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

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Abstract. The biting midges found in Saxonian amber, collected from coals near Bitter- feld, 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 bittfeldi, C. kotejai, C. miocaenicus, C. subeminens, C. succinicolus, Chimaerohelea miocaenica, Eohelea fossico- la, E. miocaenae, Fossihelea miocaenica, Stilobezzia kutscheri, S. saxonica, S. succinea, Palpomyia erikae, Forcipomyia subgedanensis, F. unciformis, F. miocaenica, F. tuberculosa, F. bifidicola, F. succinicolae, 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 (BARTHIEL & 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. succiniculus* 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. ceranoviczi*, 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 amber or with extant material.

*Culicoides* indetermined 36 (20 ♀♀, 16 ♂♂).

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

K-5, 1 ♂; K-11, 1 ♂; K-24, 1 ♂ 1 ♀ (+*Chironomidae* 8 ♂ 1 ♀); K-53, 1 ♂; K-56.b, 1 ♂ (at 56.a *Ceratopogon forcipiformis* 1 ♂); K-93, 1 ♂ (+*Ceratopogon* indet. 1 ♀); K-107, 1 ♀.
Key to named Culicoides from Baltic and Saxonian amber

Males

1. Aedeagus more or less Y-shaped, caudomedian projection single ........................................... 2
   – Aedeagus with 2 or 3 distinct apical projections ................................................................. 7
2. Gonostylus sinuous, somewhat S-shaped ...................................................................................... 3
   – Gonostylus not sinuous, C-shaped ......................................................................................... 4
3. Basal arch of aedeagus low. Apicolateral process of tergite IX slender, cylindrical ..............
   ......................................................... C. gedanensis SZADZIEWSKI (Baltic amber)
   – 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 ..............
   .................................................................................................................. C. balticus SZADZIEWSKI (Baltic amber)
   – Apicolateral process of tergite IX pointed. Tip of paramere simple ................................... .5
5. Apicolateral process of tergite IX very short. Basal radial cell without macrotrichia ........
   .................................................................................................................. C. succivarius SZADZIEWSKI (Baltic amber)
   – Apicolateral process of tergite IX long. Basal radial cell with macrotrichia ......................... .6
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 .................................................................................................................. C. prussicus SZADZIEWSKI (Baltic amber)
   – Paramere long. Caudomedian margin of tergite IX not extending beyond tip of apicolateral
   process .................................................................................................................. .8
8. Aedeagus with 3 long apical projections ..................................................................................... C. eoselficus SZADZIEWSKI (Baltic amber)
   – Aedeagus with 2 long apical projections ..............................................................................
   .................................................................................................................. C. ceranowiczi SZADZIEWSKI (Baltic and Saxonian amber)

1. Culicoides ceranowiczi SZADZIEWSKI, 1988
   Fig. 1

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

Material examined. MBI 8-165, 1 ♂.

Note. The specimen is somewhat larger than those from Baltic amber. Wing length
1.06 mm. Flagellum length 690 μm, 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).


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

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
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

**Diagnosis.** 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.** Unknown.

♂. Body blackish brown. Total length 1.6 mm. Flagellum length 816 μm, 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 μm, 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 ♂, 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 *Stilobeziini*.

**Genus Brachypgon Kieffer, 1899**

**Subgenus Brachypgon Kieffer, 1899**

*Brachypgon* (B.) indetermined.
K-46, 1 ♂; K-57a, b, 2 ♀.

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

**Males**

1. First radial cell well developed ........................................... *B. eocenicus* Szadziewski (Baltic amber)
   – Both radial cells obliterated ................................................ 2
2. Antenna with 10 flagellomeres ........................................... *B. gedanicus* Szadziewski (Baltic amber)
   – Antenna with 13 flagellomeres ........................................... 3
3. Gonostylus slender and strongly curved ................................. *B. balticus* Szadziewski (Baltic amber)
   – Gonostylus basally swollen, nearly straight ........................... *B. miocaenicus* sp. n.
4. *Brachypogon (B.) miocaenicus* sp. n.
Figs. 6 - 11

**Diagnosis.** Male with both first radial cells obliterated, almost straight gonostylus, long divergent parameres and apicolateral process of tergite IX distinct and triangular.

**Description.** Unknown.

♂. 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 ♂, MBI-8-44.

**Subgenus Isohelea KIEFFER, 1917**

*Brachypogon (Isohelea)* indetermined. K-38, 1 ♂.

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

**Males**

1. Antenna with 11 flagellomeres . . . *B.(I.) prominus*us (MEUNIER) (Baltic and Saxonian amber)
- Antenna with 13 flagellomeres ................................................................. 2

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.) prominus* (MEUNIER, 1904)

*Ceratopogon prominus* MEUNIER, 1904: 228 (Baltic amber).
*Brachypogon prominus* : SZADZIEWSKI 1988: 83 (Baltic amber).

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

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

K-10, 1 ♀; K-18, 1 ♂ 1 ♀; K-31, 1 ♂; K-45, 1 ♀; K-47, 1 ♂; K-51, 1 ♂; K-59, 1 ♂ 1 ♀; K-71, 1 ♀; K-72, 1 ♀; K-73, 1 ♂; K-74, 1 ♀; K-75, 1 ♀; K-78, 1 ♀; K-83, 1 ♀; K-89, 1 ♂; K-90, 1 ♀; K-92, 1 ♀; K-93, 1 ♀ (+Culicoides 1 ♂); K-97, 1 ♂ (+Formicidae 1); K-100, 1 ♀; K-102, 1 ♀ (+Chironomidae 1 ♂); K-106, 1 ♂.
Key to named species of *Ceratopogon* from Baltic and Saxonian amber

**Males**

1. Gonostyles when decumbent not reaching level of apicolateral process of tergite IX ........ 2
   - Gonostyles when decumbent reaching level of apicolateral process of tergite IX ........ 5
2. Gonocoxite expanded distally ........................................... *C. bitterfeldi* sp. n.
   - Gonocoxite cylindrical .................................................. 3
3. Gonocoxite 1.7-2.7 times shorter than wing length. Gonostyles 2.5-3.5 times shorter than gonocoxite ........ *C. forcipiformis* MEUNIER (Baltic and Saxonian amber)
   - Gonocoxite 3.2-3.4 times shorter than wing length. Gonostyles 1.7-2.1 times shorter than gonocoxite ........ 4
4. Tergite IX broad and short, with broad triangular apicolateral process. Gonostyles abruptly bent at the base ........................................ *C. subeminens* sp. n.
   - Tergite IX narrow and relatively long, with slender apicolateral process. Gonostyles evenly curving from the base to apex .................. *C. hennigi* SZADZIEWSKI (Baltic and Saxonian amber)
5. Aedeagus with long beak-shaped ventral projection ........................................ *C. kotejai* sp. n.
   - Aedeagus without long beak-shaped ventral projection ................................ 6
6. Parameres large, greatly diverging and extending beyond tergite IX .... 7
   - Parameres smaller, not extending beyond tergite IX ................................ 8
7. Distal part of paramere with short pointed apical projection.
   - Gonostylus somewhat curved ........................................... *C. gedanicus* SZADZIEWSKI (Baltic amber)
   - Distal part of paramere with long pointed apical projection.
     - Gonostylus greatly curved ........................................... *C. succinicolicus* sp. n.
8. Apicolateral process of tergite IX pointed ........................................... 9
   - Apicolateral process of tergite IX blunt ........................................ 11
9. Apicolateral process of tergite IX short and broad ...................... *C. eminens* MEUNIER (Baltic amber)
   - Apicolateral process of tergite IX long and slender .......................... 10
10. Aedeagus with deep basal arch ........................................... *C. gogani* SZADZIEWSKI (Baltic amber)
    - Aedeagus with low basal arch ......................................... *C. tertiaricus* SZADZIEWSKI (Baltic amber)
11. Gonostylus 2.0-2.2 times shorter than gonocoxite ......................... 12
    - Gonostylus 1.0-1.5 times shorter than gonocoxite .......................... 13
12. Gonostylus abruptly bent near the base ...................... *C. crypticus* SZADZIEWSKI (Baltic amber)
    - Gonostylus evenly curved throughout its length .......................... *C. remmicolicus* SZADZIEWSKI (Baltic amber)
13. Paramere with twisted tip. Gonostylus as long as gonocoxite ..............
    - Paramere without twisted tip. Gonostylus shorter than gonocoxite .......... 14
14. Tip of aedeagus distinctly forked ....................................... 15
   - Tip of aedeagus not forked ........................................... 16
15. Aedeagus with 2 pairs of dorsal projections. Gonocoxite 5.8 times shorter than wing length.
    - Apicolateral process of tergite IX short ................................ *C. miocaenicicus* sp. n.
    - 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 ................................
    - Gonocoxite 3.6-4.1 times shorter than the wing ........................ *C. ritzkowskii* SZADZIEWSKI (Baltic amber)
6. *Ceratopogon bitterfeldi* sp. n.
Figs. 12 - 19

**Diagnosis.** Male with big genitalia with gonoxites enlarged distally, and gonostyli, when decumbent not extending to the tips of apicolateral processes of tergite IX.

**Description.** Unknown.

♂. 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 gonoxite, with long, slender, evenly pointed apicolateral processes bearing one subapical seta. Cerci long, slender, extending beyond caudal margin of tergite IX. Gonoxite very long, 360 μm, 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 μm, 2.1 times shorter than gonoxite. 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 ♂, 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 ♂)

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

**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 ♂; 8-11, 1 ♂; 8-70, 1 ♂; 8-127, 1 ♂ 1 ♀; 8-132, 1 ♂; K-52, 1 ♂.

**Note.** Tibial spur of hind leg well developed.
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

**Diagnosis.** Male with highly modified aedeagus composed of a dorsal plate and a ventral, beak shaped, long projection.

**Description.** Unknown.

♂. 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 r₄₊₅. Microtrichia not discernible.

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 120μm. Gonostylus 88μm 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.


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.

Discussion. 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

Diagnosis. 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. Unknown.

♂. 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 r4+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 μm, 2.3 times as long as broad, 5.8 times shorter than wing length. Gonostylus 160 μm 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 σ, 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.

**Description.** ♀. Unknown.

♂. 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 ♂, MBI-8-148.
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:

<table>
<thead>
<tr>
<th>Character</th>
<th><em>C. subeminens</em> sp. n.</th>
<th><em>C. crypticus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Wing length</td>
<td>1.22 mm</td>
<td>0.95-1.16 mm</td>
</tr>
<tr>
<td>CR</td>
<td>0.60</td>
<td>0.52-0.59</td>
</tr>
<tr>
<td>Length of gonocoxite</td>
<td>375 μm</td>
<td>240-275 μm</td>
</tr>
<tr>
<td>Length of gonostylus</td>
<td>188 μm</td>
<td>124-128 μm</td>
</tr>
<tr>
<td>Wing/gonocoxite</td>
<td>3.2</td>
<td>3.8-4.4</td>
</tr>
<tr>
<td>Gonocoxite/gonostylus</td>
<td>2.0</td>
<td>2.0-2.1</td>
</tr>
</tbody>
</table>
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.** ♀ Unknown.

♂. 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 μm long, 4.8-5.0 times shorter than wing length. Gonostylus 184 μm 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 ♂, MBI-8-2. Paratype ♂, 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


Diagnosis. This genus has a unique wing venation: vein M2 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 flagellum 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 r14,5 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 *Ceratopo-gonini* is related to it. It is possible that *Wirrhohelea* 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 ....................................................... .2
   – Females ................................................... .4
2. Flagellum composed of 10 recognizable flagellomeres. Gonostylus broad, not tapering to apex ................................. *Ch. wirthi* (SZADZIEWSKI) (Baltic amber)
   – Flagellum composed of 13 recognizable flagellomeres. Gonostylus tapering to apex ................................. .3
3. CR 0.80 .................................................. *Ch. gedanica* (SZADZIEWSKI) (Baltic amber)
   – CR 0.65-67 ........................................ *Ch. nielseni* (SZADZIEWSKI) (Baltic and Saxonian amber)
4. Sensilla coeloconica present on proximal flagellomeres ................................................................. *Ch. miocaenica* sp. n. (Saxonian amber)
   – Sensilla coeloconica absent on proximal flagellomeres ................................................................. .5
5. CR 0.79-0.81 .................................................. .6
   – CR 0.66-0.76 ................................................ .7
6. Palpus short. Claws 28 μm long .................................................. *Ch. gedanica*
   – Palpus long. Claws 44-48 μm long .................................................. *Ch. sp. A* (Baltic amber)
7. AR 1.08. CR 0.76. Seminal capsule large .................................................. *Ch. sp. B* (Baltic amber)
   – AR 1.32-1.57. CR 0.66-0.72. Seminal capsule small .................................................. .8
8. Second radial cell 0.9-1.1 times as long as distance between tip of R₁ and the base of first radial cell .................................................. *Ch. nielseni*
   – Second radial cell 1.3-1.4 times as long as distance between tip of R₁ and the base of first radial cell .................................................. *Ch. sp. C*

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

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

**Description.** Female dark brown. Total length 1.2 mm. Flagellum length 716 μm, 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 μm 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 μm 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.

♂. Unknown.

**Material examined:** Holotype ♀, MBI-8-63.

    Figs. 51, 55

*Meunierhelea nielseni* SZADZIEWSKI, 1988: 150 (Baltic amber).

**Material examined:** K-20, 1 ♀.

**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 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 Palaeartic 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 ........................................... E. sakhalinica SZADZIEWSKI (Sakhalin amber)
   - Transverse vein R$_{2+3}$ between R$_1$ and R$_{4+5}$ present ........................................... 2
2. Wing without stridulatory organ ................................................................. 3
   - Wing with stridulatory organ ................................................................. 4
3. Distal portion of second radial cell narrow .............................................. E. gogani SZADZIEWSKI (Baltic amber)
   - Distal portion of second radial cell broad .............................................. E. gedanica SZADZIEWSKI (Baltic amber)
4. Stridulatory organ composed of parallel ridges ......................................... 5
   - Stridulatory organ honey-comb like or composed of wrinkled membrane .......... 6
5. Distal portion of second radial cell narrow .................................................. E. sinuosa (MEUNIER) (Baltic and Saxonian amber)
   - Distal portion of second radial cell broad .................................................. E. miocaenea sp. n.
6. Stridulatory organ honey-comb like .......................................................... E. petrunkevitchi SZADZIEWSKI (Baltic amber)
   - Stridulatory organ composed of wrinkled membrane ..................................... E. fossicola sp. n.

**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.** ♀. Body dark, very deformed. Eyes widely separated (Fig. 58). Proximal flagellomeres cylindrical (Fig. 56), their combined length 224 μm. 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 R$_{4+5}$ and free part of costa. Median and cubital veins not visible. Genitalia not modified.

♂. 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 ♀, MBI-8-72.

**16. Eohelea miocaena** sp. n.

Figs. 61 - 65

**Diagnosis.** Female is characteristic in having a stridulatory organ composed of 22 parallel ridges and the second radial cell broad on the distal portion.

**Description.** ♀. Body brown. Total length 1.5 mm. Flagellum length 552 μm, AR 0.84. All flagellomeres cylindrical (Fig. 61). Palpus 5-segmented, very short (Fig. 62). Third palpal segment about 24 μm 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.

♂. Unknown.

**Material examined**: Holotype ♀, MBI-8-81.

17. *Eohelea sinuosa* (Meunier, 1904)

*Ceratopogon sinusus* Meunier, 1904: 234 (Baltic amber).

*Eohelea stridulans* Petrunkevitch, 1957: 208 (Baltic amber).


**Material examined**: MBI-8-80, 1 ♀ (+Chironomidae 1 ♀); K-2, 1 ♀ (+Acarina 1); K-50, 1 ♀; K-103, 2 ♀ 1 ♂ (+Chironomidae 1 ♂).

**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 ♀; 8-49, 1 ♀; K-95, 1 ♀.
Key to species of *Fossihelea*

**Males**

1. Flagellomeres II-X separated. Parameres slender with straight pointed apices
   - Flagellomeres II-X fused. Parameres broad with lateromedian hook-shaped slender projections
   \[ F. \text{ gracilitarsis (MEUNIER) (Baltic amber)} \]
   \[ F. \text{ miocaenica sp. n.} \]

**Females**

1. Hind tarsus 1.3 times shorter than tibia
   - Hind tarsus equal to or slightly longer than tibia
   \[ F. \text{ gracilitarsis} \]
   \[ F. \text{ miocaenica sp. n.} \]
   - Claws of middle and hind leg greatly unequal
   \[ F. \text{ sp. B (Saxonian amber)} \]

2. Claws nearly equal on all legs
   \[ F. \text{ gracilitarsis} \]
   \[ F. \text{ miocaenica sp. n.} \]

3. Fourth tarsomeres with sinuous capitulate setae. Third palpal segment short (26 μm)
   - Fourth tarsomeres without sinuous setae. Third palpal segment long (62 μm)
   \[ F. \text{ sp. A (Baltic amber)} \]

---

**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 capitulate sensory setae.

**Description.** ♀. Body dark brown, thorax black. Total length 1.3 mm. Flagellum length 572 μm, AR 1.20 (Fig. 66). First flagellomere with sensilla coeloconica. Proximal flagellomeres cylindrical. Palpus short (Fig. 67). Third palpal segment slightly cylindrical, 26 μm 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 capitulate 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.

♂. 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 capitulate 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 gonoxoite, tapering towards apex, with distinct broad apicolateral processes.

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 ♂, MBI-8-140. Paratype ♀, MBI-8-92.
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.** ♀. Body dark. Total length 2.2 mm. Flagellum length 700 µm, 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 µm 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.

♂. Unknown.

**Material examined:** K-43, 1 ♀.
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

1. Wing length 1.7-1.9 mm. Fourth palpal segment long, only slightly shorter than third . . .
   . . . . . . . . . . . . . . . . . . . . . . . . . . . . . M. lacus (MEUNIER) (Baltic amber)
   -. Wing length 1.1-1.3 mm. Fourth palpal segment short, 1.6-2.0 times shorter than third . .
   . . . . . . . . . . . . . . . . . . . . . . . . . . . . . M. gedanica SZADZIEWSKI (Baltic and Saxonian amber)

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 *Monochelea*.

**Key to named *Monochelea* from Baltic and Saxonian amber**

1. Hind femur greatly swollen . . . . . . . . . . *M. clunipes* (LOEW) (Baltic and Saxonian amber)
   - Hind femur slightly swollen . . . . . . . . . . *M. baltica* SZADZIESKSI (Baltic amber)

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

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


**Material examined**: MBI-8-82, 1 ♀; 10-3, 1 ♀; K-99, 1♂.

**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 (SZADZIESKSI 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. Monochelea 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](image-url)
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 φ.

**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 φ, 10 φφ) 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. australa* Statz, *S. spinosifemorata* Statz) and *S. alphea* (Heyden) (Borkent & Bissett t.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* Delécolle & Braverman from Egypt) form a monophyletic group which excludes all fossil Tertiary *Serromyia* and all extant species outside of the region. Borkent & Bissett (t.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 φ; 8-93, 1 φ; 8-96, 1 φ; K-36, 1 φ; K-58, 1 φ (+ *Mantohelea gedanica*); K-65, 1 φ; K-69, 1 φ.
Key to fossil *Serromyia*

**Males**

1. Femora of fore and mid legs without strong spines ........................................................................ 2
   –. Femora of fore and mid legs with strong spines ....................................................................... 4

2. Fourth tarsomeres with one pair of sinuate setae ...................... *S. sinuosa* BORKENT (Baltic amber)
   –. Fourth tarsomeres without sinuate setae ........................................................................ 3

3. Hind femur 6.0-6.2 times as long as greatest width ........................................................................ 6
   –. Hind femur 4.0 times as long as greatest width ...................................................................... 8
   –. *S. spinigera* (LOEW) (Baltic and Saxonian amber)

4. Fore and mid femora with only ventral spines ....................... *S. succinea* SZADZIEWSKI (Baltic amber)
   –. Fore and mid femora with ventral and posterior spines ......................................................... 5

5. Fore and mid femora with anterior, ventral and posterior spines. Gonostylus with slender
   tip .............................................................................................................................. 10
   –. *S. ryszardi* BORKENT (Baltic amber)
   –. Fore femur with posterior, mid femur with ventral and posterior spines. Gonostylus with
     stout tip .................................................................................................................. 12
   –. *S. alphea* (HEYDEN) (Rott, Saxonian amber)

**Females**

1. Claws of hind leg short and equal ............................................................................................... 2
   –. Claws of hind leg long and greatly unequal ........................................................................... 3

2. Hind femur 3.6-3.8 times as long as greatest width .................. *S. anomalicornis* (LOEW) (Baltic amber)
   –. Hind femur 5.3-6.5 times as long as greatest width ................................................................ 14
   –. *S. spinigera* (LOEW) (Baltic and Saxonian amber)

3. Hind femur 5.0-5.1 times as long as greatest width. Basitarsus of mid leg with one spine
   between subbasal and apical spines ......................................................................................... 16
   –. Hind femur 3.4-4.5 times as long as greatest width. Basitarsus of mid leg with 4-7 spines
   between subbasal and apical spines ....................................................................................... 18

4. Hind femur 3.4-3.6 times as long as greatest width. Basitarsus of mid leg with 6-7 spines
   between subbasal and apical spines ....................................................................................... 20
   –. Hind femur 4.1-4.5 times as long as greatest width. Basitarsus of mid leg with 4-5 spines
   between subbasal and apical spines ....................................................................................... 22
   –. *S. alphea* (HEYDEN) (Rott, Saxonian amber)

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

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

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


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

*Serromyia spinosifemorata* STATZ, 1944: 151 (♀, 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.** ♀. 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
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.
♂. 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 ♂ of Ceratopogon alpheus, MBI-8-91, present designation. MBI-8-77, 3 ♀; 8-116, 1 ♀; 8-123, 1 ♀; 8-125, 1 ♀; K-84, 1 ♀; K-96, 1 ♀.

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 synonmys) and S. alpheas 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 ♀.

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. goetzhebueri* 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. goetzhebueri* 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
2. Wing length 2.5-2.8 mm ............................................. *S. veterana* (Meunier) (Rott)
   – Wing shorter than 1.8 mm ............................................. 3
3. Aedeagal sclerite broad, with long caudally directed extension. Paramere with broad apex
   – Aedeagal sclerite slender, simple. Paramere with pointed apex ............................. 4
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 ............................................. *S. succinea* sp.n.

Subgenus *Acanthohelea* Kieffer, 1917

*Neostilobezzia* Goetzhebuer, 1934

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

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 s; K-70, 1 q.

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

Diagnosis. 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. ♀. Unknown.

♂. 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 ♂, 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.

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

**Diagnosis.** Male of the species is characteristic in having simple arcuate aedeagal sclerites and rod-like parameres with pointed evenly curved ventrally directed apices.

**Description.** \( \varphi \). Unknown.

\( \sigma \). Body dark brown. Total length 2.03 mm. Flagellum length 1050 \( \mu \)m, AR 1.00 (Fig. 104). Third palpal segment 68 \( \mu \)m 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.


**Material examined:** Holotype \( \sigma \), 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.

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

Diagnosis. Male characteristic in having the distal projection of the parameres long and slender, with sharply curved tip.

Description. ♀. 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
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.

♂. 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. Gonocoixite 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 ♂, MBI-8-87 (+Chironomidae, Orthocladiinae, 2 ♂). The female described here, embedded in amber piece MBI-8-47, is not designated as a paratype.

**Tribe Palpomyiini**

**Genus Palpomyia** MEIGEN, 1818

**Key to Palpomyia from Baltic and Saxonian amber**

1. All femora armed with ventral spines ........................................... 2
   - Only fore femur armed with ventral spines .................................. 3
2. Claws on all legs of female short. Wing length 1.2 mm ........................  ....
   - Claws on hind leg of female long. Wing length 2.9 mm ....................
     - *P. riedeli* SZADZIEWSKI (Baltic amber)
     - *P. jantari* SZADZIEWSKI (Baltic amber)
3. Scutum with anterior tubercle .............................................. 2. succinea *SZADZIEWSKI* (Baltic amber)
   - Scutum without anterior tubercle ........................................  *P. erikae* sp. n.
29. *Palpomyia erikae* sp. n.
Figs. 119 - 124

**Diagnosis.** 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.** ♀. Body black. Total length 1.8 mm. Flagellum 840 μm long, AR 1.44 (Fig. 119). Third palpal segment short, 56 μm; 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 tarsomerses 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.


♂. Unknown.

**Material examined:** Holotype ♀, 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 ♀; K-91, 1 ♀; K-105, 1 ♂.
Key to *Forcipomyia* from Baltic and Saxonian amber

1. TR(III) lower than 1.2 .................................................. 2
   - TR(III) higher than 1.7 ........................................... 11
2. TR(II and III) 0.2-0.3 ........................................... 3
   - TR(II and III) 0.5-1.2 ........................................... 1.3
   - F.(F.) pseudomicrohelea SZADZIEWSKI (Baltic amber) ..... .3
     - TR(II) 0.8-1.2 ................................................... 4
     - F.(F.) eocostata SZADZIEWSKI (Baltic amber) ........... .4
     - TR(II) 0.8-1.2 ................................................... 5
4. Large species, wing length 1.8 mm .......................... .5
   - Small species, wing length 0.8-1.2 mm ....................... .5
5. Empodia absent in male ........................................... .6
   - Empodia well developed in male ............................. .6
6. Wing with a pattern formed by dense and sparse macrotrichia ........................................... .7
   - Wing uniformly covered with macrotrichia .................... .7
7. Third palpal segment greatly swollen in female. Female AR 1.3-1.5 .......................... .8
   - Third palpal segment not greatly swollen in female. Female AR 0.8-1.0 .......................... .8
8. Aedeagus short and broad, with strongly sclerotized triangular projection ........................................... 9
   - Distal portion of aedeagus weakly sclerotized ............... 10
9. Parameres widely separated, connected at bases by a narrow bridge at the level of aedeagal arms ........................................... 10
   - Parameres not widely separated, connected at bases by a wide bridge below the level of aedeagal arms .......................... 10
   - F.(F.) gedanicola SZADZIEWSKI (Baltic and Saxonian amber) .......................... 10
   - F.(F.) subgedanicola sp. n. ..................................... 10
10. Paramere shorter than gonocoxite ......................... 11
    - Paramere reach tip of gonocoxite .......................... 11
11. 4th and 5th palpal segments totally fused .................. 12
    - 4th and 5th palpal segments separated ..................... 13
12. Tip of gonostylus expanded ................................. 13
    - Tip of gonostylus slender ................................. 13
    - F. (sg.?) krzeminckii SZADZIEWSKI (Baltic amber) ........ 13
    - F. (Euprojoanmisia) tuberculosa sp. n. .................... 13
13. Female claws bifid, empodial setae with capitate tips ........................................... 14
    - Female claws and empodial setae simple .................... 14
14. Second radial cell long and narrow .......................... 15
    - Second radial cell short, if elongated then broad .......... 15
15. Female flagellomeres II-VII compressed and short .......... 16
    - Female flagellomeres II-VII ovoid ........................ 16
    - F. (Lasiohelea) succinea SZADZIEWSKI (Baltic amber) .... 16
    - F. (L.) sp. A (Baltic amber) ................................ 16
16. Female proximal flagellomeres compressed, AR 1.5 ........ 17
    - Female proximal flagellomeres not compressed ............. 17
17. Empodia absent in male ........................................ 17
    - Empodia present in male .................................... 17
18. Male flagellum with 10 flagellomeres ....................... 18
    - Male flagellum with 13 flagellomeres ..................... 18
19. Gonostylus with enlarged tip ................................ 18
    - Tip of gonostylus slender ................................ 18
20. Aedeagus short, as long as broad .......................... 19
    - Aedeagus long, about 2 times longer than broad .......... 19
    - Aedeagus shield-shaped. Parameres fused with apodemes of gonocoxites into U-shaped structure lacking submedian projections ........................................... 20
    - F. (E.) miocaenica sp. n. ................................... 20
22. Tip of aedeagus distinctly bilobed .......................... 21
    - Tip of aedeagus evenly pointed .......................... 21
    - F. (E.) henningseni SZADZIEWSKI (Baltic amber) ........ 21
Subgenus *Forcipomyia* MEIGEN, 1818

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

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

30. *Forcipomyia* (F.) gedanicola SZADZIEWSKI, 1988

Figs. 125 - 126

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

**Material examined:** MBI-8-103, 1 ♂; 8-143, 1 ♀.

**Note.** These specimens agree with Baltic amber specimens in all features.
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. ♀ Unknown.

♂. 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 ♂, MBI-8-105.

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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.** ♀. Unknown.

♂. 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 ♂, MBI-8-149.

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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.

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**Subgenus Euprojoannisia** Brèthes, 1914

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

**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

**Diagnosis.** 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.** ♂. 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.

♀. 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 ♂, MBI-8-152 (+Acarina, 1 specimen on dorsal surface of abdomen). Not included in the type series: MBI-8-89, 1 ♂ 1 ♀ 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. ♀. Body hairy, brown. Total length 1.7 mm. Flagellum length 960 μm, AR 1.72 (Fig. 139). Proboscis long and slender (Fig. 140). Third palpal segment slender,
116 μm long; sensory pit at midlength, opening at distal third. Fourth and fifth palpal segments totally fused, length 96 μm (Fig. 141). Legs slender with long setae. TR(I) 2.4, TR(II) 2.4, TR(III) 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.

♂. 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 unnormally 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.


Subgenus Trichohelea Goetghebuer, 1920

35. Forcipomyia (T.) bifidicola sp. n.

Figs. 147 - 151

Diagnosis. Female characteristic in having a large TR (2.5-2.6), bifid claws and empodial setae with capitate tips.

Description. ♀. 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

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.

♂: Unknown.

Material examined: Holotype ♀, 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. ♀. Body dark brown. Total length 1.0 mm. Flagellum 364 μm 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.

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.

♂. Unknown.

Material examined: Holotype ♂, 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 ♀; 8-129, 1 ♀; 8-133, 1 ♀; 8-154, 1 ♀.

Key to Dasyhelea from Baltic and Saxonian amber

Males

1. Apicolateral process of tergite IX short and broad ........................................
   −. Apicolateral process of tergite IX long and slender .................................. 2

2. Second radial cell very small. Wing length 0.7 mm ........................................
   −. Second radial cell larger. Wing length greater than 1.2 mm ......................... 3

3. Wing length 1.7 mm .......................................................................................... D. sp. A (Baltic amber)
   −. Wing length 1.2-1.3 mm ................................................................................ 4

4. Terminal flagellomere with slender apical projection. Claws stout and nearly straight
   −. Terminal flagellomere with evenly pointed apex. Claws slender and curved ..
   −. Terminal flagellomere with a rounded tip; tergite IX with distinct slender and cylindrical apicolateral processes; claws long, slender and distinctly bent.

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.

♀. Unknown.

♂. Body blackish brown. Pubescence of eyes readily visible. Flagellum length 720 μm, 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

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 ventrolateral expansions. Median projection of parameres slender with pointed tip, extending well beyond tip of aedeagus. Basal arms of aedeagus not visible.


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.
IV. DISCUSSION

In the Miocene Saxonian amber 12 species are recognized to occur in older Baltic amber. They are: Culicoides ceranowiczii, C. speciosus, Brachypogon prominulus, Ceratopogon forcipiformis, C. hennigi, Chimaerohelca nielseni, Eohelea sinuosa, Mantohelca 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 (Schumann & Wendt 1989).

The shared presence of twelve species might also be due to 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):

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

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.) \( s = 9.5 \)
- Kutsher’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.) \( s = 25.4 \)
  - MZW coll. (70 spp.) – MBI coll. (29 spp.) \( s = 23.8 \)

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).

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)

<table>
<thead>
<tr>
<th>Taxon</th>
<th>♂♂</th>
<th>♀♀</th>
<th>Total</th>
<th>%</th>
</tr>
</thead>
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<td>Ceratopogoninae</td>
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<td>117</td>
<td>223</td>
<td>66.36</td>
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<tr>
<td>Culicoidini</td>
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<tr>
<td>Culicoides</td>
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<td>68</td>
<td>20.23</td>
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<td>98</td>
<td>154</td>
<td>45.83</td>
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<td>9</td>
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<td>60</td>
<td>96</td>
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<td>7</td>
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<td>1</td>
<td>0.30</td>
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<tr>
<td>Total</td>
<td>148</td>
<td>188</td>
<td>336</td>
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Table II

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

<table>
<thead>
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<th>Taxon</th>
<th>Baltic amber</th>
<th>Saxonian amber</th>
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<td><em>Ceratopogoninae</em></td>
<td>82.05%</td>
<td>66.36%</td>
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<tr>
<td><em>Culicoidini</em> (Culicoides)*</td>
<td>17.77%</td>
<td>20.23%</td>
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<tr>
<td><em>Ceratopogonini</em></td>
<td>61.83%</td>
<td>45.83%</td>
</tr>
<tr>
<td><em>Alluaudomyia</em></td>
<td>1.45%</td>
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</tr>
<tr>
<td><em>Brachypogon</em></td>
<td>14.32%</td>
<td>2.68%</td>
</tr>
<tr>
<td>†<em>Ceratopalpomyia</em></td>
<td>+</td>
<td>-</td>
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<td><em>Ceratopogon</em></td>
<td>25.30%</td>
<td>28.57%</td>
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<td><em>Chimaerohelea</em></td>
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<td>1.79%</td>
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<td>-</td>
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<td>†<em>Mantohelea</em></td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><em>Monohelea</em></td>
<td>2.45%</td>
<td>0.90%</td>
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<tr>
<td><em>Nannohelea</em></td>
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<td>+</td>
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<td><em>Physiohelea</em></td>
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<td><em>Bezzia</em></td>
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<td>Number of specimens in a single amber piece</td>
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V. REFERENCES


