite IX (MBI-8-168).



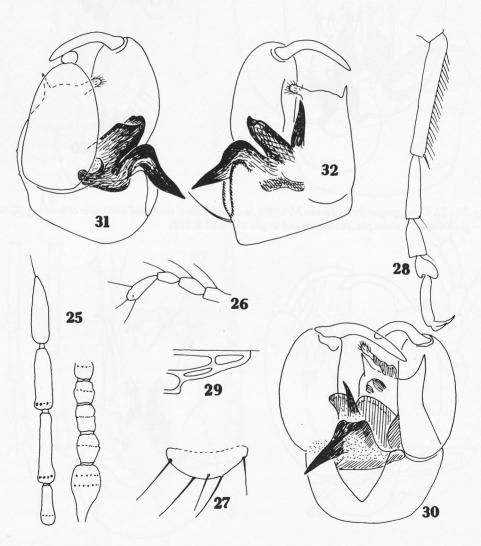
Figs. 23 - 24. Ceratopogon hennigi SZADZIEWSKI, male, K-52. 23 - genitalia, 24 - aedeagus, parameres and tergite IX.

9. Ceratopogon kotejai sp. n. Figs. 25 - 32

D i a g n o s i s . Male with highly modified aedeagus composed of a dorsal plate and a ventral, beak shaped, long projection.

Description. Q. Unknown.

σ. Body dark brown. Total length 1.1 mm. Flagellum length 503 μm, AR 0.90. All flagellomeres separate (Fig. 25). Sensilla coeloconica not visible. Third palpal segment short, measuring 28 μm; sensory pit not visible. Tibial spur of hind leg not visible. Fourth tarsomeres cordiform (Fig. 28). TR(II) 2.0, TR(III) 1.9. Wing length 0.76 mm, CR 0.64. Both first radial cells small (Fig. 29). One row of macrotrichia along wing margin present in cell r_{4+5} . Microtrichia not discernible.



Figs. 25 - 32. Ceratopogon kotejai sp. n., male, K-48. 25 – proximal 4 and distal 5 flagellomeres, 26 – palpus, 27 – scutellum, 28 – tarsus of hind leg, 29 – first radial cells, 30-32 – ventral and lateral aspects of genitalia.

Genitalia (Figs. 30-32) inverted. Sternite IX with deep v-shaped caudomedian excavation. Tergite IX relatively long, apicolateral process long and pointed. Cerci distinct, slender. Gonocoxite 6.3 times shorter than wing length, 1.36 times longer than gonostylus; length $120\,\mu m$. Gonostylus 88 μm long, slender, slightly curved, evenly pointed. Aedeagus composed of dorsal shield-shaped plate and beak shaped, sinuous, pointed, ventral projection. Paramere long, stout tapering to pointed tip, almost straight.

Material examined: Holotype o, K-48.

Etymology. The species is named in honour of Professor Jan KOTEJA of Cracow in recognition of his important contributions to the study of fossil insects preserved in amber.

D is c u s s i o n. Male genitalia of the new species are not typical of the genus Ceratopogon and are more similar to those of species of Brachypogon (subg. Isohelea) (i.e. large aedeagus). The small radial cells are also as in Brachypogon. However the separated flagellomeres, cordiform fourth tarsomeres, and five bristles on the scutellum are features present in species of Ceratopogon. It is possible that this species represents an unknown phylogenetic lineage which is not associated with either Ceratopogon or Brachypogon.

10. Ceratopogon miocaenicus sp. n. Figs. 33 - 40

D i a g n o s i s . Male with long, evenly curved gonostylus not extending to the tip of apicolateral process of tergite IX when decumbent; gonocoxite 5.8 times shorter than wing length and 1.3 times longer than gonostylus; apicolateral process of tergite IX short.

Description. Q. Unknown.

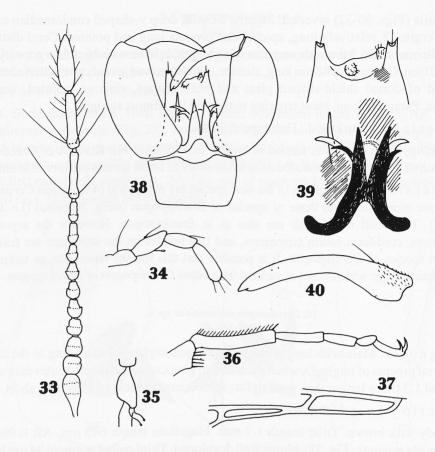
σ. Body dark brown. Total length 1.7 mm. Flagellum length 645 μm, AR 0.90. All flagellomeres separate (Fig. 33), plume well developed. Third palpal segment 34 μm long, sensory pit not discernible (Fig. 34). Scutellum bears 4 long bristles and 5 shorter setae. Tibial comb composed of 6 spines. Fourth tarsomeres subcylindrical (Figs. 35, 36). Tibial spur of hind leg not visible. TR(I) 1.7, TR(II) 2.3, TR(III) 1.7. Wing length 1.19 mm, CR 0.69. Second radial cell longer than first (Fig. 37). Single row of macrotrichia present at Wing tip in cell r_{4+5} .

Genitalia (Figs. 38-40) rotated almost 90° . Sternite IX with shallow caudomedian excavation. Tergite IX long, apicolateral process long with blunt apex bearing one apical seta. Cerci rather short. Gonocoxite somewhat bent, length 204 μ m, 2.3 times as long as broad, 5.8 times shorter than wing length. Gonostylus 160 μ m long, 1.3 times shorter than gonocoxite, somewhat curved. Aedeagus typical of the genus; basal arms slightly recurved, tips of ventral projections stout, slightly divergent, dorsal projections barely visible, probably as depicted in Fig. 39. Paramere rod-like, pointed.

Material examined: Holotype o, MBI-8-166.

11. Ceratopogon subeminens sp. n. Figs. 41 - 43

Diagnosis. Male with abruptly bent gonostylus which does not reach the tip of tergite IX when decumbent, and long triangular and pointed apicolateral process of tergite IX.



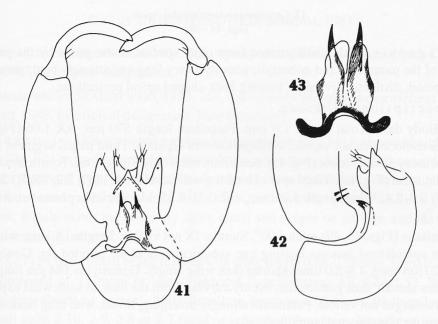
Figs. 33 - 40. *Ceratopogon miocaenicus* sp. n., male, MBI-8-166. 33 - flagellum, 34 - palpus, 35 - fourth tarsomere of fore leg, 36 - tarsus of hind leg, 37 - first radial cells, 38 - genitalia, 39 - aedeagus, parameres, tergite IX, 40 - gonostylus.

Description. q. Unknown.

o'. Body black. Total length 1.7 mm. Flagellum and palpus barely visible. Scutellum bearing 10 long and about 8 shorter setae. Tibial comb composed of 8 spines. Tibial spur of hind leg not visible. Wing length 1.22 mm, CR 0.60. Macrotrichia at wing tip present, microtrichia not discernible.

Genitalia (Figs. 41-43) inverted. Sternite IX with narrow shallow caudomedian excavation. Tergite IX short; apicolateral process long, triangular with evenly pointed apex, one subapical seta. Gonocoxite 375 μm long, 3.2 times shorter than wing length. Gonostylus 188 μm long, abruptly bent at the base, not extending to level of tergite IX when decumbent, about 2.0 times shorter than gonocoxite. Aedeagus with low basal arch; ventral projections in distal portion weakly sclerotized, plate-shaped; a pair of dorsal projections long, strongly sclerotized, pointed apices directed dorsally. Parameres barely visible; pointed apices directed ventrally.

Material examined: Holotype o, MBI-8-148.



Figs. 41 - 43. Ceratopogon subeminens sp.n., male genitalia, MBI-8-148. 41 - ventral aspect, 42 - lateral aspect, 43 - aedeagus

Discussion. Apicolateral processes of tergite IX of the male genitalia are similar to those of *C. eminens* MEUNIER and unnamed species A and C from Baltic amber (SZA-DZIEWSKI 1988). The species however, have a longer tergite IX and straighter gonostyli. The gonostyli in this new species are sharply bent at base as in *C. crypticus* SZADZIEWSKI from Baltic amber. In the latter species, the apicolateral processes of tergite IX have obliquely truncate tips bearing apical seta; moreover, tergite IX is longer and gonostyli when decumbent reach tip of tergite IX. Numerical characters of *C. crypticus* and *C. subeminens* are presented below:

	C. subeminens sp. n.	C. crypticus
wing length	1.22 mm	0.95-1.16 mm
CR	0.60	0.52-0.59
Length of gonocoxite	375 μm	240-275 μm
Length of gonostylus	188 μm	124-128 μm
Wing/gonocoxite	3.2	3.8-4.4
Gonocoxite/gonostylus	2.0	2.0-2.1

12. Ceratopogon succinicolus sp. n. Figs. 44 - 49

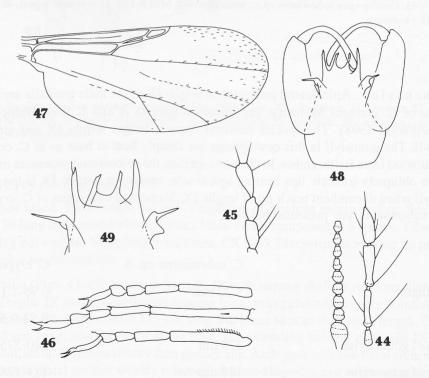
Diagnosis. Male distinguished from other species of the genus by the peculiar shape of the parameres and gonostyli; gonostyli very long and strongly bent; parameres long, broad, distinctly divergent, bearing beak-shaped apical projections.

Description. q. Unknown.

 σ . Body dark. Total length 1.6 mm. Flagellum length 570 μm, AR 1.06 (Fig. 44); sensilla coeloconica not visible; all flagellomeres separate. Third palpal segment 32 μm long, sensory pit not visible (Fig. 45). Scutellum bears only 5 long setae. Fourth tarsomeres subcylindrical (Fig. 46). Tibial spur of hind leg well developed. TR(I) 2.2, TR(II) 2.3-2.4, TR(III) 2.3-2.4. Wing length 1.05 mm, CR 0.51-0.55. Macrotrichia present at wing tip (Fig. 47).

Genitalia (Figs. 48, 49) rotated 90° . Sternite IX not visible. Tergite IX long, with long slender apicolateral process bearing one subapical seta at the pointed tip. Gonocoxite $208-220~\mu m$ long, 4.8-5.0 times shorter than wing length. Gonostylus $184~\mu m$ long, only 1.1 times shorter than gonocoxite, evenly curving from the base to somewhat expanded apex. Aedeagus not visible. Parameres strongly diverging, broad, with long beak-shaped apical projection directed laterally.

Material examined: Holotype o, MBI-8-2. Paratype o, MBI-7-5.



Figs. 44 - 49. Ceratopogon succinicolus sp. n., male; MBI-8-2 (Figs. 44-46, 49), MBI-7-5 (Figs. 47, 48). 44 - flagellum, 45 - palpus, 46 - tarsi of fore, middle and hind leg, 47 - wing, 48 - genitalia, 49 - distal portion of parameres and tergite IX.

Genus Chimaerohelea DEBENHAM, 1987

Chimaerohelea DEBENHAM, 1987: 801, type-species *Chimaerohelea caligula* DEBENHAM, 1987, by original designation.

Meunierohelea SZADZIEWSKI, 1988: 148, type-species Meunierohelea nielseni SZADZIEWSKI, 1988, by original designation. New synonymy.

D i a g n o s i s. This genus has a unique wing venation: vein M_2 is almost straight with a vein-like fold extending anteriorly towards the wing base; the first and second radial cells are separated by a fused vein which extends for a considerable distance between them; the second radial cell is long and narrow, and usually open at the distal end. In addition, female claws are relatively short, equal and simple on all legs, and the fourth tarsomeres are cylindrical.

Description. Small biting midges with wing length 0.68-0.98 mm. Female flagel-lum composed of 13 more or less cylindrical flagellomeres; AR 0.84-1.57. Sensilla coeloconica absent or present. Male flagellum composed of 13 or 10 flagellomeres, proximal units 2-10, 2-9, 2-8 or 2-7 fused or separated. Eyes bare, broadly or narrowly contiguous. Proboscis normal or very short. Palpus 5-segmented; third segment short. Scutellum bears 4-6 bristles. Legs slender and unarmed; fourth tarsomeres cylindrical; hind basitarsus with palisade setae; female claws short to moderately long, equal and simple. Wing narrow without anal lobe; venation as in diagnosis; membrane covered with indistinct microtrichia, macrotrichia absent. Intercalary fork in cell r4+5 visible in fossil species.

Female abdomen without striking modification, cerci short. Seminal capsule single. Male genitalia short, broad; inverted, rotated or in normal position. Tergite IX with broad apicolateral processes. Gonocoxites broad and short, fused basally on ventral midline or probably totally separated. Aedeagus broad with median broad apical single projection bilobed at apex, or with two submedian projections. Parameres separate or fused.

Discussion. The characteristic wing venation and other characters found in fossil species from Baltic and Saxonian amber placed in *Meunierohelea* and in a single extant species of the genus *Chimaerohelea* leads to the conclusion that they form a monophyletic group. It seems that the single extant species, *Chimaerohelea caligula* DEBENHAM, known from North Queensland in NE Australia, is a remnant of an old group which was widely distributed in the Old World. I am not able to suggest which group in the tribe *Ceratopogonini* is related to it. It is possible that *Wirthohelea* SZADZIEWSKI from Baltic amber with a similarly shaped proximal part of the radial cells, is a closely related taxon. Unfortunately the wing venation is not completely preserved in that genus.

Six species of *Chimaerohelea* are present in Baltic amber, of which three are named. The named species are based on males which are more easily identified than females. In Saxonian amber I found two females belonging to two different species.

Key to fossil species of Chimaerohelea

1. Males	
Females	
2. Flagellum composed of 10 recognizable flagellomeres. Gonostylus broad, not tapering to	
apex	
Flagellum composed of 13 recognizable flagellomeres. Gonostylus tapering to apex 3	
3. CR 0.80	
CR 0.65-67	
4. Sensilla coeloconica present on proximal flagellomeres	
	1
Sensilla coeloconica absent on proximal flagellomeres	
5. CR 0.79-0.81	
CR 0.66-0.76	,
6. Palpus short. Claws 28 m long	!
Palpus long. Claws 44-48 m long)
7. AR 1.08. CR 0.76. Seminal capsule large)
AR 1.32-1.57. CR 0.66-0.72. Seminal capsule small	;
8. Second radial cell 0.9-1.1 times as long as distance between tip of R ₁ and the base of first	
radial cell	
Second radial cell 1.3-1.4 times as long as distance between tip of R ₁ and the base of first	
radial cell	

13. Chimaerohelea miocaenica sp. n. Figs. 50, 52 - 54

Diagnosis. Female with well developed sensilla coeoloconica on at least some of the proximal flagellomeres.

Description. Q. Body dark brown. Total length 1.2 mm. Flagellum length 716 μ m, AR 1.26 (Fig. 53). Sensilla coeloconica clearly visible on flagellomeres V-VIII (Figs. 53, 54). The presence of s. coeloconica on the first flagellomere is uncertain. Third palpal segment 32 μ m long. Sensory pit not visible. Scutellum bearing 4 long setae. Tibial comb composed of 5 spines. Tibial spur of hind leg not visible. Hind basitarsus with distinct subbasal spine and palisade setae. Second and third tarsomeres of hind leg with palisade setae too. Claws (Fig. 52) simple, equal, 28-32 μ m long. TR(I) 1.9, TR(III) 2.2. Wing length 0.86 mm, CR 0.76. Wing venation as in Fig. 50. Cerci small. Seminal capsule not visible.

o. Unknown.

Material examined: Holotype Q, MBI-8-63.

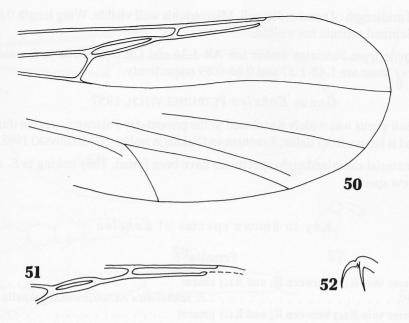
14. Chimaerohelea nielseni (SZADZIEWSKI, 1988), comb. n.

Figs. 51, 55

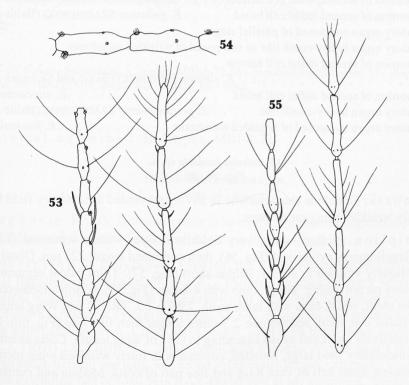
Meunierohelea nielseni SZADZIEWSKI, 1988: 150 (Baltic amber).

Material examined: K-20, 1 o.

Note. Total length 1.3 mm. Flagellum 680 µm long, AR 1.36. Proximal flagellomeres cylindrical (Fig. 55). Sensilla coeloconica absent. Scutellum with 6 long setae. Claws about 20 µm long. TR(III) 2.5. First radial cells as in Fig. 51. M₂ prolonged anteriorly to



Figs. 50 - 52. Chimaerohelea DEBENHAM, female. Ch. miocaenica sp. n., MBI-8-63 (figs. 50, 52); Ch. nielseni (SZADZIEWSKI), K-20 (fig. 51). 50 – wing venation, 51 – first radial cells, 52 – claws of fore leg



Figs. 53 - 55. Chimaerohelea Debenham, female. 53 - flagellum , 54 - flagellomeres VII and VIII of Ch. miocaenica sp. n., MBI-8-63); 55 - flagellum of Ch. nielseni (SZADZIEWSKI) (K-20)

the level of midlength of basal radial cell. Microtrichia well visible. Wing length $0.86\,\mathrm{mm}$, CR 0.72. Seminal capsule not visible.

The female from Saxonian amber has AR 1.36 and CR 0.72 while in females from Baltic amber these are 1.43-1.57 and 0.66-0.69 respectively.

Genus Eohelea PETRUNKEVITCH, 1957

This fossil genus was widely distributed in the present-day Palaearctic region during the Tertiary and is known from Baltic, Saxonian and Sakhalin amber (SZADZIEWSKI 1988, 1990).

In the material examined eight specimens have been found. They belong to *E. sinuosa* and two new species.

Key to known species of Eohelea

Females

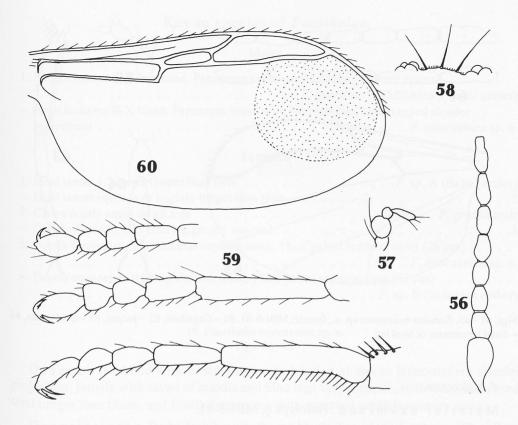
1. Transverse vein R ₂₊₃ between R ₁ and R ₄₊₅ absent
Transverse vein R ₂₊₃ between R ₁ and R ₄₊₅ present
2. Wing without stridulatory organ
Wing with stridulatory organ
3. Distal portion of second radial cell narrow E. grogani SZADZIEWSKI (Baltic amber)
Distal portion of second radial cell broad E. gedanica SZADZIEWSKI (Baltic amber)
4. Stridulatory organ composed of parallel ridges
Stridulatory organ honey-comb like or composed of wrinkled membrane
5. Distal portion of second radial cell narrow
E. sinuosa (MEUNIER) (Baltic and Saxonian amber)
Distal portion of second radial cell broad
6. Stridulatory organ honey-comb like E. petrunkevitchi SZADZIEWSKI (Baltic amber)
Stridulatory organ composed of wrinkled membrane

15. Eohelea fossicola sp. n. Figs. 56 - 60

Diagnosis. Female is characteristic in having a rounded stridulatory field formed by the finely wrinkled wing membrane.

Description. Q. Body dark, very deformed. Eyes widely separated (Fig. 58). Proximal flagellomeres cylindrical (Fig. 56), their combined length 224 μ m. Distal flagellomeres obliquely situated in amber. Palpus short (Fig. 57). Third palpal segment short, ovoid. Sensory pit not visible. Tibial comb with 4 spines (Fig. 59). Fourth tarsomeres rather short. Claws short, equal, each with inner tooth. TR(II) 2.5, TR(III) 2.8. Wing length 0.75 mm. First radial cell short, second one 2.3 times longer than first one (Fig. 60). Second radial cell relatively short and broad extending to 0.83 of wing length. Costa extending to wing tip. Stridulatory field large, rounded, covered with finely wrinkled wing membrane, situated between distal half of vein R4+5 and free part of costa. Median and cubital veins not visible. Genitalia not modified.

d Unknown



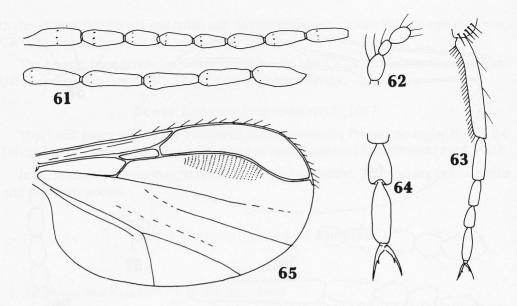
Figs. 56 - 60. *Eohelea fossicola* sp. n., female, MBI-8-72. 56 – proximal flagellomeres, 57 – palpus, 58 – eyes separation, 59 – tarsi of fore, middle and hind leg, 60 – wing.

Material examined: Holotype q, MBI-8-72.

16. Eohelea miocaenea sp. n. Figs. 61 - 65

D i a g n o s i s . Female is characteristic in having a stridulatory organ composed of 22 parallel ridges and the second radial cell broad on the distal portion.

Description. φ . Body brown. Total length 1.5 mm. Flagellum length 552 μ m, AR 0.84. All flagellomeres cylindrical (Fig. 61). Palpus 5-segmented, very short (Fig. 62). Third palpal segment about 24 μ m long, sensory pit not visible. Scutellum probably bears 4 setae. Fourth tarsomeres cylindrical (Figs. 63, 64). Basitarsus and second tarsomere of hind leg with palisade setae. Claws short, equal, each with basal inner tooth (Fig. 64). TR(I) 2.3, TR(II) 2.6, TR(III) 2.5. Tibial comb with 5 spines. Wing length 1.00 mm. First radial cell short. Second one long, and broad along entire length, extending nearly to wing tip. Costa extending just beyond vein R4+5. Distal part of M1 atrophied. Stridulatory field elliptic, covered with 22 parallel ridges, situated just posterior to R4+5 (Fig. 65). Microtrichia well developed. Genitalia not modified.



Figs. 61 - 65. Eohelea miocaenea sp. n., female, MBI-8-81. 61 - flagellum, 62 - palpus, 63 - hind tarsus, 64 - distal tarsomeres of hind leg.

o. Unknown.

Material examined: Holotype o, MBI-8-81.

17. Eohelea sinuosa (MEUNIER, 1904)

Ceratopogon sinuosus MEUNIER, 1904: 234 (Baltic amber).

Eohelea stridulans PETRUNKEVITCH, 1957: 208 (Baltic amber).

Eohelea sinuosa: SZADZIEWSKI 1988: 161 (Baltic amber, Saxonian amber).

Material examined: MBI-8-80, $1 \circ (+Chironomidae 1 \circ)$; K-2, $1 \circ (+Acarina 1)$; K-50, $1 \circ (+Chironomidae 1 \circ)$.

Note. In the material examined five females and one male have been found. In females, the stridulatory organ is composed of 13, 14, 21 and 28 ridges while in specimens from Baltic amber those vary from 9 to 21. In the female from amber piece MBI-8-80 the tibial comb is composed of six spines while in those from Baltic amber it includes four.

Genus Fossihelea SZADZIEWSKI, 1988

In the material examined only one male and five females belonging to this genus were found. This fossil genus is known from both Baltic and Saxonian ambers, and is very similar to *Congohelea* WIRTH & GROGAN, 1988 which is represented by only one recent species, *C. fuligipennis* (CLASTRIER) from the Congo Republic. The only apparent difference is in female claws, which in *C. fuligipennis* lack inner teeth.

Fossihelea indetermined: MBI-8-6, 1 o; 8-49, 1 o; K-95, 1 o.

Key to species of Fossihelea

Males

1. Flagellomeres II-X separated. Parameres slender with straight pointed apices
F. gracilitarsis (MEUNIER)(Baltic amber)
Flagellomeres II-X fused. Parameres broad with lateromedian hook-shaped slender
projections
Females
1. Hind tarsus 1.3 times shorter than tibia

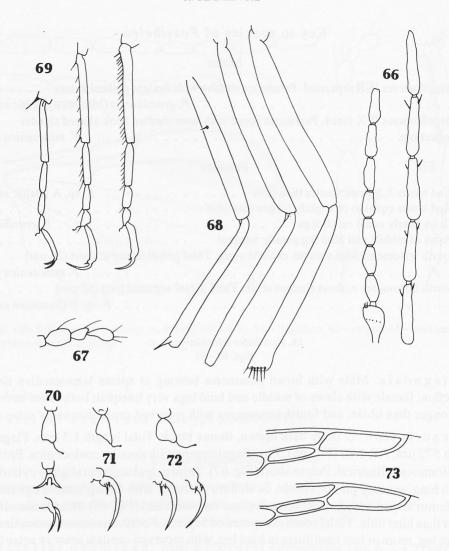
18. Fossihelea miocaenica sp. n. Figs. 66 - 81

Diagnosis. Male with broad parameres bearing at apices lateromedian slender projection; female with claws of middle and hind legs very unequal; both sexes have hind tarsi longer than tibiae, and fourth tarsomeres with recurved capitate sensory setae.

Description. Q. Body dark brown, thorax black. Total length 1.3 mm. Flagellum length 572 μ m, AR 1.20 (Fig. 66). First flagellomere with sensilla coeloconica. Proximal flagellomeres cylindrical. Palpus short (Fig. 67). Third palpal segment slightly cylindrical, 26 μ m long, sensory pit not visible. Scutellum probably with 4 long setae. Legs slender. Fore femur armed with 2 small ventral spines on basal third (Fig. 68). Hind tarsus slightly longer than hind tibia. Tibial comb composed of 5 spines. Fourth tarsomeres subcylindrical on fore leg, more or less cordiform in hind leg, with recurved capitate sensory setae (Figs. 70-72). Claws of fore leg equal, relatively short, each with inner tooth, claws of middle and hind leg greatly unequal – long claw with basal inner tooth, the other claw very short, simple (Figs. 70-72). TR(I) 1.7, TR(II) 2.1, TR(III) 2.4. Wing length 0.77 mm, CR 0.76. Both first radial cells well developed (Fig. 73). Vein M1 readily visible along its entire length, base of M2 atrophied. Wing membrane without macrotrichia. Genitalia not modified.

σ. Body dark. Flagellum 504 μm long, AR 0.92. Proximal flagellomeres II-X fused (Fig. 74). First flagellomere bears sensilla coeloconica. Flagellomere X about 2.7 times shorter than next one. Palpus short (Fig. 75). Third palpal segment about 24 μm long, sensory pit not visible. Fore femur (Fig. 76) armed with 2 ventral spines on basal third. Hind tarsus longer than hind tibia. Fourth tarsomeres (Fig. 78) cylindrical, with recurved capitate sensory setae. TR(I) 2.1, TR(II) 2.1, TR(III) 2.5. Wing length 0.76 mm, CR 0.70. First radial cells well developed (Fig. 79). Membrane without macrotrichia.

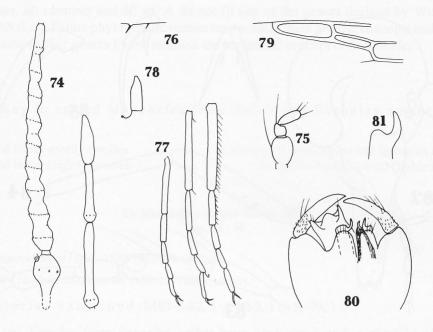
Genitalia (Figs. 80, 81) in normal position, small. Sternite IX not visible. Tergite IX longer than gonocoxite, tapering towards apex, with distinct broad apicolateral processes.



Figs. 66 - 73. Fossihelea miocaenica sp. n., female, MBI-8-92. 66 - flagellum, 67 - palpus, 68 - femora and tibiae of fore, middle and hind leg, 69 - tarsi of fore, middle and hind leg, 70 - fourth tarsomere and claws of fore leg, 71 - fourth tarsomere and claws of middle leg, 72 - fourth tarsomere and claws of hind leg, 73 - first radial cells.

Gonocoxite most probably with long and broad ventromesal lobe. Gonostyle moderately stout with evenly pointed tip. Aedeagus appears to be a slender V-shaped structure bearing an apical short projection curved ventrally. Parameres separated (?), broad; blunt apices with lateromedian slender projection directed dorsally (Fig. 81).

Material examined: Holotype of, MBI-8-140. Paratype of, MBI-8-92.



Figs. 74 - 81. Fossihelea miocaenica sp. n., male, MBI-8-140. 74 - flagellum, 75 - palpus, 76 - spines of fore femur, 77 - tarsi of fore, middle and hind leg, 79 - first radial cells, 80 - genitalia, 81 - tip of paramere.

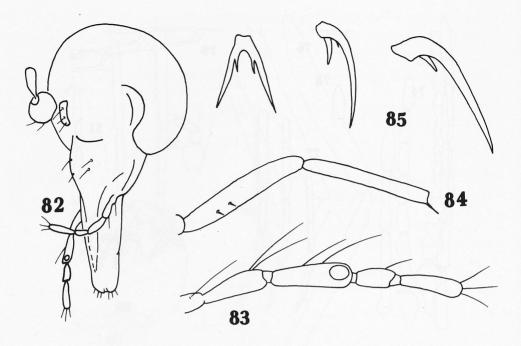
19. Fossihelea sp. B Figs. 82 - 85

Diagnosis. Female of the species has greatly unequal claws of middle and hind legs, and relatively long palpi.

Description. Q. Body dark. Total length 2.2 mm. Flagellum length 700 μ m, AR 0.94. Proximal flagellomeres cylindrical, sensilla coeloconica on first flagellomere readily visible. Eye separation not visible. Proboscis long (Fig. 82). Mandible armed with 8 coarse teeth. Palpus long (Fig. 83). Third palpal segment 62 μ m long, slender, with round sensory pit. Scutellum with at least 5 long bristles. Fore femur armed with 2 ventral spines on proximal half. Hind femur and tibia stouter than in fore or middle legs. Tibial comb composed of 6 spines. Basitarsus of middle leg with subbasal, middle and subapical strong spines. Fourth tarsomere of fore leg subcylindrical, of middle leg shorter, of hind leg nearly cordiform. Claws (Fig. 85) of fore leg equal, each with inner tooth; of middle leg distinctly unequal, long claw with inner tooth; of hind leg unequal too. TR(I) 2.0, TR(II) 2.4, TR(III) 2.7. Wing length 1.05 mm, CR 0.70. Wing membrane with distinct microtrichia, macrotrichia absent. Second radial cell twice as long as first.

o. Unknown.

Material examined: K-43, 1 o.



Figs. 82 - 85. Fossihelea sp. B, female, K-43. 82 - head, 83 - palpus, 84 - femur and tibia of fore leg, 85 - claws of fore, middle and hind leg.

Genus Mantohelea SZADZIEWSKI, 1988

Key to females

20. Mantohelea gedanica SZADZIEWSKI, 1988

Mantohelea gedanica SZADZIEWSKI 1988: 146 (Baltic amber).

Material examined: K-58, 1 ♀ (+Serromyia 1 ♂).

Note. Third palpal segment is about 56 μm long, fourth 36 μm . Fore femur armed with 8-9 cone-shaped ventral spines. TR(III) 3.1. Wing length 1.33 mm, CR 0.76.

Genus Monohelea KIEFFER, 1917, sensu lato

WIRTH & GROGAN (1988) recently revised generic concepts within the *Monohelea* complex, resulting in six newly defined genera. Of three species recognized in Baltic amber (SZADZIEWSKI 1988), *Monohelea baltica* belongs within *Schizohelea* KIEFFER.

However, M. clunipes and M. sp. A do not fit any of the genera defined by WIRTH & GROGAN (l.c.). Future phylogenetic studies may modify these generic concepts and rather than create further genera I have retained the traditional concept of Monohelea.

Key to named Monohelea from Baltic and Saxonian amber

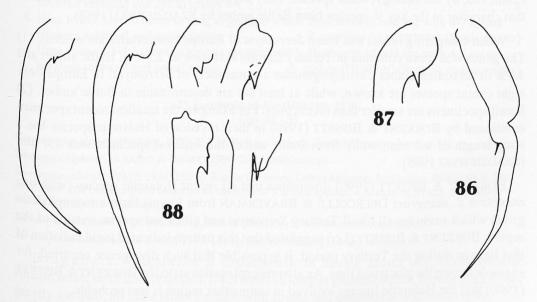
21. Monohelea clunipes (LOEW, 1850) Figs. 86 - 88

Ceratopogon clunipes LOEW, 1850: 30 (Baltic amber).

Monohelea clunipes: SZADZIEWSKI 1988: 127 (Baltic amber).

Material examined: MBI-8-82, 1 o; 10-3, 1 o; K-99, 1 o.

Note. Females from Saxonian amber have hind claws with a short basal tooth (Figs. 86, 87). In the redescription of the species from Baltic amber (SZADZIEWSKI 1988) I stated that the female hind claw was single. Re-examination of some females from the collection of Museum of the Earth in Warsaw (MZW), however, shows that they actually have a small basal tooth on the hind claw (Fig. 88) and this character was overlooked during the previous study.



Figs. 86 - 88. Monohelea clunipes (LOEW), female hind claws. 86 - MBI-8-82; 87 - base of claw, MBI-10-3; 88 - whole claws and their bases, Baltic amber, MZW 4998, 19211, 20009

Genus Nannohelea WIRTH & GROGAN, 1980

Two fossil species based on males are described from Baltic amber. In Saxonian amber only one undeterminable female has been discovered.

22. Nannohelea sp. indet.

Material examined: K-49, 1 o.

Note. Palpus short, 5-segmented, as in *N. grogani* SZADZIEWSKI. Wing length 0.54 mm, CR 0.43. Other characters typical of the genus.

Genus Serromyia MEIGEN, 1818

In the material 17 specimens (7 od, 10 od) have been found. Their determination is not easy because in addition to six fossil species from Baltic amber (SZADZIEWSKI 1988; BORKENT & BISSETT 1990) other *Serromyia* are known from Lower Miocene brown coal of Rott in Germany (HEYDEN 1870, STATZ 1944, BORKENT & BISSETT 1990). They are S. colorata STATZ (= S. austera STATZ, S. spinosifemorata STATZ) and S. alphea (HEYDEN) (BORKENT & BISETT l.c.). I propose to treat these compression fossils as a single species also present in Saxonian amber (see below under S. alphea).

The recent revision of *Serromyia* by BORKENT & BISSETT (1990) showed that the ratio of the second radial cell to the first is highly variable and is a poor tool for recognizing extant and, by the analogy, fossil species. They suggested characters to replace the use of that character in the key to species from Baltic amber by SZADZIEWSKI (1988).

When comparing recent and fossil *Serromyia* of Europe two features are evident: (1) The genus was more common in Tertiary Europe than now as 2.5% of Baltic amber and 4.8% of Saxonian amber *Ceratopogonidae* are members of *Serromyia*. In Europe only eight extant species are known, while at least six are determinable in Baltic amber. (2) Fossil specimens are smaller than recent ones. For example, the smallest recent specimen mentioned by BORKENT & BISSETT (1990) in their revision of Holarctic species has a wing length of 1.4 mm, while from Baltic amber the smallest specimen was 1.0 mm (SZADZIEWSKI 1988).

BORKENT & BISSETT (1990) discovered that all recent Holarctic species (with one exception *S. mangrovi* DELECOLLE & BRAVERMAN from Egypt) form a monophyletic group which excludes all fossil Tertiary *Serromyia* and all extant species outside of the region. BORKENT & BISSETT (l.c.) suggested that this pattern indicated rapid radiation of that lineage during the Tertiary period. It is possible that such divergence occurred, for example during the glaciation time. An alterate explanation stated by BORKENT & BISSETT (1990) that the Holarctic lineage evolved in some other region is less probable.

Serromyia indetermined: MBI-8-84, 1 ç; 8-93, 1 ơ; 8-96, 1 ơ; K-36, 1 ơ; K-58, 1 ơ(+ Mantohelea gedanica); K-65, 1 ç; K-69, 1 ç.

Key to fossil Serromyia

Males

1. Femora of fore and mid legs without strong spines	
Females	
1. Claws of hind leg short and equal	

23. Serromyia alphea (HEYDEN, 1870) Figs. 89 - 95

Ceratopogon alpheus HEYDEN, 1870: 251 (o, Rott in Germany, Lower Miocene-Aquitanian).

Serromyia alpheus: BORKENT & BISSETT 1990: 208 (combination).

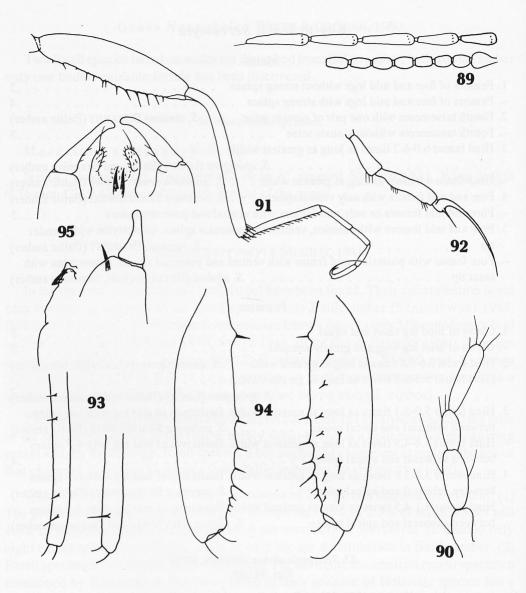
Serromyia colorata STATZ, 1944: 150 (o, Rott in Germany, Lower Miocene-Aquitanian. Borkent & Bis-SETT 1990: 206 (redescription based on all material of 3 named species, = S. austera STATZ, S. spinosife-morata STATZ). New synonymy.

Serromyia austera STATZ, 1944: 150 (o, Rott in Germany, Lower Miocene-Aquitanian).

Serromyia spinosifemorata STATZ, 1944: 151 (o, Rott in Germany, Lower Miocene).

Diagnosis. This species is characteristic in having fourth tarsomeres without sinuate setae, stout hind femora 4.1-4.5 times as long as greatest width, female hind claws greatly unequal, all male femora armed with spines and gonostylus with stout apex.

Description. Q. Body black or brown. Total length 1.7-2.0 mm. Flagellum length 713-825 μm, AR 1.35-1.44 (Fig. 89). Third palpal segment relatively short (Fig. 90). Fore



Figs. 89 - 95. Serromyia alphea (HEYDEN), male MBI-8-91, female MBI-8-77. 89 - female flagellum, 90 - female palpus, 91 - female hind leg, 92 - female hind claws, 93 - male femora of mid and fore leg, 94 - anterior and caudal aspects of male hind femur, 95 - ventral and lateral aspects of male genitalia.

and mid femora unarmed, slender. Hind femur armed with 10-12 pairs of ventral spines (Fig. 91). Basitarsus of mid leg with 4-5 spines between subbasal and apical spines. Fourth tarsomeres cylindrical, without sinuous sensory setae. Hind femur 4.1-4.5 times as long as greatest width. Hind claws greatly unequal (Fig. 92). Wing length 1.21-1.42 mm, CR 0.64-0.69. Macrotrichia present at wing tip. Second radial cell longer than first one.

 σ . Body black. Total length 2.0 mm. Flagellomere X short with a single whorl of setae, 2.5 times shorter than flagellomere XI. Third palpal segment 56 μm long. Scutellum bears about 14 long setae. All femora armed with spines. Fore femur with a single posterior spine at distal end (Fig. 93), mid femur with 3 ventral spines on proximal part and 2 long posterior spine-like setae. Hind femur 4.3 times as long as greatest width (Fig. 64). Tibiae with strong dorsal setae. Wing length 1.33-1.50 mm, CR 0.63-0.66. Macrotrichia present at wing tip.

Genitalia (Fig. 95) inverted, hidden below the tip of abdomen (Fig. 95). Gonostylus relatively broad and short with blunt apex. Aedeagus probably with trifid tip. Parameres long with pointed apices.

Material examined: Neotype σ of Ceratopogon alpheus, MBI-8-91, present designation. MBI-8-77, $3 \circ$; 8-116, $1 \circ$; 8-123, $1 \circ$; 8-125, $1 \circ$; K-84, $1 \circ$; K-96, $1 \circ$.

Discussion. Ceratopogon alpheus HEYDEN, originally found in Rott as a compression fossil was recognized by BORKENT & BISSETT (1990) as a member of Serromyia. The type was lost (STATZ 1944, SZADZIEWSKI 1988, BORKENT & BISSETT 1990). The age of the fossils from Saxonian amber and Rott is the same, and may therefore include the same species. There is no reason to treat morphologically unseparable specimens from Rott and Bitterfeld as distinct species and S. colorata (with its previously recognized synonyms) and S. alphea are considered as conspecific. The neotype of Ceratopogon alpheus is selected from amongst better preserved amber fossils.

It is not clear that actually all specimens described from Rott belong to one species because they have different pigmentation patterns. S. colorata for example is bicoloured. Most fossil biting midges from Baltic and Saxonian ambers have lost their colouration, most probably by activity of succinic acids, and this character has no diagnostic value. However, we know nothing about the colour preservation of compression fossils of biting midges.

24. Serromyia spinigera (LOEW, 1850)

Ceratopogon spiniger LOEW, 1850: 30 (Baltic amber).

Serromyia spinigera: SZADZIEWSKI 1988: 140 (Baltic amber).

Material examined: MBI-8-96, 1 c.

Note. Hind femur 6.2 times as long as greatest width. Wing length 2.09 mm, CR 0.68. Genitalia hidden under tip of abdomen. Tip of aedeagus broadly triangular.

Genus Stilobezzia KIEFFER, 1911

Amongst the Saxonian amber inclusions, eleven specimens including five well preserved males have been found. In Baltic amber six species were recognized, of which only one was named. I did not propose new names for these Baltic amber specimens because females predominated in the material and the males available had barely visible genitalia inappropriate for clear diagnoses. In contrast, in Saxonian amber I found males with readily visible genitalia, and I therefore decide to propose new names for this material.

Fossil *Stilobezzia* are known from Lower Miocene compression fossils from Rott in Germany (STATZ 1944), from Baltic amber (SZADZIEWSKI 1988), amber of Sakhalin (SZADZIEWSKI 1990), and from the presently studied Saxonian amber. From Sakhalin amber only a single male of an unnamed species was found.

All fossil species of the genus belong to the subgenus Acanthohelea (=Neostilobezzia) except for S. sp. E from Baltic amber which belongs to the subgenus Stilobezzia s.str.

S. veterana (MEUNIER, 1920) and S. goetghebueri STATZ, 1944 are described from single females from Rott and do not exhibit any diagnostic features. I consider them to be conspecific and propose to treat S. goetghebueri as a junior synonym of S. veterana. New synonymy.

Key to named fossil Stilobezzia

1. Basitarsi of all legs with 1-2 stong median spines
Basitarsi of all legs without median spines
2. Wing length 2.5-2.8 mm
Wing shorter than 1.8 mm
3. Aedeagal sclerite broad, with long caudally directed extension. Paramere with broad apex
S. kutscheri sp. n.
Aedeagal sclerite slender, simple. Paramere with pointed apex
4. Paramere simple, rod-like, with pointed evenly curved apex S. saxonica sp. n.
Paramere composed of a broad proximal portion and a slender distal projection with greatly
curved pointed apex

Subgenus Acanthohelea KIEFFER, 1917

syn. Neostilobezzia GOETGHEBUER, 1934

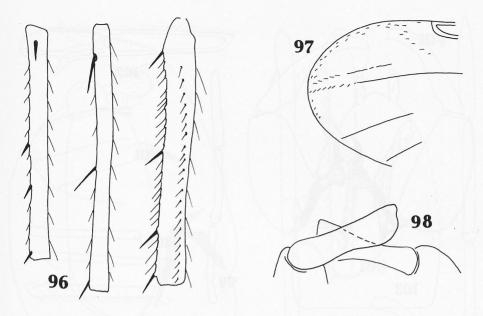
Stilobezzia (A.) indetermined: MBI-8-83, 1 ç; 8-85, 1 ç; 8-86, 1 ç; 8-88, 1 ơ; K-80, 1 ç.

25. Stilobezzia (A.) falcata (MEUNIER,1904) Figs. 96 - 98

Ceratopogon falcatus MEUNIER, 1904: 233 (Baltic amber). Stilobezzia falcata SZADZIEWSKI 1988: 117 (Baltic amber).

Material examined: K-44, 1 σ; K-70, 1 φ.

Note. Both the male and female match the species concept based on specimens from Baltic amber. The female and male have well developed median spines on the basitarsi (Fig. 96). The male wing has less macrotrichia than in the female (Fig. 97). The female is a little bit smaller, with wing length 1.64 mm. The gonostylus of the male is not so distinctly expanded as in specimens from Baltic amber (Fig. 98). However this feature varies with the angle of observation.



Figs. 96 - 98. Stilobezzia falcata (MEUNIER), female K-70, male K-44. 96 – female tarsi of fore, mid and hind leg, 97 – tip of male wing, 98 – gonostyli.

26. Stilobezzia (A.) kutscheri sp. n. Figs. 99 - 103

D i a g n o s i s. Male characteristic in having the lateral sclerites of the aedeagus broad and with a stout distinct apical prolongation directed caudally. The parameres are stout with a broad apical part which is shortly pointed.

Description. Q. Unknown.

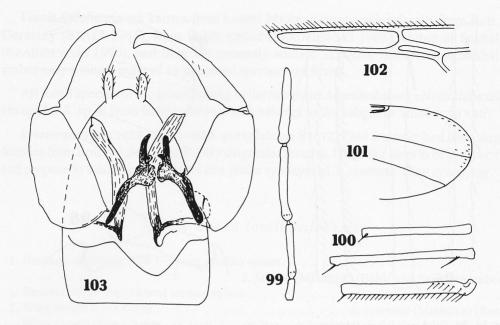
σ. Body dark. Total length 1.6 mm. Flagellum length 848 μm, AR 1.02. Flagellomere X short (Fig. 99). Third palpal segment 40 μm long, sensory pit present. Scutellum bears 4 long bristles. Legs slender. Tibial comb composed of 7 spines. Basitarsi without median spines (Fig. 100). TR(I) 1.8, TR(III) 2.1. Wing length 1.12 mm, CR 0.72. All veins except for costa devoid of setae. Macrotrichia present at wing tip (Fig. 101). Second radial cell 2.9 times longer than first (Fig. 102).

Genitalia (Fig. 103). Sternite IX with deep caudomedian excavation. Tergite IX long with pointed tip. Cerci small. Gonocoxite normal, relatively long. Gonostylus long, slender, with pointed tip. Aedeagus with pair of obliquely situated lateral sclerites, apex of each sclerite with stout caudally directed projection. Parameres separated at bases, stout and broad distally; apices with short blunt projection.

Material examined: Holotype o, K-66.

Etymology. This species is named for Mr. Manfred KUTSCHER of Sassnitz, the owner of the Saxonian amber collection.

Note. There is no species of *Stilobezzia* in the extant fauna of the Holarctic with such shaped aedeagal sclerites.



Figs. 99 - 103. Stilobezzia kutscheri sp. n., male, K-66. 99 - distal 4 flagellomeres, 100 - basitarsi of fore, mid and hind leg, 101 - tip of wing, 102 - first radial cells, 103 - genitalia.

27. Stilobezzia (A.) saxonica sp. n. Figs. 104 - 108

D i a g n o s i s. Male of the species is characteristic in having simple arcuate aedeagal sclerites and rod-like parameres with pointed evenly curved ventrally directed apices.

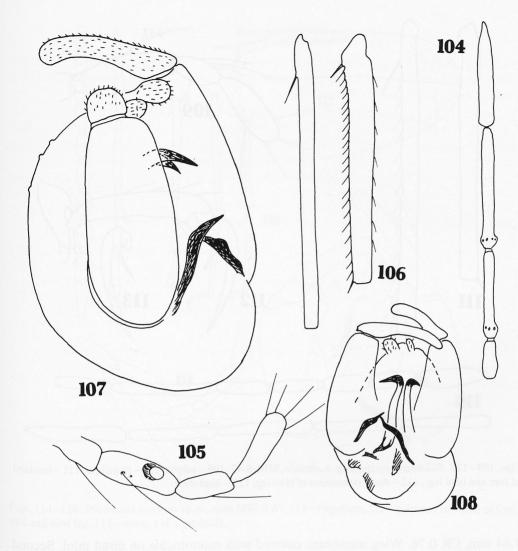
Description. q. Unknown.

 σ . Body dark brown. Total length 2.03 mm. Flagellum length 1050 μm, AR 1.00 (Fig. 104). Third palpal segment 68 μm long, sensory pit present (Fig. 105). Scutellum bears 4 long bristles. Legs slender. Tibial comb composed of 6 spines. Basitarsi without median spines (Fig. 106). TR(II) 3.0, TR(III) 2.2. Wing length 1.45 mm, CR 0.73. Macrotrichia at wing tip present.

Genitalia (Figs. 107, 108) in normal position. Sternite IX barely visible, probably with broad caudomedian excavation. Tergite IX long with rounded apex. Cerci distinct. Gonocoxite long and slender. Gonostylus long, with blunt rounded tip. Aedeagal sclerites typical of the subgenus, in shape of arcuate obliquely situated sclerites. Parameres separate, long, with beak-shaped apices directed ventrally.

Material examined: Holotype o, K-61 (+Collembola 1).

Note. Male genitalia of the new species are similar to those of extant *Stilobezzia* lutacea EDWARDS from Europe and S. pruefferi SZADZIEWSKI from Algeria. However, the extant species have the tips of parameres bifid or with a preapical tooth.

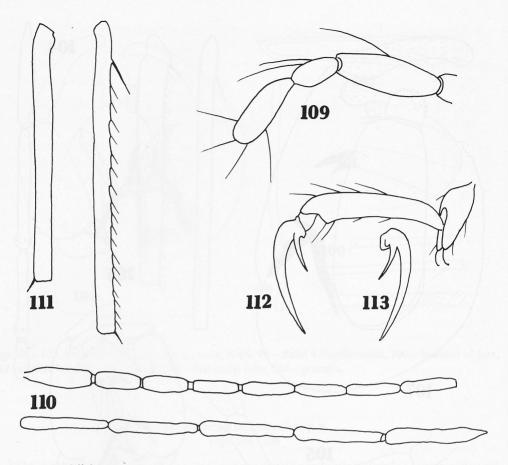


Figs. 104 - 108. Stilobezzia saxonica sp. n., male, K-61. 104 - distal 4 flagellomeres, 105 - palpus, 106 - basitarsi of of mid and hind leg, 107 - lateral aspect of genitalia, 108 - ventral aspect of genitalia.

28. Stilobezzia (A.) succinea sp. n. Figs. 109 - 118

D i a g n o s i s. Male characteristic in having the distal projection of the parameres long and slender, with sharply curved tip.

Description. φ. Body dark brown. Total length 1.9 mm. Flagellum length 1357 μm, AR 1.08 (Fig. 110). Third palpal segment 88 μm long, sensory pit not visible (Fig. 109). Scutellum bears 9 bristles. Legs slender. Tibial comb composed of 6 spines. Basitarsi without median spines (Fig. 111). Claws similar on all legs, greatly unequal (Figs. 112, 113). Fourth tarsomeres cordiform. TR(I) 2.1, TR(II) 2.6, TR(III) 2.4. Wing length



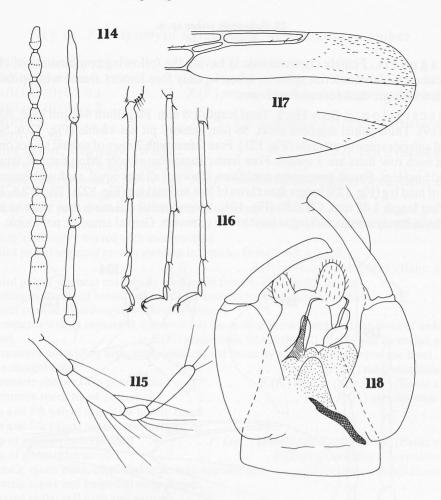
Figs. 109 - 113. *Stilobezzia succinea* sp. n., female, MBI-8-47. 109 - palpus, 110 - flagellum, 111 - basitarsi of fore and hind leg, 112 - distal tarsomeres of hind leg, 113 - hind claw.

1.64 mm, CR 0.76. Wing membrane covered with macrotrichia on distal third. Second radial cell 2.6 times longer than first one. Genital armature not visible.

 σ . Body dark brown. Total length 2.3 mm. Flagellum length 1200 μm, AR 1.10 (Fig. 114). Third palpal segment 72 μm long, sensory pit not visible (Fig. 115). Tibial comb with 6 spines. Basitarsi without median spines (Fig. 116). TR(I) 1.7, TR(II) 2.3, TR(III) 1.9. Wing length 1.78 mm, CR 0.74. Second radial cell 2.5 times longer than first (Fig. 117). Wing membrane covered with macrotrichia at apex.

Genitalia (Fig. 118) slightly rotated. Sternite IX barely visible. Tergite IX with slender apex and big ear-shaped cerci. Gonocoxite normal. Gonostylus long, almost cylindrical with short pointed apex. Aedeagal sclerites simple, slightly arcuate. Parameres barely visible on proximal portion; composed of a broad proximal portion and a distal slender long projection with hook-shaped pointed tip.

Material examined: Holotype of, MBI-8-87 (+Chironomidae, Orthocladiinae, 2 of). The female described here, embedded in amber piece MBI-8-47, is not designated as a paratype.



Figs. 114 - 118. Stilobezzia succinea sp. n., male MBI-8-87. 114 - flagellum, 115 - palpus, 116 - tarsi of fore, mid and hind leg, 117 - wing, 118 - genitalia.

Tribe *Palpomyiini*Genus *Palpomyia* MEIGEN, 1818

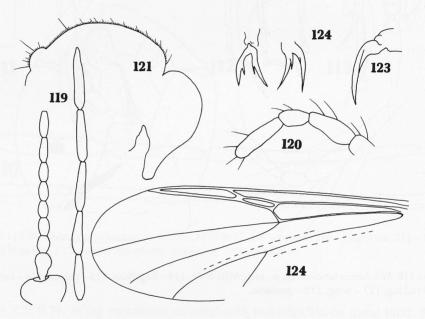
Key to Palpomyia from Baltic and Saxonian amber

1. All femora armed with ventral spines	
Only fore femur armed with ventral spines	
2. Claws on all legs of female short. Wing length 1.2 mm	
P. riedeli Szadziewski	
Claws on hind leg of female long. Wing length 2.9 mm	
3. Scutum with anterior tubercle P. succinea SZADZIEWSKI	
- Scutum without anterior tubercle	P. erikae sp. n.

29. *Palpomyia erikae* sp. n. Figs. 119 - 124

D i a g n o s i s. Female characteristic in having the following combination of characters: scutum without anterior spine or tubercle, only fore femora armed with spines, and hind claws longer than fore and mid ones.

Description. \circ . Body black. Total length 1.8 mm. Flagellum 840 μ m long, AR 1.44 (Fig. 119). Third palpal segment short, 56 μ m; sensory pit not visible (Fig. 120). Scutum without anterior spine or tubercle (Fig. 121). Fore femur with 2 rows of ventral spines on distal half; in each row there are 4 spines. Fore femur somewhat stouter than unarmed femora of mid and hind legs. Fourth tarsomeres cordiform. Claws of all legs equal, each with inner tooth. Claws of hind leg (Fig. 123) longer than claws of fore and mid leg (Fig. 122). TR(II) 2.6, TR(III) 2.4. Wing length 1.40 mm, CR 0.80 (Fig. 124). Second radial cell more than twice as long as first. Media barely sessile, forking at base of r-m crossvein. Genital armature not visible.



Figs. 119 - 124. Palpomyia erikae sp. n., female MBI-8-1. 119 - flagellum, 120 - palpus, 121 - lateral aspect of thorax, 122 - claws of fore leg, 123 - claws of hind leg, 124 - wing.

d. Unknown.

Material examined: Holotype o, MBI-8-1.

Etymology. The species is named for Dr. Erika PIETRZENIUK of the Museum für Naturkunde in Berlin, the curator of the amber collection, in recognition of her help during the present study of *Ceratopogonidae* in Saxonian amber.

Subfamily Forcipomyiinae

Genus Forcipomyia MEIGEN, 1818

Forcipomyia indetermined: K-33, 1 o; K-91, 1 o; K-105, 1 o.

Key to Forcipomyia from Baltic and Saxonian amber

1.	TR(III) lower than 1.2
	TR(III) higher than 1.7
2.	. TR(II and III) 0.2-0.3 F.(F.) pseudomicrohelea SZADZIEWSKI (Baltic amber)
	. TR(II and III) 0.5-1.2
3.	. TR(II) 0.5
	. TR(II) 0.8-1.2
4.	Large species, wing length 1.8 mm
	Small species, wing length 0.8-1.2 mm
5.	Empodia absent in male F.(F.) eotrichoheleana SZADZIEWSKI (Baltic amber)
	Empodia well developed in male
6.	Wing with a pattern formed by dense and sparse macrotrichia
	F. (F.) lyneborgi SZADZIEWSKI (Baltic amber)
	Wing uniformly covered with macrotrichia
7.	Third palpal segment greatly swollen in female. Female AR 1.3-1.5
	F.(F.) turbinata (MEUNIER)(Baltic amber)
_	Third palpal segment not greatly swollen in female. Female AR 0.8-1.0
	Aedeagus short and broad, with strongly sclerotized triangular projection
_	Distal portion of aedeagus weakly sclerotized
	Parameres widely separated, connected at bases by a narrow bridge at the level of aedeagal
٠.	arms F(F) godanicals SAADATTYVOKI (Politic and Secondary and the level of acceptable)
	arms
-	Parameres not widely separated, connected at bases by a wide bridge below the level
n	of aedeagal arms
u.	Paramere shorter than gonocoxite F.(F.) uncula (MEUNIER) (Baltic amber)
 1	Paramere reach tip of gonocoxite
11.	4th and 5th palpal segments totally fused
	4th and 5th palpal segments separated
4.	Tip of gonostylus expanded F. (sg.?) krzeminskii SZADZIEWSKI (Baltic amber)
	Tip of gonostylus slender
3.	Female claws bifid, empodial setae with capitate tips F. (Trichohelea) bifidicola sp. n.
	Female claws and empodial setae simple
4.	Second radial cell long and narrow
-	Second radial cell short, if elongated then broad
٥.	Female flagellomeres II-VII compressed and short
-	Female flagellomeres II-VII ovoid
0.	Female proximal flagellomeres compressed, AR 1.5 $F.(T.)$ succinicola sp. n.
	Female proximal flagellomeres not compressed
1.	Empodia absent in male F. (Phytohelea) eophytoheleana SZADZIEWSKI (Baltic amber)
	Empodia present in male
8,	Male flagellum with 10 flagellomeres
	F. (sg.?) eobreviflagellata SZADZIEWSKI (Baltic amber)
	Male flagellum with 13 flagellomeres
9.	Gonostylus with enlarged tip F.(sg.?) kulickae SZADZIEWSKI (Baltic amber)
	Tip of gonostylus slender
20.	Aedeagus short, as long as broad
	Aedeagus long, about 2 times longer than broad
21.	Aedeagus arch-shaped. Parameres long F.(E.) piriformis (MEUNIER) (Baltic amber)
	Aedeagus shield-shaped. Parameres fused with apodemes of gonocoxites into U-shaped
	structure lacking submedian projections F.(E.) miocaenica sp. n
22.	Tip of aedeagus distinctly bilobed F. (E.) berendti SZADZIEWSKI (Baltic amber)
	Tip of aedeagus evenly pointed F.(E.) henningseni SZADZIEWSKI (Baltic amber)

Subgenus Forcipomyia MEIGEN, 1818

Forcipomyia (F.) indetermined (57 \circ 0, 30 \circ 0). MBI-7-4, 1 \circ ; 8-33, 1 \circ (+ Mycetophilidae 1 \circ , Dolichopodidae 1); 8-42, 1 \circ ; 8-52, 1 \circ ; 8-56, 1 \circ ; 8-58, 1 \circ ; 8-61, 1 \circ ; 8-65, 1 \circ ; 8-71, 1 \circ ; 8-74, 2 \circ 9; 8-78, 1 \circ ; 8-90, 1 \circ ; 8-94, 1 \circ ; 8-97, 1 \circ ; 8-98, 1 \circ ; 8-101, 1 \circ ; 8-104, 1 \circ ; 8-106, 1 \circ ; 8-108, 1 \circ ; 8-109, 1 \circ ; 8-117, 1 \circ ; 8-119, 1 \circ ; 8-120, 1 \circ ; 8-126, 1 \circ ; 8-128, 1 \circ ; 8-130, 1 \circ ; 8-134, 2 \circ 9; 8-135, 1 \circ ; 8-146, 1 \circ ; 8-147, 1 \circ ; 8-151, 1 \circ ; 8-153, 1 \circ ; 8-155, 1 \circ ; 8-156, 1 \circ ; 8-161, 1 \circ ; 8-162, 1 \circ ; 8-163, 1 \circ ; 8-169, 1 \circ ; 9-4, 1 \circ (+Chironomidae 1 \circ); 10-1a, 1 \circ ; 10-4, 1 \circ ; 10-6, 1 \circ ; 10-8, 1 \circ ; 10-10, 1 \circ ; 11-1, 1 \circ ; 11-3, 1 \circ 1 \circ ; 11-5, 2 \circ 9.

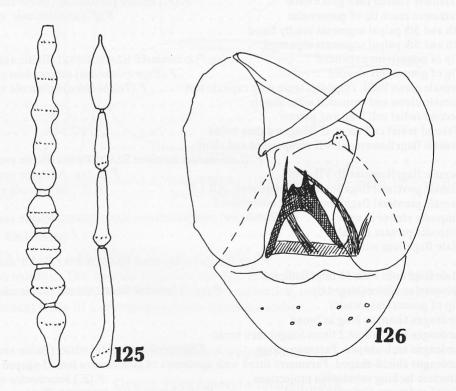
K-1, 1 o; K-3, 1 o; K-4, 1 o; K-7, 1 o; K-8, 1 o; K-9, 1 o; K-13, 1 o; K-16, 1 o; K-21, 1 o; K-22, 1 o; K-23, 1 o; K-27, 1 o (+Hymenoptera 1); K-30, 1 o; K-35, 1 o (at Brachypogon prominulus); K-34, 1 o; K-37, 1 o; K-40, 1 o; K-41, 1 o; K-42, 1 o; K-55, 1 o; K-60, 1 o; K-62, 1 o; K-63, 1 o; K-67, 1 o; K-68, 1 o; K-76, 1 o; K-77, 1 o; K-79, 1 o; K-81, 1 o; K-82, 1 o; K-86, 1 o; K-87, 1 o; K-88, 1 o; K-94, 1 o; K-101, 1 o; K-104, 1 o.

30. Forcipomyia (F.) gedanicola SZADZIEWSKI, 1988 Figs. 125 - 126

Forcipomyia gedanicola SZADZIEWSKI, 1988: 200 (Baltic amber).

Material examined: MBI-8-103, 1 o; 8-143, 1 o.

Note. These specimens agree with Baltic amber specimens in all features.



Figs. 125 - 126. Forcipomyia (F.) gedanicola SZADZIEWSKI, male MBI-8-143. 125 - flagellum, 126 - genitalia.

31. Forcipomyia (F.) subgedanicola sp. n. Figs. 127 - 130

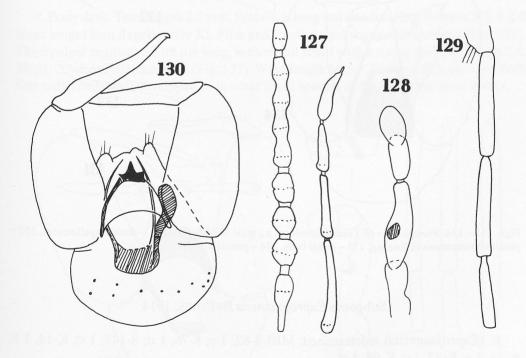
Diagnosis. This species is similar to *F. gedanicola*. Male distinguished by parameres broadly fused at the bases which are located proximad of aedeagus for a considerable distance.

Description. Q. Unknown.

σ. Body brown. Total length 1.6 mm. Flagellum length 840 μm, AR 0.86. Flagellomeres V-VIII fused (Fig. 127). Flagellomere X 1.4 times longer than flagellomere XI. Third palpal segment slender, length 72 μm, sensory pit small (Fig. 128). TR(III) 1.1 (Fig. 129). Wing length 0.95 mm, CR 0.52. Both first radial cells developed, first one small, second one distinct. Wing membrane uniformly covered with macrotrichia.

Genitalia (Fig. 130). Caudomedian excavation of sternite IX not visible. Gonocoxite simple. Gonostylus slightly sinuous on distal third, tip beak-like. Aedeagus short, well sclerotized, with a short triangular apical projection and a pair of smaller apicolateral horns. Parameres moderately long, broadly fused at bases which are situated proximad of the aedeagus. Gonocoxal apodemes long.

Material examined: Holotype of, MBI-8-105.



Figs. 127 - 130. Forcipomyia (F.) subgedanicola sp. n., male MBI-8-105. 127 - flagellum, 128 - palpus, 129 - proximal tarsomeres of hind leg, 130 - genitalia.

32. Forcipomyia (F.) unculiformis sp. n. Figs. 131 -134

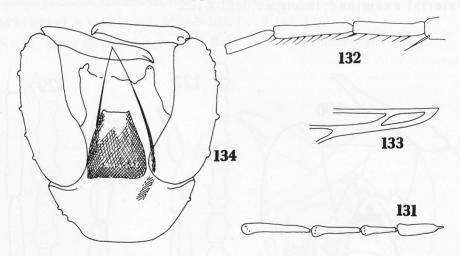
Diagnosis. This species is close to F. uncula from Baltic amber. Male distinguished by long parameres extending beyond tergite IX and lacking a first radial cell.

Description. q. Unknown.

 σ . Body black. Total length 2.0 mm. Flagellum length 773 μm, AR about 0.98. Flagellomere X 1.4 times longer than next one (Fig. 131). Palpus barely visible. Third palpal segment slightly enlarged on basal third. TR(I) 1.0 (Fig. 132). Wing length 1.14 mm, CR 0.47. Membrane uniformly covered with macrotrichia. First radial cell absent, second one distinct (Fig. 133).

Genitalia typical of the subgenus (Fig. 134). Gonocoxite slightly curved, moderately slender. Gonostylus nearly straight, with pointed beak-like tip. Aedeagus with low basal arch, distal portion barely visible, probably weakly sclerotized. Parameres broadly separated at the level of aedeagus, extending well beyond tip of tergite IX, slender, gradually tapering and converging.

Material examined: Holotype of, MBI-8-149.



Figs. 131 - 134. Forcipomyia (F.) unculiformis sp. n., male MBI-8-149. 131 - distal flagellomeres, 132 - proximal tarsomeres of fore leg, 133 - radial cells, 134 - genitalia.

Subgenus Euprojoannisia BRÈTHES, 1914

F. (Euprojoannisia) indetermined: MBI-8-62, 1 o; 8-76, 1 o; 8-145, 1 o; K-14, 1 o; K-28, 1 o; K-32, 1 o; K-98, 1 o.

Note. A female preserved in amber piece MBI-8-62 has a very transparent abdominal segment IX. Sternite IX is strongly sclerotized, broad and fused with tergite IX into a ring (Fig. 135). In extant Holarctic species of the subgenus, sternite IX is weakly sclerotized and usually divided into 2 slender lateral pieces (BYSTRAK & WIRTH 1978).

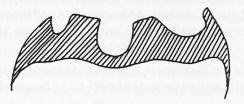


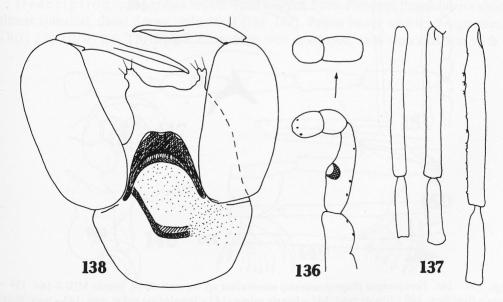
Fig. 135. Forcipomyia (Euprojoannisia) indet., female MBI-8-62. Shape of sternite IX.

33. Forcipomyia (E.) miocaenica sp. n. Figs. 136 - 138

D i a g n o s i s. Male distinguished by the following combination of characters: TR(III) 2.4-2.5; parameres and gonocoxal apodemes form an U-shaped structure, no submedian projections; aedeagus low, with broadly rounded tip.

Description. Q. Incomplete. Barely visible. Third palpal segment 84 μm long, sensory pit small. Proximal flagellomeres bottle-shaped. TR(III) 2.4. Wing length 1.26 mm.

σ. Body dark. Total length 2.3 mm. Proboscis long and slender. Flagellomere X 1.9-2.0 times longer than flagellomere XI. Fifth and fourth palpal segments separated (Fig. 136). Third palpal segment 83-88 μm long, sensory pit small with a round opening. TR(I) 2.4, TR(II) 2.3-2.6, TR(III) 2.4-2.5 (Fig. 137). Wing length 1.25-1.26 mm, CR 0.49-0.50. Both first radial cells well developed as in other fossil species of the subgenus from amber.



Figs. 136 - 138. Forcipomyia (Euprojoannisia) miocaenica sp. n., male MBI-8-152. 136 - palpus, 137 - proximal tarsomeres of fore, middle and hind leg, 138 - genitalia.

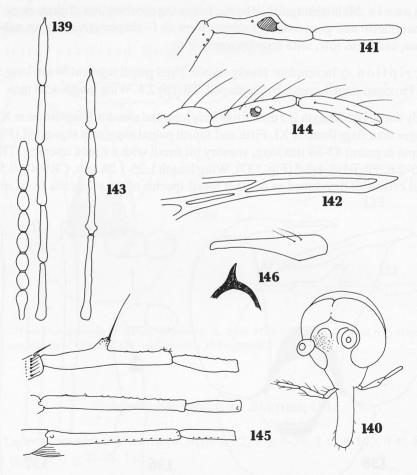
Genitalia (Fig. 138). Sternite IX barely visible. Gonocoxite and tergite IX normal. Gonostylus slender and almost straight. Aedeagus short and broad, apical portion broadly rounded. Apodemes of gonocoxites form with parameres a U-shaped bridge. Distal submedian projections of parameres not developed.

Material examined: Holotype of, MBI-8-152 (+Acarina, 1 specimen on dorsal surface of abdomen). Not included in the type series: MBI-8-89, 1 of 1 of because they are not well preserved.

34. Forcipomyia (E.) tuberculosa sp. n. Figs. 139 - 146

Diagnosis. Both sexes of the species can be readily distinguished from other fossil species by their fused 4th and 5th palpal segments.

Description. φ . Body hairy, brown. Total length 1.7 mm. Flagellum length $960\,\mu m$, AR 1.72 (Fig. 139). Proboscis long and slender (Fig. 140). Third palpal segment slender,



Figs. 139 - 146. Forcipomyia (Euprojoannisia) tuberculosa sp. n.; male K-19; female MBI-8-164. 139 – female flagellum, 140 – female head, 141 – female palpus, 142 – female first radial cells, 143 – male distal flagellomeres, 144 – male palpus, 145 – male proximal tarsomeres of hind, middle and fore leg, 146 – aedeagus and gonostylus.

 $116~\mu m$ long; sensory pit at midlength, opening at distal third. Fourth and fifth palpal segments totally fused, length $96~\mu m$ (Fig. 141). Legs slender with long setae. TR(I) 2.4, TR(II) 2.5. Empodia well developed. Wing length 1.14 mm, CR 0.70. Second radial cell long and broad, first small and narrow (Fig. 142). Membrane uniformly covered with macrotrichia.

σ. Body brown; legs, antennae and palpi pale. Total length 1.6 mm. Flagellum length 908 μm, AR about 0.66. Flagellomeres V-VIII probably fused. Flagellomere X 1.5 times longer than flagellomere XI (Fig. 143). Proboscis long and slender. Palpus slender; third palpal segment 96 μm long; sensory pit small, at midlength of segment (Fig. 144). Fourth and fifth palpal segments fused, length 92 μm. Legs slender with very long setae. TR(I) 2.3, TR(II) 2.7, TR(III) 2.1. One basitarsus of hind leg with ubnormally developed tubercle bearing long setae (Fig. 145); second basitarsus normal. Empodia well developed. Wing length 1.23 mm, CR about 0.66. Radial cells barely visible.

Genitalia barely visible because they are twisted under tip of abdomen. Sternite IX, tergite IX and gonocoxites normal. Gonostylus slender, almost straight (Fig. 146). Aedeagus arch-shaped with distinct bifid apical projection. Parameres not visible.

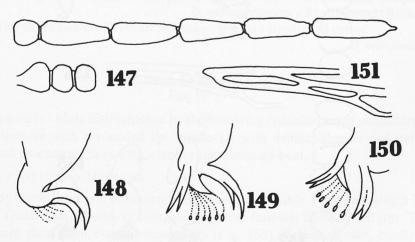
Material examined: Holotype o, K-19. Paratype o, MBI-8-164.

Subgenus Trichohelea GOETGHEBUER, 1920

35. Forcipomyia (T.) bifidicola sp. n. Figs. 147 - 151

D i a g n o s i s. Female characteristic in having a large TR (2.5-2.6), bifid claws and empodial setae with capitate tips.

Description. q. Body dark brown. Total length 1.5 mm. Proximal flagellomeres short, almost spherical, distal 5 long, cylindrical (Fig. 147). Palpus barely visible, 5-segmented. TR(I) 2.6, TR(II) 2.6, TR(III) 2.5. Empodium well developed, each empodial seta with a



Figs. 147 - 151. Forcipomyia (Trichohelea) bifidicola sp. n., female K-6. 147 - proximal 3 and distal 6 flagellomeres, 148 - lateral aspect of claws of fore leg, 149 - frontal aspect of fore claws, 150 - claws of hind leg, 151 - first radial cells.

capitate tip (Figs. 149, 150). Claws with deeply bifid tips. Wing length 0.94 mm, CR 0.60. Both first radial cells present (Fig. 151). Membrane uniformly covered with macrotrichia.

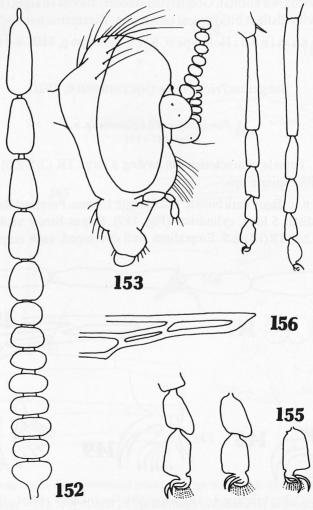
o. Unknown.

Material examined: Holotype o, K-6.

36. Forcipomyia (T.) succinicola sp. n. Figs. 152 - 156

Diagnosis. Female characteristic in having compressed proximal flagellomeres, short distal flagellomeres, simple claws, and TR(III) 2.9.

Description. φ . Body dark brown. Total length 1.0 mm. Flagellum 364 μ m long, AR 1.52. Proximal flagellomeres II-VII transverse, compressed. Distal flagellomeres relatively short (Fig. 152). Palpus 5-segmented. Third palpal segment stout and short.



Figs. 152 - 156. Forcipomyia (Trichohelea) succinicola sp. n., female MBI-8-32. 152 - flagellum, 153 - lateral aspect of head, 154 - tarsi of fore and hind leg, 155 - claws of fore, middle and hind leg, 156 - first radial cells.

Scutum moderately hairy. TR(I) 2.7, TR(II) 2.5, TR(III) 2.9 (Fig. 154). Empodia (Fig. 155) well developed, empodial hairs simple. Claws sharply curved, with simple apices (Fig. 155). Wing length 0.68 mm, CR 0.52. Both first radial cells present (Fig. 156). Wing membrane not very hairy, in basal radial cell only 3 macrotrichia are present.

o. Unknown.

Material examined: Holotype o, MBI-8-32.

Subfamily Dasyheleinae LENZ, 1934

Genus Dasyhelea Kieffer, 1911

In the material examined five specimens have been found. All unidentified females have a line-like first radial cell and a relatively well developed second one.

Dasyhelea indetermined: MBI-8-48, 1 o; 8-129, 1 o; 8-133, 1 o; 8-154, 1 o.

Key to Dasyhelea from Baltic and Saxonian amber

Males

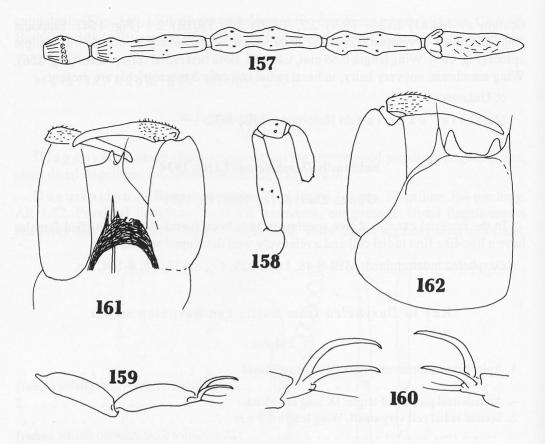
1. Apicolateral process of tergite IX short and broad
D. stanislavi SZADZIEWSKI (Baltic amber)
Apicolateral process of tergite IX long and slender
2. Second radial cell very small. Wing length 0.7 mm
Second radial cell larger. Wing length greater than 1.2 mm
3. Wing length 1.7 mm
Wing length 1.2-1.3 mm
4. Terminal flagellomere with slender apical projection. Claws stout and nearly straight
· · · · · · · · · · · · · · · · · D. eodicryptoscenica SZADZIEWSKI (Baltic amber)
Terminal flagellomere with evenly pointed apex. Claws slender and curved
· · · · · · ·

37. Dasyhelea miocaenica sp. n. Figs. 157 - 162

Diagnosis. Male distinguished by the following combination of characters: terminal flagellomere with a rounded tip; tergite IX with distinct slender and cylindrical apicolateral processes; claws long, slender and distinctly bent.

Description. q. Unknown.

σ. Body blackish brown. Pubescence of eyes readily visible. Flagellum length $720\,\mu m$, AR 0.97. Distal 4 flagellomeres elongate, length as follows: 92-88-78-80 μm. Terminal flagellomere short with evenly rounded tip (Fig. 157). Palpus slender, barely visible (Fig. 158). Third palpal segment 68 μm long. Legs slender. Tibial comb composed of 5 spines. Claws relatively long, slender, and evenly bent at basal third, apices bifid (Figs. 159, 160). Empodium obsolete. TR(II) 1.9, TR(III) 1.7. Wing length 1.19 mm, CR



Figs. 157 - 162. *Dasyhelea miocaenica* sp. n., male K-15. 157 - distal flagellomeres, 158 - palpus, 159 - distal 2 tarsomeres of middle leg, 160 - claws of middle leg, 161 - ventral aspect of genitalia, 162 - laterodorsal aspect of genitalia.

0.54. Wing membrane covered with macrotrichia except for basal radial cell. First radial cell line-like, second barely visible, distinct.

Genitalia (Fig. 161, 162), slightly rotated. Sternite IX barely visible. Tergite IX with long and slender apicolateral process and a well developed triangular expansion located more medially of it. Gonocoxite moderately slender, straight. Gonostylus slender, unmodified, slightly curved distally. Aedeagus arch-shaped, with a concave tip, and with ventro-lateral expansions. Median projection of parameres slender with pointed tip, extending well beyond tip of aedeagus. Basal arms of aedeagus not visible.

Material examined: Holotype o, K-15.

Note. The male of the species has unusually slender and long curved claws which in other recent or fossil representatives of the genus are almost straight, relatively short, and with a somewhat enlarged basal half.

s = 23.8

IV. DISCUSSION

In the Miocene Saxonian amber 12 species are recognized to occur in older Baltic amber. They are: Culicoides ceranowiczi, C. speciosus, Brachypogon prominulus, Ceratopogon forcipiformis, C. hennigi, Chimaerohelea nielseni, Eohelea sinuosa, Mantohelea gedanica, Monohelea clunipes, Serromyia spinigera, Stilobezzia falcata and Forcipomyia gedanicola. They represent 32.4% or one third of the Saxonian amber species. This suggests that during the Tertiary the evolution of biting midges was slow and species lived in stable conditions at least from the Upper Eocene (37.5 Ma) to the Lower Miocene (22 Ma), a period of 15 million years. Species common to both Saxonian and Baltic amber faunas have also been found in other groups of insects, such as the Limoniidae (SCHU-MANN & WENDT 1989).

The shared presence of twelve species might also be due a misdating of at least some Saxonian amber, which potentially may be derived from older deposits than currently thought. As such, the shared species may merely reflect a temporal overlap of the two ambers. To address this possibility, similarity indices were calculated comparing a variety of collections and comparing Saxonian and Baltic amber faunas, using the modified JACCARD's formula (SZADZIEWSKI 1983):

$$s = c \times \frac{100}{a + b - c}$$

where s – similarity index, a – the species number of one fauna, b – the species number of the other fauna, and c - the number of species in common.

The similarity indices for Baltic and Saxonian amber collections are as follows:

Saxonian amber (37 spp.) – Baltic amber (101 spp.)	s = 9.5
KUTSCHER's coll. (18 spp.) – MBI coll.(26 spp.)	s = 18.9
Baltic amber	
MZW coll.(70 spp.) – ZMC coll.(50 spp.)	s = 31.3
ZMC coll.(50 spp.) – MBI coll.(29 spp.)	s = 25.4

The similarity index between the biting midges faunas found in Saxonian and Baltic amber is the lowest one and may reflect that the biting midges actually represent faunas from different geological periods. Generally the similarity indices are low when comparing the collections. This indicates that only small part of the fauna is presently known from Saxonian amber (s = 18.9 between K and MBI coll.), and is more completely known from Baltic amber where the similarity indices between various collections are higher (23.8 to 31.3).

MZW coll.(70 spp.) – MBI coll.(29 spp.)

Only three fossil genera have been found in Saxonian amber while six are recorded in the older Baltic amber. However, this difference may be merely due to the significantly lower number of specimens of Saxonian amber available for study.

When compared to the fauna known from Baltic amber, a quantitative composition of biting midges in Saxonian amber is similar for some taxa while distinctly different for some others.

As a percentage of the total Ceratopogonidae fauna, the following genera are similar: Culicoides, Eohelea, Fossihelea, Stilobezzia, Ceratopogon, Dasyhelea (Tables I, II). However, Brachypogon at 2.7% in Saxonian amber as compared to 14.3% in Baltic amber and Monohelea with 0.9% and 2.5% respectively, were significantly lower. Forcipomyia was more common in Saxonian amber (32.1%) than in Baltic amber (15.9%). Although these differences may be due to differences in the amber producing forest, it seems more likely that the increasing importance of the genus Forcipomyia had a significant influence on the diversification of the family.

Another pattern is present which indicates a degree of faunal turnover. The genus Atrichopogon is represented by only one specimen in Baltic amber (out of a total of 1103) and was absent from Saxonian and Sakhalin ambers (SZADZIEWSKI 1988, 1990). However it is clear that the genus is common today and is readily collected by sticky traps placed in pine forests in northern Poland. For example, of 154 specimens of biting midges collected by such a trap, 18.2% were Atrichopogon and these were more common than Forcipomyia at 15.5% (unpublished data).

Table I
A composition of the Saxonian amber Ceratopogonidae († fossil genera)

Taxon	ರರ	ÇÇ	Total	%
Ceratopogoninae	106	117	223	66.36
Culicoidini				
Culicoides	50	18	68	20.23
Ceratopogonini	56	98	154	45.83
Brachypogon	5	4	9	2.68
Ceratopogon	36	60	96	28.57
Chimaerohelea	_	2	2	0.60
†Eohelea	1	7	8	2.38
†Fossihelea	1	5	6	1.79
†Mantohelea	6666 <u>-</u> 551	1	1	0.30
Monohelea	1	2	3	0.90
Nannohelea	endr <u>a</u> s ed	1	1	0.30
Serromyia	7	10	17	5.06
Stilobezzia	5	6	11	3.27
Palpomyiini				
Palpomyia	_	1	1	0.30
Forcipomyiinae		Distributions		
Forcipomyia	41 .	67	108	32.14
Dasyheleinae				
Dasyhelea	1	4	5	1.49
Total	148	188	336	100.0

Table II
A comparison of the Baltic and Saxonian amber Ceratopogonidae
(† fossil genera)

Taxon	Baltic amber	Saxonian amber
Ceratopogoninae	82.05%	66.36%
Culicoidini (Culicoides)	17.77%	20.23%
Ceratopogonini	61.83%	45.83%
Alluaudomyia	1.45%	F.J. D. 1270. Possile
Brachypogon	14.32%	2.68%
†Ceratopalpomyia	+	
Ceratopogon	25.30%	28.57%
Chimaerohelea	2.18%	0.60%
†Eohelea	4.53%	2.38%
Ceratoculicoides	real reserves top statutory by	
†Fossihelea	1.25%	1.79%
†Gedanohelea	initern). Pa# domographics.	(Cambinogr a iotars 3)
†Mantohelea	i, los tatales, anti-testado los testa	authoriti + El Alas
Monohelea	2.45%	0.90%
Nannohelea	tute Cyarama +	the state of the state of
Serromyia	2.45%	5.06%
Stilobezzia	2.63%	3.27%
†Wirthohelea	High Ald solon+ and rough	l & mol?. Ge±soyoqoni
Heteromyiini		
Neurohelea	o common o + mence o	d land snals in fre
Physohelea	+	ntossiy ter <u>a</u> nod "la
Palpomyiini		A STATE OF THE STATE OF
Bezzia	+	_
Palpomyia	+	+
Forcipomyiinae	ers wither the cesses from	
Atrichopogon	any commacts of shell	Tailer Z. T ugcZ80
Forcipomyia	15.87%	32.14%
Dasyheleinae	my. The deposits coasis	d of back grey clay
Dasyhelea	1.63%	1.49%
Leptoconopinae		TOY DISPLAY AND STREET
Leptoconops		7
Number of specimens	1103	336
Number of species	101	37
Number of specimens in a single amber piece	1.16	1.12

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