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Biting midges (*Diptera, Ceratopogonidae*) from Baltic amber

Kuczmany (*Diptera, Ceratopogonidae*) z bursztynu bałtyckiego

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ABSTRACT. The Baltic amber species of the family *Ceratopogonidae* are revised. Keys and descriptions of 101 species (17 previously known; 23 unnamed and 61 new named spp.) and 24 genera are presented.

The following new genera are described: *Fossihelea*, *Mantohelea*, *Meunierohelea*, *Wirthohelea*, *Gedanohelea* and *Ceratopalpomyia*. In addition, the following 61 new named species are described: *Culicoides dasyheleiformis*, *C. succivarius*, *C. balticus*, *C. eoselficus*, *C. ceranowiczi*, *C. gedanensis*, *C. prussicus*, *Ceratopogon hennigi*, *C. tertiaricus*, *C. grogani*, *C. crypticus*, *C. remmicolus*, *C. gedanicus*, *C. piotrowskii*, *C. ceranowiczi*, *C. ritzkowskii*, *C. margaritae*, *Brachypogon polonicus*, *B. henningseni*, *B. eocenicus*, *B. balticus*, *B. gedanicus*, *Nannohelea grogani*, *N. eocenica*, *Ceratoculicoides danicus*, *Alluaudomyia succinea*, *Monohelea baltica*, *Serromyia polonica*, *S. succinea*, *Mantohelea gedanica*, *Meunierohelea nielseni*, *M. gedanicola*, *M. wirthi*, *Wirthohelea trifida*, *Eohelea grogani*, *E. gedanica*, *Gedanohelea loewi*, *G. succinea*, *G. wirthi*, *Ceratopalpomyia eocenica*, *Palpomyia jantari*, *P. riedeli*, *P. succinea*, *Bezzia eocenica*, *Forcipomyia succinea*, *F. lyneborgi*, *F. gedanicola*, *F. eocostata*, *F. pseudomicrohelea*, *F. berendti*, *F. henningseni*, *F. eotrichoheleana*, *F. eophytoheleana*, *F. krzeminskii*, *F. kulickae*, *F. eobreviflagellata*, *Atrichopogon eocenicus*, *Dasyhelea gedanica*, *D. eodicryptoscenica*, *D. stanislavi*, and *Leptoconops succineus*.

Six new synonyms are proposed. A neotype is designated for *Ceratopogon anomalicornis* LOEW, and lectotypes are selected when necessary. A checklist of all fossil biting midges is also provided. On the basis of fossil and recent *Ceratopogonidae*, questions of systematics, age, ecology and zoogeographic relations are discussed.

CONTENTS

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I. INTRODUCTION

1. General accounts

This paper is devoted to descriptions and keys for the identification of the genera and species of biting midges found in Baltic amber, their composition, ecology and zoogeographic relations. On the basis of recent and fossil *Ceratopogonidae*, questions of systematics, phylogeny and evolution of the family are discussed.

The ambers are Tertiary or older fossil resins of various, mainly coniferous trees. Subfossil Quaternary or recent resins of angiosperm origin are described as copals. Baltic amber has its name because of its numerous occurrence sites in the Baltic region. It is currently accepted that several extinct pinacean species have contributed to the formation of this amber. In view of the difficulties in the diagnoses and descriptions of these species it has been suggested by CONWENTZ (1890) to deal with them as single compound species under the common name *Pinus* (=*Pinites*) *succinifera* (GOEPPERT) (CZECZOTT, 1961; ZALEWSKA, 1974; LARSSON, 1978).

The richest amber deposits in the world are on the Sambian (Samland) Peninsula in USSR, just northwest of Kaliningrad (old name Königsberg). These amber bearing deposits are in the lower part of the Prussian formation and belong to late Eocene (Priabonian). Their absolute age supposed is ca. 37 ± 1.5 million years (KAPLAN et al., 1977). The amber bearing sediments in the vicinity of Chłapowo, district Gdańsk, Poland, also belong to the late Eocene, ca. 37.5 ± 3 Ma (=million years ago) (PIWOCKI et al., 1985). However, in the Baltic region small amounts of amber have been recorded from the earliest Eocene (Ypresian) sediments, ca. 55 Ma, in North Jutland (LARSSON, 1978). Amber was found also in early Oligocene (Rupelian) deposits of Sambia, ca. 34 ± 3.7 Ma (KAPLAN et al., 1977). Therefore, the amber bearing forests existed here continuously at least from earliest Eocene to early Oligocene, and in Central Europe at least to early Miocene since Saxonian amber from East Germany is common in Aquitanian brown coal beds (BARTHEL and HETZER, 1982).

During the Pleistocene glaciation in the south Baltic regions the amber bearing beds were cut off by the action of the glaciers. Sea currents, glaciers and glacial rivers dispersed the detached ambers over various European regions. Today, too, the sea waves continue their action on the Tertiary amber deposits in the region of Sambia. The amber they wash out and carry away by off-shore currents, and parts of it are washed out by storms onto the beaches nearly throughout the southern coasts of the Baltic. In Poland, small amounts of amber are

found practically everywhere among Quaternary sediments, but mainly in the Baltic and its coastal area (ZALEWSKA, 1974; KOSMOWSKA-CERANOWICZ and PIETRZAK, 1982, 1985).

Baltic amber contains a rich insect fauna. Especially common in this fossil resin are flies trapped during their normal life activities. Among flies, nematocerous midges predominate. In the collection of Museum of the Earth in Warsaw midges of the suborder *Nematocera* constitute 65% (KULICKA et al., 1985), and in the Zoological Museum in Copenhagen 69% (LARSSON, 1978) of all *Diptera*. The *Ceratopogonidae* are common in Baltic amber. Their rate among nematocerous flies is from 7% in the collection from Gdańsk, and 8% in the whole collection of Museum of the Earth to 11% in the Zoological Museum in Copenhagen (KULICKA et al., 1985). Three families of *Nematocera* are more common in the amber than *Ceratopogonidae*. They are: *Chironomidae* (36–50%), *Sciaridae* (15–23%), and *Mycetophilidae* (9–19%) (KULICKA et al., l.c.).

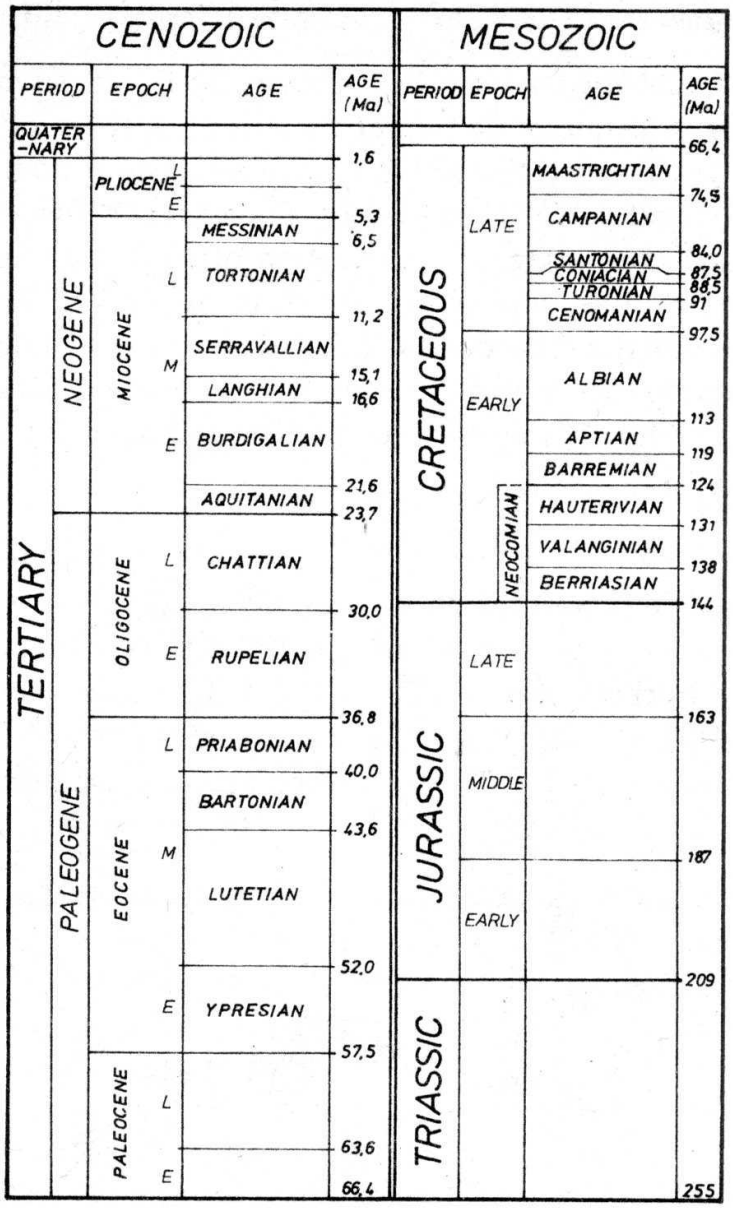
2. Recent *Ceratopogonidae*

The *Ceratopogonidae* are typical members of the *Diptera* suborder *Nematocera*, infraorder *Culicomorpha* and superfamily *Chironomoidea*. The family is apparently most closely related to *Simuliidae* and *Chironomidae*. In the recent fauna there are presently known over 4,000 species grouped in nearly 80 genera. A quarter of these species belong to the genus *Culicoides*, and a second quarter to the subfamily *Forcipomyiinae*.

The biting midges are present in nearly any semiaquatic and aquatic habitats in all regions of the world except Antarctica. They are small flies, the females of which usually require a protein-rich meal for maturation of the eggs. Species of *Culicoides*, *Leptoconops* and *Forcipomyia* (*Lasiohelea*) suck vertebrate blood, mainly of mammals and birds. Some *Atrichopogon* and *Forcipomyia* are ectoparasites on large insects or feed on dead insects or pollen. Females of many genera of the subfamily *Ceratopogoninae* are predaceous on small insects and even on their own males. Both sexes of *Ceratopogonidae* may visit flowers with easily accessible nectar. Species of the genus *Dasyhelea* are exclusively flower visiting and feeding on nectar.

Most biting midges are crepuscular but *Leptoconops* and a few others fly in full sunshine. Males of many species assemble in swarms that maintain a dancing flight. The plumose antenna of the male is an auditory organ sensitive to the wing-beat tone of the incoming female, and mating begins in flight. Some species mate on a substrate without a swarming flight, and in some of these the flagellar plume is reduced.

The immature stages of most *Ceratopogoninae* are aquatic or semiaquatic in mud or wet soil on lake, pond, stream and river margins, salt



1. Geological divisions of Cenozoic and Mesozoic (from Geologic Time Scale, published by Geological Society of America, 1983)

marshes, tree holes, water holding plants, etc. Some genera live in the benthos and a few among floating vegetation of lakes and larger streams. The larvae of this subfamily are predominantly carnivorous. Larvae of most *Forcipomyia* species are terrestrial under bark, among mosses or on wet or damp wood. Many *Dasyhelea* and *Atrichopogon* are semiaquatic on alga-covered soil, wood or rocks. Larvae of *Leptoconopinae* burrow in sand or soil, mainly of arid areas and on coastal and inland beaches. Larvae of *Leptoconopinae*, *Dasyheleinae* and *Forcipomyiinae* are saprophagous or feed on algae (WIRTH et al., 1977; DOWNES and WIRTH, 1981).

3. Fossil *Ceratopogonidae*

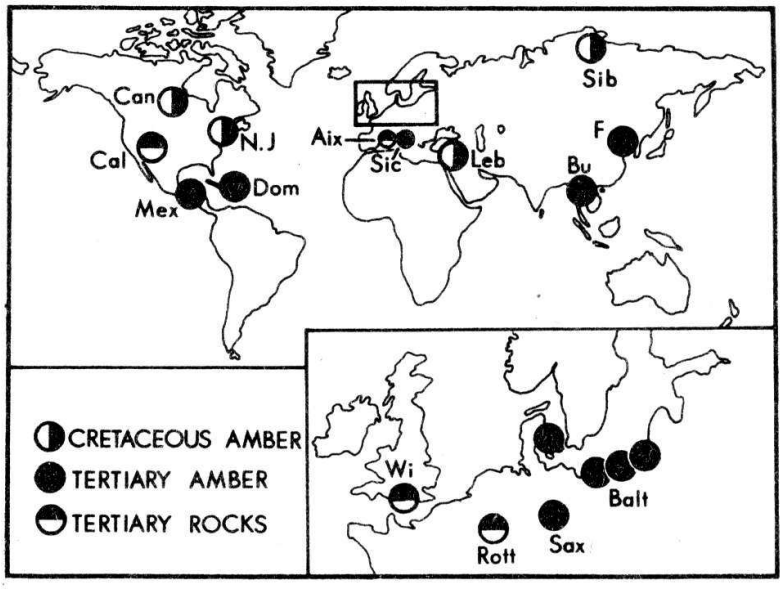
The fossil *Ceratopogonidae* are known from sedimentary rocks as impressions or three dimensional petrifications. Because of the small size of biting midges their impression findings are scanty and they have no higher taxonomical value. Fortunately, *Ceratopogonidae* are common in fossil resins and their state of preservation often is such that they allow detailed investigations, almost as complete as that of recent fauna.

Fig. 1 presents the divisions of the Mesozoic and Cenozoic Eras, and fig. 2 distribution of known sites of fossil *Ceratopogonidae*.

The abbreviation Ma used in the present paper means "million years ago".

Late Jurassic

The oldest supposed ceratopogonid-like midge was described as *Simulium* ? *humidum* by WESTWOOD (in BRODIE, 1845) from a limestone impression of Purbeck stratum in England (late Jurassic-early Cretaceous, ca. 144 Ma). HANDLIRSCH (1908) assigned the fossil to a new genus *Pseudosimulium*. CRAIG (1977) redescribed the type-specimens of *Pseudosimulium humidum* and concluded that the fossils are not *Simuliidae* and



2. Distribution of known deposits with fossil *Ceratopogonidae*; Aix — Aix-en-Provence, Oligocene; Balt — Baltic amber, Eocene; Bu — Burmese amber, ? Oligocene; Cal — calcareous nodules from California, Miocene; Can — Canadian amber, late Cretaceous; Dom — Dominican amber, Oligocene; F — Fushun or Chinese amber, Eocene; Leb — Lebanese amber, early Cretaceous; Mex — Mexican amber, Oligocene-Miocene; N. J — New Jersey amber, late Cretaceous; Rott — rocks from brown coal mine in Rott near Bonn, West Germany, Miocene; Sax — Saxonian amber from East Germany, Miocene; Sib — Siberian amber, late Cretaceous; Sic — Sicilian amber, Miocene; Wi— rocks from Isle of Wight in England, Oligocene

believed that this species belongs rather to the *Ceratopogonidae*. However, GROGAN (in litt.) and WIRTH (in litt.) are certain that these fossils are not biting midges.

GIEBEL (1856) in his manual on the fossil arthropods erronoeusly gave ceratopogonid name *Macropeza prisca* for unnamed fossil figured by BRODIE (1845, fig. 15, Pl. V) which HANDLIRSCH (1908) transferred to the new genus *Bibionites* of the family *Bibionidae*.

Cretaceous

The oldest and undoubted *Ceratopogonidae* have been found in Neocomian Lebanese amber, ca. 125–130 Ma (SCHLEE and DIETRICH, 1970). According to WIRTH (personal comm.) this material includes males and females of a ceratopogonid, which somewhat resembles *Austroconops*. The oldest named and undoubted biting midge, a species of *Culicoides* from Cenomanian New Jersey amber, ca. 94 Ma is presently being studied by GROGAN and SZADZIEWSKI.

In late Cretaceous Siberian amber from the Taymyr Peninsula (Coniacian, Santonian ?, ca. 85 Ma) REMM (1976) found the extinct genus *Atriculicoides* with two species, and seven other species which he assigned to the recent genera *Culicoides*, *Ceratopogon* and *Baeohelea* (see *Culicoidini* and *Ceratopogonini*). KALUGINA (1977) mentioned two undetermined *Leptoconopinae* from this amber.

From Campanian Canadian amber (ca. ? 80 Ma) BOESEL (1937) described a new genus *Protoculicoides* and six new species: *Lasiohelea cretea*, *L. globosa*, *Atrichopogon canadensis*, *Dasyhelea tyrrelli*, *Ceratopogon aquilonius* and *Protoculicoides depressus*. MCALPINE and MARTIN (1969) next mentioned 31 biting midges from Canadian amber preserved in the North American museums. WIRTH et al. (1974) placed *Protoculicoides* in the tribe *Ceratopogonini* (now see *Culicoidini*). REMM (1976) supposed that all species described by BOESEL (l.c.) belong to the subfamily *Ceratopogoninae* and doubted that *Forcipomyiinae* existed during Cretaceous time. DOWNES (1978) mentioned from this amber *Culicoides*, *Ceratopogonini* and *Stilobezziini*. DOWNES and WIRTH (1981) found in Canadian amber not only members of several genera of *Ceratopogoninae* but also *Leptoconops* and *Forcipomyia* too.

Eocene

HONG (1981) described a single female as *Palpomyia unca* from Chinese amber collected in the coal beds of the Guchengzi formation in the Fushun Coalfield, Liaoning Province.

Baltic amber contains a rich biting midges fauna represented by adults only.

The prominent dipterist LOEW was the first to study *Ceratopogonidae* from Baltic amber. It his paper on *Diptera* from this fossil resin LOEW (1850) mentioned 26 *Ceratopogon* species, however he presented brief diagnoses and named only three species: *C. anomalicornis*, *C. spiniger* and *C. clunipes*. Despite the fact that he later worked on these fossils (LOEW, 1864) he published nothing on this subject, and his manuscripts were not found (MEUNIER, 1904).

GIEBEL (1856) in his manual on palaeontology described the new species, *Ceratopogon escheri*, from the collection at the University of Leipzig and listed LOEW's fossils.

MEUNIER (1899) mentioned two specimens of *Ceratopogon* determined by LOEW in the collection at the Provincional Museum of Königsberg, however these specimens were not recognized in his later paper (MEUNIER, 1904). The basic publication concerning *Ceratopogonidae* from Baltic amber is the monograph of MEUNIER (1904). In the collection at the Provincional Museum of Königsberg (now Kaliningrad, USSR) MEUNIER found two of the three of LOEW's species and further described 18 new ceratopogonids in the genus *Ceratopogon*. KIEFFER (1906) in his catalogue of the world *Chironomidae* tried to place these fossil species into the genera *Culicoides*, *Ceratopogon*, *Palpomyia*, *Ceratolophus* KIEFFER, *Heteromyia* SAY and *Serromyia*, however usually incorrectly. COCKERELL (1919) placed *Ceratopon cothurnatus* and *C. sinuosus*, both described by MEUNIER, in the genus *Johannsenomyia* MALLOCH.

PETRUNKEVITCH (1957) during his studies on the Baltic amber spiders found an unusual biting midge with a stridulating organ on the wings and proposed the new genus *Eohelea* with its own subfamily *Eoheleinae*. HENNIG (1973, p. 193) however recognized this stridulatory organ as an artifact and placed *Eohelea* with its single species in the genus *Dasyhelea* with a comment "Das von PETRUNKEVITSCH (1957) vom Flügel einer fossilen Art der Gattung *Dasyhelea*... beschriebene 'Stridulationsorgan' ist sicherlich ein Artefakt". WIRTH et al. (1974) in their synopsis of the genera of *Ceratopogonidae* of the world assigned *Eohelea* to the tribe *Ceratopogonini*.

LARSSON (1978) in his Baltic amber paleobiological monograph summarized previous studies on the *Ceratopogonidae* and made known a number of specimens in the collection at the Zoological Museum of Copenhagen. KEILBACH (1982) made up a catalogue of animal inclusions in ambers and listed the known *Ceratopogonidae* from Baltic amber. He listed however nine species, the names which never have been described from Baltic amber but only labelled by LOEW in the Berendt collection. These names are typical nomina nuda (see checklist in chapter V).

SZADZIEWSKI (1984, 1985) presented a complete diagnosis of the

genus *Eohelea* and placed it in the tribe *Stilobezziini*, redescribed *E. stridulans*, and described a new species *E. petrunkevitchi* and two unnamed fossils. KULICKA et al. (1985) made known a number of *Ceratopogonidae* and other families of the suborder *Nematocera* in the Baltic amber collection at the Museum of the Earth in Warsaw.

Oligocene

Undetermined *Ceratopogonidae* have been mentioned by HURD et al. (1962) from Mexican amber (Chiapas, 25–35 Ma), and by SCHLEE and GLÖCKNER (1978) from Dominican amber (Haiti, 35 Ma).

COCKERELL (1919) briefly described *Johannsenomyia swinhoei* from Burmese amber.

From Oligocene rocks of Gurnet Bay, Isle of Wight in England, COCKERELL (1921) described a new badly preserved impression of *Palpomyia edwardsi.*

Also from Aix-en-Provence, south of France, undetermined *Ceratopogon* has been mentioned (SERRES, 1829; after HANDLIRSCH, 1908).

Miocene

Rich impressions of the *Ceratopogonidae* have been found in the Aquitanian rocks of Rott in Siebengebirge near Bonn, West Germany. From these deposits HEYDEN (1870) described *Ceratopogon alpheus,* and MEUNIER (1920) *Tetragoneura veterana.* MEUNIER (1922) removed the latter species from the family *Mycetophilidae* and placed it in the genus *Ceratopogon.* STATZ (1944) among 75 females, 1 male, and 55 pupae found a large number of species. He redescribed MEUNIER's species and placed it in the genus *Stilobezzia*, and described new species in the following genera: *Atrichopogon* (1), *Culicoides* (12), *Stilobezzia* (1), *Serromyia* (4), *Bezzia* ? (1), unnamed adults as "*Ceratopogon*" (3), and unnamed pupae as "*Ceratopogon* pupae" (13). According to STATZ (l.c.) the type of *C. alpheus* is lost and perhaps this fossil does not belong to the *Ceratopogonidae.*

Quite recently a new Saxonian amber (22 Ma) has been discovered in the brown coal mine at Bitterfeld near Halle, East Germany (BARTHEL and HETZER, 1982). I recently received from the Museum für Naturkunde in Berlin about 200 biting midges enclosed in this amber.

Unusually well preserved biting midges have been found in Miocene (20 Ma) calcareous nodules from the Calico Mts., Mojave Desert, California (PALMER, 1957; PIERCE, 1959, 1966). The *Ceratopogonidae* found in the nodules are mostly silicified, three dimensional with even some internal organs preserved which were free from the enclosing matrix using special methods. Unfortunately, they are immature stages

mainly poorly known on a world-wide basis. PALMER (1957) described from the nodules *Dasyhelea stenoceras* (pupa), *Culicoides megacanthus* (pupa) and a subspecies of the modern species *Dasyhelea australis* WIRTH (all stages). PIERCE (1966) redescribed all species found by PALMER and described pupae of another 15 new species of the following genera: *Dasyhelea* (4), *Culicoides* (4), *Neoculicoides* (1), *Paraculicoides* (1), *Johannsenomyia* (1), *Miopalpomyia* (1), *Neopalpomyia* (2) and *Parapalpomyia* (1). He unwisely proposed new genera based solely on pupae: *Neoculicoides*, *Paraculicoides*, *Miopalpomyia*, *Neopalpomyia* and *Parapalpomyia*. GROGAN and WIRTH (1979 b) synonymized the three last genera with the recent genus *Palpomyia*, but the systematic position of the other two is still uncertain. It is worth-while to note that PIERCE (1966) isolated 38 *Dasyhelea* eggs from the nodules.

RONDANI (1840) stated that two undetermined males figured and placed in the genus *Dasypogon* (*Asilidae*) by GUÉRIN-MENEVILLE (1838: 170, figs. 15, 16) from Sicilian amber actually belong to *Ceratopogon*. However one of the males presented by GUÉRIN-MENEVILLE on fig. 15 has long palpi and long, slender legs that suggest it is a chironomid. The other male illustrated in fig. 16 also does not resemble typical *Ceratopogonidae*. This does not mean that in Sicilian amber biting midges are absent. I saw a photograph made by Dr. A. SKALSKI (Regional Museum of Częstochowa) showing a well preserved female probably of *Brachypogon* enclosed in this amber from the Italian collections.

Quaternary

Radiocarbon analysis of selected copal specimens by BURLEIGH and WHALLEY (1983) proved them to be younger than 100 years old. Therefore four *Ceratopogon* spp. described by MEUNIER (1912) from Madagascar copals should be included in the recent fauna.

II. MATERIALS AND METHODS

For the present study 1103 specimens (only imagines) of *Ceratopogonidae* enclosed in 954 pieces of Baltic amber from seven collections have been utilized (table 1). The following abbreviations of collections (plus one collector) in the paper are used:

IMGPUG — Institut und Museum für Geologie und Paläontologie der Georg-August-Universität, Göttingen
IZPAN — Institute of Zoology, Polish Acad. Sci., Warsaw
MBI — Museum für Naturkunde, Paläontologisches Museum, Berlin (Mikropaläontologie, Bernstein Inklusion)

MM — Castle Museum of Malbork (Muzeum Zamkowe, on deposit at MZW)
MZW — Museum of the Earth (Muzeum Ziemi), Warsaw
RSz — Author's collection (R. SZADZIEWSKI)
TG — T. GIECEWICZ, the collector of inclusions from Gdańsk at MZW
ZMC — Zoologisk Museum, Copenhagen

Table 1. *Ceratopogonidae* from Baltic amber available for the present study

Collection	Number of amber pieces	Number of specimens
MZW	485	587
ZMC	253	282
MBI	128	144
IMGPUG	58	63
IZPAN	13	16
MM	10	10
RSz	7	10
Total	954	1103

The Polish inclusions (MZW, MM, IZPAN, RSz) originate from secondary Quaternary deposits found on Polish Baltic coasts, especially of the Gdańsk region. However, during 1960ties Sambian amber was imported from the USSR to Polish jewellery workshops (KOSMOWSKA-CERANOWICZ and PIETRZAK, 1985). It may be then that some Polish inclusions are from the amber mine on the Sambian Peninsula. The richest material studied comprising 578 biting midges is from the MZW collection which has been gradually extended since 1951. A large number of these inclusions at MZW has been collected by M.Sc. T. GIECEWICZ from known localities of Gdańsk.

Most of the inclusions from ZMC collection probably have been found on Danish Baltic coasts (LARSSON, 1978). In that collection there are also amber specimens from Sambia, Gdańsk (old name Danzig), or of unknown origin, for example labelled as "German amber 1966" (see *Culicoides* indet. ZMC 81, 180, 226).

The oldest collections of *Ceratopogonidae* studied belong to MBI, of which the THOMAS collection has been deposited at the Museum in 1859, G. C. BERENDT of Gdańsk in 1873, KÜHL of Berlin in 1888, and KÜNOW of Königsberg in 1890 (HIEKE and PIETRZENIUK, 1984).

From among Baltic amber inclusions of the collection at IMGPUG only the types of *Ceratopogonidae* described by MEUNIER (1904) have been available. Previously they belonged to the large collection at the Provincional Museum of Königsberg, and it seems that at least most of them, or all, originated from the Sambian Peninsula.

Usually each amber specimen is provided with its own inventory number which makes it possible to find the material again. Originally the amber pieces from the ZMC collection were labelled only by name of donator, date, or eventually the place of finding, but without inventory numbers. Each of 253 specimens of amber containing *Ceratopogonidae* from this collection has been marked with a number independently of donators and dates (No. 1–253). Similarly the amber specimens from the MM collection have been marked. When a single lump of amber containing several insects has been divided into several pieces, then each of these is provided with an additional mark a, b, c, and so on.

The best for entomological purposes are golden and transparent amber pieces ground and polished into thin cubicoid plates in which the insects studied are in the most suitable position for examination. Because of these reasons most of the amber specimens obtained for the study needed further time-consuming manual preparations i.e. cutting, grinding and polishing.

When an amber piece was too large or insects in the piece required their separation it has been cut with an ordinary hack-saw or with a jewellery saw. A sufficiently small amber piece was ground along the most suitable planes, and then polished. A coarse-grained abrasive paper No. 200–300 or less was used for grinding, and then a water-proof abrasive paper No. 500–800 to obtain a semi-polished surface. The thin plates were then polished with a chalk powder in a wax-paraffin spread on the inner surface of a leather strap, or with toothpaste spread on a scrap of flannel.

Almost all amber specimens from old collections of MBI, MM, and ZMC required further grinding because of the relatively rapid breakdown of the amber in the atmospheric conditions. The pieces which were formerly golden in colour now have a dull, reddish-brown tint (or even dark brown as in some specimens of BERENDT collection), and their surface over time has become crack into a fine network. These pieces are distinctly more fragile than fresh ones. It is worth noting that the amber pieces of the THOMAS collection deposited at MBI in 1859 and mounted on slides in Canada balsam have been effectively protected against atmospheric oxidation. It seems that since Canada balsam possesses a similar refractory index to that of amber, this resin is a good and

practical medium that can be used for the preservation of amber inclusions. In contrast, the amber pieces embedded in the cubes of an artificial resin (Hobby-Plast) from MBI, presumably because of the refractions, are not very good for more detailed examination. However, when the artificial resin was ground to the level of the amber, then the inclusion was suitable for examination. Unfortunately, in many cases this resin reached the insect body and many important morphological characters are barely visible now.

Sometimes one or two small openings that reach the insect body were made with specially prepared entomological pins No. 0–2, and then the empty insect body was filled with Canada balsam. It is a rather difficult operation since usually air bubbles are resistant to being filled with the balsam. Fossil biting midges filled with Canada balsam usually become transparent, and usually internal structures of the male genitalia, flagella, and macrotrichia on the wing membrane are visible. However, the effects of this procedure depend on the state of preservation of the inclusion. Nothing new has been found in the specimens that were formerly filled with amber resin or covered with a milky film which presumably was formed by body fluids mixed with fresh amber resin, and possibly when genitalia were surrounded with ejaculated sperm or excrements. Often, especially those insects laying between two different layers of the resin, were not fully enclosed in the amber and the Canada balsam penetrated them through slits without additional openings.

Small amber pieces have been mounted in Canada balsam on microscopic cover glasses and covered with a smaller piece of cover slip. Also, inclusions laying on or nearby the rough amber surface have been covered with Canada balsam.

The amber plates with inclusions usually have been fastened to plasticine directly or indirectly using a cover slip on a microscope slide in a position suitable for examination. To avoid reflections and refractions of the light at obliquely situated planes, additional horizontal cover slips have been applied and the space between the amber and cover slip was filled with Canada balsam or immersion oil. Canada balsam and immersion oil have also been used to temporarily glue the amber pieces to cover glasses or for the submersion of irregular pieces.

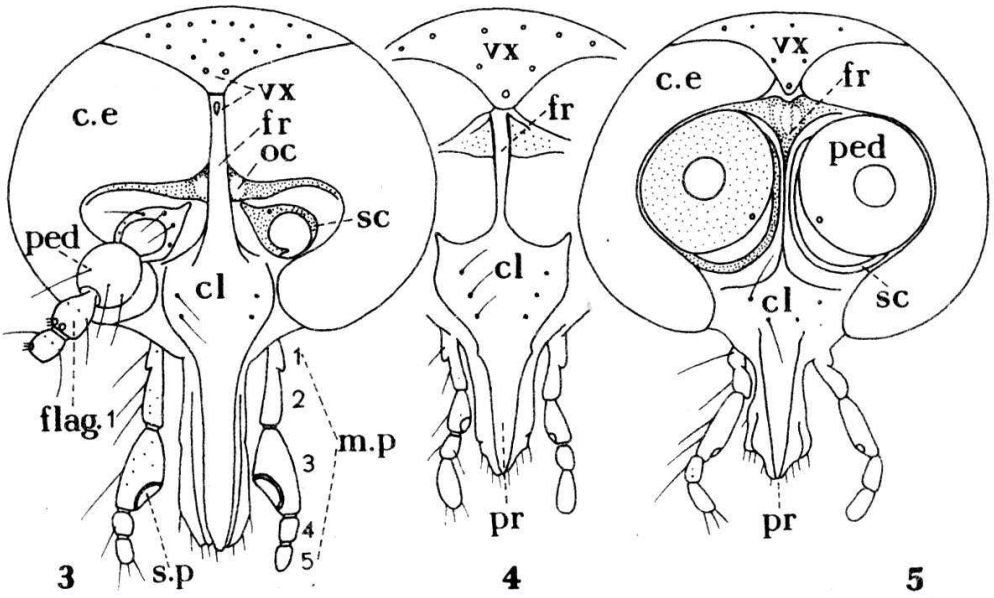
For examination typical Polish stereoscopic and biological microscopes have been used at magnifications of 40 × to 240 ×, and sometimes 480 ×. All measurements have been made with the aid of an ocular micrometer (10 ×), and drawings with a prismatic drawing ocular (10 ×). Strong, adjustable transmitted and reflected lights were utilized, usually simultaneously.

III. MORPHOLOGY AND TERMINOLOGY OF ADULT

Body length was measured from the base of the pedicel to the tip of abdomen.

Colour

As a rule colour is not considered here as a diagnostic character, since in the amber specimens it was destroyed or changed through ages, and depends mainly on the state of preservation. The biting midges lying between two different layers of the resin are black, and those totally enclosed in amber are black, blackish brown or brown. The specimens filled with Canada balsam usually became brown or pale brown. In some specimens paler tarsi or pale rings were found, for example in *Forcipomyia lyneborgi* **sp. n.**



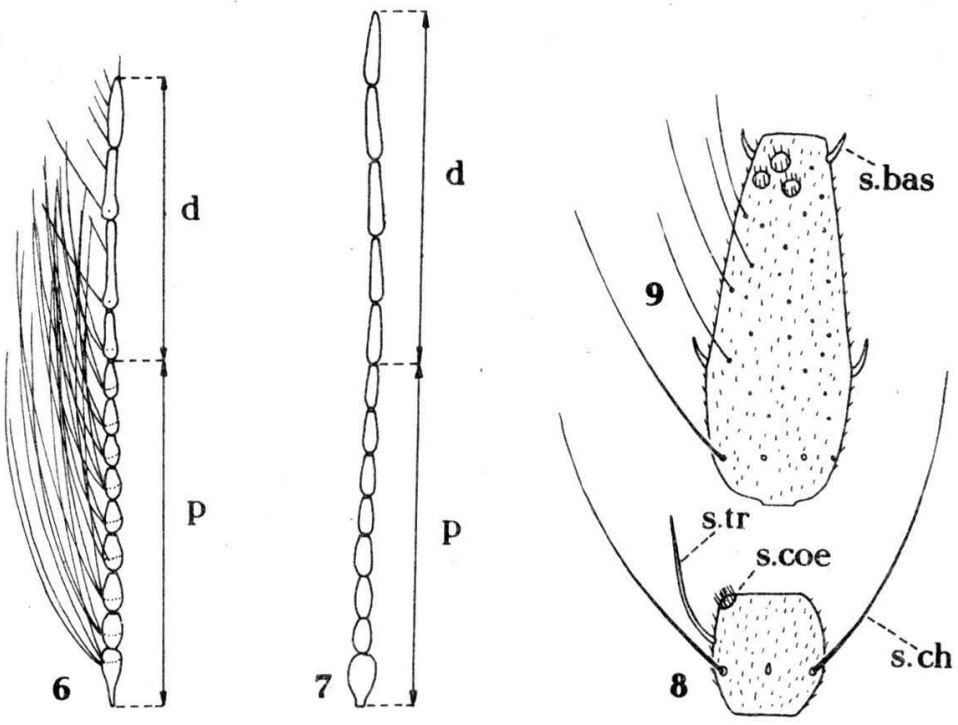
3–5. Frontal view of female (3, 4) and male head (5) of *Culicoides* spp. (3, 5) and *Ceratopogon* sp. (4); c. e — compound eye; cl — clypeus; flag. 1 — first flagellomere; fr — frons; m. p — maxillary palpus; oc — ocellar tubercle; ped — pedicel; pr — proboscis; sc — scape; s. p — sensory pit; vx — vertex

Wing patterns that are usually present in the recent *Culicoides*, *Alluaudomyia*, *Monohelea* and some other genera were not found in the material examined since the pigment responsible for the wing pattern in *Ceratopogonidae* was decomposed in the amber. Previously, Lane (1981) discovered that the wing pattern of spots characteristic of most *Culicoides* and some other genera is not formed by varying densities of microtrichia as suggested by some authors, and the ultrastructural modifications found in *Alluaudomyia* and *Monohelea* add only to the contrast in the wing pattern.

HEAD

The head is a subspherical to slightly flattened structure. Externally the main parts of the head capsule (fig. 3) are reniform eyes laterally, vertex dorsally, occiput above and postgenae below posteriorly, frons and clypeus anteriorly. Antennae and proboscis are appendages.

Eyes bare or with short pubescence between the facets. In the amber specimens pubescence as a rule is not visible, and because of that is not included in diagnoses of genera and species. Eyes are widely separated in *Leptoconopinae*, or contiguous to more or less narrowly separated, usually by vertex (figs. 4, 5) in other *Ceratopogonidae*. In females of *Culicoides* eyes are separated partly by dorsal projection of frons (fig. 3) and partly by vertex. It seems the transverse interocular suture in *Culicoides* is a secondary reinforcement of the frontal area of the head (ATCHLEY, 1970). The upper part of the interocular plate with long seta belongs to vertex, but not to frons as previously suggested by ARNAUD (1956), ATCHLEY (1970) and others. In the *Ceratopogonidae* the frons is fused with the clypeus into the frontoclypeus, in *Leptoconopinae* females however, it is widely fused with vertex also. The convex clypeus usually bears distinct setae. Usually present are two inconspicuous ocellar



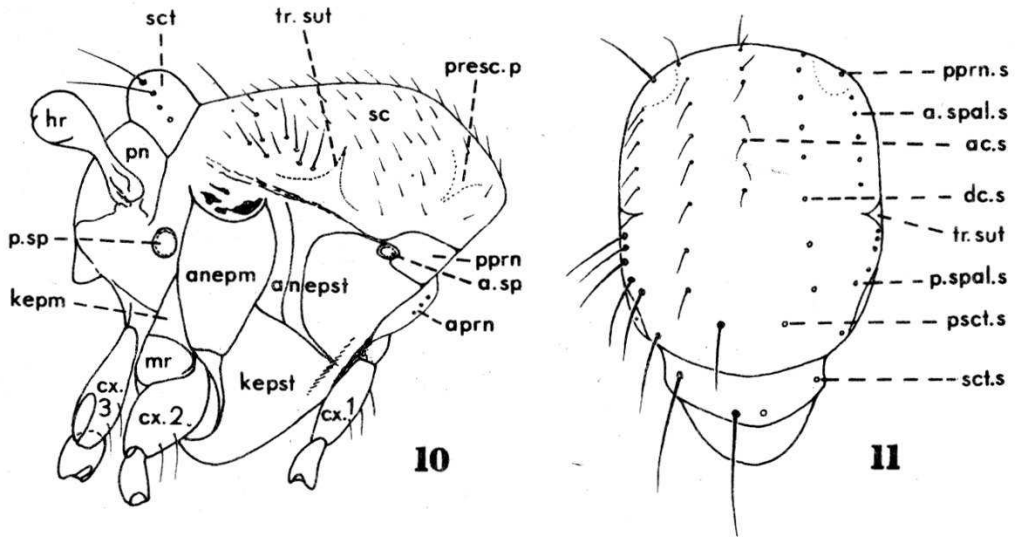
6–9. Flagellum; 6 — male flagellum showing measurements, 7 — female flagellum showing measurements, 8, 9 — flagellomere III (8) and flagellomere XI (9) of female of *Culicoides* sp.; d — distal flagellomeres; p — proximal flagellomeres; s. bas — sensillum basiconicum; s. coe — sensillum coeloconicum; s. ch — sensillum chaeticum; s. tr — sensillum trichodeum

tubercles located on frons above the bases of antennae (fig. 3). In males eyes usually fused or only narrowly separated by vertex (fig. 5), in *Leptoconops* however they are widely separated.

Antenna consists of three segments: scape, pedicel and flagellum. The scape is usually reduced to a ring-shaped structure hidden by the enlarged second antennal segment, the pedicel. The pedicel is considerably larger in the males (fig. 5). Flagellum usually consists of 13 units called flagellomeres. Proximal 8 flagellomeres of the females are usually shorter than the elongated distal 5, in *Leptoconops* only the apical one elongated. Flagellomeres 1–8 of female usually bear a basal ring of long verticils (sensilla chaetica) and a subapical pair of hyaline setae (sensilla trichodea) (fig. 8). Distal 5 flagellomeres of female usually bear shorter basal verticils and scattered short setae and short cone-shaped sensilla basiconica (WIRTH and NAVAI, 1978) (fig. 9). Most *Culicoidini* and *Ceratopogonini* have sensilla coeloconica on at least the first flagellomere (figs. 8, 9) visible as pits surrounded by numerous short setae. Male flagellum with 2–9 or 10 proximal flagellomeres short and similar bearing usually oblique whorls of long erect verticils on flagellomeres 1 or 2–10 forming more or less a dense plume (fig. 6). In some recent and fossil genera the plume is reduced. First flagellomere of male bears one or two rings of long verticils. One, three or four of the most distal flagellomeres in male are prolonged, but usually only three last with short verticils. The female flagellum is reduced to 10–12 in *Leptoconops*, 12 in *Rhynchohelea*, and occasionally to 12 or 11 flagellomeres in *Brachypogon*. The number of male flagellomeres is reduced to 12–6 in certain genera such as *Baeohelea*, *Nannohelea*, *Baeodasymyia*. Also in males of many genera flagellomeres 2–11(10) are more or less fused.

Female antennal ratio (AR) is obtained by dividing the combined lengths of the distal five flagellomeres by the combined lengths of the proximal eight flagellomeres (fig. 7). Male AR is the ratio of combined lengths of distal four flagellomeres to the proximal units of the flagellum (fig. 6).

Proboscis is well developed, usually adapted for piercing and stronger in females than in males. Proboscis consists of three unpaired elements, i.e. labrum forming dorsal wall, labium forming ventral wall and hypopharynx projecting between labrum and labium; and two paired lateral elements arising between the labium and labrum are mandibles usually armed with strong teeth, and the laciniae (parts of maxillae) usually armed with fine teeth. Maxilla bears the maxillary palpus. Palpus typically is five segmented, in some genera last two segments are more or less fused. First palpal segment is usually weakly delineated from the second, and sometimes totally fused with it. Third palpal segment bears



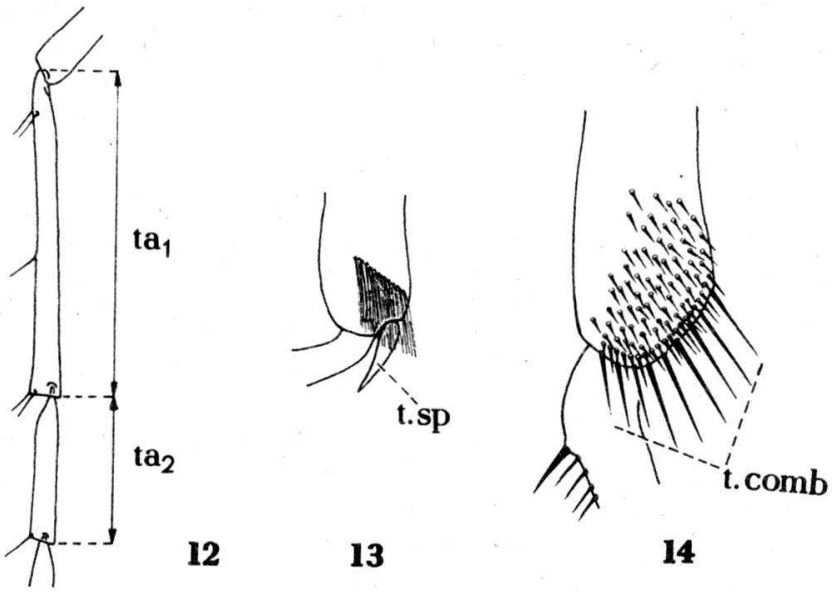
10, 11. Lateral (10) and dorsal view (11) of thorax of *Culicoides* sp. (10) and *Stilobezzia* sp. (11); ac. s — acrostichal setae; anepm — anepimeron; anepst — anepisternum; aprn — antepronotum; a. sp — anterior spiracle; a. spal. s — anterior supraalar setae; cx 1, 2, 3 — coxa of fore, middle and hind leg; dc. s — dorsocentral setae; hr — halter; kepm — katepimeron; kepst — katepisternum; mr — meron; pn — postnotum; pprn — postpronotum; pprn. s — postpronotal setae; presc. p — prescutal pit; psct. s — prescutellar setae; p. sp — posterior spiracle; p. spal. s — posterior supraalar setae; sc — scutum; sct — scutellum; sct. s — scutellar setae; tr. sut — transverse suture

on its inner surface a characteristic sensory area which usually is invaginated as a sensory pit (fig. 3) containing capitate sensilla = sensilla capitata of SAETHER (1980). In the amber, the piercing elements of the proboscis usually are barely visible.

THORAX

Thorax is dorsally convex and extends anteriorly over the head slightly (fig. 10). Antepronotum is divided by anterior part of scutum into lateral halves hidden below postpronotum (humerus). In predatory biting midges, antepronotum is usually well developed, collar-like. Mesothorax is greatly enlarged and mesonotum includes the entire dorsum, i.e. prescutum, scutum, scutellum and postnotum (postscutellum). Prescutum is greatly reduced and its position coincides with the prescutal (humeral) pits well visible in some genera. In this paper the prescutum is treated as a part of the scutum. The posterior portion of scutum before scutellum is usually flattened. Sometimes scutum bears a small tubercle in the middle of anterior margin. Laterally it has a pair of indistinct transverse sutures as depressed lines. Scutum is covered with unordered setae, eventually with distinct prescutal and supraalar setae (fig. 10). In some genera however, distinct setal groups are developed (fig. 11), i.e. acrostichals, dorsocentrals, supraalars, prescutellars and postpronotals

(humerals). The acrostichal setae are located on the midline of scutum. The dorsocentral setae lie lateral to the acrostichals. The supraalar (prealar) setae include anterior and posterior groups of usually stronger setae. Usually one pair of long prescutellar setae is located on flattened prescutellar surface of scutum. Sometimes distinct setae are found on postpronotum. Scutellum bears different number of long, or long and short setae. The postnotum is bare and void of a longitudinal suture. Pleural sclerites of mesothorax are usually bare (fig. 10).



12–14. Legs of *Ceratopogon* sp.; 12 — proximal tarsomeres of middle leg showing measurements, 13 — apex of fore tibia, 14 — apex of hind tibia; ta_1 —first tarsomere; ta_2 — second tarsomere; t. comb — tibial comb; t. sp — tibial spur

Legs are rather short and stout with characteristic modifications, especially in the female sex. One or more pairs of femora may be swollen and armed with distinct ventral spines. Apex of fore tibia bears an articulate spur and a transverse row of modified fine hairs (fig. 13), middle tibia without spur, while hind tibia usually possesses an indistinct spur and a tibial comb composed of a number of strong spines (fig. 14). In the genus *Ceratopogon* the entire outer apical part of hind tibia adjoining the tibial comb is covered with numerous spines. Usually only single row of weaker spines proximal of tibial comb is present. Tibiae, especially of hind legs, usually bear long dorsal setae.

Tarsomeres with or without spines. Fourth tarsomeres cylindrical, subcylindrical or cordiform, in male usually subcylindrical or cylindrical. Basitarsi longer, equal or shorter than second tarsomeres. Tarsal ratio (TR) is the length of the basitarsus divided by the length of second tarsomere; of fore leg — TR(I), middle leg — TR(II), hind leg — TR(III).

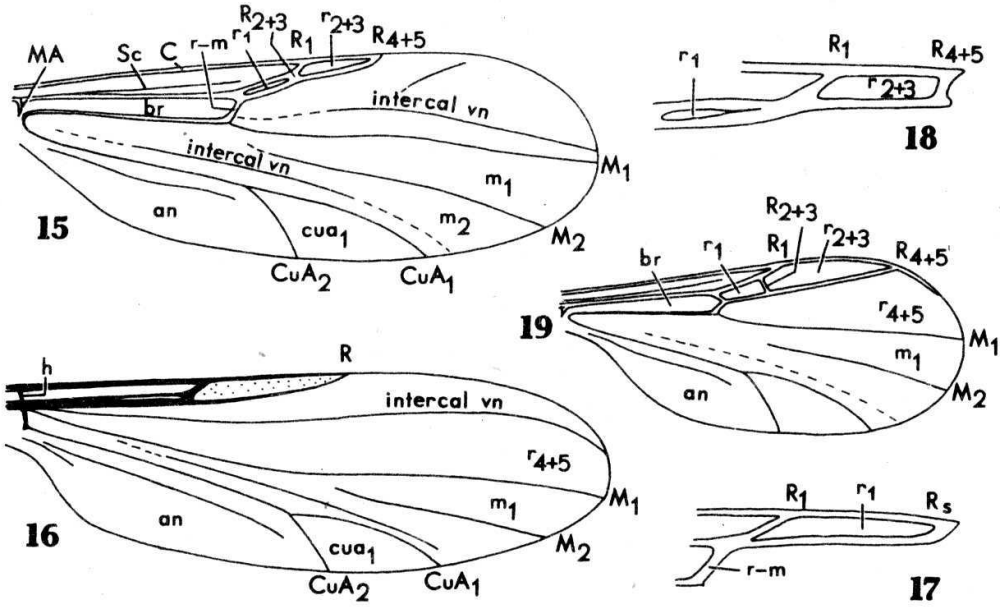
Length of second tarsomere was measured excluding basal portion hidden in the basitarsus and because of that usually invisible (fig. 12). Hind basitarsus is often bent near the base, somewhat swollen and bearing a ventral spine near the base and usually with ventral palisade of spine-like setae.

Female claws with simple apices, may be short and equal, long and equal, long and more or less unequal, with or without inner and outer basal teeth, trifid, similar on all legs or not, etc. Empodium rudimentary, only well developed and branching in most *Forcipomyiinae*. Male claws nearly always simple and equal on all legs, usually with bifid apices.

Wing moderately broad, in male narrower, with apex usually evenly rounded, alula usually indistinct. Wing membrane is usually covered with very short microtrichia which are of uniform density and long macrotrichia varying in density, distribution and size. Development or reduction of the microtrichia and macrotrichia usually are well visible in the specimens impregnated with Canada balsam.

The nomenclature of the wing veins follows the McAlpine (1981) venational pattern proposed for *Diptera*, and Downes and Wirth (1981) as concerns the *Ceratopogonidae*.

According to McAlpine (l.c.) each of six primary veins called costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), and anal vein (A) consists of two branches: a convex anterior branch (A) and a concave



15–19. Wing venation of *Ceratopogonidae*; 15 — *Fossihelea gracilitarsis* (Meunier), 16 — *Leptoconops succineus* sp. n., 17 — *Mantohelea lacus* (Meunier), 18 — *Dasyhelea stanislavi* sp. n., 19 — *Eohelea sinuosa* (Meunier): br — basal radial cell; intercal vn — intercalary vein. For explanation of other abbreviations see text

posterior branch (P), except for the C and Sc which are single veins. The anterior branch of R is called R_1, the posterior branch called radial sector (Rs) consists of four veins R_2–R_5. Anterior branch of M i.e. MA (= basal arculus) is reduced and occurs as a transverse short vein at wing base. The posterior branch MP has only three free veins $M_1 - M_3$, since M_4 never occurs as a free vein in *Diptera*. Base of M is atrophied. The anterior branch of Cu is forked into CuA_1 and CuA_2 veins, the posterior branch is CuP. In the case of A the anterior branch is called A_1 and the posterior branch A_2.

In the *Ceratopogonidae* (figs. 15–19) C is usually short, sometimes elongated to wing tip. Subcosta well visible, however rarely reaching costal vein. A humeral cross-vein often is indistinct. Vein R_1 usually reaches wing margin at middle of the wing length. R_s typically branching into R_{2+3} and R_{4+5} to form cell r_1 and r_{2+3}, which usually are termed as the first and second radial cells respectively (WIRTH, 1952). Sometimes R_{2+3} running forward to R_1 is not developed (fig. 17). In the cell r_{4+5} there is single (fig. 16) or forked (fig. 15) intercalary or false vein. The cell br is a basal radial cell (figs. 15, 19). The radial-medial (r-m) crossvein is absent only in *Leptoconops* and in the anomalous genus of *Ceratopogonini* (GROGAN and WIRTH, in prep.). Veins M_1 and M_2 usually are well developed, sessile or petiolate, sometimes the base of M_2 is atrophied or this vein is totally reduced in some genera. A false vein is often evident in cell m_2 (fig. 15). Cubital fork is well developed, CuP and A weak and not reaching the wing margin.

The wing length was measured from the MA (= basal arculus) to the wing tip. The costal ratio (CR) is obtained by dividing the length of costa by wing length.

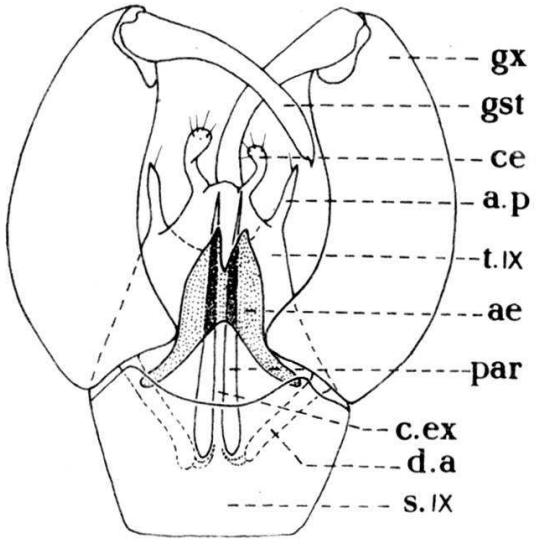
ABDOMEN

Abdomen is ten-segmented. Sometimes the tergites of the two first segments are fused.

The female abdomen is usually short and bears on its caudal end one-segmented cerci, which are distinctly elongated only in *Leptoconops*. In the *Ceratopogonidae* elements of segments VIII–X form the female genitalia (SZADZIEWSKI, 1986). Sternite VIII caudally bears usually short gonapophyses recognizable as submedian caudal lobes. The gonapophyses VIII are strongly developed in *Eohelea gedanica* **sp. n.** (fig. 534). Sternite IX is strongly reduced and fused with tergite IX, and with more or less developed gonapophyses IX (subgenital plate) ventrally. Sternite IX in females in amber is not visible being hidden under sternite VIII. The small sternite X and tergite X are usually fused and continuous around the entire segment. The cerci are appendages of segment XI, which is reduced and thus they belong to segment X. The spermathecae

usually consist of 1–3 strongly sclerotized seminal capsules. Unfortunately, only in a few of the specimens dissected in amber the seminal capsules have been found.

The male abdomen is more slender than in the female. The male genitalia (fig. 20) are formed by modified elements of segments IX and X.



20. Male genitalia of *Ceratopogon grogani* sp. n., ventral view: ae — aedeagus; a. p — apicolateral process of tergite IX; ce — cercus; c. ex — caudomedian excavation of sternite IX; d. a — dorsal apodeme of gonocoxite; gst — gonostylus; gx — gonocoxite; par — paramere; s. IX — sternite IX; t. IX — tergite IX

They may be inverted, rotated or in the normal position. Sternite IX is small and fused with tergite IX, and its caudomedian margin is usually more or less emarginated. Tergite IX is usually enlarged to cover the other elements of genitalia, and often bears two divergent apicolateral processes. The lateral gonopods are composed of the large proximal gonocoxite and the slender distal gonostylus. The gonostyli bear an articulated subapical spine only in *Leptoconops*. The aedeagus is a usually more or less triangular or Y-shaped structure. Above the aedeagus a pair of parameres is present and are usually symmetrical and separated, articulating with the dorsal apodemes of the gonocoxites. Segment X is usually strongly reduced and shifted onto the ventral surface of tergite IX. The slender male cerci are usually visible on the distal margin of tergite IX.

IV. SYSTEMATICS

1. Arrangement of the genera from Baltic amber. Key for the indentification of subfamilies

The arrangement of the subfamilies and tribes is discussed in chapter VII. Related genera and species are grouped. More plesiomorphic groups of species usually precede these more apomorphic. Extinct genera are marked with "+".

Subfamily *Ceratopogoninae* NEWMAN (78 species)

Tribe *Culicoidini* KIEFFER (11 species)

1. Genus *Culicoides* LATREILLE (11 species)

Tribe *Ceratopogonini* NEWMAN (27 species)

2. Genus *Ceratopogon* MEIGEN (15 species)
3. Genus *Brachypogon* KIEFFER (7 species)
4. Genus *Nannohelea* GROGAN et WIRTH (2 species)
5. Genus *Ceratoculicoides* WIRTH et RATANAWORABHAN (1 species)

\+ 6. Genus *Fossihelea* **gen. n.** (2 species)

Tribe *Stilobezziini* WIRTH (34 species)

7. Genus *Alluaudomyia* KIEFFER (2 species)
8. Genus *Stilobezzia* KIEFFER (6 species)
9. Genus *Monohelea* KIEFFER (3 species)
10. Genus *Serromyia* MEIGEN (6 species)

\+ 11. Genus *Mantohelea* **gen. n.** (2 species)
\+ 12. Genus *Meunierohelea* **gen. n.** (6 species)
\+ 13. Genus *Wirthohelea* **gen. n.** (1 species)
\+ 14. Genus *Eohelea* PETRUNKEVITCH (4 species)
\+ 15. Genus *Gedanohelea* **gen. n.** (3 species)
\+ 16. Genus *Ceratopalpomyia* **gen. n.** (1 species)

Tribe *Heteromyiini* WIRTH (2 species)

17. Genus *Neurohelea* KIEFFER (1 species)
18. Genus *Physohelea* GROGAN et WIRTH (1 species)

Tribe *Palpomyiini* ENDERLEIN (4 species)

19. Genus *Palpomyia* MEIGEN (3 species)
20. Genus *Bezzia* KIEFFER (1 species)

Subfamily *Forcipomyiinae* LENZ (18 species)

21. Genus *Forcipomyia* MEIGEN (17 species)
22. Genus *Atrichopogon* KIEFFER (1 species)

Subfamily *Dasyheleinae* LENZ (4 species)

23. Genus *Dasyhelea* KIEFFER (4 species)

Subfamily *Leptoconopinae* NOÉ (1 species)

24. Genus *Leptoconops* SKUSE (1 species)

Key for the identification of subfamilies

1. Wing without crossvein r-m. Female cerci long. Male antenna with only apical flagellomere elongated. . . . . *Leptoconopinae*
—. Wing with distinct crossvein r-m. Female cerci short. Male antenna with distal 3–4 flagellomeres elongated. 2
2. Empodium well developed and branching, at least in female. Claws distinctly curved. Apical flagellomere with distinct terminal papilla. . . . . *Forcipomyiinae*
—. Empodium vestigial. Claws slightly curved. Apical flagellomere with blunt or slightly pointed tip. 3
3. Male antenna with distal four flagellomeres elongate, flagellomere IX usually as long as next distal one. Flagellomeres sculptured. Tip of vein R_{4+5} usually concave. Female claws short and equal. . . . . *Dasyheleinae*
—. Male antenna with distal three flagellomeres elongate, flagellomere IX usually distinctly shorter than next one. Flagellomeres not sculptured. Tip of vein R_{4+5} rounded or blunt. Female claws various. . . . . *Ceratopogoninae*

2. Subfamily *Ceratopogoninae* Newman, 1834

DIAGNOSIS

Eyes contiguous or separated. Female antenna usually with 13 flagellomeres, distal 5 elongate; only the distal flagellomere elongate in the recent *Rhynchohelea monilicornis* WIRTH et BLANTON; flagellomeres reduced. Last flagellomere without terminal papilla. Third palpal segment the latter. Sensilla coeloconica present at least on the first flagellomere in the tribes *Culicoidini* and *Ceratopogonini*. The typical number of 13 male flagellomeres reduced in some genera to 12–6, and plume may also be reduced. Last flagellomere without terminal papilla. Third palpal segment with or without sensory pit. Sometimes fourth and fifth palpal segments fused, and rarely 1 and 2 or 1–3.

Antepronotum sometimes well developed, collar-like. Prescutal pits well developed or absent. Legs may be modified. Basitarsi longer than second tarsomeres. Female claws various. Empodium rudimentary. Wing membrane usually with microtrichia, macrotrichia present or absent. Transverse vein r-m almost always present. Tip of R_{4+5} blunt or rounded. Sometimes all radial veins totally fused. Media petiolate or sessile. Female cerci short. Male genitalia various.

RECENT ECOLOGY, DISTRIBUTION AND CLASSIFICATION

The larvae of most *Ceratopogoninae* are predominantly carnivorous and inhabit a wide variety of aquatic, semiaquatic and moist habitats.

Females are usually adapted to blood sucking on mammals and birds or are predaceous on small insects. Both sexes may visit flowers. Most species are crepuscular.

It is the largest subfamily distributed worldwide and containing over 70 of the over 80 recent genera. The subfamily is divided into seven tribes: *Culicoidini*, *Ceratopogonini*, *Stilobezziini*, *Heteromyiini*, *Sphaeromiini*, *Palpomyiini*, and *Stenoxenini*.

Fossils

The oldest findings, Cretaceous in age, belong to the tribe *Culicoidini* (see below). No fossils of the tribes *Sphaeromiini* and *Stenoxenini* have been reported until now. Remm (1976) suggested that the species described by Boesel (1937) from Canadian amber as *Atrichopogon*, *Dasyhelea* and *Lasiohelea* actually belong to this subfamily. The genera *Neoculicoides* and *Paraculicoides* described by Pierce (1966) from Miocene Californian nodules may also belong to this subfamily, however, their tribal position is uncertain at this time (see chapter V).

The male of *Johannsenomyia swinhoei* briefly described from Burmese amber by Cockerell (1919) and placed in that genus of the tribe *Sphaeromiini* has no characters justifing its generic and tribal position. It may also be a member of the *Heteromyiini* or *Palpomyiini*. The vein M_2 certainly forks proximal to the level of crossvein r-m, and femora its lack ventral spines (B. Townsend, personal comm.). Also, *Johannsenomyia rouseae* from Californian nodules (Pierce, 1966) is of doubtful generic and tribal position.

The *Ceratopogoninae* predominate in Baltic amber, 82% of all specimens examined (table 3).

Ceratopogoninae indetermined (1 ♂, 8 ♀)

MBI 138, Kühl, 1 ♀; 187, Künow, 1 ♀; 189, Künow, 1 ♀; 190, Künow, 1 ♀; 193, Künow, 1 ♀; 204, Künow, 1 ♀; Thomas 186, 1 ♀; Thomas 221, 1 ♀; ZMC 24, Ostpreussen, Min. Mus., 1 ♂.

Key to Baltic amber tribes of *Ceratopogoninae*

1. Veins M_1 and M_2 forking distal of crossvein r-m 2
—. Veins M_1 and M_2 forking at or proximal of crossvein r-m . . . 4
2. First flagellomere with sensilla coeloconica or sensilla basiconica . . . 3
—. First flagellomere without sensilla coeloconica or sensilla basiconica . . . . . *Stilobezziini*
3. Claws of both sexes moderately small, equal and simple. Wing membrane usually with abundant macrotrichia . . . . *Culicoidini*

—. Female claws large, equal or unequal, or very small and equal. Wing membrane with macrotrichia at wing tip or bare . . . *Ceratopogonini*

4. Fifth tarsomere of fore leg inflated or swollen . . . . *Heteromyiini*

—. Fifth tarsomere of fore leg slender . . . . . *Palpomyiini*

Tribe *Culicoidini* Kieffer, 1911

Diagnosis

Eyes separated or contiguous. Antenna in both sexes with 13 flagellomeres, in female distal 5 or 4, in male distal 3 elongate. Palpus five segmented, in *Austroconops* Wirth et Lee and in some *Paradasyhelea* Macfie the last two segments are fused. Third palpal segment usually with distinct sensory pit. Sensilla coeloconica present not only on first but usually on some others or all flagellomeres. Female proboscis usually adapted for piercing mammals or birds. Antepronotum small. Prescutal pits usually well developed. Legs moderately slender, unmodified, fourth tarsomeres cylindrical. Female claws short, equal and simple on all legs. Wing membrane covered with distinct microtrichia and usually with abundant macrotrichia. Costa usually short. Usually both first radial cells present. Veins M_1 and M_2 petiolate, base of M_2 usually atrophied.

Parameres in male genitalia usually well developed, slender with curling tips and separated. Apicolateral processes of tergite IX usually long, slender and pointed.

Recent ecology, distribution and classification

To this tribe belong three recent genera, i.e. *Culicoides*, *Paradasyhelea* and *Austroconops*. *Paradasyhelea* includes only six recent species and is distributed from North America via Patagonia to New Zealand and Australia (Wirth, 1981). It differs from *Culicoides* mainly in having a short proboscis, and long and abundant macrotrichia covering the entire wing. The monotypic genus *Austroconops* from Australia showing diurnal activity has four segmented palpi (as *Leptoconops*), wing membrane without macrotrichia, media with long petiole, mandible with small number of teeth, low TR(III), and highly modified male genitalia.

Fossils

The undoubted oldest findings of *Culicoidini* are late Cretaceous *Culicoides* (see below), *Atriculicoides* Remm and *Protoculicoides* Boesel. It seems that the Neocomian ceratopogonids from Lebanese amber

which according to WIRTH (personal comm.) resemble in some ways *Austroconops* may also belong to this tribe. Also, it is probable that the Miocene genera *Neoculicoides* and *Paraculicoides* from California (PIERCE, 1966) known from pupa stages belong to the *Culicoidini.*

Atriculicoides from Cretaceous Siberian amber (REMM, 1976) undoubtedly belongs to this tribe, however its relation to *Culicoides*, *Protoculicoides* and *Paradasyhelea* is not quite clear. It has a short proboscis similar to *Paradasyhelea* and a long costa (CR 0.70–0.75) like some recent *Culicoides* from South America (WIRTH and BLANTON, 1973) and from Oriental region (*Culicoides* subg. *Haemophoructus* MACFIE; WIRTH, personal comm.) or *Protoculicoides* and *Austroconops*. All other characters are typical for "average" *Culicoides* except for sensilla capitata scattered over the whole surface of third palpal segment as in subg. *Haemophoructus* (WIRTH, personal comm.). It is worth-while to note that *Atriculicoides squamaticrus* (REMM, 1976) was diagnosed by lanceolate scales present on the wing margin which seem to be an artifact. Often normal setae in the amber are in a sheath of air and because of this they appear stouter or lanceolate.

The late Cretaceous *Protoculicoides* including its single species *depressus* (BOESEL, 1937) from Canadian amber should probably be included to the tribe *Culicoidini.* The holotype female of this species preserved in Dept. of Entomology, Royal Ontario Museum, Toronto, examined through the present course is characterized as follows: Eyes pubescent, separate. Flagellum with only 4 last units elongate. Pedicel unusually long, cylindrical. Sensilla coeloconica not visible. Proboscis long. Palpus long and slender, 5-segmented. Wing length 1.72 mm, CR 0.87. Both first radial cells long, macrotrichia absent, microtrichia distinct, media with long petiole. Legs slender. Spur of fore tibia serrated, fourth tarsomeres cylindrical, claws small and equal. Proximal tarsomeres with several spine-like setae and more distinct apical spines. Prescutal pits distinct. Cerci short. Proximal flagellomeres with long, strong verticils.

This species is very close to *Culicoides cylindricornis* (WIRTH and BLANTON, 1973) from the Amazon Basin which has no macrotrichia on wing membrane; a long single first radial cell, CR 0.83; proximal flagellomeres with stout verticils. Only two characters of *Protoculicoides* are not present in *Culicoides*, i.e. long cylindrical pedicel and short flagellomere IX. The elongated nature of the pedicel may not be natural, since upper part of head, thorax and abdomen are depressed in the amber. WIRTH et al. (1974) placed *Protoculicoides* in the tribe *Ceratopogonini.*

In the Baltic amber only *Culicoides* has been found.

1. Genus *Culicoides* Latreille, 1809

Diagnosis

Small midges. Eyes large, separated or contiguous. Flagellum always consists of 13 flagellomeres. Some or all flagellomeres with sensilla coeloconica. In female the distal 5, in male the distal 3 flagellomeres elongate. Male plume well developed. Palpus 5-segmented. Third palpal segment usually with distinct sensory pit. Proboscis long, adapted for piercing. Prescutal pits large and always distinct. Scutum covered with short hairs and longer setae of no taxonomic value. Scutellum bears various number of long and shorter setae. Legs slender, unmodified. Tibial comb composed of 4–8 long spines. Fourth tarsomeres cylindrical. Female claws short, equal and simple on all legs. Wing usually covered with dense microtrichia and with more or less abundant macrotrichia. Female CR 0.53–0.83. Cells r_1 and r_{2+3} usually well developed. Vein M_2 usually well visible.

Male genitalia moderately large, sometimes slightly rotated. Tergite IX usually with long and slender apicolateral processes. Gonostylus usually with slightly swollen and setosed base, and slender and nearly bare distal portion with incurved tip. Aedeagus usually Y-shaped with a caudomedian process directed ventrally. Parameres usually separate with slender smooth or pectinate, often curling tips. Cerci usually shifted to ventral surface of tergite IX.

Recent ecology, distribution and classification

The larvae are adapted to aquatic and semiaquatic habitats, and are active swimmers. They are found in a wide variety of moist habitats including margins of water reservoirs, wet soils, animal manure, decaying plants, etc. Larvae feed on organic rotting material including micro-organisms or are predaceous. Adult females take blood from mammals and birds. Mating typically takes place in flight.

The genus is distributed worldwide including about 1,000 recent species grouped in over 20 subgenera. However the subgeneric classification of *Culicoides* is still poorly understood.

Fossils

Twenty two species of fossil *Culicoides* outside of Baltic amber have been described (see chapter V). The oldest *Culicoides* has been recorded from late Cretaceous New Jersey amber (ca. 94 Ma) by Grogan and Szadziewski (in prep.). Remm (1976) from Siberian amber described four species of the genus, and Statz (1944) from Aquitanian deposits of Rott

impressions a further 12 species (only females). PALMER (1957) and PIERCE (1966) described silicified pupae from Miocene nodules found in California of five species. Unfortunately all named impressions are void of diagnostic characters good enough to compare them with the amber fossils or with recent species. Also, these species which are based on pupae which are poorly known in the genus and have no taxonomic value.

Previously only a single species of *Culicoides* has been described from Baltic amber by MEUNIER (1904). In present material 196 specimens belonging to 11 distinct species have been found.

Culicoides indetermined 64 (25 ♂, 39 ♀)

IMGPUG 6586, paralectotype ♂ of *Forcipomyia uncula*; MBI 143, KÜHL, at *Alluaudomyia succinea*, 1 ♀; 152, KÜNOW, 1 ♂; 185, KÜNOW, 1 ♀; 222, THOMAS, 1 ♀; THOMAS 452, 1 ♂; MM 4, 1 ♀; MZW 393 b′, b″, 2 ♂, 1 ♀; 469/40, 1 ♂; 469/184, 1 ♀; 1832/9, 1 ♀; 3705, 1 ♀; 4388, 1 ♀; 4835, TG, 1 ♂; 5015, TG, 1 ♂; 5137, TG, 2 ♂; 5207, TG, 1 ♀; 5307, TG, 1 ♀; 6482 b, 1 ♂; 7237 (+ *Empididae* 1 ♂), 1 ♀; 7634 (+ *Cecidomyiidae* 1 ♂), 1 ♂, 2 ♀; 7674 (+ *Mycetophilidae* 1 ♀), 1 ♂; 8390 a (+ *Aranei* 1), 1 ♀; 10282, 1 ♀; 12662, 1 ♀; 12803, 1 ♀; 13204, TG, 1 ♀; 13989, TG, 1 ♂; 14008, TG, 1 ♀; 14584, TG, 1 ♂; 15746, TG, 1 ♀; 18553 c (+ *Chironomidae* 1 ♀), 1 ♀; 18879, TG (+ *Chironomidae* 1 ♀), 1 ♂; ZMC 23, BÓRGE MORTENSEN, 23–2 1965, 1 ♂; 26, Ostpreussen, Min. Mus., 1 ♂; 36, C. V. HENNINGSEN, 1–12 1966, 1 ♀; 69 b, A. HENNINGSEN, 9–9 1974, 1 ♂; 71, C. V. HENNINGSEN, 1–4 1970, 1 ♀; 81, C. V. HENNINGSEN, 1–7 1966, German amber, 1 ♂; 82, TH. HANSEN, Mou, 16–1 1961, 1 ♀; 88, A. K. ANDERSEN, 28–3 1968, 1 ♂; 100, C. V. HENNINGSEN, 1–1 1966, 1 ♂; 124, C. V. HENNINGSEN, 8–7 1965, 1 ♀; 126, C. V. HENNINGSEN, 3–5 1960, 1 ♀; 136, Libau, Kóbmand Tidemand, Min. Mus., 1940–43, 1 ♀; 156, Jyll. Vestkyst., S. HANSEN, Min. Mus., 1919–299, 1 ♀; 164, A. K. ANDERSEN, 28–3 1968, 1 ♀; 172, A. HENNINGSEN, 9–9 1974, 1 ♀; 180, C. V. HENNINGSEN, German amber, 1–7 1966, 1 ♂; 187, C. V. HENNINGSEN, 12–4 1957, 1 ♀; 199, A. HENNINGSEN, 9–9 1974, 1 ♀; 202, C. V. HENNINGSEN, 24–1 1963, 1 ♂; 205, A. HENNINGSEN, 9–9 1974, 1 ♂; 206, A. K. ANDERSEN, 28–3 1968, 1 ♀; 212, A. HENNINGSEN, 9–9 1974, 1 ♀; 224, C. V. HENNINGSEN, 1–5 1967, 1 ♀; 226, C. V. HENNINGSEN, German amber, 1–7 1966, 1 ♀; 246, A. HENNINGSEN, 9–9 1974, 1 ♀.

Key to Baltic amber species of *Culicoides*

Males

1. Aedeagus more or less Y-shaped, caudomedian projection single 2

impressions a further 12 species (only females). PALMER (1957) and PIERCE (1966) described silicified pupae from Miocene nodules found in California of five species. Unfortunately all named impressions are void of diagnostic characters good enough to compare them with the amber fossils or with recent species. Also, these species which are based on pupae which are poorly known in the genus and have no taxonomic value.

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Key to Baltic amber species of *Culicoides*

Males

1. Aedeagus more or less Y-shaped, caudomedian projection single 2

—. Aedeagus with 2 or 3 distinct apical projections 9

2. Gonostylus sinuous, somewhat S-shaped . . . . . 10. *C.* (subg.?) *gedanensis* sp. n.

—. Gonostylus not sinuous, C-shaped 3

3. Apicolateral processes of tergite IX blunt. Tip of paramere with fringe of setae . . . . . 7. *C.* (*Oecacta*) *balticus* sp. n.

—. Apicolateral processes of tergite IX pointed. Tip of paramere void of setae 4

4. Apicolateral processes of tergite IX very short. Basal radial cell without macrotrichia . . . . . 6. *C.* (*Oe.*) *succivarius* sp. n.

—. Apicolateral processes of tergite IX long. Basal radial cell with macrotrichia 5

5. Apicolateral processes of tergite IX broad . . . . . 2. *C.* (*Oe.*) *dasyheleiformis* sp. n.

—. Apicolateral processes of tergite IX slender 6

6. Apical projection of aedeagus blunt . . . . . 5. *C.* (*Oe.*) sp. C

—. Apical projection of aedeagus evenly pointed 7

7. Distal part of parameres long and stout . . . . 3. *C.* (*Oe.*) sp. A

—. Distal part of parameres short and slender 8

8. Basal arch of aedeagus very high. Tip of parameres slightly curved . . . . . 4. *C.* (*Oe.*) sp. B

—. Basal arch of aedeagus moderately low. Tip of parameres strongly curved . . . . . 1. *C.* (*Oe.*) *speciosus* (MEUNIER)

9. Parameres short. Caudomedian margin of tergite IX extending beyond tips of the apicolateral processes . . . . . 11. *C.* (subg.?) *prussicus* sp. n.

—. Parameres long. Caudomedian margin of tergite IX not extending beyond tips of the apicolateral processes 10

10. Aedeagus with 3 long apical projections . . . . . 8. *C.* (subg.?) *eoselficus* sp. n.

—. Aedeagus with 2 long apical projections . . . . . 9. *C.* (subg.?) *ceranowiczi* sp. n.

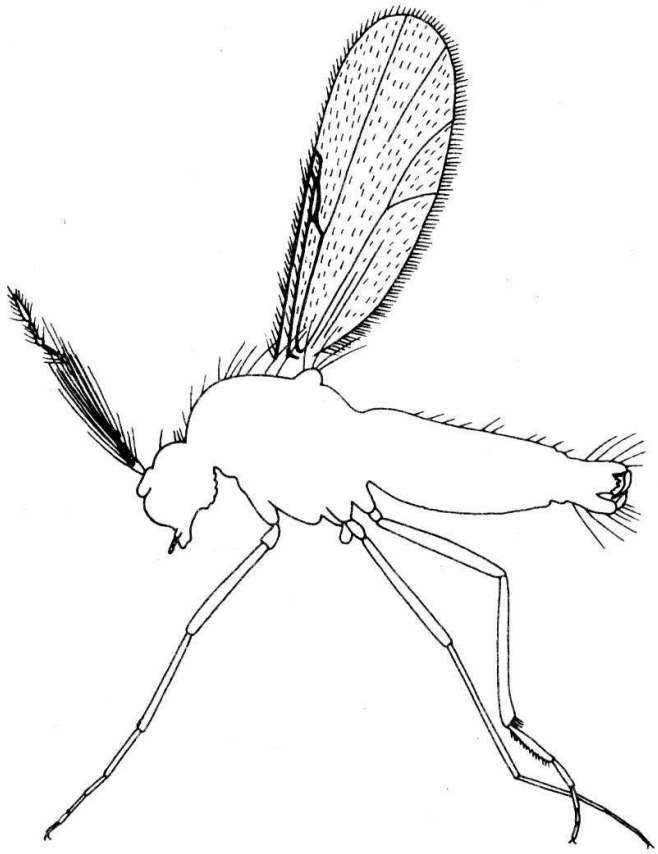
Subgenus *Oecacta* Poey, 1851

DIAGNOSIS

Third palpal segment with distinct sensory pit. Wing membrane usually with abundant macrotrichia. Apicolateral processes of tergite IX present. Parameres separate. Aedeagus triangular or Y-shaped. Spermathecae with two ovoid seminal capsules.

RECENT ECOLOGY, DISTRIBUTION AND CLASSIFICATION

Ecology of *Oecacta* as of the genus *Culicoides*. This worldwide distributed subgenus inclades large number of often very similar species separated mainly using wing pattern, distribution of sensilla coeloconica on female flagellum, details of male genitalia, seminal capsules, etc. The classification of this ill defined subgenus is poorly understood on the worldwide basis. In the Palaearctic region *Oecacta* is divided into species groups (cf. GUCEVIČ, 1973). Some of these groups are treated by some authors as distinct subgenera (for example GLUCHOVA, 1979).



21. *Culicoides speciosus* (MEUNIER), total habitus of male, MZW 19303

FOSSILS

It seems that the late Cretaceous *Culicoides* presently under study by GROGAN and SZADZIEWSKI, *C. succineus* REMM and *C. sphenostylus* REMM may be included in this subgenus. Seven of 11 species of *Culicoides* from Baltic amber are included in *Oecacta*.

1. *Culicoides* (*Oecacta*) *speciosus* (Meunier, 1904)
(Figs. 21–32)

Ceratopogon speciosus MEUNIER, 1904: 229(♂, ♀, Baltic amber).
Culicoides speciosus: KIEFFER, 1906: 1 (combination); ARNAUD, 1956: 148 (combination).

DIAGNOSIS

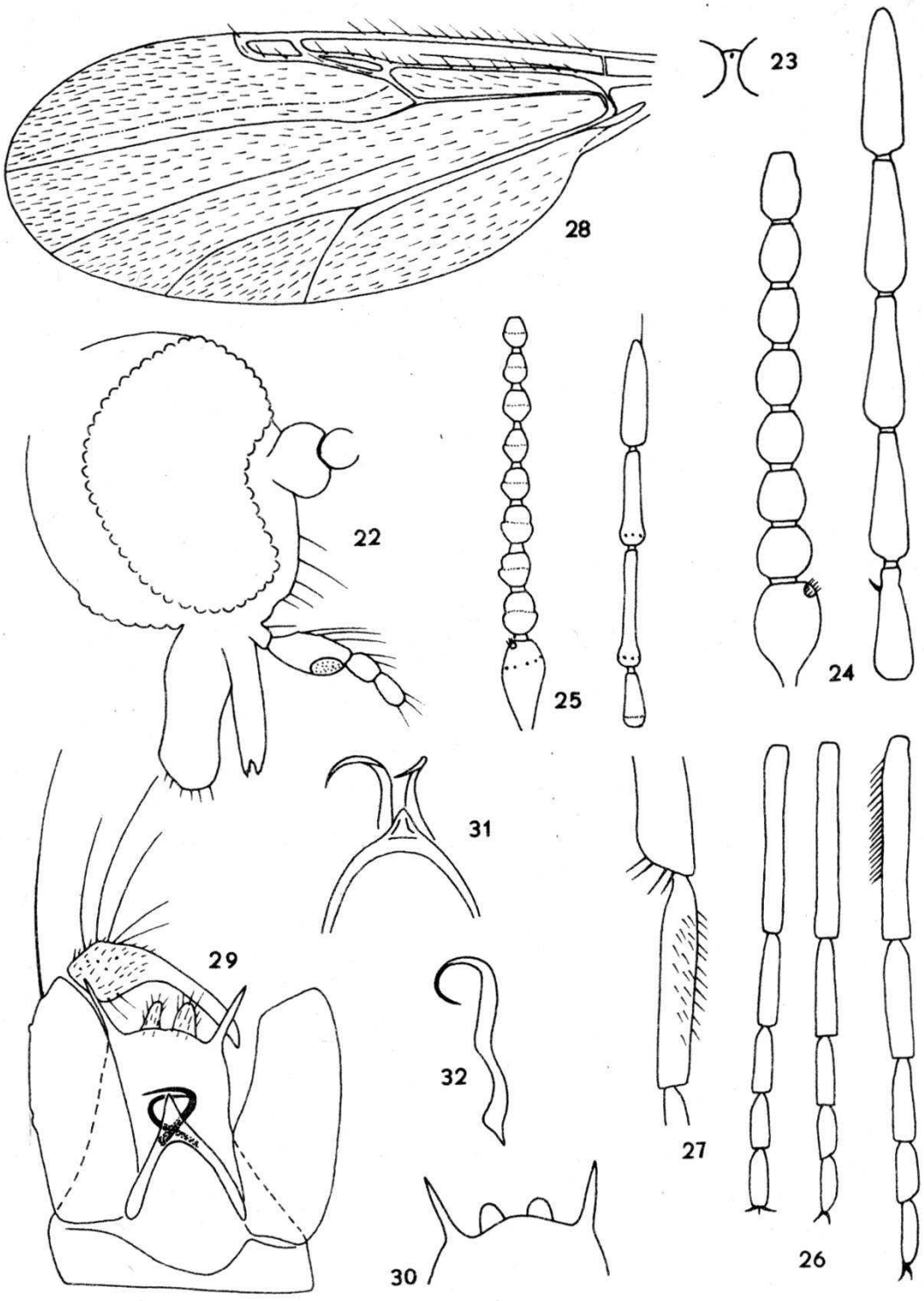
The species is characteristic in having the entire wing membrane including basal radial cell densely covered with macrotrichia, apicolateral processes of tergite IX in male genitalia long, slender and pointed, parameres with slender curved tips, aedeagus with moderately high basal arch and apical projection of aedeagus short and evenly pointed.

DESCRIPTION

♀. Body blackish brown. Total length 1.3–2.0. Eyes widely separated (fig. 23). Flagellum length 533–680 µm, AR 1.18–1.26. Sensilla coeloconica on first flagellomere visible, proximal flagellomeres spherical to slightly elongate (fig. 24). Proboscis rather short (fig. 22). Third palpal segment distinctly swollen with large sensory pit; length 48–64 µm. Prescutal pits well developed. Legs slender. Tibial comb composed of 4, sometimes 3, spines. Hind basitarsus with distinct spine-like palisade setae (fig. 26). TR(I) 1.8–2.0, TR(II) 2.0–2.2, TR(III) 1.7–1.8. Wing length 0.94–1.39 mm, CR 0.58–0.62. Wing membrane covered with distinct microtrichia and with abundant macrotrichia over entire surface (fig. 28).

♂. Similar to female with the usual sexual differences. Body length 1.4–1.5 mm. Total habitus as in fig. 21. Flagellum length 642–710 µm, AR 0.92–1.04. First flagellomere with sensilla coeloconica (fig. 25). Third palpal segment 44–64 µm long, sensory pit distinct. Tibial comb composed of 3–5 spines (fig. 27). TR(I) 1.8–2.0, TR(II) 1.9–2.1, TR(III) 1.5–2.0. Wing length 0.96–1.26 mm, CR 0.53–0.58. Membrane including basal radial cell covered with long abundant macrotrichia.

Genitalia (figs. 29–32). Sternite IX with distinct caudomedian excavation. Tergite IX with long, slender and pointed divergent apicolateral processes. Cerci usually extending beyond caudal margin of tergite IX. Gonocoxite slender and long. Gonostylus with distinctly enlarged base bearing long setae, distal part slender with evenly pointed apex. Aedeagus Y-shaped, basal arch moderately high, apical projection short with evenly pointed apex. Parameres separate with slender and curved apices void of setae.



22–32. *Culicoides speciosus* (MEUNIER); 22 — female head, MZW 7462; 23 — eyes separation of female, IMGPUG 5893; 24 — female flagellum, IMGPUG 5893; 25 — male flagellum, MZW 7812; 26 — tarsi of fore, middle and hind leg of female, IMGPUG 5893; 27 — tip of hind tibia and first tarsomere of male, MZW 7812; 28 — female wing, IMGPUG 5893; 29 — male genitalia, MZW 19303; 30 — apicolateral processes of tergite IX, MZW 12898; 31 — aedeagus and parameres, MZW 8484; 32 — paramere, MM 8

MATERIAL EXAMINED (78 ♂, 26 ♀)

Types. Only female syntypes have been available for present study. Lectotype: IMGPUG Z 5893, 1 ♀. Paralectotypes: IMGPUG Z 4620, 1 ♀; 5577, 1 ♀, presumably another species; 5758, 1 ♀; 7867, 1 ♀; 7957, 1 ♀; 8873, 1 ♀. By present designation.

IZPAN 41/73, 1 ♂; MM 2, 1 ♂; 3, 1 ♂; 8, 1 ♂; MZW 469/106, 1 ♂; 1310, 1 ♂; 1347, 1 ♂; 3877 a (+ *Chironomidae* 1 ♂), 1 ♂; 3877 b, 1 ♂ 1 ♀; 4578, 1 ♂; 4698, TG, 1 ♂; 4832, TG, 1 ♀; 4859, TG, 1 ♀; 4920, TG, 1 ♀; 5003, TG, 1 ♀; 5019, TG, 1 ♂; 5068, TG, 1 ♀; 6482 a, 1 ♂; 6965, 1 ♂ 1 ♀; 7462, 1 ♀; 7812 (+ *Forcipomyia* indet. 1 ♀), 6 ♂ 2 ♀; 7964, 1 ♀; 8484, 1 ♂; 8521 a,b, 2 ♀; 8709 b, 1 ♂; 9059 b, c, d, 2 ♂ 1 ♀; 9624, 1 ♂; 9733, 6 ♂; 10044, 1 ♂; 10309 a, b, 1 ♂ 1 ♀; 11389, TG, 1 ♂; 12327, 1 ♂; 12824, 1 ♂; 12838 (+ *Chironomidae* 1 ♀), 3 ♂; 13182, TG, 1 ♂; 13189, TG, 1 ♀; 13800, TG, 1 ♂; 14082, TG, 1 ♂; 14405, TG, 1 ♂; 14520, TG, 1 ♂; 15733, TG, 1 ♂; 16414, TG, 1 ♂; 16578, TG, 1 ♂ 1 ♀; 16591, TG, 1 ♂; 16685, TG, 2 ♂; 17299, TG, 2 ♂; 17465, TG, 1 ♂; 17496, TG, 1 ♀; 17525, TG, 1 ♂; 17919, TG, 1 ♂; 18168, TG, 1 ♂; 18174, TG, 1 ♂; 18194, TG, 1 ♀; 18886, TG, 2 ♂; 19303, TG, 1 ♂; 19746, TG, 1 ♂; 19956 a, b, c, 3 ♂; 19985, 1 ♂; 20011, TG, 1 ♂; 20013, TG, 1 ♂; 20279, TG, 2 ♂; 20280, TG, 1 ♂; ZMC 83, C. V. HENNINGSEN, 31–5 1961, 1 ♂; 101, THORV. HANSEN, Mou, 4 ♂; 181 a, b, C. V. HENNINGSEN, 306 1953, 2 ♂; 248, C. V. HENNINGSEN, 3–5 1960, 1 ♂.

DISCUSSION

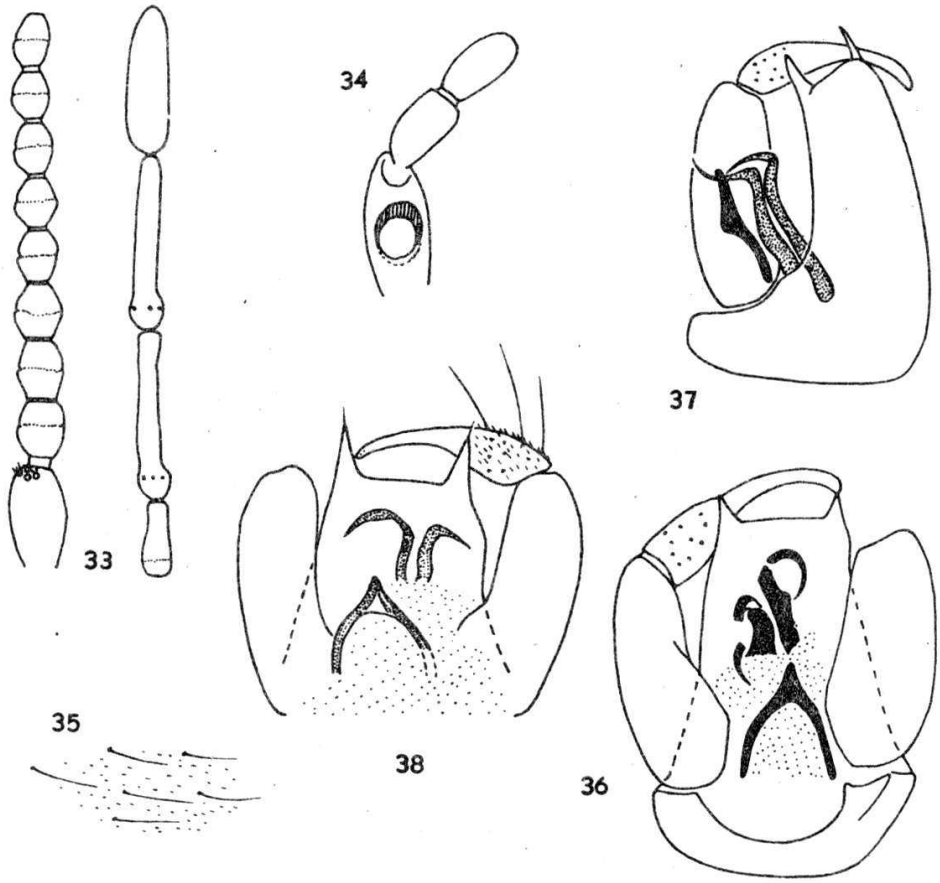
C. speciosus is a typical member of the subgenus *Oecacta* and belongs to this worldwide distributed species group, which in the Palaearctic region is called *pictipennis* (GUCEVIČ, 1973) or *odibilis* (KREMER et al., 1973). The group includes many very similar species separated mainly using wing pattern, distribution of sensilla coeloconica, shape of seminal capsules, details of male genitalia, etc. Therefore the fossil *C. speciosus* is void of important characters not visible in the amber and most probably it is a species complex.

It is the most common species representing more than 53% of all *Culicoides* examined. Males predominate, their rate is 75%. Single amber pieces contain up to 4 males (ZMC 101) or 6 males and 2 females (MZW 7812). The data above suggest, that *C. speciosus*, and *Culicoides* on the whole, were trapped in the yet soft resin probably from the swarm aggregations formed chiefly by males.

2. *Culicoides* (*Oecacta*) *dasyheleiformis* sp. n.
(Figs. 33–38)

DIAGNOSIS

This new species is characteristic in having the wing membrane including basal radial cell densely covered with long macrotrichia, apicolateral processes of tergite IX in male genitalia broad, long and pointed, parameres with moderately slender curved tips, aedeagus moderately high with evenly pointed, short apical projection and long tergite IX.



33–38. *Culicoides dasyheleiformis* sp. n., male; 33 — flagellum of holotype, 34 — palpus of holotype, MBI 99; 35 — macrotrichia and microtrichia on wing membrane of paratype, MBI 99; 36–38 — genitalia, 36 — holotype MBI 99; 37 — paratype, MBI 99; 38 — paratype, MBI 145

DESCRIPTION

♀. Unknown.

♂. Body dark brown. Total length 1.7–1.9 mm. Scutum shining. Flagellum length 938 μm, AR about 1.0. First flagellomere with ca. 6 sensilla coeloconica (fig. 33). Third palpal segment 75–76 μm long with

deep sensory pit (fig. 34). Scutum covered with long setae, scutellum with ca. 8 long and several short setae. Prescutal pits well developed. Tibial comb composed of 5 spines. Hind basitarsus with spine-like palisade setae. TR(I) 1.9–2.0, TR(II) 1.9–2.1, TR(III) 1.6–1.7. Wing length 1.45–1.70 mm, CR 0.58–0.59. Membrane with long appressed macrotrichia covering entire wing including basal radial cell (fig. 35).

Genitalia (figs. 36–38). Sternite IX with broad caudomedian excavation. Tergite IX longer than gonocoxite; apicolateral processes long, broad, apices pointed. Gonostylus normal. Basal arch of aedeagus moderately high, apical projection short with evenly pointed tip. Parameres separate, apical portion moderately slender and curved.

MATERIAL EXAMINED (4 ♂)

Holotype — ♂, MBI 99, BERENDT. Paratypes: MBI 99, 1 ♂ (+*Formicidae* 1), in the same amber piece with the holotype; MBI 145, KÜHL, 1 ♂.

Badly preserved 1 ♂, MZW 19983, TG, is not included in the type-series of the species.

3. *Culicoides* (*Oecacta*) sp. A
(Fig. 39)

DIAGNOSIS

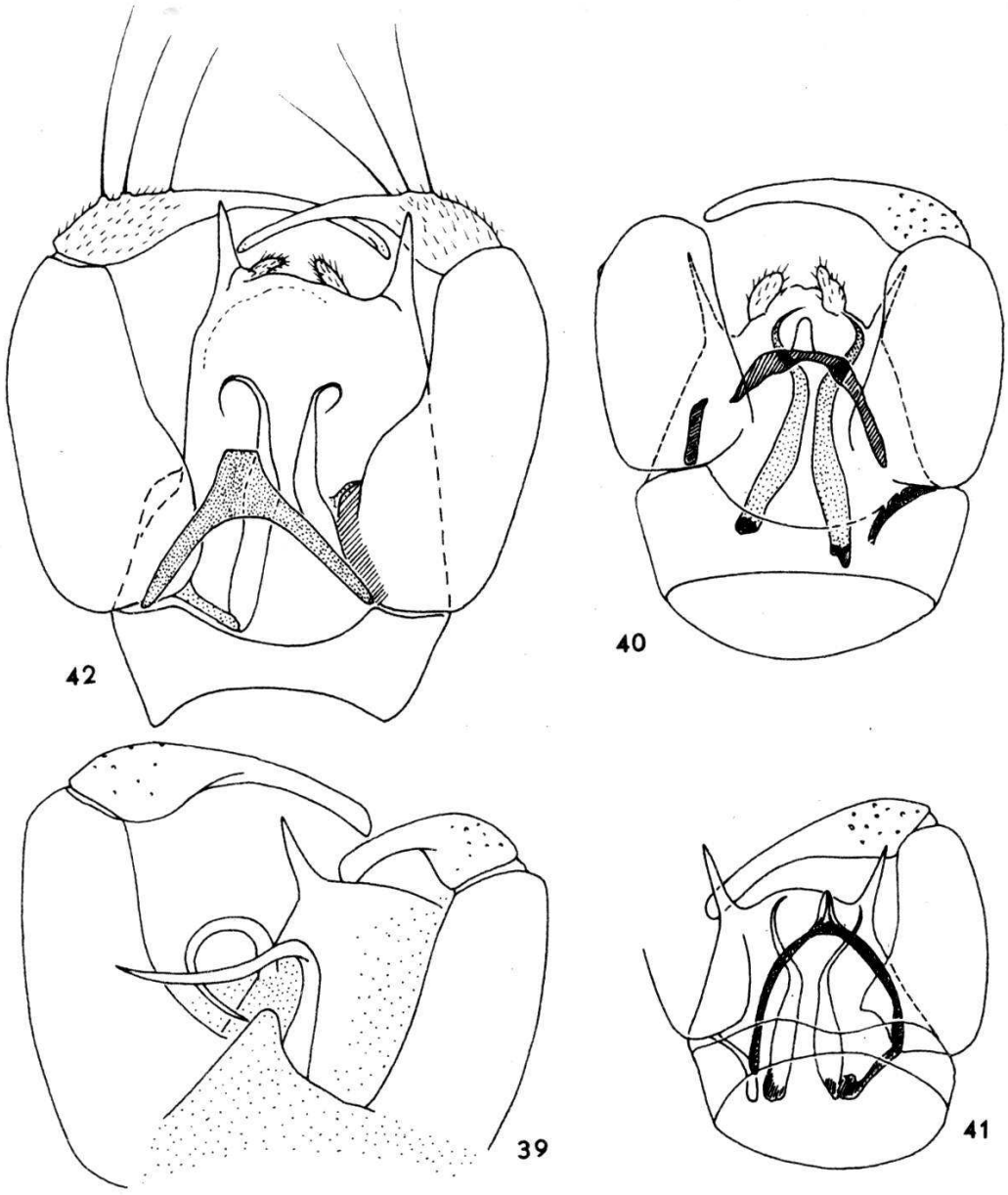
The species is characteristic in having wing membrane including basal radial cell densely covered with macrotrichia, apicolateral processes of tergite IX in male genitalia slender and long, and parameres with very long and stout apical portion.

DESCRIPTION

♀. Unknown.

♂. Body dark brown, thorax darker. Total length 1.8 mm. Flagellum length about 630 μm, AR ca. 0.84. TR(I) 1.8, TR(II) 2.0, TR(III) 1.7. Hind basitarsus with palisade setae on basal half. Wing length 1.06 mm, CR 0.57. Membrane including basal radial cell densely covered with long macrotrichia. Sensilla coelocanica visible on first flagellomere.

Genitalia as in fig. 39. Aedeagus and sternite IX not visible. Apicolateral processes of tergite IX long, slender and pointed. Gonocoxite and gonostylus normal. Parameres separate, distal portion long, stout, evenly tapering to pointed tip; about distal third deeply curved.



39–42. Male genitalia; 39 — *Culicoides* sp. A, MZW 11575; 40, 41 — *Culicoides* sp. B, MZW 7985 (40), ZMC 175 (41); 42 — *Culicoides* sp. C, MZW 8150

MATERIAL EXAMINED (1 ♂)

MZW 11575, TG, 1 ♂ (+*Acarina* 1).

NOTE

This species differs from *C. speciosus* mainly in having longer and stouter parameres. Unfortunately the aedeagus is not visible.

4. *Culicoides* (*Oecacta*) sp. B
(Figs. 40, 41)

DIAGNOSIS

The species is characteristic in having wing membrane including basal radial cell densely covered with long macrotrichia, short tergite IX in male genitalia with long, slender and pointed apicolateral processes, and aedeagus with very high basal arch.

DESCRIPTION

♀. Unknown.

♂. Body dark brown. Flagellum length 750 μm, AR 1.00; first flagellomere with 4 sensilla coeloconica. Eyes bare. Tibial comb composed of 5 spines, middle one longest. TR(II) 2.0, TR(III) 1.8. Hind basitarsus with palisade setae on proximal half. Wing length 1.14–1.26 mm, CR 0.58. Wing membrane including basal radial cell densely covered with long macrotrichia; in basal radial cell ca. 30.

Genitalia (figs. 40, 41). Sternite IX with distinct caudomedian excavation. Tergite IX shorter than gonocoxite; apicolateral processes long, slender and with pointed apices. Gonocoxite short, gonostylus normal. Aedeagus with very high basal arch and with small evenly rounded apical projection. Parameres separate with slender slightly inward curving tips.

MATERIAL EXAMINED (2 ♂)

MZW 7985, 1 ♂; ZMC 175, C. V. HENNINGSEN, 1–1 1966, 1 ♂.

DISCUSSION

This unnamed species is close to *C. speciosus*. It differs in having aedeagus with very high basal arch and the parameres only slightly curved inward at the tips. It may be that the length of tergite IX is normal, and its "shortness" is caused by its oblique position in the amber piece.

5. *Culicoides* (*Oecacta*) sp. C
(Fig. 42)

DIAGNOSIS

Male of this species is characteristic in having wing membrane including basal radial cell densely covered with long macrotrichia, tergite

IX with long and pointed apicolateral processes, apical projection of aedeagus broad and blunt, parameres with tips slender and sharply curved.

DESCRIPTION

♀. Unknown.

♂. Body dark. Head barely visible. Scutum shining with long setae. Tibial comb composed of 5 spines. TR(I) 1.9, TR(III) 1.5. Wing length 1.17 mm, CR 0.59. Membrane covered with long appressed setae, each ca. 40 μm long; basal radial cell with about 20 macrotrichia.

Genitalia (fig. 42). Sternite IX with shallow caudomedian excavation. Tergite IX long with long and pointed apicolateral processes. Gonostylus with very slender distal portion. Aedeagus with moderately high basal arch, apical projection short, broad with truncate tip. Parameres moderately long with slender strongly outward curving tips.

MATERIAL EXAMINED (1 ♂)

MZW 8150, 1 ♂.

DISCUSSION

The species is similar to *C. speciosus*. It differs only in the structure of the male genitalia in which the apical projection of aedeagus is broad, short and its tip is truncate, and the parameres are curved only in their apical portion.

6. *Culicoides* (*Oecacta*) *succivarius* sp. n.
(Figs. 43–47)

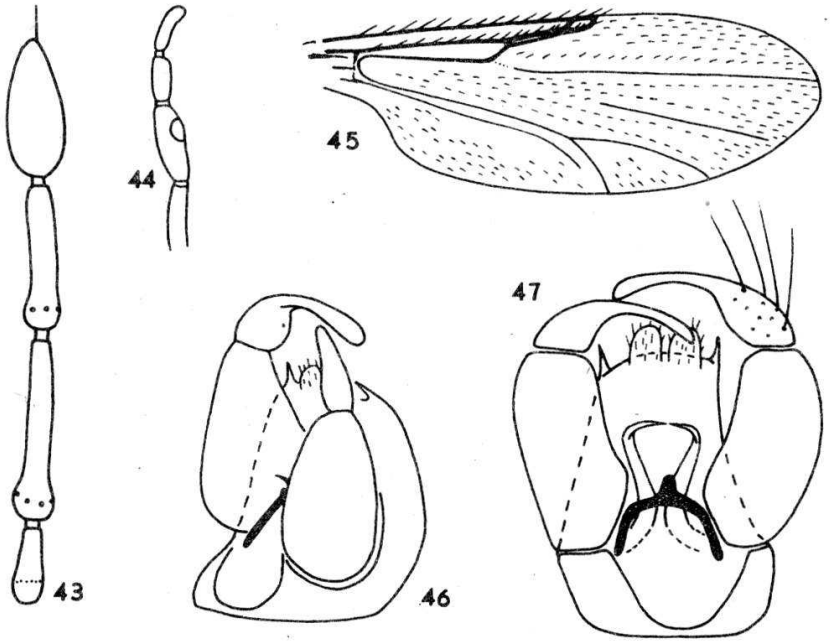
DIAGNOSIS

Male of the new species is characteristic in having wing membrane covered with sparse macrotrichia, basal radial cell bare, short tergite IX with slender apicolateral processes, and aedeagus short.

DESCRIPTION

♀. Unknown.

♂. Body blackish brown, thorax black. Flagellum length 524 μm, AR 0.90. Distal flagellomeres as in fig. 43. Palpus slender, third palpal segment 36 μm long, sensory pit well defined (fig. 44). Sensilla coeloconica visible on first flagellomere. Tibial comb composed of 4 spines. TR(I)



43–47. *Culicoides succivarius* sp. n., male, MZW 11926; 43 — distal flagellomeres, 44 — palpus, 45 — wing, 46, 47 — lateral and ventral view of genitalia

1.8, TR(II) 2.0, TR(III) 1.8. Wing length 0.80 mm, CR 0.51. Wing membrane with sparse macrotrichia arranged in rows, basal radial cell without macrotrichia (fig. 45).

Genitalia (figs. 46, 47). Sternite IX with very deep caudomedian excavation. Tergite IX long, tapering caudally; apicolateral processes short and pointed. Gonostylus on distal two third probably somewhat flattened. Aedeagus broad and short, basal arch broad and low, apical projection short and blunt. Parameres moderately long, S-shaped, apices bent mesally nearly 90° and sharply pointed.

MATERIAL EXAMINED (1 ♂)

Holotype — ♂, MZW 11926.

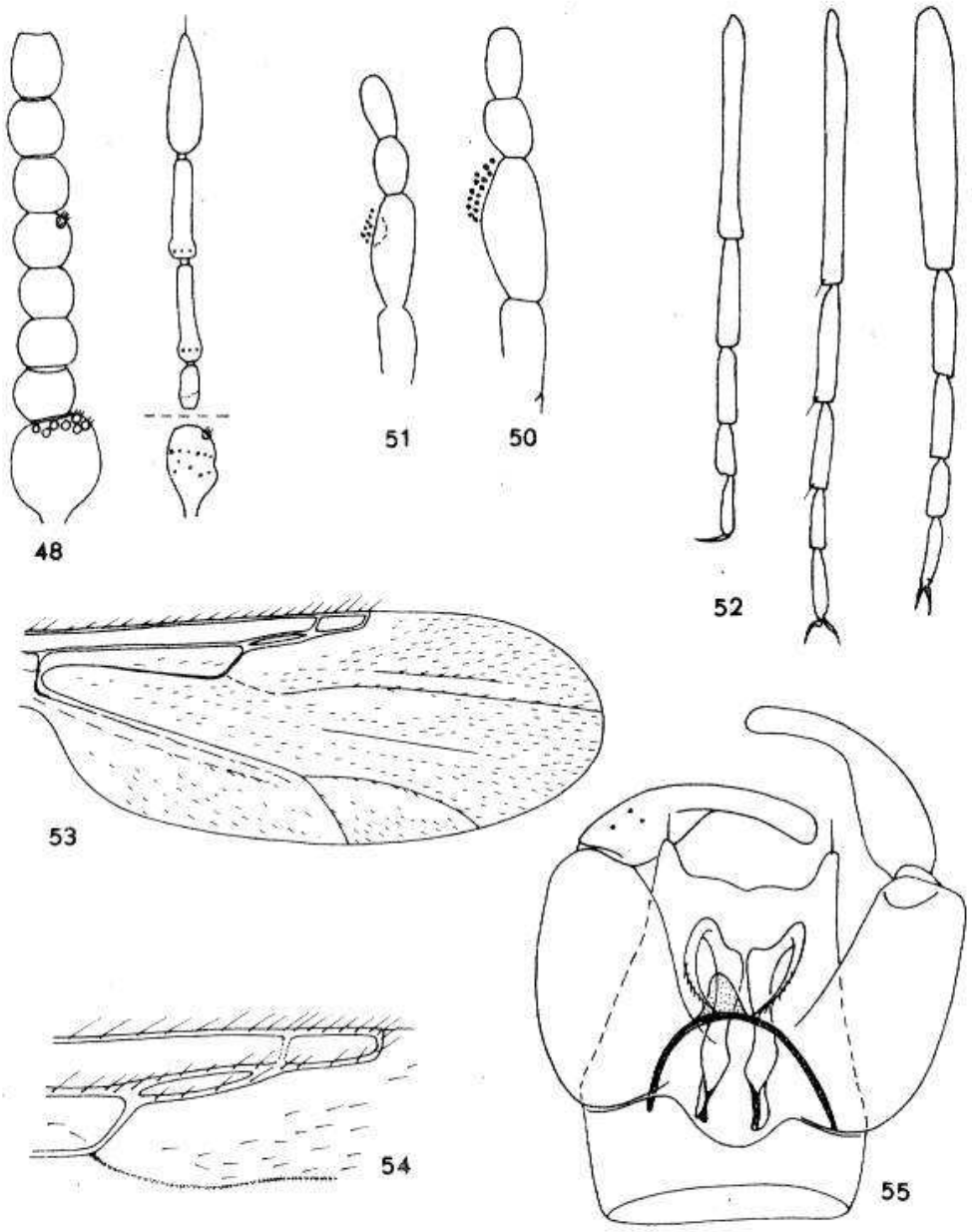
7. *Culicoides* (*Oecacta*) *balticus* sp. n.
(Figs. 48–55)

DIAGNOSIS

Male of the new species is characteristic in having broad and blunt apicolateral processes of tergite IX and parameres bearing fringe of setae.

DESCRIPTION

♀. Incomplete. Proximal flagellomeres spherical to slightly elongate; first flagellomere with numerous sensilla coeloconica, fifth flagellomere



48–55. *Culicoides balticus* sp. n., 48 — female proximal flagellomeres, 49 — male flagellomeres I and IX–XIII, 50 — female palpus, 51 — male palpus, 52 — male tarsi of fore, middle and hind leg, MZW 1990; 53, 54 — male wing, ZMC 70 a; 55 — male genitalia, MZW 1990

with a single s. coeloconica (fig. 48). AR ca. 1.7. Third palpal segment enlarged, a shallow sensory pit present (fig. 50). Proboscis long. Few macrotrichia present in basal radial cell.

♂. Body brown, thorax darker. Total length 1.4 mm. Flagellum length 636 μm, AR 0.99. First flagellomere with sensilla coeloconica (fig. 49). Palpus slender (fig. 51). Third palpal segment 44–52 μm long, sensory pit present. Tarsi as in fig. 52. TR(I) 2.2–2.4, TR(II) 2.2–2.4, TR(III) 2.3–2.6. Tibial comb not visible. Wing length 0.97–1.03 mm,

CR 0.61–0.62. Membrane covered with sparse macrotrichia, basal radial cell with 5 setae (figs. 53, 54).

Genitalia (fig. 55). Sternite IX with small but distinct caudomedian excavation. Tergite IX with moderately long, stout, blunt apicolateral processes. Gonocoxite and gonostylus normal. Aedeagus with slender arch-shaped basal sclerite, apical projection distinct and blunt. Parameres straight and broad in basal two third, apical third abruptly slender and curved, tips with fringe of setae.

MATERIAL EXAMINED (2 ♂, 1 ♀)

Holotype — ♂, MZW 19193, TG. Paratype — ♂, ZMC 70 a, A. HENNINGSEN, 20–3 1975. Incomplete female embedded with the holotype is not a member of the type-series. In 70 b — *Limoniidae* 1 ♂.

DISCUSSION

C. balticus sp. n. belongs to the recent species group *similis* (GUCEVIČ, 1973). In the Palaearctic this group is restricted to warmer regions (Mediterranean, Middle Asia, Japan). In Europe *C. semimaculatus* CLASTRIER of this group was found even as far north as Czechoslovakia (ORSZÀGH, 1980). All Palaearctic species of this group have a long apical projections slender, blunt, shorter than median one, tip bent inward. worldwide distributed.

8. *Culicoides* (subg. ?) *eoselficus* sp. n.
(Figs. 56–60)

DIAGNOSIS

Male of this species is characteristic in having an aedeagus with three long apical projections and very small apicolateral processes on tergite IX.

DESCRIPTION

♀. Unknown.

♂. Body brown, thorax darker. Total length 1.2–1.3 mm. Flagellum length 520–738 μm, AR 0.96–1.00. First flagellomere with sensilla coeloconica, distal flagellomeres as in fig. 56. Proboscis relatively short, about half of head length. Palpus slender (fig. 57). Third palpal segment 40–44 μm long, with a sensory pit. Prescutal pits distinct. Scutellum with 2 lateral and 2 submedian long setae. Tarsomeres of fore and middle legs each with apical spine, hind leg void of apical spines (fig. 58). TR(I)

1.9–2.1, TR(II) 2.3, TR(III) 2.1. Wing length 0.83–0.87 mm, CR 0.56–0.57. Wing membrane covered with sparse macrotrichia, basal radial cell bare. Tibial comb composed of 4 spines.

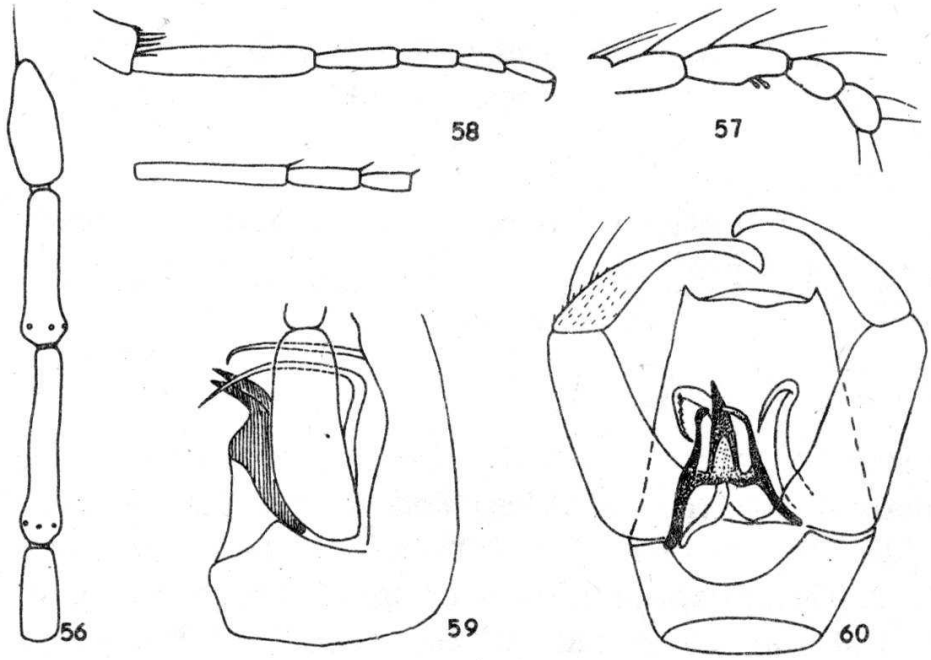
Genitalia (figs. 59, 60). Sternite IX with broad caudomedian excavation. Tergite IX long, tapering posteriorly. Apicolateral processes very short, triangular. Gonocoxite slender and long. Gonostylus with slender distal half. Aedeagus broad with low basal arch; three long apical projections present; median one long, triangular with pointed tip; lateral projections slender, blunt, shorter than median one, tip bent inward. Parameres long, but not extending beyond tip of aedeagus; sharply bent at the middle; tips presumably bare (or serrated ?).

MATERIAL EXAMINED (3 ♂)

Holotype — ♂, MZW 5205, TG. Paratypes: MZW 11577, TG, 1 ♂; ZMC 211, C. V. HENNINGSEN, 8–12 1954, 1 ♂.

DISCUSSION

The systematic position of *C. eoselficus* **sp. n.** and *C. ceranowiczi* **sp. n.** described below is uncertain. It seems that both species may be related to the recent subgenus *Selfia* KHALAF. This subgenus including 7 species is restricted to western North America (ATCHLEY, 1970), and seems to be a relictal group. Males in this subgenus have the aedeagus with 2 or



56–60. *Culicoides eoselficus* sp. n., male, MZW 5205; 56 — distal flagellomeres, 57 — palpus, 58 — hind tarsus and tarsomeres 1–3 of fore leg, 59, 60 — lateral and ventral view of genitalia

3 long apical projections, the parameres however are strongly reduced and male wing is bare.

A bifid aedeagus is characteristic for the subgenus *Monoculicoides* KHALAF, which contains large species with long apicolateral processes of tergite IX and broad, fused parameres. In the subgenus *Macfiella* FOX and in some species of the subgenera *Oecacta* and *Haematomyidium* GOELDI the aedeagus bears 3–4 apical projections, but they are short (cf. WIRTH and BLANTON, 1974).

9. *Culicoides* (subg.?) *ceranowiczi* sp. n.
(Figs. 61–67)

DIAGNOSIS

Male of the species is characteristic in having an aedeagus with two long apical projections and very long, slender parameres.

DESCRIPTION

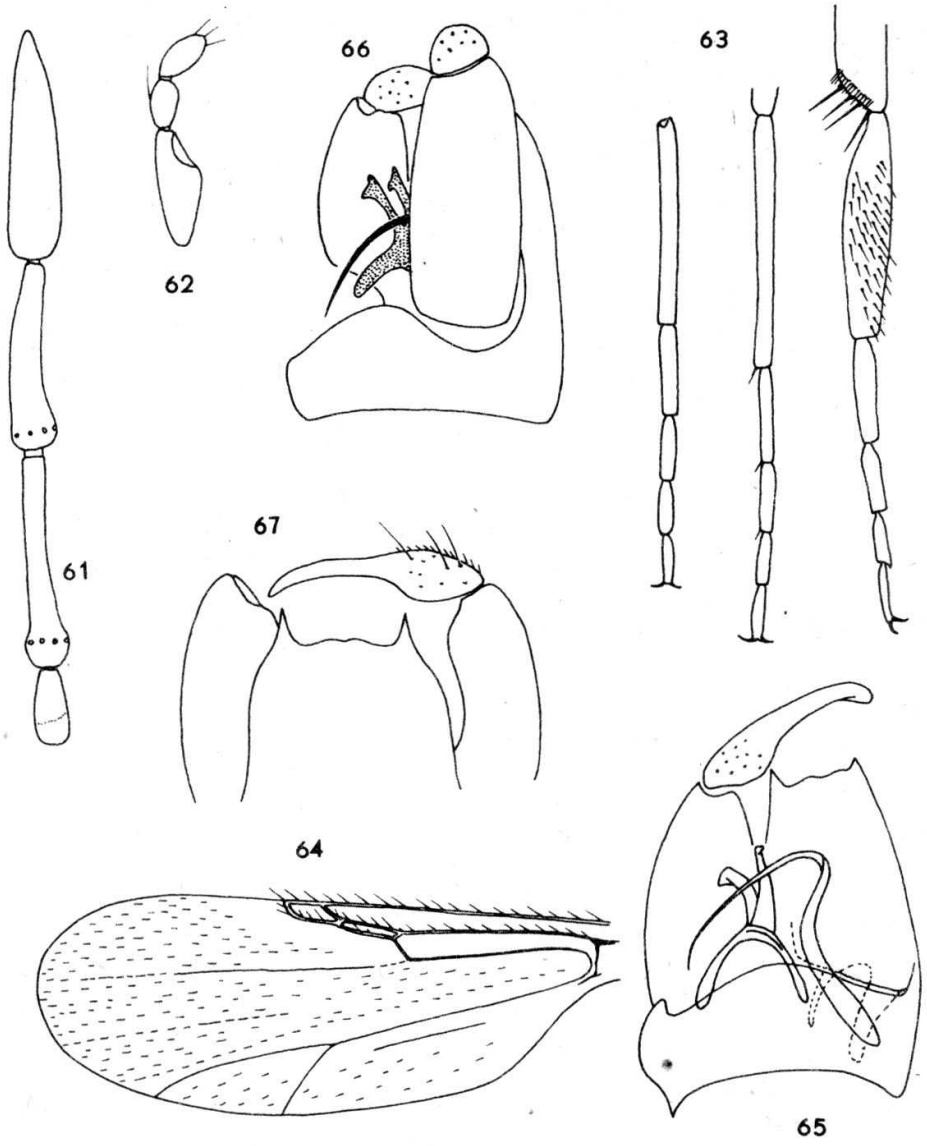
♀. Unknown.

♂. Body brown, thorax darker. Total length 1.3–1.5 mm. Flagellum length 585–666 μm, AR 0.96–1.03. First flagellomere with 1–2 sensilla coeloconica, distal flagellomeres as in fig. 61. Third palpal segment moderately swollen with distinct sensory pit, length 36–48 μm (fig. 62). Scutellum with several long and short setae. Tibial comb composed of 4 spines (fig. 63). Hind basitarsus with spine-like palisade setae almost along the entire length of this distinctly swollen segment. Tarsomeres 1–3 of middle leg with apical spines, in some paratypes proximal tarsomeres of fore leg with apical spines also. Tarsomeres of hind leg without apical spines. TR(I) 2.2–2.6, TR(II) 2.6–3.1, TR(III) 1.9–2.4. Wing length 0.86–0.97 mm, CR 0.56–058. Wing membrane covered with sparse macrotrichia arranged in rows, basal radial cell bare (fig. 64).

Genitalia (fig. 65–67). Sternite IX with shallow caudomedian excavation. Tergite IX long and broad, apicolateral processes triangular, moderately short. Gonocoxite and gonostylus normal. Aedeagus with low basal arch and with two long apical projections, each with expanded triangular tip. Parameres separate, very long and sharply bent beyond midportion; tip slender directed ventrally toward base of aedeagus.

MATERIAL EXAMINED (7 ♂)

Holotype — ♂, MZW 4827, TG. Paratypes: MBI 133, KÜHL, 1 ♂; MZW 2353/18, 1 ♂; MZW 4888, TG, 1 ♂; MZW 17471, TG, 1 ♂; MZW 17989, TG, 1 ♂; MZW 19061, TG, 1 ♂.



61–67. *Culicoides ceranowiczi* sp. n., male; 61 — distal flagellomeres, MBI 133; 62 — palpus, MZW 4827; 63 — tarsi of fore, middle and hind leg, MZW 4827; 64 — wing, MZW 17471; 65–67 — genitalia, MZW 17471 (65), MZW 4827 (66), MZW 17989 (67)

ETYMOLOGY

This species is named for Docent Dr. B. KOSMOWSKA-CERANOWICZ of the Museum of the Earth in Warsaw, in recognition of her valuable contributions to the knowledge of Baltic amber.

10. *Culicoides* (subg.?) *gedanensis* sp. n.
(Figs. 68–75)

DIAGNOSIS

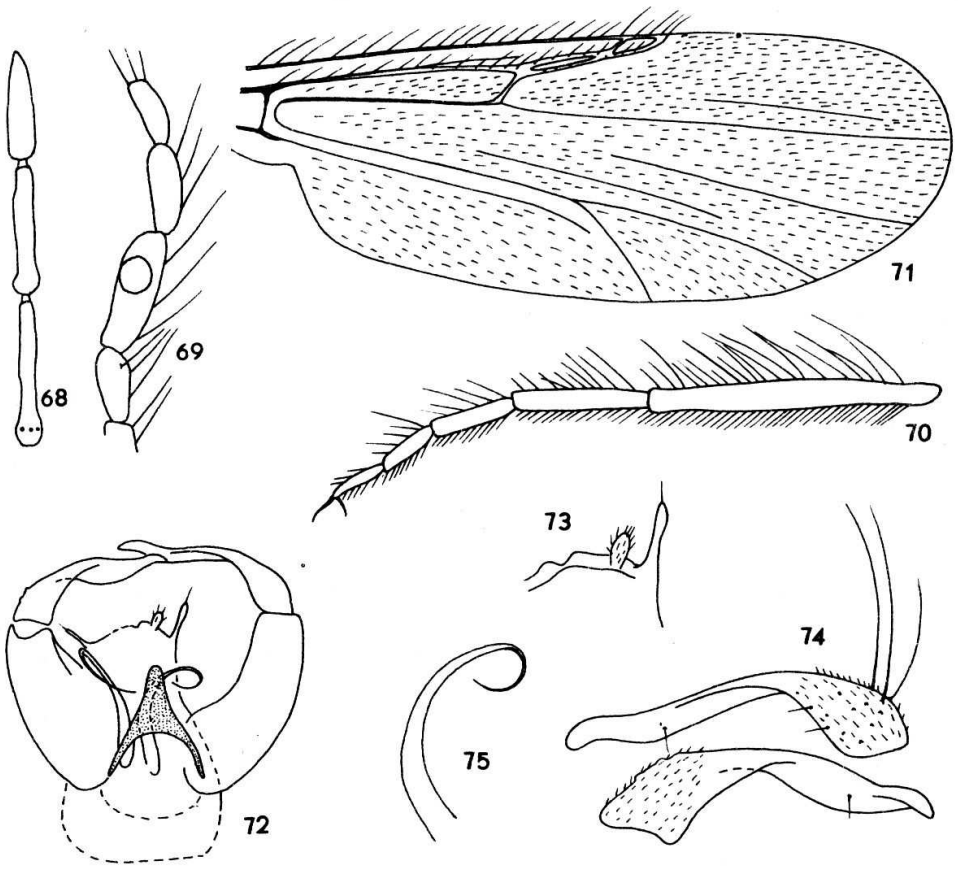
Male of the new species is characteristic in having long, sinuous gonostyli, wing membrane including basal radial cell densely covered with macrotrichia, and long cylindrical apicolateral processes of tergite IX.

DESCRIPTION

♀. Unknown.

♂. Body blackish brown; scutum black, shining. Total length 1.7 mm. Flagellum length 735 μm, AR 1.09. Sensilla coeloconica not visible on first flagellomere. Flagellomere X 5.6 times shorter than flagellomere XI. Three distal flagellomeres as in fig. 68. Proboscis long. Palpus slender (fig. 69). Third palpal segment cylindrical, length 56 μm, sensory pit rounded. Scutum covered with long setae, scutellum with ca. 8–10 long and several shorter setae. Legs with long and abundant setae (fig. 70). TR(III) 2.2. Wing length 1.25 mm, CR 0.59. Membrane including basal radial cell covered with dense, long and appressed macrotrichia (fig. 71).

Genitalia (figs. 72–75). Sternite IX barely visible. Tergite IX with long, cylindrical, and somewhat constricted at midportion. Cerci very small. Gonocoxite normal. Gonostylus long, almost as long as gonocoxite, sinuous or S-shaped. Aedeagus nearly triangular with low basal arch and long and broad apical portion. Parameres separate, slender, gradually tapering to strongly recurved tips.



68–75. *Culicoides gedanensis* sp. n., male, MZW 18558; 68 — last three flagellomeres, 69 — palpus, 70 — hind tarsus, 71 — wing, 72 — genitalia, 73 — apicolateral process of tergite IX, 74 — gonostyli, 75 — paramere

MATERIAL EXAMINED (2 ♂)

Holotype — ♂, MZW 18558. Another male, MZW 8280, is not recognized as a paratype since it has wing delaminated, incomplete legs and the head is missing.

DISCUSSION

The sinuous gonostyli are unusual for the genus *Culicoides* and there are no recent species with similarly shaped male genitalia.

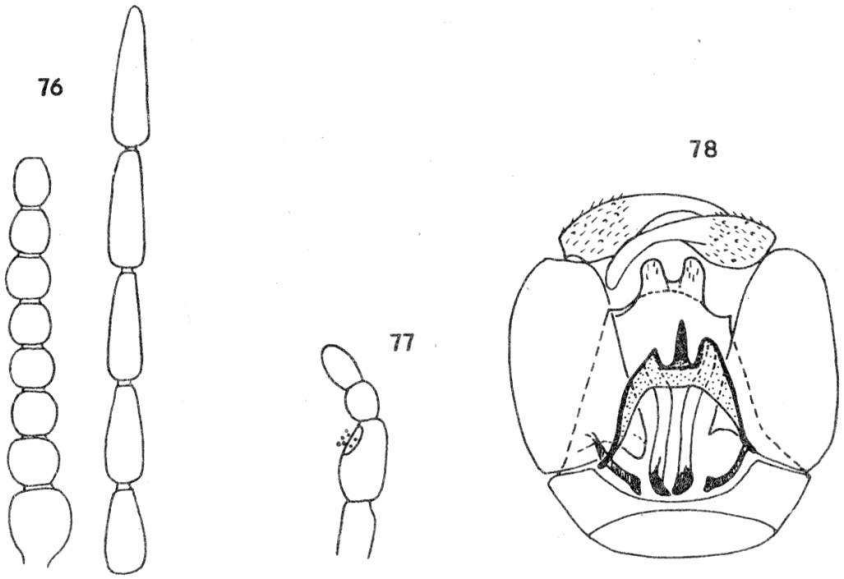
11. *Culicoides* (subg.?) *prussicus* sp. n.
(Figs. 76–78)

DIAGNOSIS

Male of this species is characteristic in having extremely short apicolateral processes of tergite IX, distinctly convex caudal margin of tergite IX, and aedeagus with spine-like caudomedian projection and two apicolateral extensions.

DESCRIPTION

♀. Body brown. Flagellum length 433 μm, AR 1.39. Proximal flagellomeres spherical to slightly ovoid (fig. 76). Sensilla coeloconica not visible. Palpus short (fig. 77). Third palpal segment 40 μm long, sensory pit shallow but distinct. Scutellum with ca. 12 long setae. Legs slender,



76–78. *Culicoides prussicus* sp. n., MBI 122; 76 — female flagellum, 77 — female palpus, 78 — male genitalia

tibial comb composed of 4 spines. TR(I) 1.9, TR(II) 2.4–2.6, TR(III) 1.9. Wing length 0.78 mm, CR 0.58. Wing membrane covered with sparse macrotrichia, basal radial cell with 12 setae.

♂. Body length 1.25 mm. Flagellum length 548 μm, AR 0.86. First flagellomere with at least 3 sensilla coeloconica. TR(II) 2.1, TR(III) 1.8. Length of costal vein 390 μm. Wing on distal half with sparse macrotrichia, basal radial cell with 4 macrotrichia in single row.

Genitalia (fig. 78). Sternite IX with broad and deep caudomedian excavation. Tergite IX shorter than gonocoxite. Apicolateral processes of the tergite extremely small. Caudal margin of tergite distinctly convex extending beyond level of apicolateral processes. Cerci large and appearing as submedian lobes of tergite IX. Gonocoxite stout, dorsal apodemes long. Gonostylus normal. Aedeagus broad with high basal arch; apical part with stout spine-like projection and two apicolateral extensions. Parameres separate, basal parts parallel, distal parts divergent, tips not visible.

MATERIAL EXAMINED (1 ♂, 3 ♀)

Holotype — ♂, MBI 122, "*Ceratopogon* sp. 8, *Heinei*, Original Dr BERENDT". In this piece of amber there are 3 females which are not included in the type-series.

DISCUSSION

Despite this species has characteristic male genitalia, its subgeneric position is unknown. Among the recent species of *Culicoides* I was not able to find any similar male genitalia. It may be that *C. prussicus* **sp. n.** belongs to the subgenus *Avaritia* FOX or *Oecacta*.

Tribe *Ceratopogonini* Newman, 1834

DIAGNOSIS

Eyes contiguous or separated. First flagellomere with sensilla coeloconica or sensilla basiconica. Female antenna usually with 13 flagellomeres, distal 5 elongate; in some *Brachypogon* reduced to 12 or rarely 11; in *Rhynchohelea monilicornis* WIRTH et BLANTON with 12 flagellomeres, only the last flagellomere is elongated. Male flagellum with dense plume, which is absent in *Echinohelea* MACFIE and highly reduced in *Nannohelea*, *Baeodasymyia*, and *Baeohelea*; usually 3 distal flagellomeres elongate; the basic number of 13 flagellomeres reduced to 12 or rarely 11 in some *Brachypogon*, 7 or 8 in *Nannohelea*, 8 in *Baeodasymyia*, and 6 in

Baeohelea; in the following genera flagellomeres 2–11 (10–9) are fused: *Brachypogon*, *Baeodasymyia* and in some *Nannohelea*. The female proboscis adapted to feeding on insects, but is usually short. Third palpal segment usually with sensory pit. Fourth and fifth palpal segments fused in some genera, and more rarely one and two.

Antepronotum small and hidden below postpronotum. Prescutal pits usually well developed, sometimes absent. Legs usually slender and unmodified. Fore femur armed with ventral spines in *Fossihelea* **gen. n.** and a new genus from Africa (WIRTH and GROGAN, in prep.). Tarsi usually armed with ventral spines. Fourth tarsomeres from cylindrical to cordiform. Female claws long, equal, subequal or unequal, similar on all legs or not, inner basal teeth often present and rarely outer ones; in some genera claws very small, equal and simple. Wing membrane with or without microtrichia, macrotrichia usually present at wing tip. Costa usually short. Both first radial cells present or first, second or both cells may be reduced. Media petiolate, base of M_2 often distinctly atrophied or totally absent.

Tergite IX in male genitalia usually with well developed apicolateral processes. Parameres usually separated, long and stout, occasionally fused or rarely absent.

RECENT ECOLOGY, DISTRIBUTION AND CLASSIFICATION

The females of this tribe are predaceous on other small insects. For the present 14 recent genera have been described, some of which are restricted, or more common, in the Holarctic region. The *Ceratopogonini* are separated from the next tribe *Stilobezziini* by only a single character — presence of sensilla coeloconica or s. basiconica at least on first flagellomere, and it may be that the *Stilobezziini* is not a monophyletic group.

FOSSILS

The oldest findings of *Ceratopogonini* are late Cretaceous. They are found in Siberian and Canadian ambers and possibly belong to the genera *Ceratopogon* and *Brachypogon* (see below). An uncertain systematic position has fossil male described by REMM (1976) from Siberian amber as *Baeohelea taimyrica*. This male has short palpi with only one segment distal to that bearing sensory pit; a relatively long first radial cell, second one absent; cell r_{4+5} with distinct intercalary veins; the flagellum composed of 9 units, and the proximal flagellomeres are fused; and the male genitalia with well developed apicolateral processes. Because none of these characters is found in *Baeohelea* WIRTH et

BLANTON (WIRTH and BLANTON, 1970 b) except for palpus, then it cannot be assigned to this genus. It seems that *taimyrica* may be included in the genus *Leptohelea* WIRTH et BLANTON with its single recent species *L. micronyx* WIRTH et BLANTON from Colombia (WIRTH and BLANTON, 1970 a). Unfortunately, the fossil species *taimyrica* is based on male while recent species *L. micronyx* on female. The wing venation and palpi of *taimyrica* are such similar to these of *L. micronyx* that it is quite plausible they both belong to the same genus. *L. taimyrica* has well developed vein M_2 which is absent in *L. micronyx*. However it is not important difference (see *Brachypogon*).

The *Ceratopogonini* is the most common tribe in Baltic amber comprising 45% of all specimens (table 3). In the material examined 27 species belonging to 5 genera have been found.

Ceratopogonini indetermined (4 ♂, 28 ♀)

MBI 150, KÜNOW, 1 ♀; 186, KÜNOW, 1 ♀; 194, KÜNOW, 1 ♀; 207, KÜNOW, 1 ♀; 223, THOMAS (+*Chironomidae* 1 ♂), 1 ♀; THOMAS 309, "*Ceratopogon eucerus, Dolichodea diaphorus*", (+ *Dolichopodidae* 3), 1 ♀; THOMAS 318, "*Ceratopogon ungulatus*", 1 ♂; MZW 393 d, 1 ♀; 1796, 1 ♀; 4712, TG, 1 ♀; 5244, TG, 1 ♀; 5266, TG, 1 ♂; 5339, TG, 1 ♀; 5921, TG, 1 ♀; 5974 (+*Mycetophilidae* 2), 1 ♀; 9002, 1 ♀; 9707, 1 ♀; 11997 (+*Chironomidae* 1 ♀), 1 ♀; 12466, 1 ♀; 12916 a (+*Chironomidae* 1 ♂), 1 ♀; 13157, TG (+*Aranei* 1), 1 ♀; 13306, TG, 1 ♀; 17977, TG, 1 ♀; 18553 b, 1 ♂; 20006, TG, 1 ♀ (at *Brachypogon prominulus*); ZMC 20, C. V. HENNINGSEN, 1–5 1967, 1 ♀; 68, A. HENNINGSEN, 9–9 1974, 1 ♂; 79, C. V. HENNINGSEN, 1–4 1970, 1 ♀; 113, Sydsjalland, Aage Madsen, Min. Mus., 1906–6, 1 ♀; 131, Th. HANSEN, Mou, 16–1 1961, 1 ♀; 147, A. K. ANDERSEN, 28–3 1968, 1 ♀; 210, A. HENNINGSEN, 9–9 1974, 1 ♀.

Key to Baltic amber genera of *Ceratopogonini*

1. Fore femur armed with ventral spines . . . . *Fossihelea* gen. n.
—. Fore femur unarmed 2
2. Male 3
—. Female 8
3. Antenna with 13 flagellomeres 4
—. Antenna with 8–11 flagellomeres 7
4. All flagellomeres separated . . . . . *Ceratopogon*
—. Flagellomeres 2–10 or 2–11 fused 5
5. First and second radial cells obsolete . . . *Brachypogon* (*B.*) (in part)
—. First or second or both radial cells present 6
6. First or both radial cells present . . . . *Brachypogon* (*Isohelea*)

—. Only second radial cell well developed . . . . . *Ceratoculicoides*

7. Antenna with 10 or 11 flagellomeres . . . *Brachypogon* (in part)
—. Antenna with 8 flagellomeres . . . . . *Nannohelea*

8. First and second radial cells obliterated . . . *Brachypogon* (*B.*)
—. At least first or second radial cell present 9

9. Claws very short, equal and similar on all legs . . . *Nannohelea*
—. Claws long, at least on fore leg 10

10. Claws of all legs similar 12
—. Claws at least of fore leg strongly unequal 11

11. Claws of fore leg strongly unequal, of middle and hind legs small and equal . . . . . *Brachypogon* (*Isohelea*) (in part)
—. Claws of fore and middle legs strongly unequal, of hind leg small and equal . . . . . *Ceratoculicoides*

12. Eyes separated. Fourth tarsomeres usually cordiform. First and second radial cells well developed . . . . . *Ceratopogon*
—. Eyes contiguous. Fourth tarsomeres subcylindrical or cylindrical. First and second radial cells small or second one obliterated . . . . . *Brachypogon* (*Isohelea*) (in part)

2. Genus *Ceratopogon* Meigen, 1803

DIAGNOSIS

Eyes separated. Flagellum of male composed of 13 free units, plume well developed; proximal 8 flagellomeres of female moderately to very short, distal 5 moderately elongated. Palpus 5 segmented, third palpal segment usually slender with or without small ill defined sensory pit. Prescutal pits well developed. Legs unarmed. Tarsi usually with distinct spines. Fourth tarsomeres of recent species usually deeply cordiform with apical recurved sensory setae; in males of fossil species cordiform, subcylindrical or even cylindrical. Female claws similar on all legs, moderately short to long and usually slightly unequal, each with or without inner basal teeth. Scutellum with 5–10 long and several shorter setae. Wing membrane with fine microtrichia, macrotrichia usually present at wing tip. Both first radial cells always well developed. CR of recent females 0.60–0.80, but ranging from 0.52 to 0.68 in males of fossil species.

Aedeagus usually lightly sclerotized along its midline, and usually with a pair of dorsal and ventral divergent projections. Parameres usually long and stout, separate. Tergite IX with or without long, pointed or blunt apicolateral processes. Male cerci long and slender, usually extending beyond caudal margin of tergite IX.

RECENT ECOLOGY, DISTRIBUTION

The *Ceratopogon* is a typical boreal faunal element (fig. 767) occurring in the cooler parts of Holarctic and more southwardly in peat bogs or in the mountains. It ranges as far south as 35° N latitude in North America (GROGAN and WIRTH, 1980 b). This genus includes about 40 recent species. The insectivorous females feed on other small *Diptera* (DOWNES, 1978).

FOSSILS

Two species probably of *Ceratopogon* are known from late Cretaceous Siberian amber — *C. macronyx* (REMM, 1976), and Canadian amber — *C. aquilonius* (BOESEL, 1937). These species have well developed first and second radial cells. The holotype female of *C. macronyx* has also distinctly short (? cordiform) fourth tarsomere of hind leg and eyes separated as typical *Ceratopogon*. WIRTH and GROGAN (personal comm.) suppose that they both belong to the genus *Brachypogon*.

In Baltic amber *Ceratopogon* is the most common genus with 279 specimens, i.e. 25.3% of all biting midges. In this paper I describe 15 species in the genus, of which only two have been described previously by MEUNIER (1904). The other species placed by LOEW (1850) and MEUNIER (l.c.) in *Ceratopogon* belong to other genera.

Ceratopogon indetermined (28 ♂, 171 ♀)

IZPAN 47/73, 1 ♀; 91/65 (+*Chironomidae* 1 ♀), 1 ♀; MBI 98, BERENDT, a, 1 ♀ at *Dasyhelea eodicryptoscenica*, b, 1 ♂ 1 ♀; 103, BERENDT, 1 ♂; 105, BERENDT, 1 ♀; 117, BERENDT, "*Ceratopogon* sp. 2, *ungulatus*, Original Dr B.", 1 ♀; 118, BERENDT, "*Ceratopogon* sp. 3, *ungulinus*, Original Dr B.", 1 ♀; 119, BERENDT, "*Ceratopogon* ♀, sp. 4, *pectinatus*, Original Dr B.", 1 ♀; 127, BERENDT, "*Rhamphom.* sp. 15 *pteropa* ♀, orig. Dr B", (+*Acarina* 1, and *Empididae* 1 ♀), 1 ♀; 134, KÜHL, 1 ♀; 135, KÜHL, 1 ♀; 141, KÜHL, 1 ♀; 142, KÜHL, 1 ♀; 146, KÜHL, 1 ♂; 147, KÜHL, 1 ♀; 151, KÜNOW, 1 ♀; 155, KÜNOW, 1 ♀; 173, KÜNOW, 1 ♀; 174, KÜNOW, 1 ♀; 177, KÜNOW, 1 ♀; 198, KÜNOW, 1 ♀; 214, BERENDT, 1 ♀; THOMAS 48, "*Tip. culicif. Ceratopogon ungulatus* ♀", 1 ♀; THOMAS 275, "*Tip. culiciformia, Ceratopogon ungulatus* ♀", 1 ♀; THOMAS 413, "*Tip. culiciformia, Ceratopogon ungulatus* ♀", 1 ♀; MM 7, 1 ♀; MZW 469/32, 1 ♀; 469/70, 1 ♀; 1257, 1 ♀; 1526 a, b, 2 ♀; 1884/3 b′, b″, 1 ♂ 1 ♀; 1927/34, 1 ♀; 2353/20, 2 ♀; 2881 (+*Empididae* 1), 1 ♂ 1 ♀; 3187, 1 ♀; 3980, 1 ♂; 4480 a, b, 2 ♀; 4511, 2 ♀; 4532, 1 ♀; 4679, TG (+*Chironomidae* 1 ♀), 1 ♀; 4777, TG, 1 ♀; 4778, TG, 1 ♀; 4879, TG, 1 ♀; 4947, TG, 1 ♀; 5081, TG, 1 ♀; 5185, TG, 1 ♀; 5250, TG, 1 ♀; 5252, TG, 1 ♀; 5280, TG, 1 ♀; 5308, TG, 1 ♀; 5343, TG, 1 ♀; 5346, TG, 1 ♀; 5350, TG, 2 ♀; 5360, TG, 2 ♀; 5383, TG, 1 ♀; 7222

(+*Chironomidae* 1 ♀), 1 ♀; 7479 a, 1 ♀; 7481 a (+*Chironomidae* 1), 1 ♀; 7588, 1 ♀; 8013, 1 ♀; 8398, 1 ♀; 8954, 1 ♀; 8964, 1 ♀; 9011, 1 ♀; 9053, 1 ♀; 9256, 1 ♀; 9265, 1 ♀; 9348, 1 ♀; 9631, 1 ♀; 10161, 1 ♀; 10169, 1 ♀; 10200, 1 ♀; 10221, 1 ♀; 10339 (+*Chironomidae* 1 ♂), 1 ♀; 10604, 1 ♀; 10683, 1 ♀; 11446 (+*Chironomidae* 1 ♂), 1 ♀; 11551, TG, 1 ♂; 12046 (+*Chironomidae* 1 ♀), 1 ♀; 12187, TG, 1 ♂; 12340 a, b, 2 ♀; 12342, 1 ♀; 12465, 1 ♂; 12712, 1 ♀; 12878, 1 ♀; 13000, 1 ♀; 13126, TG, 1 ♀; 13144, TG, 1 ♀; 13177, TG, 1 ♀; 13186, TG, 1 ♀; 13192, TG, 1 ♀; 13210, TG, 1 ♀; 13565 (+*Chironomidae* 2 ♀), 1 ♀; 13579, 1 ♀; 14001, TG, 1 ♂; 14968, TG, 1 ♀; 15774, TG, (+*Chironomidae* 1 ♀), 1 ♀; 16121, TG, 1 ♀; 16405 (+*Chironomidae* 1 ♀) TG, 1 ♀; 16438, TG, 1 ♀; 16563, TG, 1 ♀; 16826, TG (+*Acarina* 1), 1 ♀; 17181, 1 ♀; 17258, 1 ♀; 17475, TG, 1 ♀; 17543, TG, 1 ♀; 18171, TG, 1 ♀; 18191, TG, 1 ♀; 18221, TG, 1 ♀; 18227, TG, 1 ♀; 18235, TG, 1 ♀; 18633, TG, 1 ♂; 18850, TG, 1 ♀; 18867, TG, 1 ♀; 18916, TG, 1 ♂; 18917, TG, 1 ♀; 19002, TG, 1 ♀; 19032, TG, 1 ♀; 19064, TG (+*Chironomidae* 1 ♀), 1 ♀; 19182, 1 ♀; 19231, TG (+*Acarina* 1), 1 ♀; 19244, TG, 1 ♀; 19272, TG, 1 ♀; 19460, 2 ♂ 2 ♀; 20012, TG (+*Thysanoptera* 1), 1 ♀; 20274, TG, 1 ♀; 20275, TG (+*Chironomidae* 1 ♀), 1 ♀; 20276, TG, 1 ♀; 20277, TG, 1 ♀; 20283, TG, 1 ♂; ZMC 2, Tysk Raw, C. V. HENNINGSEN, 1–7 1966, 1 ♀; 3, A. K. ANDERSEN, 28–3 1968, 1 ♀; 4, Libau, Köbmand TIDEMAND, Min. Mus. 1940–43, 1 ♀; 6, Bórge MORTENSEN, 1–9 1960, 1 ♂; 9, Bórge MORTENSEN, 1–11 1964, 1 ♀; 16, C. V. HENNINGSEN, 22–6 1953, 1 ♀; 19, Bórge MORTENSEN, 1–9 1960, 1 ♀; 22, C. V. HENNINGSEN, 19–11 1958, 1 ♀; 28, C. V. HENNINGSEN, 1–2 1969, 1 ♀; 29, Th. HANSEN, Mou, 16–1 1961, 1 ♀; 34, A. HENNINGSEN, 9–9 1974 (+*Chironomidae* 1 ♂), 1 ♀; 37, C. V. HENNINGSEN, 1–2 1969, 1 ♀; 44, C. V. HENNINGSEN, 25–3 1961, 1 ♀; 49, C. V. HENNINGSEN, 22–6 1953, 1 ♂; 50, C. V. HENNINGSEN, 1–4 1970, 1 ♂; 73, C. V. HENNINGSEN, 1–5 1967, 1 ♀; 85 a, C. V. HENNINGSEN, 28–3 1968 (+*Phoridae* 1), 1 ♂; 97, Gulds med HENNINGSEN, Min. Mus. 1951–22, 1 ♂; 104, C. V. HENNINGSEN, 12–7 1957, 1 ♂; 109, C. V. HENNINGSEN, 11–10 1963, 1 ♀; 115, A. K. ANDERSEN, 28–3 1968, 1 ♀; 116, A. K. ANDERSEN, 28–3 1968, 1 ♀; 119, C. V. HENNINGSEN, 31–5 1961, 1 ♀; 120, C. V. HENNINGSEN, 15–10 1962, 1 ♀; 121, Bórge MORTENSEN, 5–1 1961 (+*Chironomidae* 1 ♂), 1 ♀; 137, Hirshals, Fyrassitent HANSEN, Min. Mus. 1913–25, 1 ♀; 139, A. HENNINGSEN, 9–9 1974, 2 ♂; 142, C. V. HENNINGSEN, 9–3 1967, 1 ♀; 150, C. V. HENNINGSEN, German amber, 1–7 1966, 1 ♀; 155, Klarskov ANDERSEN, 16–5 1957, 1 ♀; 163, C. V. HENNINGSEN, 1–1 1966, 1 ♂; 165, A. HENNINGSEN, 9–9 1974, 1 ♀; 166, Th. HANSEN, Mou, 16–1 1961, 1 ♂; 169, A. HENNINGSEN, 9–9 1974, 1 ♀; 174, A. HENNINGSEN, 9–9 1974 (+*Chironomidae* 2 ♂), 2 ♀; 177, A. HENNINGSEN, 9–9 1974, 1 ♀; 179, A. HENNINGSEN, 9–9 1974, 1 ♀; 183, C. V. HENNINGSEN, 1–7 1966,

German amber, 1 ♂; 184, A. HENNINGSEN, 9–9 1974, 1 ♀; 190, C. V. HENNINGSEN, 1–7 1966, Ostpreussen, 1 ♂; 198, A. HENNINGSEN, 9–9 1974, 1 ♀; 203, A. HENNINGSEN, 9–9 1974, 1 ♀; 204, LEHMAN, 1888–601, Min. Mus. (at *Brachypogon prominulus*), 1 ♀; 208, A HENNINGSEN, 9–9 1974, 1 ♀; 209, A. HENNINGSEN, 9–9 1974, 1 ♀; 213, C. V. HENNINGSEN, 30–6 1953, 1 ♀; 222, A. HENNINGSEN, 9–9 1974, 1 ♀; 228, A. HENNINGSEN, 9–9 1974, 1 ♀; 241, A. HENNINGSEN, 9–9 1974, 1 ♀; 242, A. HENNINGSEN, 9–9 1974, 1 ♀; 247, Uden Oplysninger, Zool. Mus., 1 ♂; 244, A. HENNINGSEN, 9–9 1974 (+*Dolichopodidae* 1 ♀), at *Forcipomyia* (*F.*) indet., 1 ♀; 253 c, A. HENNINGSEN, 9–9 1974, 1 ♀.

Key to Baltic amber species of *Ceratopogon*

Males

1. Tip of gonostylus not reaching level of apex of apicolateral processus of tergite IX 2
—. Tip of gonostylus reaching level of apex of apicolateral processus of tergite IX 3
2. Gonocoxite long, 390–525 µm. Gonostylus 2.5–3.5 times shorter than gonocoxite. Wing 1.7–2.7 times longer than length of gonocoxite . . . . . 1. *C. forcipiformis* MEUNIER
—. Gonocoxite shorter, 255–308 µm. Gonostylus 1.7–2.1 times shorter than gonocoxite. Wing 3.2–4.3 times longer than length of gonocoxite . . . . . 2. *C. hennigi* sp. n.
3. Apicolateral processes of tergite IX short and blunt. Tergite IX broad . . . . . 10. *C.* sp. B
—. Apicolateral processes of tergite IX long, blunt or pointed. Tergite IX distinctly tapering caudally 4
4. Distal portion of parameres broad and divergent . . . . . 11. *C. gedanicus* sp. n.
—. Distal portion of parameres slender 5
5. Apicolateral processes of tergite IX pointed 6
—. Apicolateral processes of tergite IX blunt 10
6. Apicolateral processes of tergite IX short and broad, triangular . . 8
—. Apicolateral processes of tergite IX long and slender 7
7. Aedeagus with high basal arch, apical projections blunt. Gonostylus 1.6 times shorter than gonocoxite . . . . . 4. *C. grogani* sp. n.
—. Aedeagus with low basal arch, apical projections pointed. Gonostylus 1.8–2.1 times shorter than gonocoxite . . 3. *C. tertiaricus* sp. n
8. Second radial cell 1.7 times shorter than first one. Wing 6.3 times longer than gonocoxite . . . . . 6. *C.* sp. A.
—. Second radial cell 1.1–1.2 times shorter than first one. Wing 3.6–4.3 times longer than gonocoxite 9

Table 2. Comparison of certain quantitative characters of males of *Ceratopogon*

Species	Wing L [mm]	CR	Gx L [μm]	Gst L [μm]	Gx/gst	r_1/r_{2+3}	Wing/gx
1. *C. forcipiformis* MEUNIER	0.91–1.16	0.57–0.63	390–525	150–188	2.5–3.5	1.0–1.3	1.7–2.7
2. *C. hennigi* sp. n.	0.91–1.09	0.60–0.64	255–308	136–150	1.7–2.1	0.8–1.3	3.2–4.3
3. *C. tertiaricus* sp. n.	0.91–1.05	0.58–0.66	192–218	98–116	1.8–2.1	0.9–1.2	4.3–5.0
4. *C. grogani* sp. n.	0.98	—	180	113	1.6	—	5.4
5. *C. eminens* MEUNIER	1.11–1.45	0.62–.066	270–352	130–160	1.7–2.1	1.1–1.2	4.1–4.3
6. *C.* sp. A	1.33	0.62	212	152	1.4	1.7	6.3
7. *C.* sp. C	0.90–0.94	0.59–0.62	233–263	120–128	1.9–2.1	—	3.6–3.9
8. *C. crypticus* sp. n.	0.95–1.16	0.52–0.59	240–275	124–128	2.0–2.1	1.8–2.0	3.8–4.4
9. *C. remmicolus* sp. n.	0.81–0.89	0.62–0.63	188–195	90	2.1–2.2	0.8–1.0	4.3–4.5
10. *C.* sp. B	1.09	0.61	220	150	1.5	1.2	5.0
11. *C. gedanicus* sp. n.	1.36	0.63	203	165	1.2	1.3	6.7
12. *C. piotrowskii* sp. n.	1.31	0.62	180	173	1.0	1.5	7.3
13. *C. ceranowiczi* sp. n.	0.73	0.58	128	92	1.4	>2.0	5.7
14. *C. ritzkowskii* sp. n.	0.63–0.74	0.61	176–180	120–128	1.4–1.5	1.5	3.6–4.1
15. *C. margaritae* sp. n.	0.87–0.91	0.57–0.60	128–132	120	1.1	1.1–1.3	6.7–6.8

Abbreviations: gx — gonocoxite, gst — gonostylus, B — breadth, L — length, r_1 and r_{2+3} — lengths of first and second radial cells

9. Wing 3.6–3.9 times longer than gonocoxite . . . . . 7. *C.* sp. C
—. Wing 4.1–4.3 times longer than gonocoxite . . . . . 5. *C. eminens* MEUNIER
10. Gonostylus 2.0–2.2 times shorter than gonocoxite 11
—. Gonostylus 1.0–1.5 times shorter than gonocoxite 12
11. Gonostylus abruptly bent near the base . . . 8. *C. crypticus* sp. n.
—. Gonostylus evenly curved throughout its length . . . . . 9. *C. remmicolus* sp. n.
12. Parameres with twisted tip. Gonostylus slender, as long as gonocoxite . . . . . 14. *C. piotrowskii* sp. n.
—. Parameres without twisted tip. Gonostylus shorter than gonocoxite 13
13. Tip of aedeagus distinctly forked. Parameres strong and long . . . . . 15. *C. margaritae* sp. n.
—. Tip of aedeagus not forked. Parameres slender and short . . . 14
14. Parameres straight. Wing 5.7 times longer than gonocoxite . . . . . 13. *C. ceranowiczi* sp. n.
—. Tips of parameres perpendicular to the aedeagus. Wing 3.6–4.1 times longer than gonocoxite . . . . . 14. *C. ritzkowskii* sp. n.

1. *Ceratopogon forcipiformis* Meunier, 1904
(Figs. 79–95)

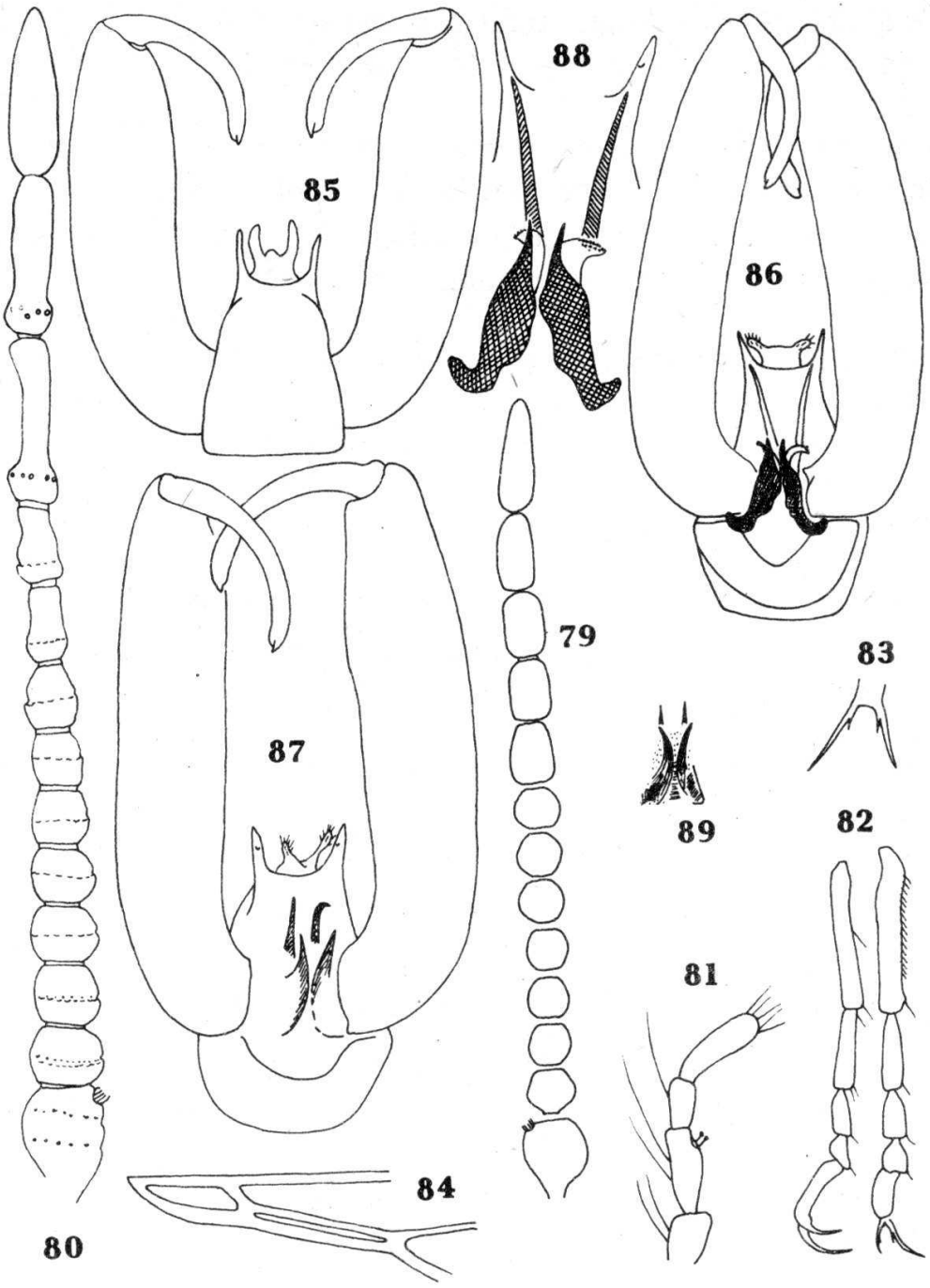
Ceratopogon forcipiformis MEUNIER, 1904: 235 (♂, Baltic amber).
C. defectus MEUNIER, 1904: 229 (♀, Baltic amber), **syn. n.**
Ceratolophus defectus: KIEFFER, 1906: 1 (combination).

DIAGNOSIS

Male of the species is characteristic in having large genitalia with short tergite IX and gonostyli. Gonocoxite is 1.7–2.7 times shorter than wing length only, but 2.5–3.5 times longer than gonostylus.

DESCRIPTION

♀. Body dark. Total length 1.2–1.4 mm. Eyes separated. Flagellum length 328–403 μm, AR 0.93–1.08. Sensilla coeloconica visible on first flagellomere (figs. 79, 90). Proximal 8 flagellomeres spherical, distal 5 elongate. Proboscis moderately long. Palpus slender (fig. 91). Third palpal segment 28–36 μm long, with distinct sensory pit. Scutum covered with distinct setae. Scutellum with 5 long and several shorter setae (fig. 95). Fourth tarsomeres cordiform (fig. 82). Claws slightly unequal, each with inner basal tooth (figs. 83, 93). TR(I) 1.7–2.3, TR(II) 2.0–2.1, TR(III) 2.0. Microtrichia not visible on wing membrane, macrotrichia at



79–89. *Ceratopogon forcipiformis* MEUNIER; 79 — female flagellum, MZW 17268; 80 — male flagellum, IMGPUG 5981; 81 — male palpus, MZW 17659; 82 — female tarsi of middle and hind leg, MZW 17268; 83 — female claws of fore leg, MZW 17268; 84 — first radial cells of male wing, MZW 8023; 85 — male genitalia, IMGPUG 6533; 86 — male genitalia, MZW 10077; 87 — male genitalia, MZW 8597; 88 — aedeagus, parameres and apicolateral processes of tergite IX, MZW 10077; 89 — aedeagus and parameres, IMGPUG 6533

wing tip present (fig. 94). Wing length 0.81–0.95 mm, CR 0.63–0.67. Second radial cell slightly longer than first one.

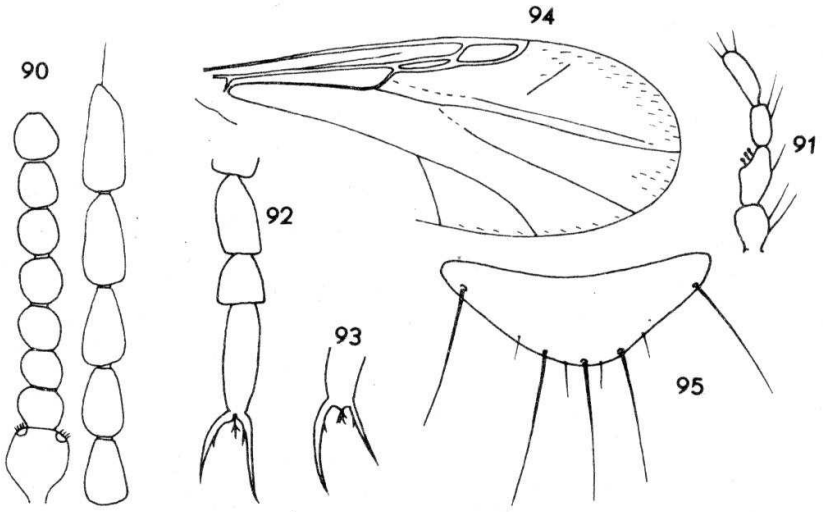
♂. Body brown, thorax dark. Total length 1.5–2.0 mm. Flagellum length 570–652 μm, AR 0.87–0.97. First flagellomere with sensilla

coeloconica (fig. 80). Palpus slender (fig. 81). Third palpal segment 40–42 μm long, sensory pit small. Scutellum with 5–8 long and several short setae. Prescutal pits distinct. Fourth tarsomeres cordiform to slightly subcylindrical. TR(I) 1.8, TR(II) 2.1–2.3, TR(III) 1.8–2.2. Wing length 0.91–1.16 mm, CR 0.57–0.63. Second radial cell 1.0–1.3 times shorter than first one (fig. 84). Macrotrichia at wing tip present, microtrichia not visible.

Genitalia (figs. 85–89) inverted, rotated or in normal position. Sternite IX narrow with distinct caudomedian excavation. Tergite IX very short in relation to gonocoxite with long, slender and pointed apicolateral processes bearing a single subapical seta. Segment X bearing long and slender cerci that extend well beyond caudal margin of tergite IX. Gonocoxite slender and very long, 390–525 μm; 1.7–2.7 times shorter than wing length; 4.2–6.0 times as long as broad. Gonostylus slender, slightly curved, not reaching level of apicolateral processes of tergite IX, 2.5–3.5 times shorter than gonocoxite, apex with small tooth-like projection. Aedeagus lightly sclerotized along midline, short; basal arms distinctly recurved; tips of ventral projections pointed and divergent, dorsal projections broad and covered with small spinules. Parameres slender and long, gradually tapering at their pointed and ventrally curving tips.

MATERIAL EXAMINED (14 ♂, 3 ♀)

Types: Lectotype male of *C. forcipiformis*, IMGPUG Z 6533. Paralectotypes: IMGPUG Z 5523, 1 ♂; 5951, 1 ♂; 5716, 1 ♂. By present



90–95. *Ceratopogon forcipiformis* MEUNIER, female; 90 — flagellum, 91 — palpus, 92 — distal tarsomeres of middle leg, 93 — claws of hind leg, 94 — wing, IMGPUG 8376; 95 — scutellum, MŻW 10336

designation. The paralectotype male IMGPUG Z 5716 does not belong to *C. forcipiformis* but to *C. eminens* (wing length 1.31 mm, CR 0.65). Holotype female of *C. defectus*, IMGPUG Z 8376.

MBI 168, KÜNOW, 1 ♂; MZW 8023, 1 ♂; 8597, 1 ♂; 10336, 1 ♂ 1 ♀; 12285 (+*Dolichopodidae* 1 ♀), 1 ♂; 10077, 1 ♂; 12724, 1 ♂; 17268, TG, 1 ♂ 1 ♀; 17659, TG, 1 ♂; ZMC 160, Ostpreussen, C. V. HENNINGSEN, 1–7 1966, 1 ♂; 219, A. HENNINGSEN, 9–9 1974, 1 ♂.

DISCUSSION

It may be that *C. forcipiformis* is a species complex. This species has extremely large male genitalia, as large as any fossil or recent species, except for the recent *C. gigaforceps* REMM (REMM 1973, 1974 a). The latter species which is known from East Palaearctic (Mongolia, Yakutia and Sakhalin) has gonocoxite 420 μm long, i.e. 3.6 times shorter than wing length. However it is larger species having long gonostyli and blunt apicolateral processes of tergite IX, and male wing is without macrotrichia.

2. *Ceratopogon hennigi* sp. n.
(Figs. 96–102)

DIAGNOSIS

Male of the new species is distinguished by the following combination of characters: gonocoxite 255–308 μm long, 3.2–4.3 times shorter than wing length, and 1.7–2.1 times longer than gonostylus. Gonostylus when decumbent not quite reaching apicolateral processus of tergite IX.

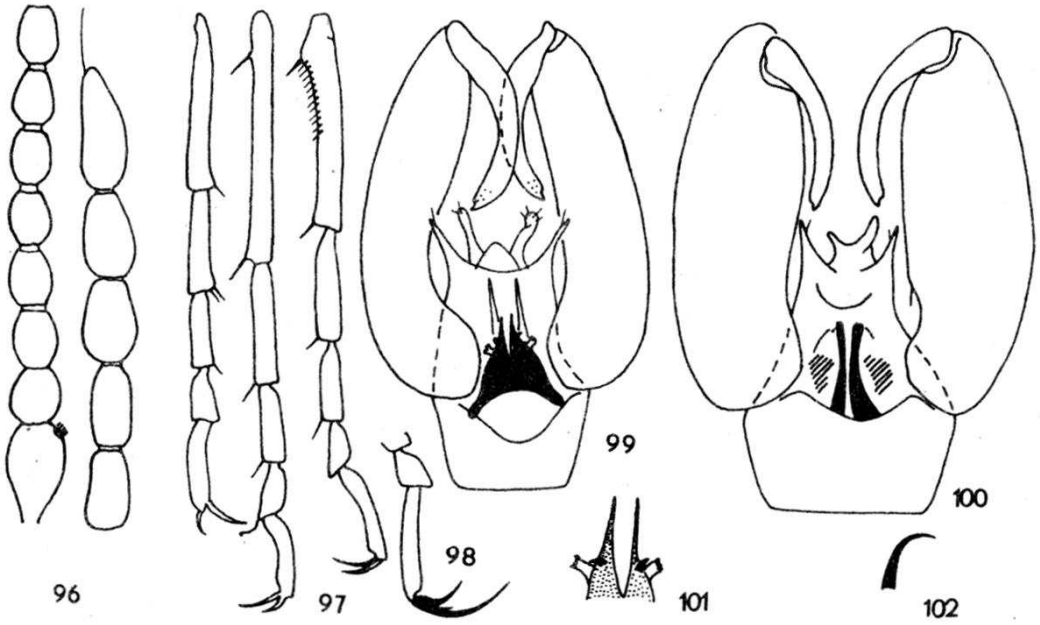
DESCRIPTION

♀. Much deformed due to preservation. Body brown. Total length 1.4 mm. Flagellum length 426 μm, AR 0.90. First flagellomere with single sensillum coeloconicum (fig. 96), proximal 8 flagellomeres slightly elongate. Fourth tarsomeres cordiform. Claws unequal, each with inner basal tooth (fig. 98). TR(III) 2.1. Wing length 0.98 mm, CR 0.66. Both first radial cells equal.

♂. Body brown or dark brown. Total length 1.3–1.6 mm. Flagellum length 428–615 μm, AR 0.89–0.97. Third palpal segment 36–40 μm long, sensory pit distinct. Scutellum with 4–5 long and several shorter setae (ca. 10). Tibial comb composed of 6–8 spines. Fourth tarsomeres subcylindrical (fig. 97). TR(I) 1.9, TR(II) 1.9–2.0, TR(III) 1.9–2.0. Wing

length 0.91–1.09 mm, CR 0.60–0.64. Second radial cell 0.8–1.3 as long as first one. Macrotrichia at wing tip present, microtrichia not visible.

Genitalia moderately large, inverted, rotated or in normal position (figs. 99–102). Sternite IX narrow with shallow caudomedian excavation. Tergite IX short in relation to gonocoxite, apicolateral processes long and pointed with distinct subapical seta. Cerci very long and slender,



96–102. *Ceratopogon hennigi* sp. n.; 96 — female flagellum, MZW 4504; 97 — male tarsi of fore, middle and hind leg, MZW 10748; 98 — female claws of fore leg, 99 — male genitalia, MZW 4504; 100 — male genitalia, MZW 10748; 101 — tip of aedeagus, MZW 4504; 102 — tip of paramere, MZW 17501

extending well beyond caudal margin of tergite IX. Gonocoxite 3.2–4.3 times shorter than wing length and 1.7–2.1 times longer than gonostylus (table 2). Gonostylus slender, not tapering to tip which has an apical spinelike process. Apex of gonostylus when decumbent not quite reaching apicolateral processes of tergite IX. Aedeagus with low basal arch and distal portion with slender deeply forked tip. Dorsal projections of aedeagus short and blunt, bearing small spinules on apex. Parameres long, slender, tips pointed and curved ventrally.

MATERIAL EXAMINED (6 ♂, 1 ♀)

Holotype — ♂, MZW 4504. Paratypes: MZW 4504, 1 ♀; 1831/23 b, 1 ♂; 10748, 1 ♂.

MZW 6475, 1 ♂; 17501, TG, 1 ♂; ZMC 21, A. HENNINGSEN, 20–3 1975, 1 ♂.

ETYMOLOGY

The species is named in honour of the late Professor WILLI HENNIG in recognition of his valuable contributions to the study of *Diptera*.

NOTE

This species differs from *C. forcipiformis* mainly in having shorter gonocoxites in male genitalia.

3. *Ceratopogon tertiaricus* sp. n.
(Figs. 103–110)

DIAGNOSIS

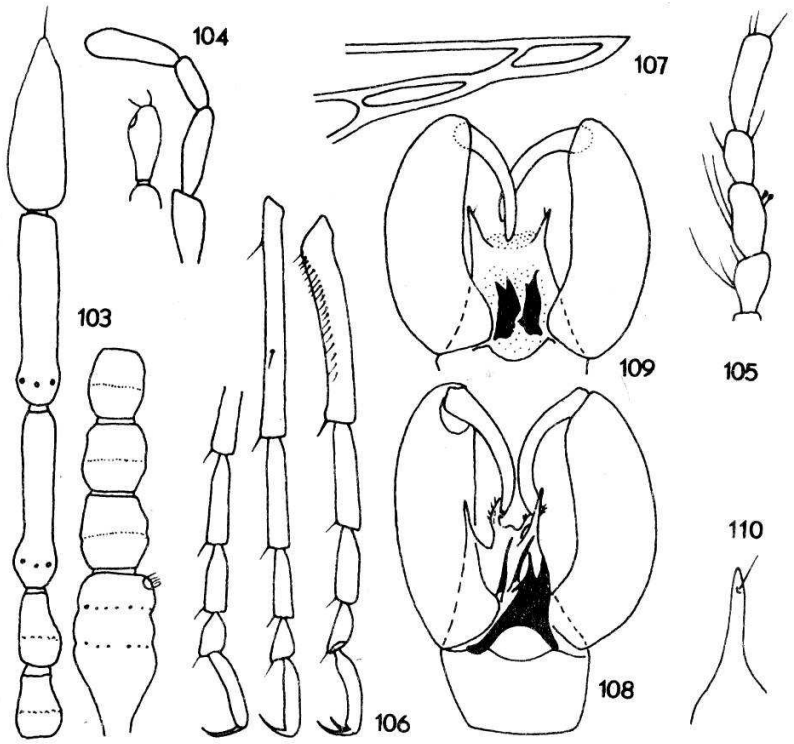
Male of the new species is distinguished by the following combination of characters: gonocoxite moderately long, 4.3–5.0 times shorter than wing length and 1.8–2.1 times longer than gonostylus. Gonostyli reaching below the level of the apicolateral processes of tergite IX when decumbent. Ventral projections of aedeagus slender and pointed.

DESCRIPTION

♀. Unknown.

♂. Body brown or blackish brown, thorax darker. Total length 1.4–1.8 mm. Flagellum length 528–593 μm, AR 0.89–0.92. First flagellomere with easily visible sensilla coeloconica (fig. 103). Palpus slender (figs. 104, 105). Third palpal segment 32–38 μm long, sensory pit present. Scutum covered with sparse setae. Scutellum bears 5–6 long and several shorter setae. Fourth tarsomeres subcylindrical. Tibial comb composed of 6–8 spines. TR(I) 1.7–1.8, TR(II) 2.2–2.3, TR(III) 1.9–2.1. Wing length 0.91–1.05 mm, CR 0.58–0.66. Macrotrichia at wing tip present. Second radial cell 0.9–1.2 as long as first one (fig. 107). Intercalary veins in cell r_{4+5} well visible.

Genitalia slightly rotated or in normal position (figs. 108–110). Sternite IX relatively long with shallow caudomedian excavation. Tergite IX reaching middle length of gonocoxite; apicolateral processes long, slender and pointed, each with subapical seta. Cerci long and slender extending beyond caudal margin of tergite IX. Gonocoxite slender and moderately long, 192–208 μm, 4.3–5.0 times shorter than wing length and



103–110. *Ceratopogon tertiaricus* sp. n., male; 103 — proximal and distal flagellomeres, 104 — palpi, MZW 16125; 105 — palpus, MZW 16582; 106 — tarsi of fore, middle and hind leg, 107 — first radial cells, 108 — genitalia, MZW 16125; 109 — genitalia, MZW 16582; 110 — apicolateral process of tergite IX, MZW 16125

1.8–2.1 times longer than gonostylus. Gonostylus slender, reaching below level of apicolateral processes of tergite IX. Aedeagus with low basal arch and long, slender and pointed ventral projections; dorsal projections pointed and slender. Parameres moderately long with slender, pointed tips.

MATERIAL EXAMINED (8 ♂)

Holotype — ♂, MZW 16125, TG. Paratypes: MZW 10618, 1 ♂; 14988, TG, 1 ♂; 16156, TG, 1 ♂; 16582, TG (+*Chironomidae* 1 ♀), 1 ♂; 20278, TG, 1 ♂.

Specimens not included in the type-series: MBI 219, THOMAS, 1 ♂; ZMC 95, C. V. HENNINGSEN, 1–5 1967, 1 ♂.

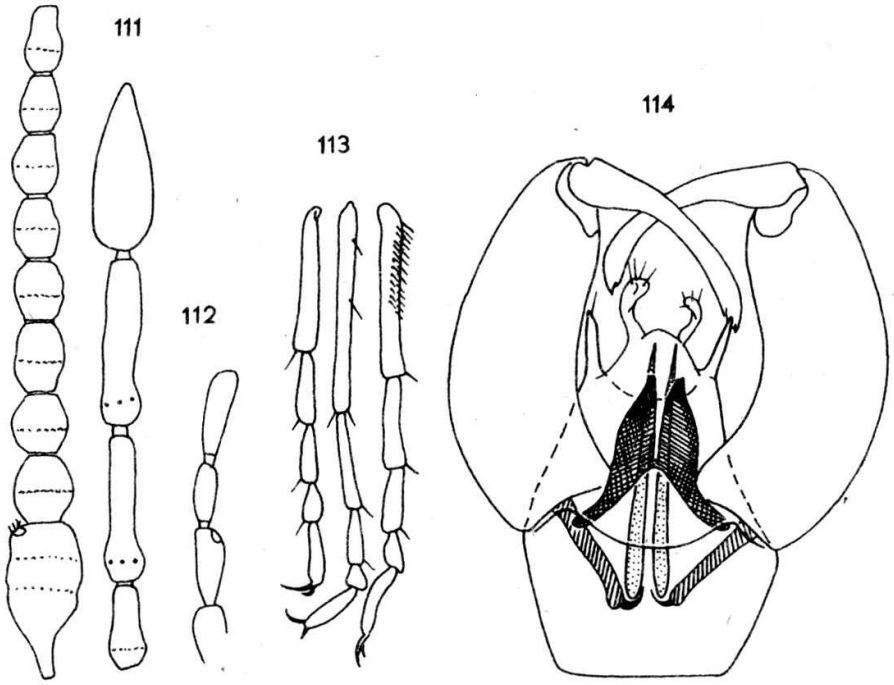
DISCUSSION

The male genitalia of *C. tertiaricus* **sp. n.** are of the same type as of all species described above. However the new species has shorter gonocoxites and gonostyli extending below the level of the apicolateral processes of tergite IX.

4. *Ceratopogon grogani* sp. n.
(Figs. 111–114)

DIAGNOSIS

Male of the new species is distinguished by the following combination of characters: aedeagus large reaching bases of apicolateral processes of tergite IX; ventral projections broad and blunt. Parameres straight. Gonocoxites moderately long, with long, straight dorsal apodemes. Gonostyli reaching level of tergite IX which bears long and slender apicolateral processes.



111–114. *Ceratopogon grogani* sp. n., male, MZW 11411; 111 — flagellum, 112 — palpus, 113 — tarsi of fore, middle and hind leg, 114 — genitalia

DESCRIPTION

♀. Unknown.

♂. Body black, tarsi paler. Total length 1.5 mm. Flagellum length 563 μm, AR 0.88. First flagellomere with sensilla coeloconica (fig. 111). Palpus slender (fig. 112). Third palpal segment 36 μm long, with small apical sensory pit. Proboscis moderately long. Scutum covered with sparse long setae. Scutellum with 5 long setae. Fourth tarsomeres rather subcylindrical (fig. 113). Tibial comb composed of 7 spines. TR(I) 2.0, TR(II) 2.1, TR(III) 2.0. Wing length 0.98 mm. Macrotrichia at wing tip present, microtrichia not visible.

Genitalia (fig. 114). Sternite IX relatively long with shallow caudomedian excavation. Tergite IX moderately long, slender, pointed apicolateral processes, each with subapical seta. Cerci very long, slender proximally but capitate distally, extending well beyond caudal margin of tergite IX and apicolateral processes. Gonocoxite moderately long, 180 μm, 5.4 times shorter than wing length. Gonostylus relatively long, slightly curved and slender, 1.6 times shorter than gonocoxite, apex with toothlike projection. Tips of gonostyli reaching level of distal part of tergite IX. Aedeagus large with high basal arch and long basal arms; ventral projections blunt and slightly divergent, dorsal projections absent. Parameres long and straight, reaching middle of apicolateral processes of tergite IX. Dorsal apodeme of gonocoxite long and straight.

MATERIAL EXAMINED (1 ♂)

Holotype — ♂, MZW 11411, TG.

ETYMOLOGY

The species is named for Dr. W. L. GROGAN, Jr. of Salisbury State College, Salisbury, Maryland, in recognition of his valuable contributions to the study of the world *Ceratopogonidae*.

5. *Ceratopogon eminens* Meunier, 1904
(Figs. 115–126)

Ceratopogon eminens MEUNIER, 1904: 229 (♀, Baltic amber).
Ceratolophus eminens: KIEFFER, 1906: 1 (combination).

DIAGNOSIS

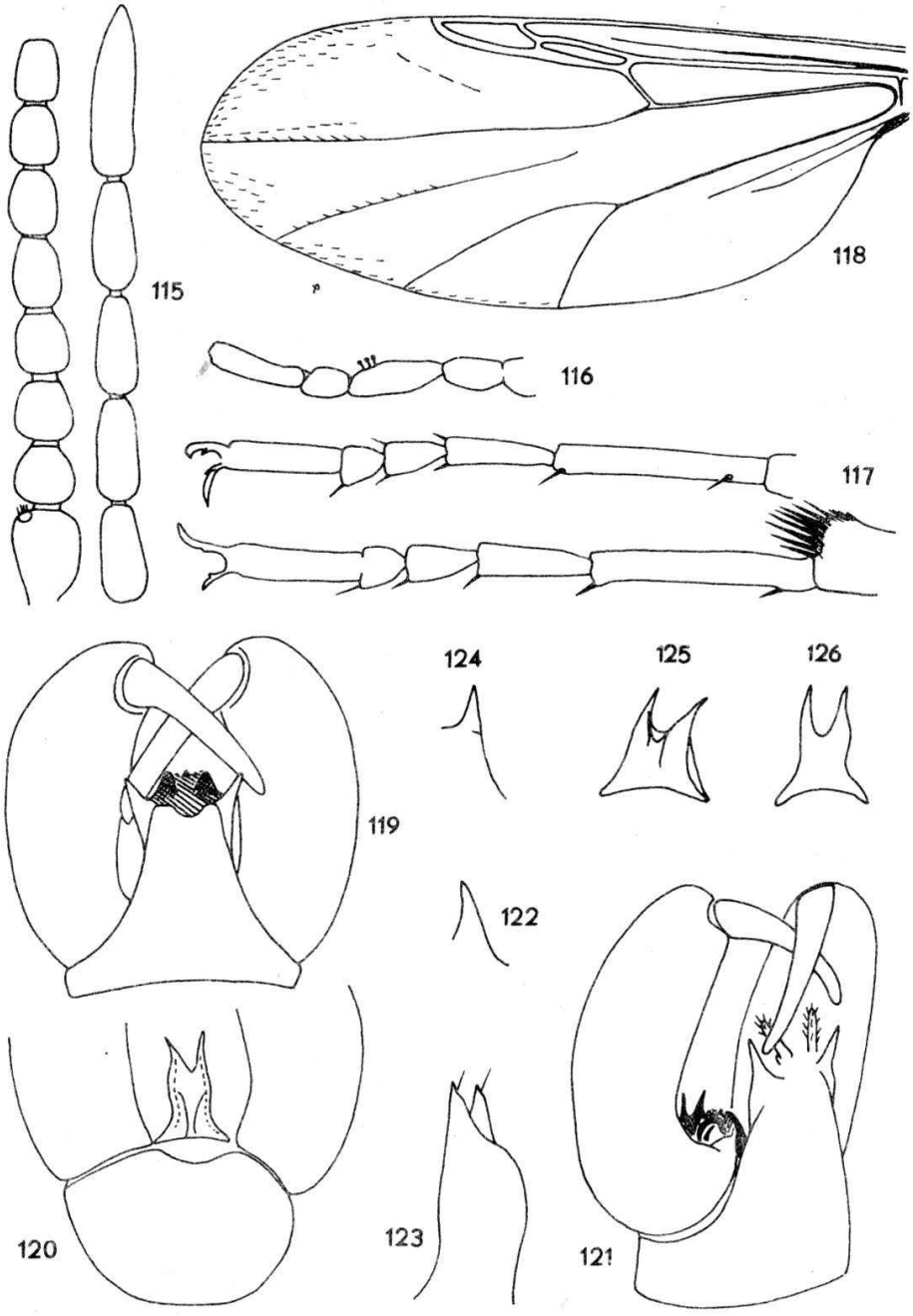
Relatively large species. Male is characteristic in having stout genitalia, apicolateral processes of tergite IX long, broad, triangular, gonocoxite 4.1–4.3 times shorter than wing length and gonostyli reaching tergite IX when decumbent.

DESCRIPTION

♀. All measurements given concern the lectotype. Body dark brown. Total length 1.9 mm. Flagellum length 530 μm, AR 1.0. Proximal flagellomeres spherical to slightly elongated, first flagellomere with sensilla coeloconica (fig. 115). Palpus slender (fig. 116). Third palpal segment 48 μm long, sensory pit small. Prescutal pits distinct. Scutellum with 6 long and several shorter setae. Fourth tarsomeres cordiform.

Claws unequal, each with inner basal tooth (fig. 117). TR(II) 1.9, TR(III) 2.1. Wing length 1.20 mm, CR 0.66; membrane with macrotrichia at wing tip, microtrichia not visible (fig. 118).

♂. Body dark brown or blackish brown. Total length 1.7–1.9 mm. Flagellum length 638–795 μm, AR 0.93. First flagellomere with sensilla



115–126. *Ceratopogon eminens* MEUNIER; 115 — female flagellum, IMGPUG 4003; 116 — female palpus, IMGPUG 6628; 117 — female tarsi of middle and hind leg, 118 — female wing, IMGPUG 4003; 119, 120 — dorsal and ventral view of male genitalia, RSz 5; 121 — lateral view of male genitalia, MZW 19246; 122–124 — apicolateral processes of tergite IX, MZW 20014 (122), MZW 17187 (123), MZW 19239 (124); 125 — aedeagus, MZW 17187; 126 — aedeagus, MZW 20014

coeloconica. Third palpal segment 40–46 μm long. Scutellum with 6 long and several shorter setae. Fourth tarsomeres subcylindrical. Tibial comb composed of 6–7 spines. TR(I) 1.8, TR(II) 1.9–2.3, TR(III) 1.7–2.0. Wing length 1.11–1.45 mm, CR 0.62–0.66. Macrotrichia present at wing tip. Second radial cell 1.1–1.2 times shorter than first one.

Genitalia inverted or not (figs. 119–126). Sternite IX long with very shallow caudomedian excavation. Tergite IX moderately short, reaching midlength of gonocoxite, apicolateral processes long, broad and triangular. Cerci very slender and long, extending with segment X beyond caudal margin of tergite IX. Gonocoxite stout, 4.1–4.3 times shorter than wing length, and 1.7–2.1 times longer than gonostylus (table 2). Gonostylus slightly curved. Aedeagus rather small with no basal arch and with 2 widely separated apical projections. Parameres short and slender with tips curved ventrally.

MATERIAL EXAMINED (10 ♂, 9 ♀)

Types: Lectotype — ♀, IMGPUG Z 4003. Paralectotypes: IMGPUG Z 4374, 1 ♀; 4546, 1 ♀; 4989, 1 ♀; 5445, 1 ♀; 6628, 1 ♀; 7528, 1 ♀; 8671, 1 ♀. By present designation.

IMGPUG Z 5716, 1 ♂, paralectotype of *C. forcipiformis*; MZW 8827, 1 ♂; 12253, 1 ♂; 12567 (+*Chironomidae* 1 ♂), 1 ♂ 1 ♀; 17187, 1 ♂; 19239, TG, 1 ♂; 19246, TG, 1 ♂; 20014, TG, 1 ♂; RSz 5, 1 ♂; ZMC 245, Uden Oplysninger, Zool. Mus., 1 ♂.

DISCUSSION

MEUNIER (1904) in his original description of this species mentioned 9 females, however at IMGPUG collection there are only 8 females. A large female I designate as the lectotype. It may be that the paralectotypes belong to several different species as *C. eminens* is distinguished mainly by quantitative characters.

6. *Ceratopogon* sp. A
(Figs. 127–132)

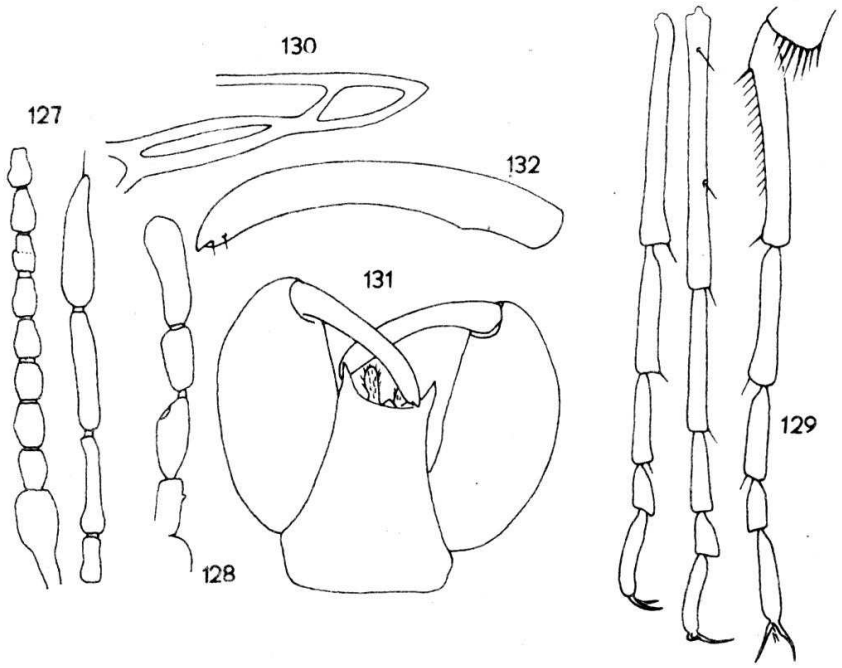
DIAGNOSIS

Large species. Male is characteristic in having short and stout genitalia with gonocoxite 6.3 times shorter than wing length, and long almost straight gonostylus 1.4 times shorter than gonocoxite. Apicolateral processes of tergite IX triangular.

DESCRIPTION

♀. Unknown.

♂. Body blackish brown. Total length 1.5 mm. Flagellum length 713 μm, AR 0.90 (fig. 127). Palpus slender (fig. 128). Third palpal segment ca. 36 μm long, sensory pit small. Scutellum with 5 or 6 long setae. Fourth tarsomeres subcylindrical (fig. 129). TR(I) 2.0, TR(II) 2.0, TR(III) 1.6. Wing length 1.33 mm, CR 0.62. Macrotrichia present at wing tip, microtrichia not visible. Second radial cell 1.7 times shorter than first one (fig. 130).



127–132. *Ceratopogon* sp. A, male, ZMC 221; 127 — flagellum, 128 — palpus, 129 — tarsi of fore, middle and hind leg, 130 — first radial cells, 131 — dorsal view of genitalia, 132 — gonostylus

Genitalia rotated 90° (figs. 131, 132). Tergite IX relatively long with broad, triangular apicolateral processes. Cerci extending beyond caudal margin of tergite IX. Gonocoxite short and broad, 6.3 times shorter than wing length, and 1.4 times longer than gonostylus. Gonostylus long and slightly bent, reaching tergite IX.

MATERIAL EXAMINED (1 ♂)

ZMC 221, A. K. ANDERSEN, 30–1 1958, 1 ♂.

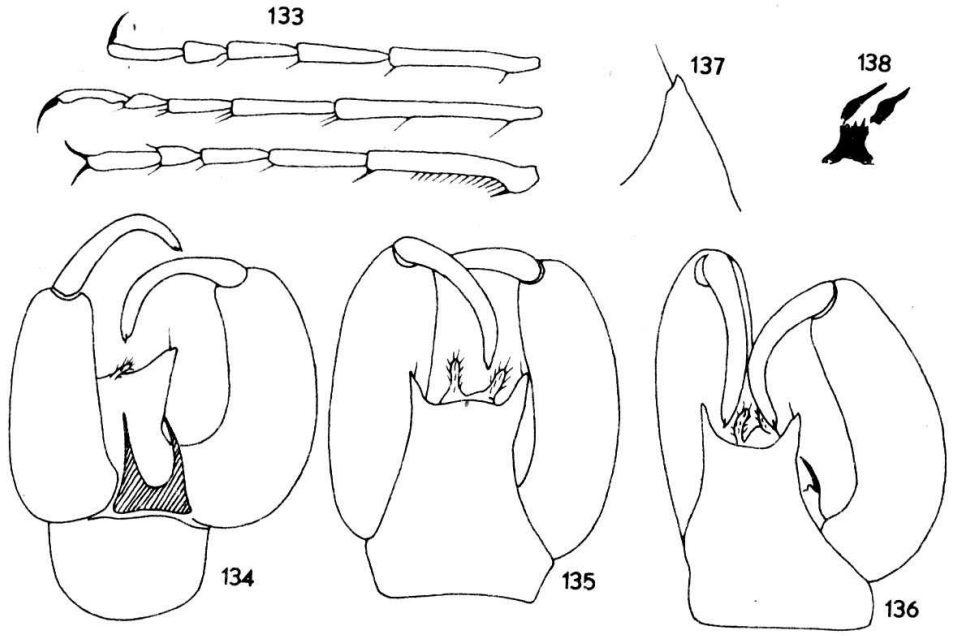
DISCUSSION

This species is very close to *C. eminens*, however second radial cell is short and some other quantitative characters are quite different (table 2). Unfortunately aedeagus and parameres of *C.* sp. A are not visible.

7. *Ceratopogon* sp. C
(Figs. 133–138)

DIAGNOSIS

This species is close to *C. eminens* and *C.* sp. A but is distinctly smaller. Male is characteristic in having stout genitalia, gonocoxite 3.6–3.9 times shorter than wing length, gonostylus slightly curved reaching tergite IX when decumbent, apicolateral processes of tergite IX triangular.



133–138. *Ceratopogon* sp. C, male, ZMC 7; 133 — tarsi of fore, middle and hind leg, 134–136 — genitalia, 137 — apicolateral process of tergite IX, 138 — aedeagus

DESCRIPTION

♀. Unknown.

♂. Body dark brown, thorax black. Total length ca. 1.4 mm. Flagellum length 555 μm, AR 1.00. Palpus barely visible. Fourth tarsomeres subcylindrical (fig. 133). TR(I) 1.8, TR(II) 1.9, TR(III) 1.8. Wing length 0.90–0.94 mm, CR 0.59–0.62. Second radial cell slightly shorter than first one. Macrotrichia present at wing tip.

Genitalia inverted (figs. 134–138). Tergite IX short, with broad, triangular apicolateral processes. Cerci long extending well beyond caudal margin of tergite IX. Gonocoxite 3.6–3.9 times shorter than wing length and 1.9–2.1 times longer than gonostylus. Gonostylus slender, curved distally. Apical projections of aedeagus broadly separated. Parameres not visible (see also table 2).

MATERIAL EXAMINED (3 ♂)

ZMC 7, C. V. HENNINGSEN, 28–3 1968 (+*Phoridae* 1), 3 ♂.

8. *Ceratopogon crypticus* sp. n.
(Figs. 139–145)

DIAGNOSIS

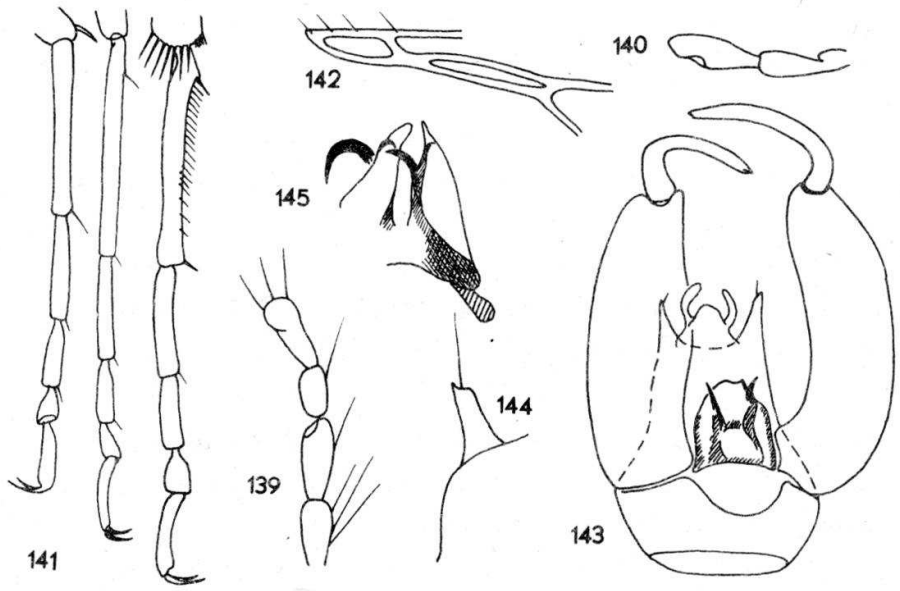
Male of the new species is characteristic in having gonostyli sharply bent near the base and long, blunt apicolateral processes of tergite IX.

DESCRIPTION

♀. Unknown.

♂. Body blackish, dark brown or brown, thorax darker. Total length 1.4–1.8 mm. Flagellum length 585–608 μm, AR 0.84–0.86. Proximal flagellomeres separate. Palpus slender (figs. 139, 140). Third palpal segment 36–40 μm long, sensory pit small. Scutellum bearing 5–8 long and several shorter setae. Fourth tarsomeres subcylindrical (fig. 141). TR(I) 1.7–1.9, TR(II) 1.9–2.5, TR(III) 1.8–1.9. Wing length 0.95–1.16 mm, CR 0.52–0.59. Second radial cell 1.8–2.0 times shorter than first one (fig. 142). Macrotrichia present at wing tip, microtrichia not visible.

Genitalia rotated or inverted (figs. 143–145). Sternite IX with distinct caudomedian excavation. Tergite IX short; apicolateral processes long



139–145. *Ceratopogon crypticus* sp. n., male, ZMC 249 a; 139 — palpus, 140 — proximal three palpal segments, 141 — tarsi of fore, middle and hind leg, 142 — first radial cells, 143 — genitalia, 144 — apicolateral process of tergite IX, 145 — aedeagus and parameres

with obliquely truncate tip bearing long apical seta. Cerci very slender and long extending with segment X beyond caudal margin of tergite IX. Gonocoxite slender, 3.8–4.4 times shorter than wing length and 2.0–2.1 times longer than gonostylus. Gonostylus slender and strongly bent at the base, reaching tip of tergite IX when decumbent. Aedeagus barely visible. Parameres separate, tips strongly curved ventrally.

MATERIAL EXAMINED (8 ♂)

Holotype — ♂; ZMC 249 a, C. V. HENNINGSEN, 1–4 1970, specimen with open gonostyli. Paratypes: ZMC 249 a, 2 ♂ together with the holotype; MZW 20169, 1 ♂; RSz 3, Gdańsk 1985, 2 ♂; ZMC 52, A. K. ANDERSEN, 28–3 1968, 1 ♂. Paratypes from the author's collection will be deposited in MZW.

MZW 8163, 1 ♂ is not included in the type-series of *C. crypticus*.

9. *Ceratopogon remmicolus* sp. n.
(Figs. 146–154)

DIAGNOSIS

Male of the species is characteristic in having very small flagellomere X, distinctly curved gonostyli tapering to pointed tip, apicolateral processes of tergite IX with obliquely truncate tip and cylindrical fourth tarsomeres.

DESCRIPTION

♀. Unknown.

♂. Body brown, thorax darker. Total length 1.1–1.4 mm. Flagellum length 488–495 μm, AR 0.98–1.06. Sensilla coeloconica not visible. Flagellomere X very short (fig. 146). Proboscis moderately long. Palpus slender (figs. 147, 148). Third palpal segment 39–44 μm long, with deep sensory pit. Scutellum bearing 5 long setae. Tibial comb composed of ca. 10 spines (fig. 149). Fourth tarsomeres cylindrical. TR(I) 1.8, TR(II) 1.8–2.1, TR(III) 1.6–1.8. Wing length 0.81–0.89 mm, CR 0.62–0.63. Both first radial cells equal or second one slightly longer (fig. 150). Macrotrichia present at wing tip, microtrichia not visible.

Genitalia inverted (figs. 151–154). Sternite IX with shallow caudomedian excavation. Tergite IX relatively long and distinctly tapering caudally; apicolateral processes broad and long with obliquely truncate tip bearing short apical seta. Gonocoxite slender and moderately short, 4.3–4.5 times shorter than wing length. Gonostylus short and distinctly

curved, tapering to evenly pointed tip, and reaching tergite IX when decumbent. Aedeagus with high basal arch; apicomedian part short, lightly sclerotized in midportion, tip slightly concave; 2 pairs of small apical projections at tip present. Parameres separate, pointed, tips indistinctly curved or straight, basal apodemes straight.

MATERIAL EXAMINED (4 ♂)

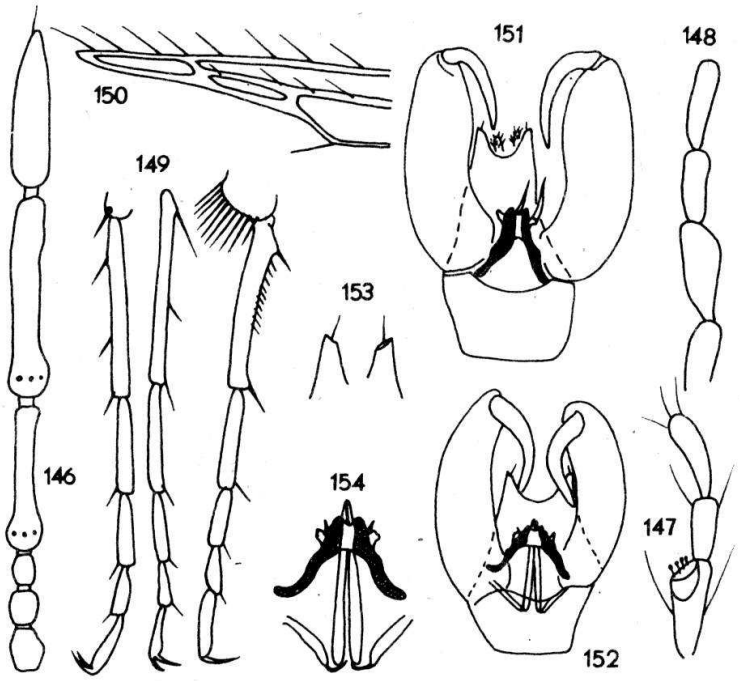
Holotype — ♂, MZW 15788, TG. Paratypes — 3 ♂ together with the holotype. A single amber piece containing 4 males embedded has been divided into 3 pieces. The holotype is in a triangular amber piece mounted in Canada balsam on a cover glass.

ETYMOLOGY

The species is named in honour of the late Dr. HANS REMM (previously of University of Tartu, Estonia) in recognition of his contributions to the study of the Palaearctic *Ceratopogonidae*.

DISCUSSION

This species is unlike any other *Ceratopogon* because of its very small flagellomere X and distinctly cylindrical fourth tarsomeres, and the



146–154. *Ceratopogon remmicolus* sp. n., male, MZW 15788; 146 — distal flagellomeres, 147, 148 — palpi, 149 — tarsi of fore, middle and hind leg, 150 — first radial cells, 151, 152 — genitalia, 153 — apicolateral processes of tergite IX, 154 — aedeagus and parameres

sensory pit of third palpal segment is deep. These characters are not typical for the genus, however the male genitalia including the aedeagus with two pairs of apical projections, and other characters suggest that it is a member of *Ceratopogon*. In the specimens examined sensilla coeloconica were not visible.

10. *Ceratopogon* sp. B
(Figs. 155–158)

DIAGNOSIS

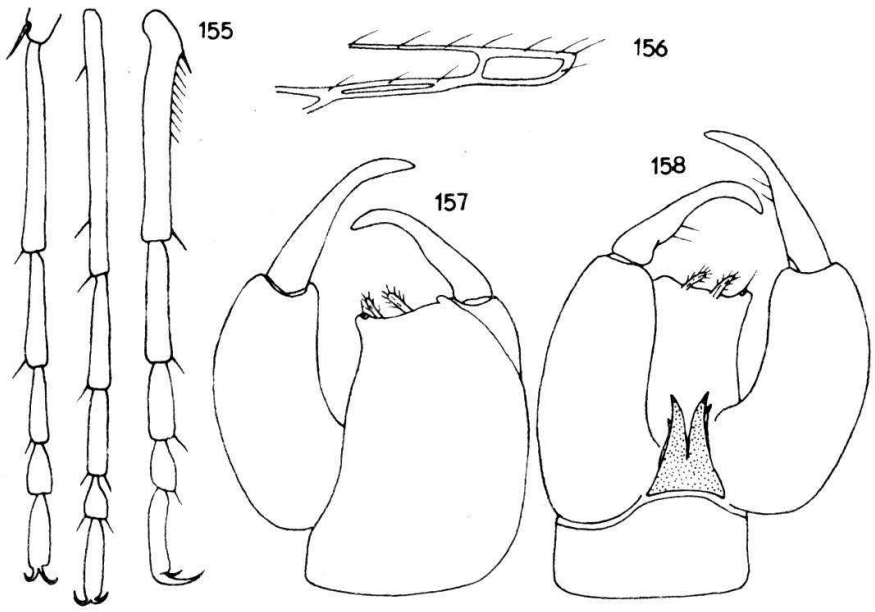
Male of the species is characteristic in having tergite IX broad and long and reaching tips of gonocoxites, stout gonocoxites and long gonostyli.

DESCRIPTION

♀. Unknown.

♂. Body black, legs dark brown. Total length 2.2 mm. Flagellum length 615 μm, AR 0.91. Third palpal segment 44 μm long. Scutellum with 5 long and 2 short setae. Tibial comb composed of 7 spines. Fourth tarsomeres subcylindrical (fig. 155). Wing length 1.09 mm, CR 0.61. Second radial cell slightly shorter than first one (fig. 156). Macrotrichia present at wing tip, microtrichia not visible.

Genitalia rotated (figs. 157, 158). Sternite IX broad, caudal margin



155–158. *Ceratopogon* sp. B, male, ZMC 243; 155 — tarsi of fore, middle and hind leg, 156 — first radial cells, 157, 158 — dorsal and ventral view of genitalia

produced distally. Tergite IX broad and long extending nearly to level of tips of gonocoxites; apicolateral processes very short and blunt. Cerci slender, extending beyond caudal margin of tergite IX. Gonocoxite stout, 5.0 times shorter than wing length. Gonostylus tapering slightly distally with apical 1/3 slightly bent. Aedeagus with low basal arch, deeply forked distally; dorsal and ventral apical projections distinct and pointed. Parameres not visible.

MATERIAL EXAMINED (1 ♂)

ZMC 243, C. V. HENNINGSEN, 26–2 1955, 1 ♂.

11. *Ceratopogon gedanicus* sp. n.
(Figs. 159–164)

DIAGNOSIS

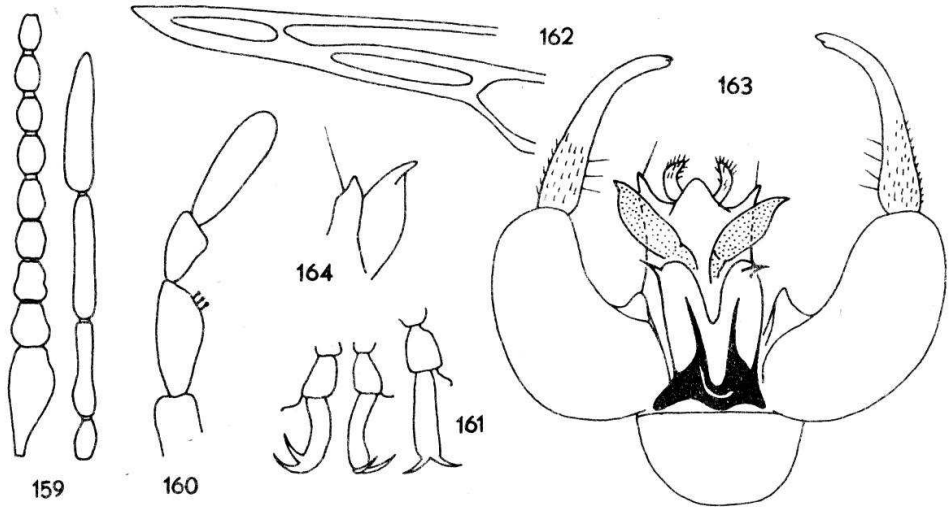
Male of the new species is characteristic in having very large and broad apical portion of parameres, and stout divergent gonocoxites.

DESCRIPTION

♀. Unknown.

♂. Body black. Total length 2.1 mm. Flagellum length 725 μm, AR 0.92 (fig. 159). Palpus moderately stout (fig. 160). Third palpal segment 52 μm long, a small sensory pit present. Scutellum with 5 long setae. Tibial comb composed of 6 spines. Fourth tarsomeres cordiform (fig. 161). TR(II) 2.6, TR(III) 2.1. Wing length 1.36 mm, CR 0.63. Second radial cell shorter than first one 1.3 times (fig. 162). Wing membrane with macrotrichia along distal margin, microtrichia not visible.

Genitalia rotated (figs. 163, 164). Sternite IX moderately long, caudal margin straight. Tergite IX long and narrow; apicolateral processes moderately long with evenly pointed tip bearing long subapical seta. Cerci long and slender, extending beyond caudal margin of tergite IX. Gonocoxite stout, strongly divergent, at base with prominent subtriangular mesal projection; 6.7 times shorter than wing length. Gonostylus slightly tapering distally to somewhat curved apical 1/3; 1.2 times shorter than gonocoxite. Aedeagus large, distally divided into 2 broad lobes, each armed with sharp apicolateral projection. Distal portion of parameres large, in shape of bird wing, extending beyond tergite IX and aedeagus, distinctly divergent.



159–164. *Ceratopogon gedanicus* sp. n., male, MZW 4483; 159 — flagellum, 160 — palpus, 161 — last two tarsomeres of fore, middle and hind leg, 162 — first radial cells, 163 — genitalia, 164 — tip of paramere and apicolateral process of tergite IX

MATERIAL EXAMINED (1 ♂)

Holotype — ♂, MZW 4483.

DISCUSSION

C. gedanicus **sp. n.** from Baltic amber is related to recent species from North Korea which I have in my collection (? *C. unguis* TOKUNAGA). The latter species has broad male genitalia with broad and strongly divergent parameres; however aedeagus has long and slender apical projections, tergite IX devoid of apicolateral processes, gonocoxites and gonostyli stouter and wing membrane without macrotrichia.

12. *Ceratopogon piotrowskii* sp. n.
(Figs. 165–170)

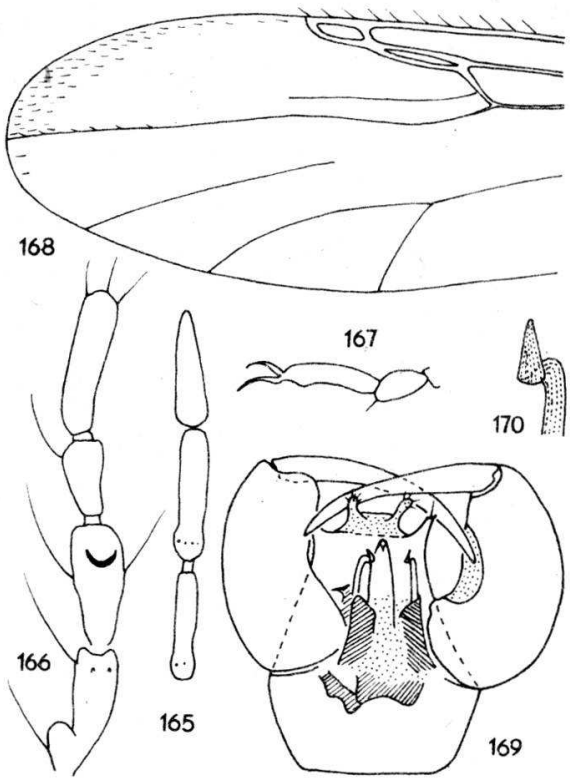
DIAGNOSIS

Male of the species is characteristic in having aedeagus with long caudomedian projection; parameres long and slender with twisted tips; and gonostyli slender and as long as gonocoxites.

DESCRIPTION

♀. Unknown.

♂. Body dark brown. Total length 2.0 mm. Flagellum 728 μm long, AR 0.87. Distal flagellomeres as in fig. 165. Palpus long and slender



165–170. *Ceratopogon piotrowskii* sp. n., male, ZMC 223; 165 — distal flagellomeres, 166 — palpus, 167 — last two tarsomeres of hind leg, 168 — distal part of wing, 169 — genitalia, 170 — tip of paramere

(fig. 166). Third palpal segment 56 μm long, a small sensory pit present. Eyes pubescent. Scutellum with 5 long and several short setae. Fourth tarsomeres cordiform. Tibial comb composed of 8 spines. TR(III) 1.9. Wing length 1.31 mm, CR 0.62. Second radial cell 1.5 times shorter than first one. Macrotrichia present at wing tip (fig. 168), microtrichia not visible.

Genitalia inverted (fig. 169, 170). Sternite IX broad. Tergite IX long, slightly tapering distally; apicolateral processes moderately long with blunt apices bearing a single seta. Cerci slender, extending with segment X beyond caudal margin of tergite IX. Gonocoxite stout and short, 7.3 times shorter than wing length (table 2). Gonostylus long and slender, gradually curved and tapering distally to an evenly pointed tip, as long as gonocoxite. Aedeagus barely visible, with long and pointed apicomedian projection curved ventrally. Parameres slightly shorter than apicomedian projection of aedeagus, distal portion slender with apex twisted or recurved.

MATERIAL EXAMINED (1 ♂)

Holotype — ♂, ZMC 223, J. FLAUENSGAARD, 15–9 1962.

ETYMOLOGY

This species is named for Professor Dr. F. PIOTROWSKI of University of Gdańsk in recognition of his helpful suggestions and criticism throughout my studies on recent and fossil *Ceratopogonidae*.

13. *Ceratopogon ceranowiczi* sp. n.
(Figs. 171–174)

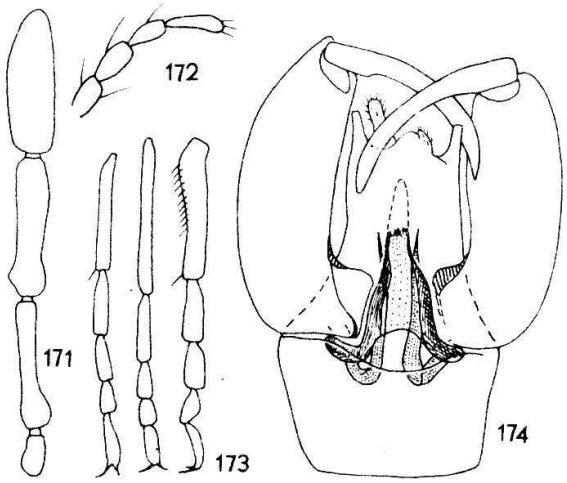
DIAGNOSIS

Male of the species is distinguished by the following combination of characters: apicolateral processes of tergite IX long and blunt. Gonocoxite short, 128 μm, 5.7 times shorter than wing length. Gonostylus long and slender, 1.4 times shorter than gonocoxite. Aedeagus probably with long hyaline apicomedian projection. Parameres short and straight.

DESCRIPTION

♀. Unknown.

♂. Body pale brown. Total length 1.2 mm. Flagellum length 412 μm, AR 0.98. Distal flagellomeres as in fig. 171. Palpus slender (fig. 172). Third palpal segment 20 μm long, sensory pit not visible. Scutum covered with sparse fine setae. Scutellum presumably with 4 long and several short setae. Fourth tarsomeres subcylindrical (fig. 173). TR(I) 1.9, TR(II) 2.3, TR(III) 2.1. Wing length 0.73 mm, CR 0.58. Second radial cell slightly more than 2.0 times longer than first one. Macrotrichia present at wing tip.



171–174. *Ceratopogon ceranowiczi* sp. n., male, MZW 18553 d; 171 — distal flagellomeres, 172 — palpus, 173 — tarsi of fore, middle and hind leg, 174 — genitalia

Genitalia rotated 90° (fig. 174). Sternite IX long and with very shallow caudomedian excavation. Tergite IX long and slender, apicolateral processes long and blunt. Cerci long and slender extending beyond caudal margin of tergite IX. Gonocoxite slender, 128 μm long, 5.7 times shorter than wing length. Gonostylus long, slender, slightly curved, 1.4 times shorter than gonocoxite. Aedeagus barely visible; basal arch low, main body long with long triangular caudomedian projection. Parameres separate, short and straight with pointed tip.

MATERIAL EXAMINED (1 ♂)

Holotype — ♂, MZW 18553 d (together with *Ceratopogonini* indet. 1 ♂; *Culicoides* indet. 1 ♀; *Chironomidae* 1 ♀; *Ceratopogon ritzkowskii* **sp. n.** 1 ♂ 2 ♀).

ETYMOLOGY

This species is named for Docent Dr. B. KOSMOWSKA-CERANOWICZ of Museum of the Earth in Warsaw in recognition of her contributions to the study of Polish Baltic amber.

14. *Ceratopogon ritzkowskii* sp. n.
(Figs. 175–182)

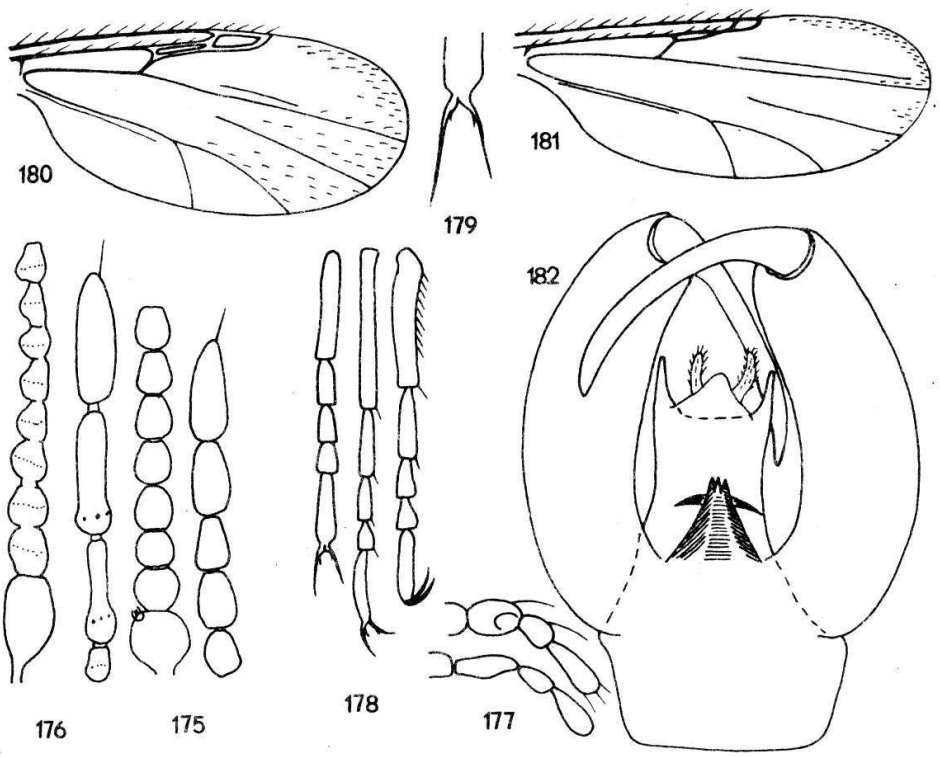
DIAGNOSIS

Male of the new species is distinguished from *C. ceranowiczi* **sp. n.** by the following combination of characters: gonocoxite 176–180 μm long i.e. 3.6–4.1 times shorter than wing length; aedeagus void of apicomedian projection; tips of parameres strongly divergent.

DESCRIPTION

♀. Body black. Total length 1.0 mm. Flagellum length 306 μm, AR 0.97. First flagellomere with sensilla coeloconica (fig. 175). Eyes separate. Proboscis short. Scutum shining. Scutellum with 4–6 long setae. Tibial comb composed of 6 spines. Fourth tarsomeres slightly subcylindrical. Claws long, unequal, each with inner basal tooth (figs. 178, 179). TR(I) 2.3, TR(II) 2.4, TR(III) 2.0. Wing length 0.71–0.72 mm, CR 0.61–0.64. Membrane with macrotrichia on distal half of wing (fig. 180), microtrichia readily visible. Second radial cell slightly shorter than first one.

♂. Body dark brown, thorax black. Total length 1.2 mm. Proximal



175–182. *Ceratopogon ritzkowskii* sp. n.; 175 — female flagellum, MZW 18553 a; 176 — male flagellum, ZMC 89 b; 177 — male palpi, 178 — female tarsi of fore, middle and hind leg, 179 — female claws of fore leg, 180 — female wing, 181 — male wing, 182 — male genitalia, MZW 18553 a

flagellomeres probably separated (fig. 176). Length of flagellum 368 μm, AR 0.96. Proboscis short. Palpus short (fig. 177). Third palpal segment ca. 28 μm long, sensory pit present. Scutum shining. Scutellum with only short setae visible. Tibial comb composed of 6 spines. Fourth tarsomeres subcylindrical. Wing length 0.63–0.74 mm, CR 0.61. Macrotrichia present at wing tip, microtrichia fine but recognizable. Second radial cell 1.5 times shorter than first one (fig. 181).

Genitalia rotated 90° (fig. 182). Tergite IX long and narrow with long and blunt apicolateral processes. Cerci slender and long extending with segment X beyond caudal margin of tergite IX. Gonocoxite long and slender, 3.6–4.1 times shorter than wing length. Gonostylus long and slender, slightly curved distally with pointed tip and 1.4–1.5 times shorter than gonocoxite. Aedeagus barely visible, but tapering distally with serrated tip. Parameres short and strongly divergent, almost perpendicular to tip of aedeagus.

MATERIAL EXAMINED (2 ♂, 2 ♀)

Holotype — ♂, MZW 18553 a. Paratypes: MZW 18553 a, 2 ♀ together with the holotype; ZMC 89 b, A. HENNINGSEN, 9–9 1974, 1 ♂.

Specimens embedded together with the holotype and paratypes in amber piece MZW 18553 are listed at *C. ceranowiczi* **sp. n.**

ETYMOLOGY

The species is named for Dr. S. RITZKOWSKI of Institut und Museum für Geologie und Paläontologie der Georg-August-Universität in Göttingen, a curator of the Baltic amber inclusions.

DISCUSSION

The wing membrane of this species is covered with easily visible microtrichia which are difficult to see in most recent and fossil species.

15. *Ceratopogon margaritae* sp. n.
(Figs. 183–188)

DIAGNOSIS

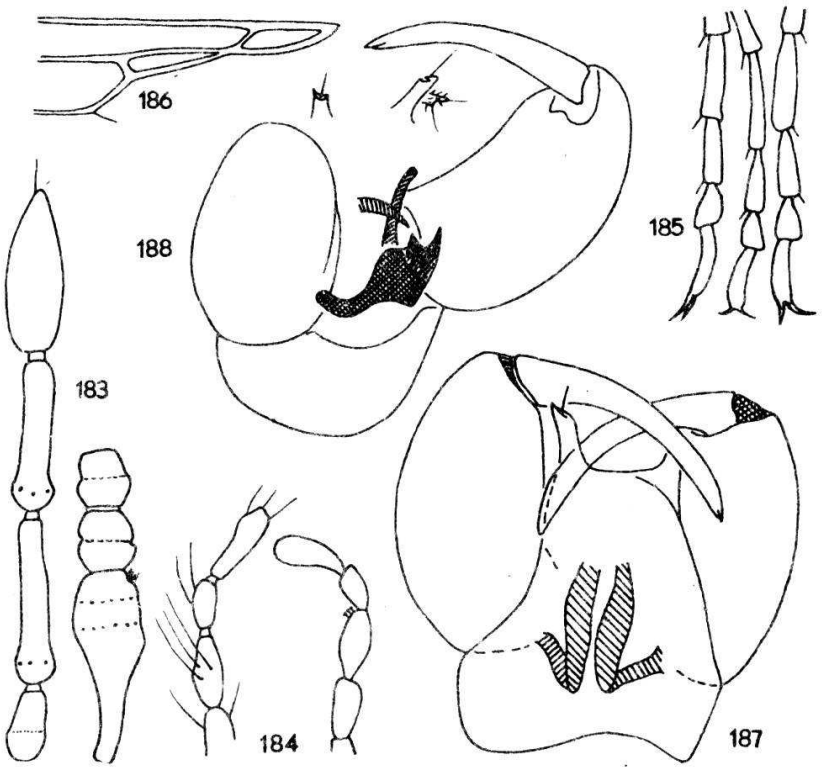
Male of the new species is distinguished by the following combination of characters: gonocoxites short and broad, 6.7–6.8 times shorter than wing length; apicolateral processes of tergite IX long and blunt; gonostyli long and slender; aedeagus with forked tip.

DESCRIPTION

♀. Unknown.

♂. Body brown, thorax darker. Total length 1.2–1.5 mm. Flagellum length 503–540 μm, AR 0.85–0.91. First flagellomere with sensilla coeloconica (fig. 183). Palpus slender (fig. 184). Third palpal segment 30–32 μm long, sensory pit small. Scutellum with 5 long and several short setae. Tibial comb composed of 8 spines. Fourth tarsomeres subcylindrical (fig. 185). Wing length 0.87–0.93 mm, CR 0.57–0.60. Second radial cell 1.1–1.3 times shorter than first one. Macrotrichia present at wing tip, microtrichia not visible.

Genitalia in normal position or slightly rotated (figs. 187, 188). Sternite IX short with shallow caudomedian excavation. Tergite IX long with long, broad and obliquely blunt apicolateral processes. Gonocoxite short and broad, 6.7–6.8 times shorter than wing length. Gonostylus long and slender, slightly curved and tapering distally with beaklike tip, 1.1 times shorter than gonocoxite. Aedeagus broad and short, basal arch low, basal arms long and slightly recurved, tip broadly bifid. Parameres separate, strong with stout pointed apices curved ventrally.



183–188. *Ceratopogon margaritae* sp. n., male, MZW 10945 a; 183 — proximal and distal flagellomeres, 184 — palpi, 185 — distal tarsomeres of fore, middle and hind leg, 186 — first radial cells, 187, 188 — genitalia

MATERIAL EXAMINED (4 ♂)

Holotype — ♂, MZW 19078, TG. Paratypes: MZW 4762, TG, 1 ♂; 10945 a, 2 ♂.

ETYMOLOGY

This species is named for my wife MARIA MAŁGORZATA.

3. Genus *Brachypogon* Kieffer, 1899

DIAGNOSIS

Eyes contiguous. Antenna with 13, rarely 12, 11 or 10 flagellomeres, first flagellomere with sensilla coeloconica. In male plume well developed and proximal flagellomeres II-X or XI fused. Palpus 5 segmented, third palpal segment with distinct sensory pit. Female claws small to moderately long, equal, subequal to unequal, usually with basal inner teeth. Fourth tarsomeres cylindrical to subcylindrical. Scutellum with 4 long

setae. CR less than 0.65. First radial cells variable, varying from completely obsolete to a single complete first or second radial cell. Vein M_2 absent or present. Wing membrane with or without distinct microtrichia, macrotrichia present at wing tip or absent. Male genitalia various. Parameres separated or fused by transverse bridge, usually long. Tergite IX usually without apicolateral processes, and aedeagus usually shield-shaped.

Recent distribution and classification

In the recent fauna there are known about 80 species, mainly in the Palaearctic region. *Brachypogon* including two subgenera *Isohelea* and *Brachypogon* s. str. as proposed Grogan (1982) is an ill defined genus close to *Ceratopogon*.

Fossils

The oldest *Brachypogon* (*B.*) is recorded from the late Cretaceous Siberian amber (see below). The oldest and undoubted *B.* (*Isohelea*) is recorded at present from Baltic amber.

In the material examined 158 specimens of *Brachypogon* belonging to 7 distinct species have been found.

Key to Baltic amber species of *Brachypogon*

Males

1. Both first radial cells present . . . . . subgenus *Isohelea* 2
—. Second or both first radial cells obliterated . . . . . subgenus *Brachypogon* 5
2. Antenna with 11 flagellomeres . . . 1. *B.* (*I.*) *prominulus* (Meunier)
—. Antenna with 13 flagellomeres 3
3. Gonostylus long and slender with enlarged and bilobed tip . . . . . 4. *B.*(*I.*) *henningseni* sp. n.
—. Gonostylus short and stout with blunt or pointed tip 4
4. Parameres longer than gonocoxite, stout . . . 3. *B.*(*I.*) *polonicus* sp. n.
—. Parameres shorter than gonocoxite, indistinct . . . 2. *B.*(*I.*) sp. A
5. First radial cell well developed . . . . . 5. *B.*(*B.*) *eocenicus* sp. n.
—. Both first radial cells obliterated 6
6. Antenna with 10 flagellomeres . . . . 7. *B.*(*B.*) *gedanicus* sp. n.
—. Antenna with 13 flagellomeres . . . . . 6. *B.*(*B.*) *balticus* sp. n.

Subgenus *Isohelea* Kieffer, 1917

DIAGNOSIS

Wing with first and second radial cells of equal size, usually small but well recognizable. Fourth palpal segment with 2 (rarely 1) setae.

RECENT DISTRIBUTION

In the recent fauna there are known slightly more than 50 species, 41 of them from the Palaearctic region. Some species of the subgenus have been described from Nearctic, Afrotropical, Oriental and Australian regions.

FOSSILS

The oldest and undoubted *Isohelea* species are recorded at present from Baltic amber. In the material examined 132 specimens belonging to 4 species have been found.

Brachypogon (*Isohelea*) indetermined (3 ♂, 5 ♀)

MBI 140, KÜHL (+*Dolichopodidae* 1 ♀), 1 ♀; IZPAN 42/78, 1 ♂ 1 ♀; 41/73, 1 ♂; MZW 469/106, 1 ♀; 10333 (+*Chironomidae* 1 ♂), 1 ♂; 12750, 1 ♀; 18270, TG (+*Diptera Cyclorrhapha* 1), 1 ♀.

1. *Brachypogon* (*Isohelea*) *prominulus* (Meunier, 1904), comb. n.

(Figs. 189–203)

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

DIAGNOSIS

Female claws of middle and hind legs short, simple and equal, on fore leg one claw very long but the other one very short, barb-like. Male antenna composed of 11 flagellomeres. Tergite IX in male genitalia with long, finger-like apicolateral processes.

DESCRIPTION

♀. Body brown, thorax dark or black. Total length 0.9–1.1 mm. Eyes separated. Flagellum length 264–296 μm, AR 1.04–1.11. Proximal flagellomeres 8 spherical, distal 5 slightly elongated (fig. 189). Proboscis slightly curved caudally (fig. 192). Palpus slender (fig. 193). Third palpal segment ca. 20 μm long, sensory pit distinct. Fourth palpal segment very short with 2 setae, fifth one long and very slender. Scutum covered with sparse setae, prescutal pits distinct. Scutellum with 4 long setae. Tibial comb composed of 5–6 spines. Fourth tarsomere of fore leg short and

cordiform, of middle and hind legs subcylindrical (figs. 197, 198). Claws of fore leg strongly unequal (fig. 197), of hind and middle legs short, equal and simple (fig. 198). TR(III) 2.1. Wing length 0.54–0.75 mm, CR 0.54–0.60. Macrotrichia present at wing tip, microtrichia readily visible. Both first radial cells present. Vein M_2 with atrophied base.

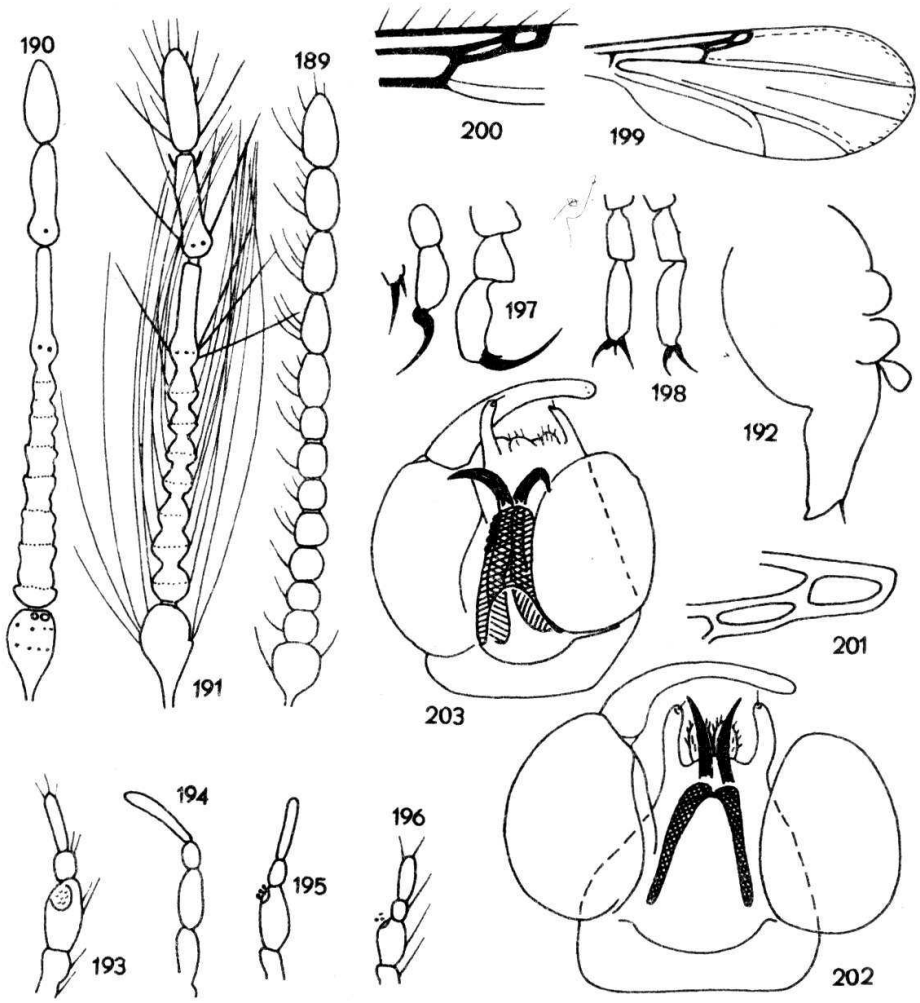
♂. Similar to female with the usual sexual differences. Total length 0.8–1.0 mm. Flagellum length 269–304 μm, AR 1.11–1.17. Flagellomeres II–IX fused, terminal 2 units separated (figs. 190, 191). Flagellum composed of 11 units. Plume well developed. First flagellomere with sensilla coeloconica. Palpus slender (figs. 194–196). Third palpal segment 22–32 μm long. Scutellum with 4 long setae, in some specimens shorter setae present also. Fourth tarsomeres cylindrical. Tibial comb composed of 5–6 spines. TR(I) 2.0, TR(II) 2.3–2.6, TR(III) 2.1–2.4. Wing length 0.51–0.68 mm, CR 0.47–0.54. First radial cell small (figs. 200, 201). Macrotrichia present along distal margin of wing (fig. 199).

Genitalia not inverted, broader than caudal part of abdomen (figs. 202, 203). Sternite IX short with shallow caudomedian excavation. Tergite IX longer than gonocoxite with long finger-like apicolateral processes bearing a single apical seta. Cerci broad, extending just beyond caudal margin of tergite IX. Gonocoxite stout and broad. Gonostylus long, slightly curving and tapering distally to blunt tip. Aedeagus triangular with nearly straight basal arms, tip broadly rounded. Parameres separated, long, with pointed tips strongly divergent and curved ventrally.

MATERIAL EXAMINED (25 ♂, 91 ♀)

Types: Lectotype — ♀, IMGPUG Z 8550. Paralectotypes: IMGPUG 4282, 1 ♀; 5469, 1 ♀; 5711, 1 ♀. By present designation.

IZPAN 41/73, 1 ♀; MBI 100, BERENDT, 1 ♀; 108, BERENDT, 1 ♀; 123, BERENDT, 1 ♀; 203, KÜNOW, 1 ♀; MBI THOMAS 106, 1 ♀; THOMAS 461, "*Ceratopogon eucerus* ♂", 1 ♀; MZW 469/33, 1 ♀; 469/38, 1 ♀; 469/41, 1 ♂; 469/126, 1 ♀; 2189/19, 1 ♀; 4582, 1 ♀; 4803, TG, 1 ♀; 4960, TG, 1 ♂; 4989, TG, 1 ♀; 5055, TG (+*Chironomidae* 1 ♀), 1 ♀; 5256, TG, 2 ♂ 4 ♀ (+*Chironomidae* 1 ♀); 5328, TG, 1 ♂; 5329, TG, 1 ♂; 5338, TG, 1 ♀; 5379, TG, 1 ♂; 8687, 1 ♀; 8746, 1 ♀; 9226 a (+*Acarina* 1, *Chironomidae* 1 ♀), 1 ♀; 9721 a (+*Hymenoptera* 1), 3 ♂; 10122, 1 ♀; 10160, 1 ♀; 10663 (+*Chironomidae* 1 ♀), 1 ♀; 11566, 1 ♂; 12437, 1 ♀; 12457, 1 ♀; 12471, 1 ♀; 12512, 1 ♀; 12827 (+*Chironomidae* 1 ♂), 1 ♀; 13185, TG, 1 ♀; 13193, TG, 1 ♀; 13769, TG, 1 ♀; 13782, TG, 2 ♀; 14403, TG, 1 ♂; 14760, TG, 1 ♂; 14948, TG, 1 ♀; 16096, TG, 1 ♀; 16184, TG, 1 ♀; 16343, TG, 1 ♀; 16364,



189–203. *Brachypogon* (*Isohelea*) *prominulus* (MEUNIER); 189 — female flagellum, IMGPUG 8550; 190 — male flagellum, MZW 18630; 191 — male flagellum, ZMC 14; 192 — lateral view of female head, ZMC 229; 193 — female palpus, IMGPUG 5469; 194 — male palpus, ZMC 138; 195 — male palpus, MZW 18630; 196 — male palpus, ZMC 14; 197 — female claws of fore leg, IMGPUG 8550, MZW 20006; 198 — female claws of middle and hind leg, IMGPUG 8550; 199 — male wing, ZMC 14, 138; 200 — first radial cells of male, ZMC 14; 201 — first radial cells of male, ZMC 138; 202 — male genitalia, ZMC 14; 203 — male genitalia, MZW 18630

TG, 1 ♀; 16421, TG, 1 ♀; 17320, TG, 1 ♀; 16433, TG, 1 ♂ 1 ♀; 16555, TG, 1 ♀; 18101, 1 ♀; 18152, TG, 1 ♀; 18241, TG, 1 ♀; 18630, TG, 1 ♂; 18873, TG, 1 ♂; 18996, TG, 1 ♀; 19074, TG, 1 ♀; 19248, TG, 1 ♀; 19681, TG, 1 ♀; 19801, TG, 2 ♀; 20004, TG, 1 ♀; 20005, TG, 1 ♀; 20006, TG (+*Dasyhelea* indet. 1 ♀, *Ceratopogonini* indet. 1 ♀, *Chironomidae* 1 ♂ 1 ♀), 1 ♀; 20281, TG, 1 ♀; ZMC 8, Th. HANSEN, Mou, 16–1 1961, 1 ♀; 14, Ostpreussen, C. V. HENNINGSEN, 1–7 1966, 1 ♂; 33, C. V. HENNINGSEN, 1–1 1966, 1 ♂; 38, Klarskov ANDERSEN, 30–1 1958, 1 ♀; 40, Th. HANSEN, Mou, 22–6

1955, 1 ♀; 41, C. V. HENNINGSEN, 12–4 1957, 1 ♀; 53, Th. HANSEN, Mou, 16–1 1961, 1 ♂ 1 ♀; 89 a, A. K. ANDERSEN, 28–3 1968, 1 ♀; 90, A. K. ANDERSEN, 1 ♀ at *Stilobezzia* sp. F; 102, Uden OPLYSNINGER, 1 ♂; 110, C. V. HENNINGSEN, 30–6 1953, 1 ♀; 123, Preussen, 1 ♂; 130, Th. HANSEN, Mou, 22–6 1953, 1 ♂; 134, C. V. HENNINGSEN, 8–12 1954, 1 ♀; 138, Balticum, Fru LARSEN, Min. Mus., 5/10–1946, 1 ♂; 145, C. V. HENNINGSEN, 1–5 1967, 5 ♀; 146, C. V. HENNINGSEN, 1–7 1966, 1 ♀; 152, C. V. HENNINGSEN, 3–5 1960, 1 ♀; 158, C. V. HENNINGSEN, 1–5 1967, 1 ♀; 161, C. V. HENNINGSEN, Ostpreussen, 1–7 1966, 1 ♀; 167, German amber, C. V. HENNINGSEN, 1–7 1966, 1 ♂; 197, A. HENNINGSEN, 9–9 1974, 1 ♀; 204, LEHMAN, 1888–601, Min. Mus. (+*Ceratopogon* indet. 1 ♀), 1 ♀; 207, C. V. HENNINGSEN, 1–7 1966, 1 ♀; 214, Th. HANSEN, Mou, 16–1 1961, 1 ♀; 217, A. K. ANDERSEN, 28–3 1968, 1 ♀; 218, C. V. HENNINGSEN, 3–5 1960, 1 ♀; 220, A. HENNINGSEN, 9–9 1974, 1 ♀; 229, C. V. HENNINGSEN, 17–5 1963, 1 ♂ 1 ♀; 230, A. HENNINGSEN, 9–9 1974, 1 ♀; 232, A. HENNINGSEN, 20–3 1975, 1 ♀; 240, A. HENNINGSEN, 9–9 1974, 1 ♀.

NOTE

This is the most common species comprising 10.5% of all biting midges examined.

2. *Brachypogon* (*Isohelea*) sp. A
(Figs. 204–213)

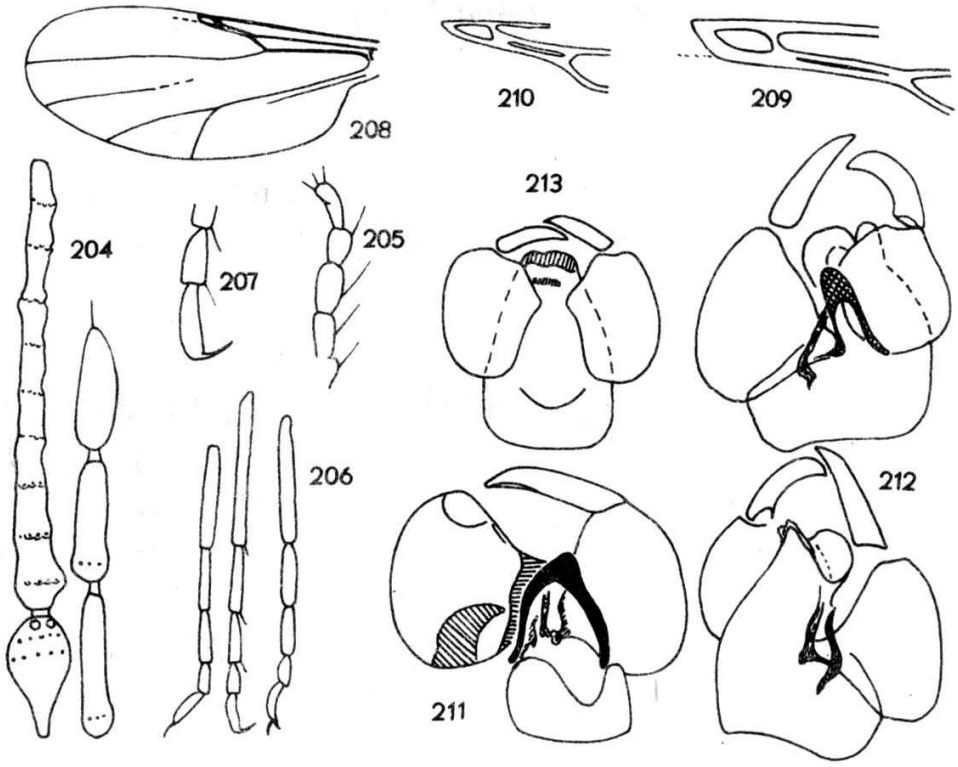
DIAGNOSIS

Male of the species is distinguished by the following combination of characters: both first radial cells present, the first one slit-like; genitalia stout, tergite IX without apicolateral processes; gonostyli short and stout.

DESCRIPTION

♀. Unknown.

♂. Body brown, thorax darker. Total length 1.0–1.1 mm. Flagellum length 405–440 μm, AR 0.91. Flagellomeres II–X fused; first flagellomere with sensilla coeloconica (fig. 204). Palpus slender (fig. 205). Third palpal segment 20 μm long, sensory pit not visible. Prescutal pits present. Scutum with sparse setae. Scutellum bearing 4 long setae. Legs slender. Tibial comb composed of 5–6 spines. Fourth tarsomeres cylindrical (figs. 206, 207). TR(I) 1.6, TR(II) 2.2–2.4, TR(III) 2.0–2.4. Wing length



204–213. *Brachypogon* (*Isohelea*) sp. A, male; 204 — flagellum, ZMC 253 a; 205 — palpus, 206 — tarsi of fore, middle and hind leg, 207 — last two tarsomeres of middle leg, 208 — wing, 209 — first radial cells, ZMC 182; 210 — first radial cells, ZMC 253 a; 211 — genitalia, ZMC 182; 212 — genitalia, ZMC 253 a; 213 — genitalia, ZMC 192

0.59–0.71 mm, CR 0.51–0.55. First radial cell slit-like, second one subtriangular (figs. 209, 210). Vein M_2 present. Wing membrane without macrotrichia or microtrichia (fig. 208).

Genitalia broad, in normal position (figs. 211–213). Sternite IX moderately long with deep caudomedian excavation. Tergite IX as long as gonocoxite, apicolateral processes absent. Gonocoxite short and stout. Gonostylus short, stout, slightly curved, tip pointed. Aedeagus barely visible, triangular; basal arch high. Parameres barely visible, short.

MATERIAL EXAMINED (4 ♂)

MZW 8943 (+ *Acarina* 1), 1 ♂; ZMC 182, B. MORTENSEN, 1–11 1964, 1 ♂; 192, C. V. HENNINGSEN, 28–5 1959, 1 ♂; 253 a, A. HENNINGSEN, 9–9 1974, 1 ♂ (in 253 b, *Dolichopodidae* 1 ♀, *Chironomidae* ♂♂).

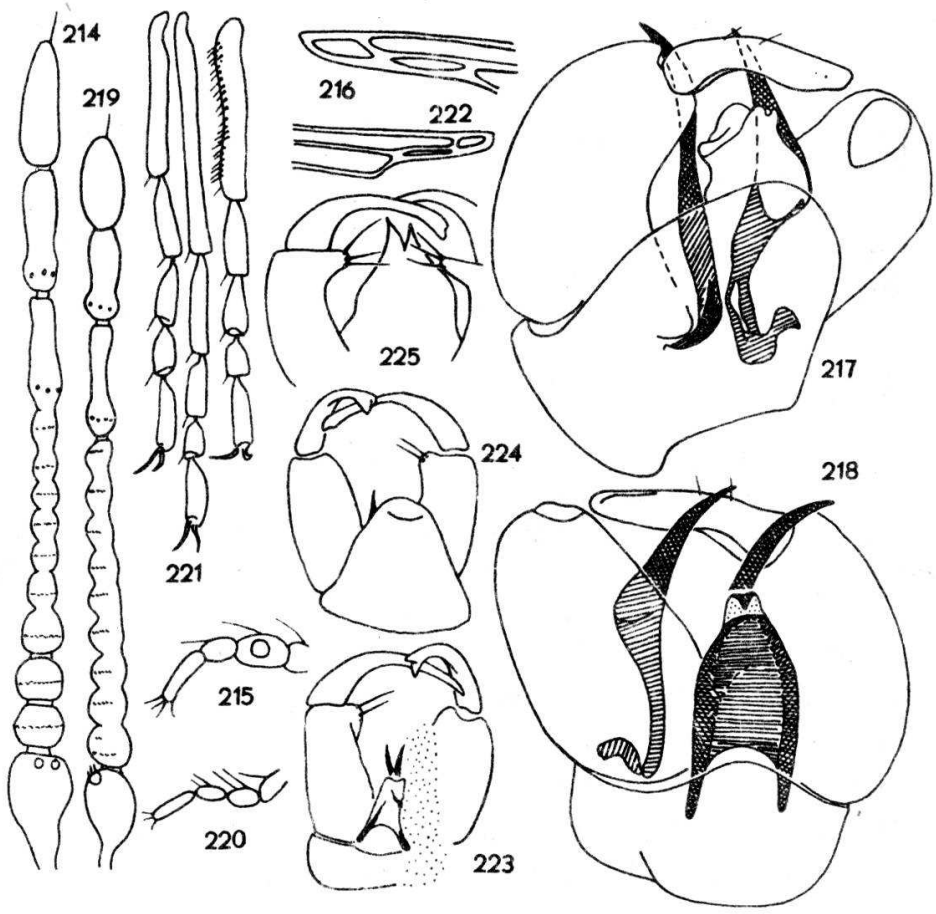
DISCUSSION

This species is a typical member of the subgenus *Isohelea*, similar to many recent Palaearctic species (cf. REMM, 1974 a). The stout male genitalia are barely visible and because of that the ventral structures may be quite different and *B.*(*I.*) sp. A may include more than one species.

3. *Brachypogon* (*Isohelea*) *polonicus* sp. n.
(Figs. 214–218)

DIAGNOSIS

Male of the species is characteristic in having both first radial cells and stout genitalia with very long and stout parameres.



214–225. *Brachypogon* (*Isohelea*) *polonicus* sp. n. and *B.*(*I.*) *henningseni* sp. n. *B. polonicus* sp. n., male, IZPAN 41/73 (214–218): 214 — flagellum, 215 — palpus, 216 — first radial cells, 217, 218 — dorsal and ventral view of genitalia. *B. henningseni* sp. n., male (219–225): 219 — flagellum, 220 — palpus, 221 — tarsi of fore, middle and hind leg, 222 — first radial cells, 223, 224 — ventral and dorsal view of genitalia, ZMC 144; 225 — ventral view of genitalia, MZW 16171

DESCRIPTION

♀. Unknown.

♂. Body dark brown, thorax darker. Total length 1.1 mm. Flagellum length 360 μm, AR 0.98. Proximal flagellomeres IV–XI fused (fig. 214). Proboscis moderately long. Palpus as in fig. 215. Third palpal segment 24 μm long, sensory pit present. Prescutal pits well developed. Scutellum

with 4 long and 2 shorter setae. Tibial comb composed of 6 spines. Fourth tarsomeres cylindrical. TR(II) 2.2, TR(III) 1.5. Wing length 0.65 mm, CR 0.49. Both first radial cells developed (fig. 216). Membrane covered with easily visible microtrichia and with a single row of sparse macrotrichia along wing margin in cell r_{4+5}.

Genitalia slightly rotated, stout and broad (figs. 217, 218). Sternite IX short with convex caudal margin. Tergite IX broad and short without apicolateral processes. Segment X distinctly extending beyond caudal margin of tergite IX. Cerci not visible or absent. Gonocoxite stout. Gonostylus stout slightly sinuous, tip distinctly blunt. Aedeagus long and narrow; basal arch low; apical part short and broad with pointed and curved ventrally apex. Parameres separate, long and stout, longer than gonocoxite; apices gradually tapering to pointed tips that curve ventrally.

MATERIAL EXAMINED (1 ♂)

Holotype — ♂, IZPAN 41/73.

4. *Brachypogon* (*Isohelea*) *henningseni* sp. n.
(Figs. 219–225)

DIAGNOSIS

Male of the species is characteristic in having both first radial cells and small genitalia provided with long and slender gonostyli with enlarged, bilobed tips.

DESCRIPTION

♀. Unknown.

♂. Body brown, thorax darker. Total length 0.7–0.8 mm. Antenna composed of 13 flagellomeres. Flagellum length 324–400 μm, AR 0.76–0.85. Flagellomeres II–X fused (fig. 219). Palpus slender (fig. 220). Third palpal segment 12 or 16 μm long. Scutellum with only 2 long submedian setae. Tibial comb composed of 5 spines. Fourth tarsomeres rather cylindrical (fig. 221). Wing length 0.54–0.62 mm, CR 0.48–0.49. Both first radial cells small (fig. 222). Membrane with few macrotrichia at wing tip, microtrichia not visible.

Genitalia small, not inverted (figs. 223–225). Tergite IX short without apicolateral processes. Gonocoxite slender with distinct apicoventral lobe bearing strong setae. Gonostylus slender and long, evenly curved, tip enlarged, bilobed. Aedeagus small subrectangular, basal arch low, tip slightly concave. Parameres barely visible, longer than aedeagus, apices slender and pointed.

MATERIAL EXAMINED (3 ♂)

Holotype — ♂, ZMC 144, C. V. HENNINGSEN. Paratypes: MZW 16171, TG, 1 ♂; 18929, TG, 1 ♂.

ETYMOLOGY

The species is named for C. V. HENNINGSEN, the collector of the holotype.

NOTE

Shape of gonostylus is unique in the subgenus *Isohelea*.

Subgenus *Brachypogon* Kieffer, 1899

DIAGNOSIS

Wing with both first radial cells completely obliterated or with first or second radial cell. Fourth palpal segment with 0–1 (rarely 2) setae. Tergite IX in male genitalia usually without apicolateral processes.

RECENT DISTRIBUTION AND CLASSIFICATION

Brachypogon (*B.*) including 28 recent species is almost worldwide distributed (see chapter VIII). They are distributed in particular regions as follows: Afrotropical — 11 spp., Australian — 6, Palaearctic — 6, Neotropical — 3, Nearctic — 1 and Oriental — 1 species. SZADZIEWSKI and HAVELKA (1984) suggested that the subgenus *Brachypogon* originated in warm climate, since amongst the Palaearctic species only *B.*(*B.*) *vitiosus* (WINNERTZ) occurs in the cooler parts of Europe and Asia. The other five species of this subgenus are found only at the southern borders of the Palaearctic.

It is worth-while to note that the Eocene *B.*(*B.*) *balticus* **sp. n.** and *B.*(*B.*) *eocenicus* **sp. n.** described below have macrotrichia at wing tip, well developed vein M_2 and fourth palpal segment with long setae while all recent species have no macrotrichia on wing membrane, usually atrophied vein M_2 and usually 0–1 seta on fourth palpal segment.

FOSSILS

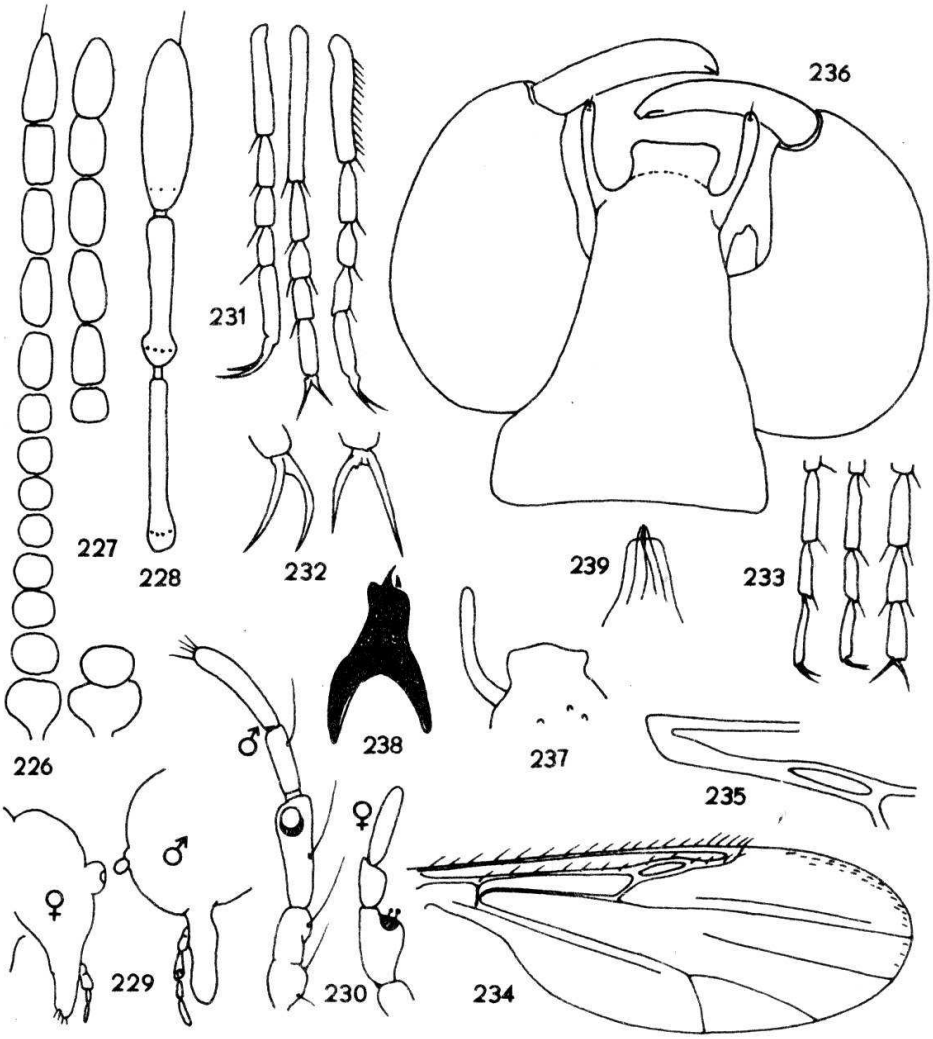
According to GROGAN (personal comm.) *Ceratopogon* (*Fanthamia*) *frigidus* described by REMM (1976) from late Cretaceous Siberian amber should be placed in the subgenus *Brachypogon*.

In the material examined 26 specimens of the subgenus belonging to 3 species have been found.

5. *Brachypogon* (*B.*) *eocenicus* sp. n.
(Figs. 226–239)

DIAGNOSIS

The species is characteristic in having only first radial cell and male genitalia with very long and slender apicolateral processes of tergite IX.



226–239. *Brachypogon* (*B.*) *eocenicus* sp. n.; 226 — female flagellum, MZW 13822; 227 — proximal and distal female flagellomeres, ZMC 103; 228 — male distal flagellomeres, ZMC 238 a; 229 — female and male head, 230 — female and male palpus, ZMC 103; 231 — female tarsi of fore, middle and hind leg, MZW 13822; 232 — female claws of fore and middle leg, 233 — male distal tarsomeres of fore, middle and hind leg, 234 — female wing, ZMC 103; 235 — first radial cells of male, 236 — male genitalia, ZMC 238 a; 237 — tip of tergite IX, 238 — aedeagus, 239 — tip of aedeagus and parameres, ZMC 103

DESCRIPTION

♀. Body dark brown, thorax darker. Total length 1.1–1.2 mm. Flagellum length 320 μm, AR 1.0. Proximal flagellomeres spherical, distal short and cylindrical (figs. 226, 227). Proboscis long (fig. 229). Palpus slender (fig. 230). Third palpal segment 32–40 μm long, somewhat enlarged, with distinct sensory pit. Scutellum with 4 long and several shorter setae. Legs slender. Fourth tarsomeres subcylindrical (fig. 231). Claws long, slightly unequal, probably without inner teeth (fig. 232). RT(I) 2.4, TR(II) 2.5–2.8, TR(III) 2.1–2.3. Wing length 0.74–0.81, CR 0.61–0.62. Second radial cell absent (fig. 234). Membrane covered with small microtrichia, macrotrichia present at wing tip. Wing with brownish tint.

♂. Body dark brown. Total length 1.5–1.6 mm. Eyes pubescent. Flagellum length 555 μm, AR 0.85. Flagellum composed of 13 units, first flagellomere with sensilla coeloconica. Proximal flagellomeres probably separated. Distal flagellomeres as in fig. 228. Proboscis long (fig. 229). Palpus slender (fig. 230). Third palpal segment slender with small but distinct sensory pit, length 48–50 μm. Fourth and fifth palpal segments long and slender. Prescutal pits distinct. Scutellum bearing 5 long and 8 shorter setae. Legs slender, fourth tarsomeres cylindrical (fig. 233). TR(I) 2.1, TR(II) 2.2, TR(III) 1.6–2.0. Wing length 0.91–1.01 mm, CR 0.55. First radial cell as in fig. 235. Wing membrane without macrotrichia, microtrichia not visible.

Genitalia broad, not inverted (figs. 236–239). Sternite IX not visible. Tergite IX long with very long, slender, finger-like apicolateral processes reaching tip of gonocoxites. Tip of tergite IX broadly prolonged to midlength of the processes. Cerci not visible. Gonocoxite stout curved mesally. Gonostylus short, stout and slightly curved distally, tip beaklike. Aedeagus strongly sclerotized, Y-shaped with high basal arch and with broad and probably blunt apical projection. Parameres short, extending just past tip of aedeagus.

MATERIAL EXAMINED (3 ♂, 2 ♀)

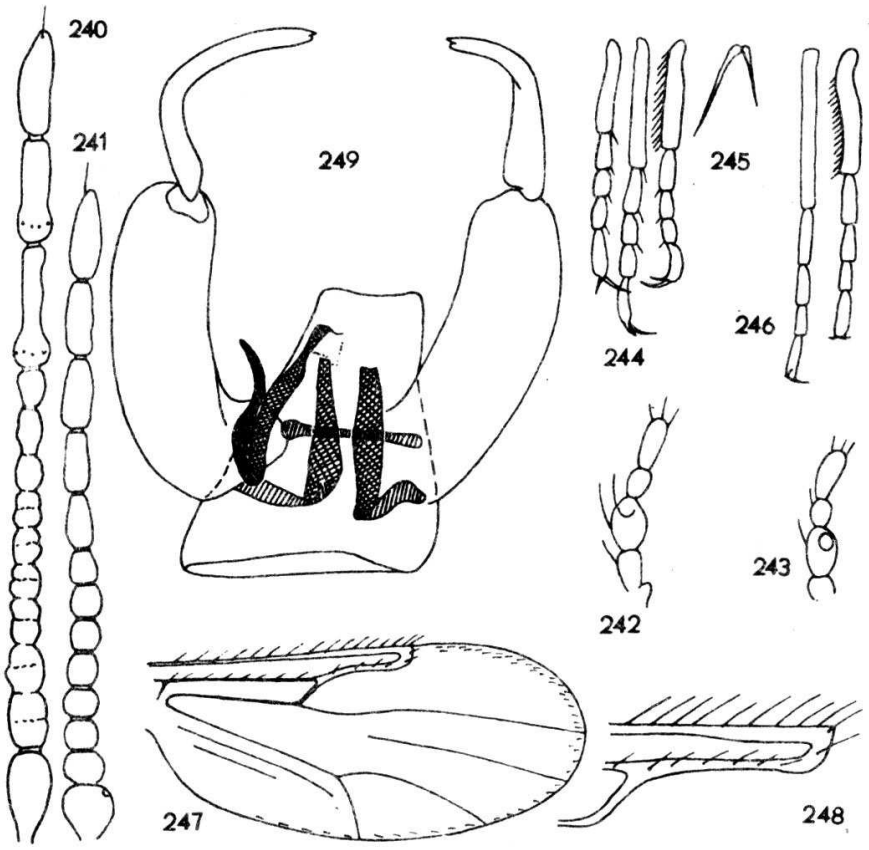
Holotype — ♂, ZMC 238 a, C. V. HENNINGSEN, 25–3 1961. Paratypes: MZW 13822, TG, 1 ♀; 17963, TG, 1 ♀; ZMC 103, Danzig, O. JACOBSEN, 24–3 1916, 1 ♂ 1 ♀.

ZMC 238 b, head of male together with the holotype.

DISCUSSION

Brachypogon eocenicus **sp. n.** is not a typical member of the subgenus because it has very long apicolateral processes of tergite IX in male

genitalia and only first radial cell well developed. Of the presently described species only *Brachypogon* (*B.*) *maai* TOKUNAGA from New Guinea has a similar first radial cell (TOKUNAGA, 1964), and the fossil *Ceratopogon frigidus* from the Cretaceous Siberian amber (REMM, 1976) allocated by GROGAN and WIRTH (personal comm.) in *Brachypogon* (*B.*) which has a similar first radial cell and apicolateral processes on tergite IX in male genitalia. However, female of the latter species has long and strongly unequal claws on hind legs, which of fore and middle legs are very small.



240–249. *Brachypogon* (*B.*) *balticus* sp. n.; 240 — male flagellum, 241 — female flagellum, 242 — female palpus, 243 — male palpus, MBI THOMAS 380; 244 —female tarsi of fore, middle and hind leg, ZMC 173; 245 — female claws of middle leg, 246 — male tarsi of middle and hind leg, 247 — female wing, 248 — female tip of costa and radial veins, MBI 101; 249 — male genitalia, MBI THOMAS 380

6. *Brachypogon* (*B.*) *balticus* sp. n.
(Figs. 240–250)

DIAGNOSIS

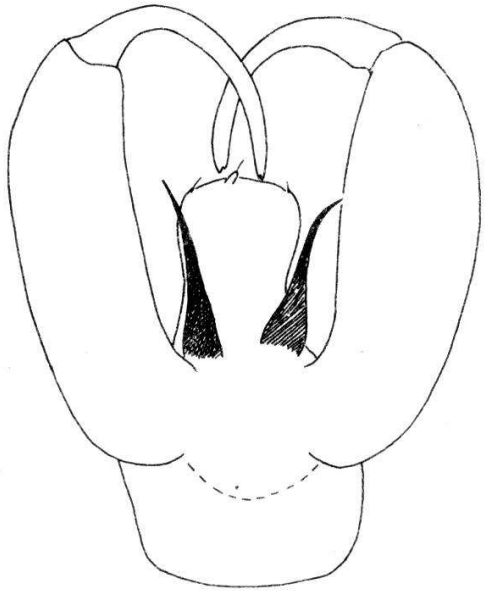
Male of the species is characteristic in having slender strongly curved gonostyli, long and slender gonocoxites, and very long, divergent parameres.

DESCRIPTION

♀. Body black or brown. Total length 0.8–1.2 mm. Flagellum length 288–356 μm, AR 1.14–1.24. Proximal flagellomeres spherical to slightly elongated (fig. 241). Palpus short (fig. 242). Third palpal segment 20–22 μm long, sensory pit visible. Fourth palpal segment with one distinct seta. Prescutal pits readily visible. Scutellum bearing 4 long setae. Tibial comb composed of ca. 5–6 spines. Fourth tarsomeres subcylindrical (fig. 244). Claws long and unequal without recognizable basal teeth (fig. 245). TR(I) 2.4, TR(II) 2.8–3.0, TR(III) 2.3–2.4. Wing length 0.49–0.72 mm, CR 0.57–0.62. Vein R_1 totally fused with Rs, vein M_2 present (figs. 247, 248). Wing membrane with readily visible microtrichia, macrotrichia present along distal margin and in cell r_{4+5} in 2 rows.

♂. Similar to female with the usual sexual differences. Body length 0.9 mm. Eyes pubescent. Flagellum composed of 13 units, length 340–356 μm, AR ca. 0.9. Flagellomeres II-X or XI fused (fig. 240). Palpus as in fig. 243. Third palpal segment 22 μm long. Tibial comb composed of 6 spines. Fourth tarsomeres cylindrical (fig. 246). TR(I) 1.9–2.1, TR(II) 2.6–3.0, TR(III) 2.3–2.5. Wing length 0.69 mm, CR 0.52–0.54. Microtrichia and macrotrichia on wing membrane not visible.

Genitalia large, rotated (figs. 249, 250). Tergite IX short with truncate tip, apicolateral processes absent. Cerci short, barely visible. Gonocoxite slender and long. Gonostylus slender, strongly bent at midportion. Aedeagus barely visible. Parameres very long, widely separated, tips pointed and strongly divergent.



250. *Brachypogon* (*B.*) *balticus* sp. n., male genitalia, RSz 6

MATERIAL EXAMINED (3 ♂, 12 ♀)

Holotype — ♂, MBI 101, BERENDT. Paratypes: MBI 101, BERENDT, 4 ♀; MBI THOMAS 380, "*Tip. culiciform. Ceratopogon*", 1 ♂ 1 ♀ in copula; RSz 6, 1 ♂.

IZPAN 41/73 (+*Dasyhelea* indet. 1 ♀, *Chironomidae* 1 ♀), 1 ♀; MBI 113, BERENDT, 2 ♀; MZW 5270, TG (+*Chironomidae* 1 ♂), 1 ♀; 17467, TG, 1 ♀; ZMC 25, C. V. HENNINGSEN, 3–1 1956, 1 ♀; 173, Libau, Kóbm. TIDEMAND, Min. Mus. 1940–43 (+*Chironomidae* 1 ♂), 1 ♀.

7. *Brachypogon* (*B.*) *gedanicus* sp. n.
(Figs. 251–258)

DIAGNOSIS

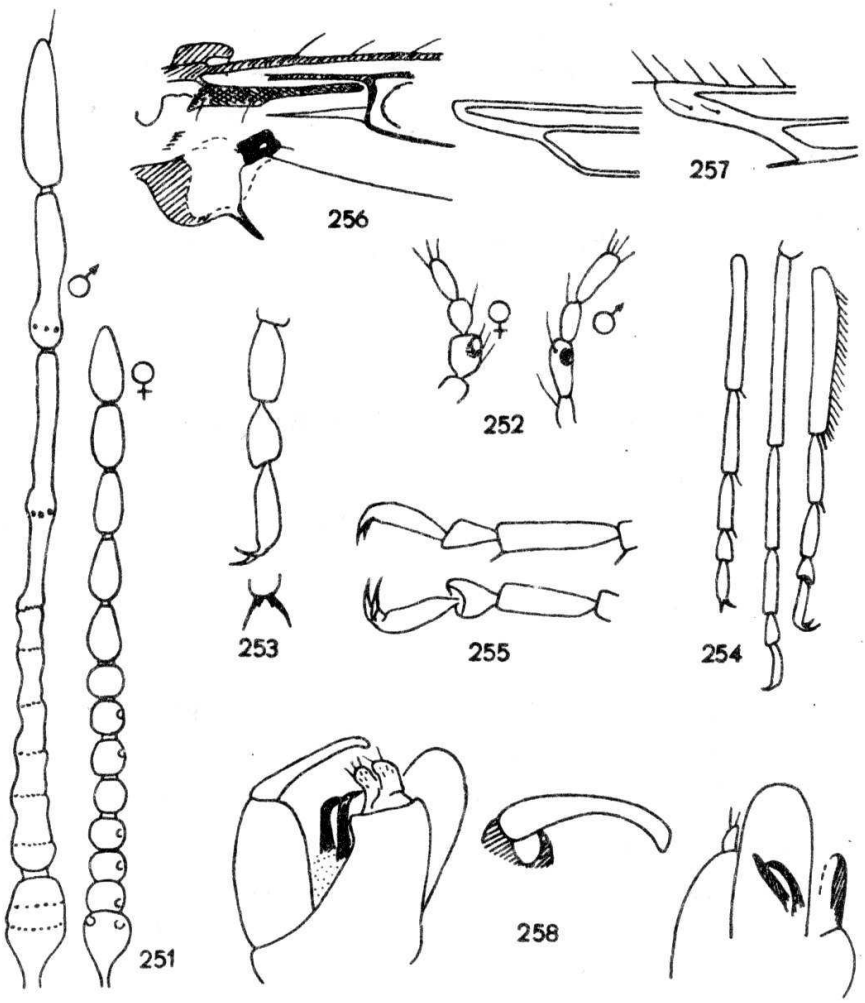
This species is distinguished by the following combination of characters: female claws very short and equal; male antenna with 10 recognizable flagellomeres; first radial cells absent; squama of wing bearing distinct spine.

DESCRIPTION

♀. Body dark brown, thorax darker. Total length 0.8–0.9 mm. Eyes widely separated. Flagellum length 296 μm, AR 1.06. Proximal flagellomeres spherical, first flagellomere with sensilla coeloconica which are also present on 2–4 and 6–7 flagellomeres (fig. 251). Proboscis short. Palpus short (fig. 252). Third palpal segment with distinct sensory pit, 20 μm long. Scutellum bearing 4 long setae. Fourth tarsomeres subcylindrical (fig. 253). Claws very short and equal on all legs, probably with basal inner teeth. TR(I) 2.3, TR(II) 2.5–2.6, TR(III) 2.6. Wing length 0.59–0.60 mm, CR 0.44–0.47. First radial cells obsolete, vein M_2 visible but obsolete basally. Wing membrane with distinct microtrichia, macrotrichia present at wing tip.

♂. Body brown or dark brown, thorax darker. Total length 0.7–1.1 mm. Eyes separated. Antenna composed of 10 flagellomeres. Flagellum length 430–510 μm, AR 1.06. Plume well developed, proximal flagellomeres II-VIII fused (fig. 251). Sensilla coeloconica not visible on first flagellomere. Proboscis short. Palpus slender and short (fig. 252). Third palpal segment 20–24 μm long, with distinct pit. Scutum covered with distinct and sparse setae. Scutellum with 4 long setae. Tibial comb composed of 6–7 spines. Fourth tarsomeres subcylindrical (fig. 254). TR(I) 1.6–1.8, TR(II) 2.0–2.2, TR(III) 2.1–2.4. Wing length 0.68–0.72 mm, CR 0.44–0.46. First radial cells absent, anastomosed radial veins very

short (fig. 257). Vein M_2 well developed. Few macrotrichia present at wing tip, microtrichia barely visible. Wing squama (or upper calypter) well developed and armed with strong spine on caudolateral margin (fig. 256).



251–258. *Brachypogon* (*B.*) *gedanicus* sp. n.; 251 — flagellum of male (ZMC 96) and female (ZMC 227); 252 — palpi, MZW 20007, ZMC 227; 253 — female distal tarsomeres of hind leg, ZMC 227; 254 — male tarsi of fore, middle and hind leg, 255 — male distal tarsomeres of fore, middle and hind leg, MZW 20007; 256 — wing base of male, ZMC 96; 257 — tip of costa and radial veins of male, 258 — male genitalia, ZMC 96, MZW 20007

Genitalia slightly rotated (fig. 258). Sternite IX not visible. Tergite IX long and broad with short and blunt apicolateral processes. Cerci broad, distingtly extending beyond caudal margin of tergite IX. Gonocoxite short, straight. Gonostylus slender, slightly curved distally. Aedeagus barely visible. Parameres well developed, with long, pointed apices curved dorsally.

MATERIAL EXAMINED (2 ♂, 3 ♀)

Holotype — ♂, MZW 20007, TG. Paratypes: MZW 17519, TG, 1 ♀; 17932, TG, 1 ♀; ZMC 96, C. V. HENNINGSEN, 1–7 1966, Ostpreussen, 1 ♂; 227, A. K. ANDERSEN, 28–3 1968, 1 ♀.

4. Genus *Nannohelea* Grogan et Wirth, 1980

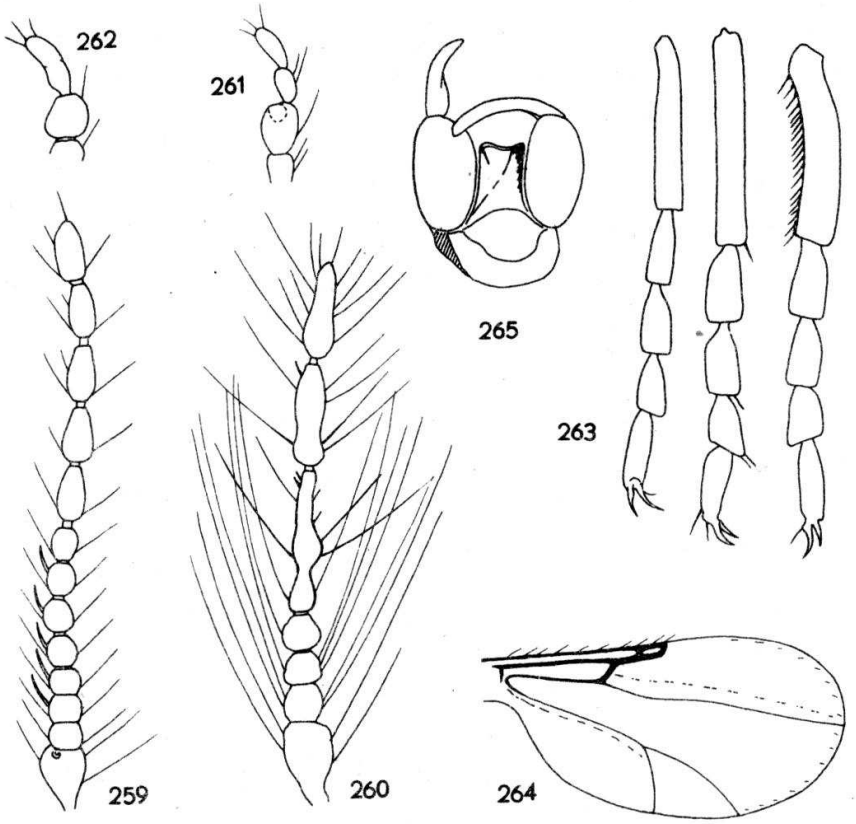
DIAGNOSIS

Female flagellum composed of 13 flagellomeres; first flagellomere with sensilla basiconica; male antenna with 7–8 flagellomeres, distal 2–3 units elongated, flagellomeres separated or V–VI fused in *N. grogani* **sp. n.** Eyes contiguous or narrowly separated. Third palpal segment enlarged, elongated or ovoid with distinct sensory pit. Palpus 3-segmented in recent species, 5-segmented in fossil species. Fourth and fifth palpal segments separated in fossil species, or fused in recent species. Legs slender. Fourth tarsomeres cylindrical or subcylindrical. Female claws very short, equal and simple on all legs. Costa extending to 0.44–0.58 of wing length, only second radial cell developed. Vein M_2 absent. Membrane covered with microtrichia, macrotrichia usually present at wing tip. Male genitalia with broad tergite IX, gonostyli slender and long, parameres strongly reduced.

RECENT ECOLOGY, DISTRIBUTION AND CLASSIFICATION

In the genus *Nannohelea* there are 3 known recent species: *N. bourioni* (CLASTRIER, 1961; Algeria, southern France), *N. clastrieri* GROGAN et WIRTH, 1980 (Colombia), and *N. fuscipennis* (TOKUNAGA, 1964; New Guinea and Malaysia) (GROGAN and WIRTH, 1980 a) (see chapter VIII). *N. bourioni* was reared by CLASTRIER (1961) from rotting wood.

Nannohelea belongs to a group of related genera distinguished by unspecialized and very short female claws, strongly reduced mouthparts, wing venation and male flagellum. They are: *Baeohelea* WIRTH et BLANTON (1 species, Colombia, Dominica, Ecuador), *Leptohelea* WIRTH et BLANTON (1 recent species from Colombia, 1 fossil species from Siberian amber) and *Baeodasymyia* CLASTRIER et RACCURT (1 species, Haiti). It seems that this group of the genera is of Laurasian origin and probably evolved from a *Brachypogon*-like ancestor (DOWNES, 1976; GROGAN and WIRTH, 1980 a). The extinctions of intermediate forms and the reduction process caused certain *Brachypogon*-like forms to evolve into many small, reduced genera. In the Baltic amber there are



259–265. *Nannohelea grogani* sp. n., ZMC 106; 259 — female flagellum, 260 — male flagellum, 261 — female palpus, 262 — male palpus, 263 — female tarsi of fore, middle and hind leg, 264 — female wing, 265 — male genitalia

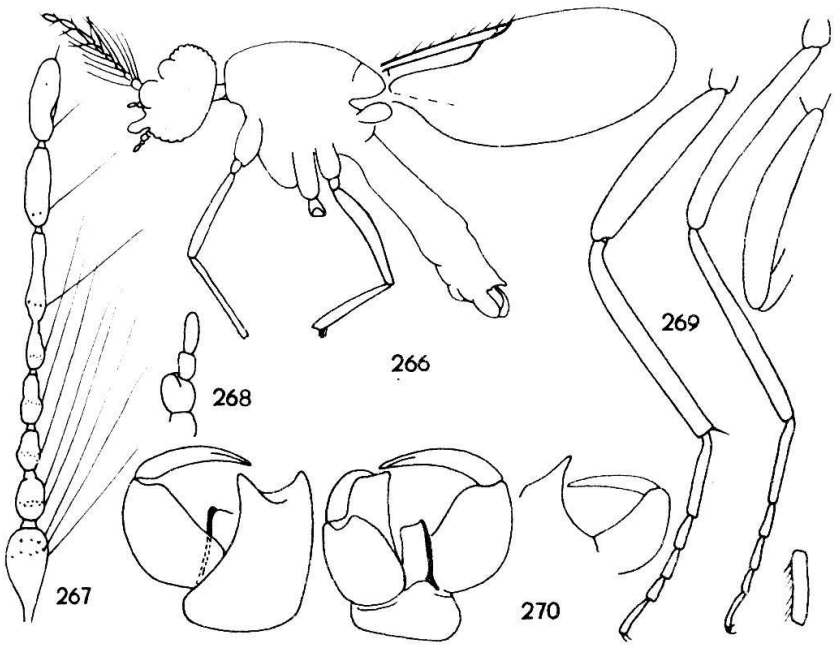
unquestionably *Nannohelea* which have a relatively normal 5-segmented palpi with a moderately enlarged, ovoid third palpal segment while all recent species have 3-segmented palpi in which the primitive third palpal segment is strongly enlarged and elongated and the first segment is composed of the fused 1 and 2, while the third segment is composed of the primitive 4+5. The greatly enlarged third palpal segment is to be found in only one fossil female (fig. 274), and the incompletely fused fifth and fourth palpal segments of one palpus of the male of *N. grogani* **sp. n.** (fig. 262).

FOSSILS

This is the first record of fossil *Nannohelea*. In the material examined 12 specimens of the genus have been found belonging to 2 distinct species.

Nannohelea indetermined (7 ♀)

MBI 175, KÜNOW (+*Acarina* 1), 1 ♀; 195, KÜNOW, 1 ♀; MZW 4769, TG, 1 ♀; 5311, TG, 1 ♀; 10297, 1 ♀; ZMC 42, C. V. HENNINGSEN, 19–11 1958, 1 ♀; 45, C. V. HENNINGSEN, 25–3 1961, 1 ♀.



266–270. *Nannohelea grogani* sp. n., male, ZMC 200; 266 — total habitus, 267 — flagellum, 268 — palpus, 269 — fore and middle legs, hind femur and hind basitarsus, 270 — genitalia

Key to Baltic amber species of *Nannohelea*

Males

1. Plume well developed, flagellomeres V–VI fused . . . . . 1. *N. grogani* sp. n.
—. Plume very short, all 8 flagellomeres separated 2. *N. eocenica* sp. n.

1. *Nannohelea grogani* sp. n.
(Figs. 259–270)

DIAGNOSIS

Male of the species is distinguished by the following combination of characters: plume composed of long setae, flagellomeres V and VI fused.

DESCRIPTION

♀. Body brown, thorax darker. Eyes separated. Flagellum length 268 μm, AR ca. 1.00. Proximal flagellomeres spherical (fig. 259). First flagellomere with sensilla basiconica. Proboscis short. Palpus short, 5-segmented (fig. 261). Third palpal segment rather spherical, with

distinct sensory pit, last 2 palpal segments separated. Scutellum with 4 long and 2 shorter setae. Fourth tarsomeres subcylindrical (fig. 263). Claws short, equal and simple. TR(I) 2.4, TR(II) 2.8, TR(III) 2.5. Wing length 0.60 mm, CR 0.46. First radial cell obliterated, second one small (fig. 264). Vein M_2 absent. Wing membrane covered with microtrichia, macrotrichia present along wing tip.

♂. Body brown, thorax darker. Total length 0.7–0.8 mm. General habitus as in fig. 266. Flagellum length 244–291 μm. Plume composed of long setae (figs. 260, 267). Antenna with 8 flagellomeres, distal 3 flagellomeres elongated, flagellomeres V and VI fused. Proboscis short. Palpus short (figs. 262, 268). Third palpal segment spherical, ca. 16 μm long. Fifth and fourth palpal segments separated or incompletely fused (figs. 262, 268). Scutellum with 4 long and several shorter setae. Fourth tarsomeres cylindrical (fig. 269). Tibial comb composed of 5 spines. TR(I) 2.4, TR(II) 2.5, TR(III) 2.3. Wing length 0.47–0.57 mm, CR 0.43–0.46. Wing membrane covered with microtrichia, sparse macrotrichia in single row present at wing tip.

Genitalia inverted or rotated (figs. 265, 270). Sternite IX short with shallow caudomedian excavation. Gonocoxite moderately stout. Gonostylus long and slender, slightly curved distally to pointed tip, as long as gonocoxite. Tergite IX broad with short and blunt apicolateral processes. Aedeagus plate-shaped, basal arch low, apex slightly concave.

Material examined (3 ♂, 1 ♀)

Holotype — ♂, ZMC 106, A. K. Andersen, 28–3 1968. Paratypes: ZMC 106, 1 ♀ together with the holotype; ZMC 76, C. V. Henningsen, 1–2 1969, 1 ♂; 200, Kunskamere Min. Mus., 1 ♂.

Etymology

The species is named for Dr. W. L. Grogan, Jr. of Salisbury State College, Salisbury, Maryland in recognition of his valuable contributions to study of the tribe *Ceratopogonini*.

Discussion

This species differs from known recent species (Grogan and Wirth, 1980 a) in having fused male flagellomeres V and VI, and the palpus with five segments.

2. *Nannohelea eocenica* sp. n.
(Figs. 271–273)

DIAGNOSIS

Male of the species is distinguished by the following combination of characters: flagellum composed of 8 separate flagellomeres, plume reduced to normal setae, and palpus 5-segmented.

DESCRIPTION

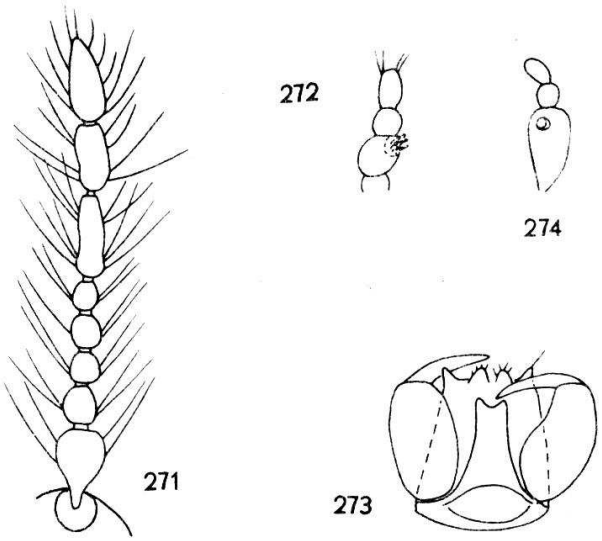
♀. Unknown.

♂. Body dark. Total length 0.7 mm. Flagellum 200 μm long. All 8 flagellomeres separated (fig. 271). Flagellomere V short, plume reduced in length to those of normal setae. Palpus short, 5-segmented (fig. 272). Third palpal segment spherical with distinct sensory pit. Scutellum with 4 long setae. TR(I) 2.3, TR(III) 2.1. Wing length ca. 0.45–0.46 mm, barely visible.

Genitalia inverted, small (fig. 273). Sternite IX short with shallow caudomedian excavation. Tergite IX broad and long with distinct triangular apicolateral processes bearing a single seta. Gonocoxite straight, not extending past level of tergite IX. Gonostylus slender, shorter than gonocoxite. Aedeagus plate-shaped, long and narrow with concave apex, and basal low arch.

MATERIAL EXAMINED (1 ♂)

Holotype — ♂, ZMC 140, C. V. HENNINGSEN, 24–5 1962.



271–274. *Nannohelea eocenica* sp. n. and *Nannohelea* indet. *N. eocenica*, male, ZMC 140 (271–273): 271 — flagellum, 272 — palpus, 273 — genitalia; *N.* indet., female, ZMC 42 (274): 274 — palpus

5. Genus *Ceratoculicoides* Wirth et Ratanaworabhan, 1971

DIAGNOSIS (based on recent species only)

Female eyes distinctly separated. Distal flagellomeres of female antenna moderately elongated. Male flagellum with well developed plume, proximal flagellomeres fused. Palpus short, 5-segmented. Third palpal segment with sensory pit. Legs slender. Fourth tarsomeres subcylindrical. Female claws of fore and sometimes middle legs long, subequal or slightly unequal, of hind leg short and equal, simple. Wing broad. First radial cell obliterated, second one small. Microtrichia on wing membrane distinct, macrotrichia present at wing tip. Male genitalia with long apicolateral processes of tergite IX. Parameres separated. Aedeagus shield-shaped.

RECENT DISTRIBUTION

The genus includes only 4 or 5 recent species restricted to the Holarctic. In North America there are 3 known species (WIRTH and RATANAWORABHAN, 1971). In the Palaearctic, 2 species are described: *C. gracilipes* (REMM, 1967) from Caucasus and *C. tontoeguri* (HAVELKA, 1980) from West Germany. It seems that these two species are synonymous, however priority would be C. *tontoeguri*, but not C. *gracilipes* because of the homonymy (*Ceratopogon gracilipes* WINNERTZ). In my collection I have also females of *Ceratoculicoides* from Yugoslavia and North Korea.

FOSSILS

This is the first record of fossil *Ceratoculicoides*. Only single poorly preserved female has been found which is distinctly different from recent species of the genus.

1. *Ceratoculicoides danicus* sp. n.
(Figs. 275–280)

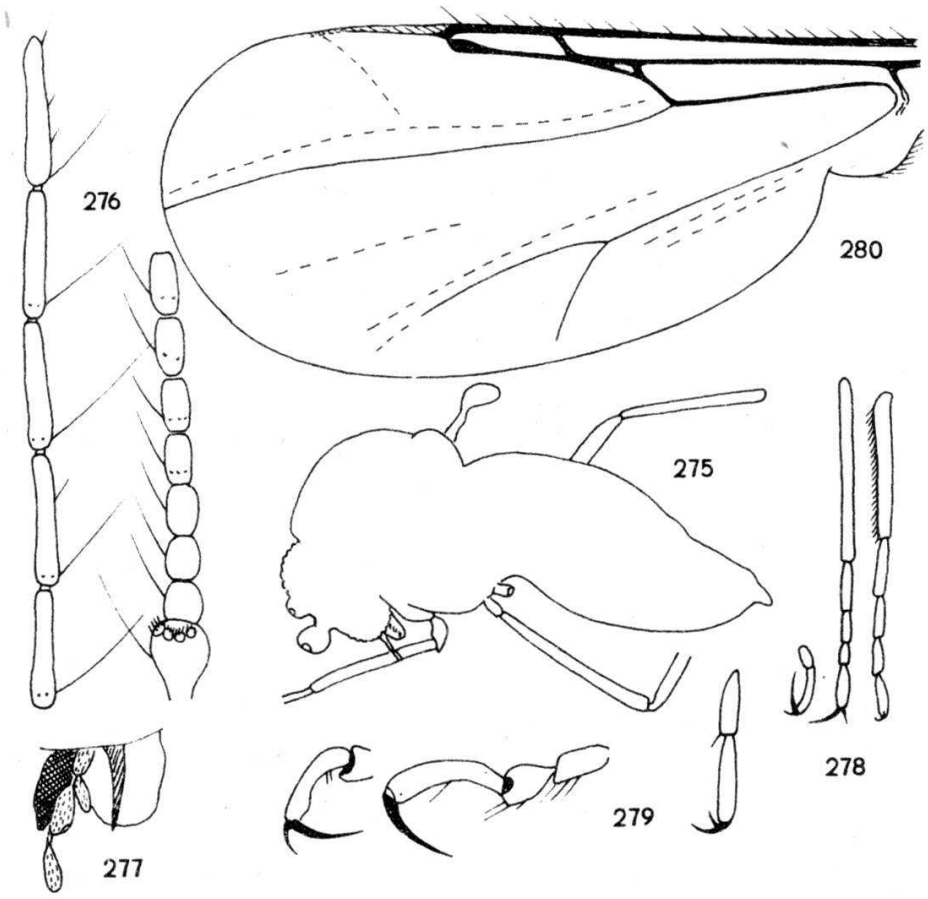
DIAGNOSIS

Female of *C. danicus* **sp. n.** differs from recent species in having fourth and fifth palpal segments fused, large second radial cell and small first one, wing membrane without macrotrichia, and claws of fore and middle legs strongly unequal.

DESCRIPTION

♀. Body brown, thorax darker. Total habitus as in fig. 275. Total length 0.8 mm. Eyes separation not visible. Flagellum length 503 μm, AR 1.50. Proximal 8 flagellomeres subcylindrical, distal 5 long, cylindrical (fig. 276). First flagellomere with sensilla coeloconica. Proboscis short. Palpus short, barely visible (fig. 277). Third palpal segment with small sensory pit. Fifth and fourth palpal segments apparently fused. Scutum covered with sparse normal setae. Scutellum presumably with 4 long setae. Legs slender and unarmed. Tibial comb composed of 4 or 5 spines. Fourth tarsomeres of fore and middle legs subcylindrical, of hind leg cylindrical (figs. 278, 279). Claws of fore and middle legs long and strongly unequal, of hind leg short and equal; all claws simple without basal inner teeth (fig. 279). TR(II) 4.2, TR(III) 2.4. Wing length 0.60 mm, CR 0.62. First radial cell very small, second one long and broad (fig. 280). Wing broad with distinct anal lobe and alula. Membrane covered with distinct microtrichia, macrotrichia absent.

♂. Unknown.



275–280. *Ceratoculicoides danicus* sp. n., female, ZMC 127; 275 — total habitus, 276 — flagellum, 277 — palpi and proboscis, 278 — last two tarsomeres of fore leg and tarsi of middle and hind leg, 279 — claws of middle and hind legs, 280 — wing

MATERIAL EXAMINED (1 ♀)

Holotype — ♀, ZMC 127, C. V. HENNINGSEN, 6–3 1958.

6. *Fossihelea* gen. n.

Type-species *Ceratopogon gracilitarsis* MEUNIER, by present designation.

DIAGNOSIS

Both sexes are characteristic in having sensilla coeloconica on first flagellomere and fore femur armed with 1–3 slender ventral spines.

DESCRIPTION

Small biting midges. Eyes probably narrowly contiguous. Antenna with 13 flagellomeres, first one with 4 or more sensilla coeloconica. Proximal 8 flagellomeres of female cylindrical, distal 5 1.5 times longer than proximal 8, AR 1.0–1.1. Male flagellomeres separated, plume well developed, flagellomere X relatively long. Proboscis moderately long. Palpus 5-segmented. Third palpal segment cylindrical with small, deep, sensory pit. Antepronotum small. Scutum without anterior tubercle, prescutal pits present. Scutellum with 5–8 long and several shorter setae. Legs slender or moderately stout. Fore femur armed with 1–3 slender ventral spines on proximal half, middle and hind femora unarmed. Fourth tarsomeres in female subcylindrical, in male cylindrical. Female claws moderately long, nearly equal, each with inner basal tooth. Wing membrane covered with distinct microtrichia, macrotrichia absent. Both first radial cells well developed. Intercalary veins in cell r_{4+5} well visible, base of M_2 atrophied. Female CR 0.72–0.75, male CR 0.64–0.69.

Female abdomen without modifications. Male genitalia inverted or in normal position. Tergite IX with long and broad apicolateral processes bearing several apical setae. Aedeagus short and broad; basal arch low, apex slightly concave with a subapical ventral tubercle. Parameres separate, short, with pointed slender tip.

DISCUSSION

In the tribe *Ceratopogonini* there is only one other recent species having ventral spines on femora and first flagellomere with sensilla coeloconica. The recent species *Serromyia fuligipennis* CLASTRIER. This species from Congo (only female known) was excluded by DE MEILLON and WIRTH (1983) from the genus *Serromyia* and is being described as

a new genus by WIRTH and GROGAN (in prep.). It may be related to *Fossihelea*. According to the redescription given by DE MEILLON and WIRTH (l.c.) *fuligipennis* has sensilla coeloconica on first flagellomere, moderately swollen hind femur (as *F.* sp. A), fore femur armed with 3 short, stout ventral spines, fourth tarsomeres short and subcylindrical (not cordiform) as *Fossihelea* from Baltic amber. However it has subequal claws on fore legs, and unequal on middle and hind legs, and all claws are simple.

In the material examined there are 6 females and 8 males belonging to 2 species.

Key to Baltic amber species of *Fossihelea*

Males

1. Hind leg stout, tarsus 1.3 times shorter than tibia . . . 2. *F.* sp. A
—. Hind leg slender, tarsus equal or slightly longer than tibia . . . . . 1. *F. gracilitarsis* (MEUNIER)

1. *Fossihelea gracilitarsis* (Meunier, 1904), comb. n.

(Figs. 281–297)

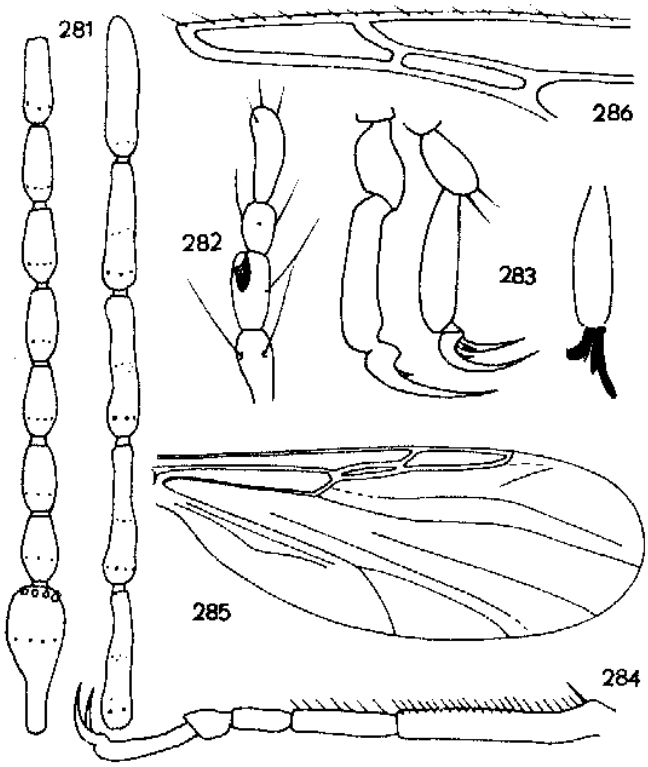
Ceratopogon gracilitarsis MEUNIER, 1904: 235 (♂, Baltic amber).

DIAGNOSIS

Hind tarsus of male equal to somewhat shorter than hind tibia.

DESCRIPTION

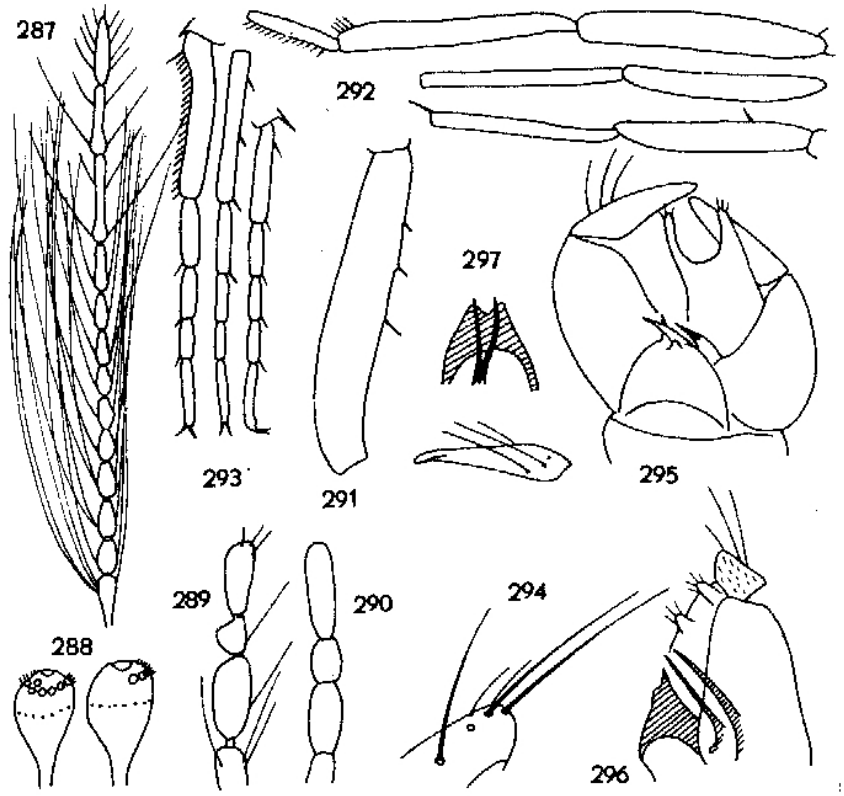
♀. Body brown or dark brown. Total length 1.3–1.5 mm. Eyes probably narrowly contiguous. Flagellum length 575–636 µm, AR 1.00–1.13. Proximal flagellomeres cylindrical, first one with 4 sensilla coeloconica (fig. 281). Palpus slender (fig. 282). Third palpal segment 36–38 µm long, sensory pit small and deep. Scutellum with 5 long and several shorter setae. Fore femur with 2–3 ventral spines on proximal half. Fourth tarsomeres rather subcylindrical (figs. 283, 284). Claws long and nearly equal, each with inner basal tooth. Spur of fore tibia long. TR(I) 1.9–2.1, TR(II) 2.1–2.2, TR(III) 2.1–2.4. Wing length 0.78–0.95 mm, CR 0.72–0.75. Second radial cell distinctly longer than first one (fig. 286). Intercalary veins well visible, M_1 sinuous, base of M_2 atrophied (fig. 285). Wing membrane covered with distinct microtrichia, macrotrichia absent.



281–286. *Fossihelea gracilitarsis* (MEUNIER), female; 281 – flagellum, 282 — palpus, 283 — claws of fore, middle and hind leg, MZW 16425; 284 – tarsus of hind leg, 285 wing, MZW 20302; 286 — first radial cells, MZW 16425

♂. Body brown or dark brown. Total length 1.0–1.2 mm. Flagellum length 508–582 μm, AR 0.83–0.95. All flagellomeres separate, plume well developed, first flagellomere with several sensilla coeloconica (figs. 287, 288). Flagellomere X long, about 2 times shorter than next one. Palpus slender (figs. 289, 290). Third palpal segment 32–38 μm long. Scutellum with 5–8 long and several shorter setae (fig. 294). Legs slender, hind leg slightly stouter than others. Fore femur armed with 1–3 slender ventral spines on proximal half (figs. 291, 292). Tibial spur of fore leg long. Tibial comb composed of 5 spines. Fourth tarsomeres cylindrical (fig. 293). Hind basitarsus with stout basal ventral spine. Tarsus of hind leg equal or slightly longer than hind tibia. TR(I) 2.0–2.1, TR(II) 2.0–2.3, TR(III) 2.2–2.5. Wing length 0.78–1.05 mm, CR 0.64–0.69. Second radial cell larger than first one. Membrane without macrotrichia.

Genitalia in normal position or inverted (figs. 295–297). Sternite IX short and probably without caudomedian excavation. Tergite IX moderately long with broad and distinct apicolateral processes bearing several apical setae. Cerci not visible. Gonocoxite moderately stout. Gonostylus straight, tapering to blunt tip slightly. Aedeagus broad with low basal arch, tip bilobed, a ventral expansion present at tip. Parameres short, separate, with pointed tips.



287–297. *Fossihelea gracilitarsis* (MEUNIER), male; 287 — flagellum, IMGPUG 5732; 288 — first flagellomeres, IZPAN 41/73 b; 289 — palpus, IMGPUG 5732; 290 — palpus, IZPAN 41/73 b; 291 — fore femur, IMGPUG 5732; 292 — femora and tibiae of fore, middle and hind leg, IZPAN 41/73 b; 293 — tarsi of fore, middle and hind leg, IMGPUG 5732; 294 — lateral view of scutellum, IZPAN 41/73 b; 295 — ventral view of genitalia, ZMC 87; 296 — lateral view of genitalia, 297 — aedeagus, parameres and gonostylus, IZPAN 41/73 b

MATERIAL EXAMINED (7 ♂, 6 ♀)

Holotype — ♂, IMGPUG Z 5732.

MBI 109, BERENDT, 1 ♀; 156, KÜNOW, 1 ♂; IZPAN 41/73 a, b, 2 ♂; MZW 1296, 1 ♂; 7902 (+*Chironomidae* 1 ♀), 1 ♀; 8857, 1 ♀; 16425, TG, 1 ♀; 16690, TG, 1 ♂; 20168 b, 1 ♀; 20302, 1 ♀; ZMC 87, A. K. ANDERSEN, 28–3 1968, 1 ♂.

2. *Fossihelea* sp. A
(Figs. 298–302)

DIAGNOSIS

Male of this species differs from *F. gracilitarsis* in having stouter legs, especially of hind pair and by short hind tarsus 0.77 the length of the hind tibia.

DESCRIPTION

♀. Unknown.

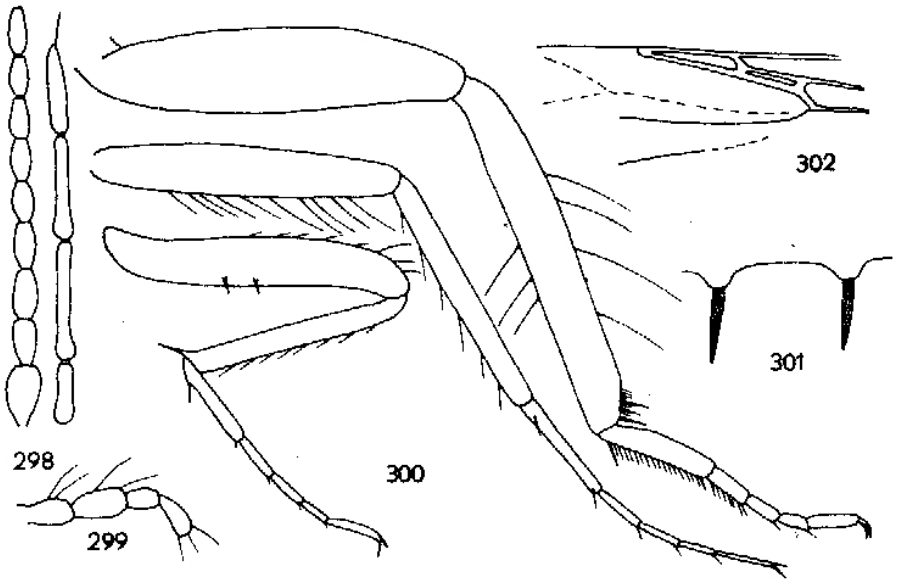
♂. Body dark brown. Total length 1.6 mm. Flagellum length 672 μm, AR 0.90 (fig. 298). Palpus as in fig. 299. Third palpal segment 46 μm long. Scutum covered with sparse strong setae. Scutellum with about 8 large and several shorter setae. Femora and tibiae of fore and middle legs moderately stout, of hind leg stouter (fig. 300). Fore femur armed with 2 ventral spines (fig. 301). Hind tibia with strong and long dorsal and ventral setae. Tibial comb composed of stout and long spines. Hind tarsus stout and short, 1.3 times shorter than hind tibia. Middle tarsus long and slender. Fourth tarsomeres cylindrical. Wing length 1.09 mm, CR 0.64. First radial cells as in fig. 302, intercalary veins well visible. Genitalia inverted, barely visible.

MATERIAL EXAMINED (1 ♂)

IMGPUG Z 4642, 1 ♂ determined by MEUNIER (1904) as *Ceratopogon clunipes* LOEW.

NOTE

This species superficially resembles some species of *Monohelea* in the tribe *Stilobezziini*.



298–302. *Fossihelea* sp. A, male, IMGPUG 4642; 298 — flagellum, 299 — palpus, 300 — fore, middle and hind leg, 301 — ventral spines of fore femur, 302 — first radial cells

Tribe *Stilobezziini* Wirth, 1952

DIAGNOSIS

This tribe is separated from the tribe *Ceratopogonini* by lacking sensilla coeloconica and sensilla basiconica on first flagellomere.

Eyes contiguous or separated. Female antenna always with 13 flagellomeres, distal 5 elongate. Male flagellum with dense plume, reduced only in *Fanthamia* DE MEILLON, *Eohelea*, *Camptopterohelea* and *Gedanohelea* **gen. n.**; usually 3 last flagellomeres elongated. Number of 13 basic male flagellomeres reduced to 12 in *Eohelea*, 11 in *Camptopterohelea*, and to 10 in *Meunierohelea wirthi* **sp. n.** Occasionally proximal flagellomeres fused. Female proboscis usually long, adapted to feeding on insects. Third palpal segment with or without sensory pit. Fourth and fifth palpal segments fused in some genera.

Thorax usually robust. Antepronotum sometimes strongly developed, collar-like. Legs usually highly modified. Femora armed or unarmed, sometimes distinctly swollen. Tarsi usually with strong ventral spines. Fourth tarsomeres from cylindrical to cordiform. Female claws often distinctly enlarged and unequal, reduced to single claw or equal and simple. Wing membrane usually with distinct microtrichia, macrotrichia present or absent. Costa long or short. First and second radial cells or only first one present. Vein M_2 forking distal of the level of r-m with base often atrophied. Male genitalia various, inverted or not, usually stout. Apicolateral processes of tergite IX usually ill defined. Parameres often separated.

RECENT ECOLOGY, DISTRIBUTION AND CLASSIFICATION

Females of *Stilobezziini* are predaceous on other insects. The larvae are predaceous and live in various aquatic and semiaquatic habitats. The tribe including 15 recent genera is distributed worldwide. It may be that this tribe is not a monophyletic group.

FOSSILS

The oldest, however undetermined, *Stilobezziini* are recorded from late Cretaceous Canadian amber (DOWNES, 1978). *Stilobezzia* and *Serromyia* have been found in Miocene rocks from Rott in West Germany (STATZ, 1944).

In Baltic amber the *Stilobezziini* are not common comprising only 16.9% of all specimens (table 3). However in the material studied have been found 34 species belonging to 10 genera of which 6 became extinct.

Stilobezziini indetermined (1 ♀)
ZMC 170, A. HENNINGSEN, 9–9 1974, 1 ♀.

Key to Baltic amber genera of *Stilobezziini*

1. Female claws trifid . . . . . *Wirthohelea* gen. n.
—. Female claws not trifid 2
2. Costa very long, prolonged beyond R_{4+5} almost to wing tip . . . . . *Eohelea*
—. Costa shorter, not prolonged beyond R_{4+5} 3
3. Fore femur swollen and armed with strong ventral spines 4
—. Fore femur slender and unarmed 5
4. Only first radial cell present. Female claws unequal . . . . . *Mantohelea* gen. n.
—. Both first radial cells present. Female claws equal . . . . . *Ceratopalpomyia* gen. n.
5. Hind femur swollen 6
. Hind femur slender 7
6. Hind femur armed with numerous strong ventral spines *Serromyia*
. Hind femur unarmed or with some indistinct spine-like setae . . . . . *Monohelea*
7. Only first radial cell present. Female legs with single long claw. Male flagellum without plume . . . . . *Gedanohelea* gen. n.
—. Both first radial cells present. Female legs with 2 claws. Male flagellum with plume 8
8. Female claws equal. First and second radial cells broadly separated by anastomosed R_1 and R_{4+5} veins . . . . *Meunierohelea* gen. n.
—. Female claws strongly unequal. Both first radial cells not broadly separated 9
9. Proximal flagellomeres of male fused. Parameres long, strongly curved dorsally or ventrally . . . . . *Alluaudomyia*
—. Proximal flagellomeres of male separated. Parameres not strongly curved dorsally or ventrally . . . . . *Stilobezzia*

7. Genus *Alluaudomyia* Kieffer, 1913

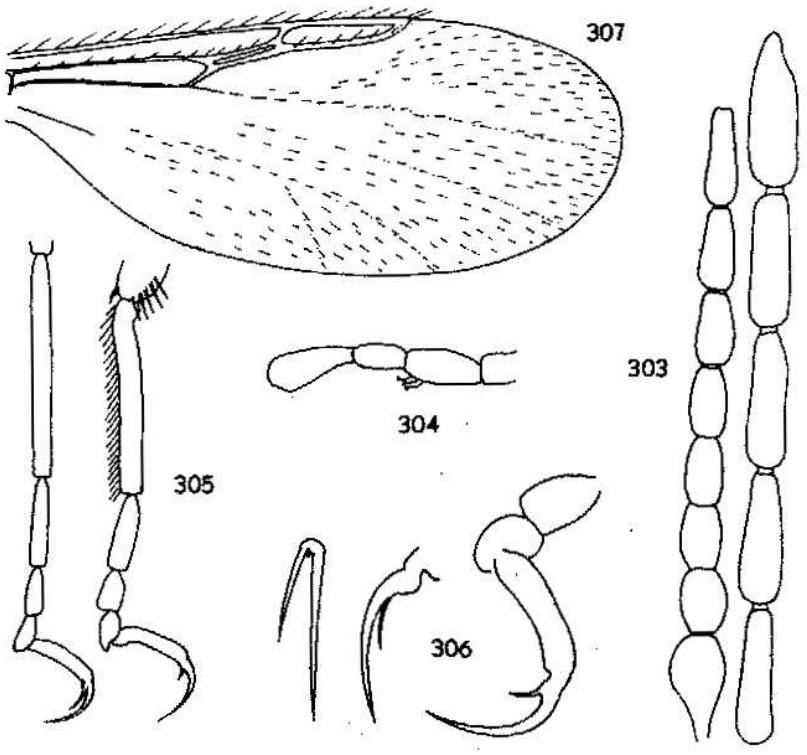
DIAGNOSIS

Eyes contiguous or separated. Flagellum in both sexes composed of 13 units. Male flagellomeres II–IX or X more or less completely fused, plume well developed. Palpus 5-segmented, with or without sensory pit. Legs slender, unarmed. Fourth tarsomeres cordiform. Female claws long

and simple, distinctly unequal or subequal on all legs, or equal on one or more pairs of legs. Wing usually with short slit-like first radial cell. In some Neotropical species r_1 totally reduced (SPINELLI and WIRTH, 1984). Some Micronesian species with indistinct slit-like first radial cell and with larger second one (TOKUNAGA and MURACHI, 1959, fig. 81) while the Baltic amber *Alluaudomyia* species have both first radial cells well developed. Wing membrane void of distinct microtrichia, macrotrichia usually abundant on distal part of wing. Male genitalia with simple gonocoxite and gonostylus. Tergite IX usually long and with distinct apicolateral processes. Distal portion of aedeagus usually highly modified. Parameres separated, usually large and characterstic for each species.

RECENT DISTRIBUTION

More than 140 species of the genus have been described mainly from subtropics and tropics of the World. Largest number of *Alluaudomyia* species is known from the African continent and from the Oriental region. In Nearctic only about 10 species occur while in the Palaearctic there are known about 24 species. In Central and North Europe only 4 species are present and are rarely collected.



303–307. *Alluaudomyia succinea* sp. n., female; 303 — flagellum, MBI 143; 304 — palpus, MZW 7631; 305 — tarsi of middle and hind leg, 306 — claws of fore, middle and hind leg, MZW 11416; 307 — wing, ZMC 39

FOSSILS

This is the first record of fossil *Alluaudomyia*. In the material examined 16 specimens have been found. The species described below are not typical members of *Alluaudomyia*, resembling in some ways *Stilobezzia* and *Kolenohelea* WIRTH et DE MEILLON.

Key to Baltic amber species of *Alluaudomyia*

Males

1. Wing with macrotrichia on distal half, microtrichia not visible. Gonostylus slender . . . . . 1. *A. succinea* sp. n.
—. Wing with macrotrichia at wing tip, microtrichia distinct. Gonostylus with enlarged apex . . . . . 2. ? *A.* sp. A

1. *Alluaudomyia succinea* sp. n.
(Figs. 303–317)

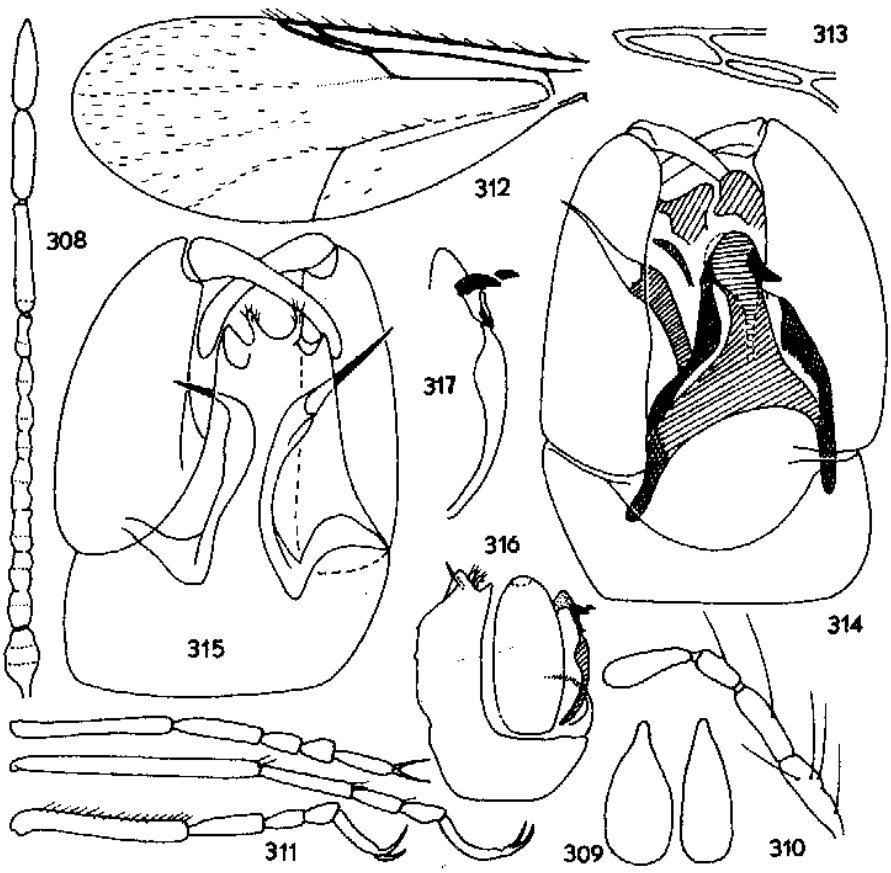
DIAGNOSIS

Both first radial cells well developed. Aedeagus large with swollen apex bearing two strong lateral hooks. Parameres long with slender and pointed tips curved dorsally.

DESCRIPTION

♀. Body dark brown or black. Total length 1.3 mm. Flagellum length 471–594 μm, AR 0.97–1.14. Distal flagellomeres moderately elongated, last one distinctly pointed (fig. 303). Sensilla coeloconica absent. Proboscis moderately long. Third palpal segment without sensory pit (fig. 304), length 24–32 μm. Eyes contiguous. Scutum covered with sparse moderately long setae. Scutellum with 6 long setae. Tibial comb composed of 5 spines. Fourth tarsomeres cordiform (fig. 305). Hind basitarsus without ventral basal spine. Claws long and strongly unequal, simple and similar on all legs (fig. 306). TR(I) 1.9–2.1, TR(II) 2.0–2.5, TR(III) 2.7–2.9. Wing length 0.92–1.19 mm, CR 0.62–0.68. Wing membrane without microtrichia, macrotrichia abundant on distal half (fig. 307). Both first radial cells present, first one short and narrow, second one large. Vein M_2 developed, atrophied at base.

♂. Body brown. Total length 1.2–1.4 mm. Flagellum length 516–542 μm, AR 0.93–1.00. Proximal flagellomeres II–IX or X fused (fig. 308). Terminal flagellomere distinctly pointed (fig. 309). Proboscis moderately long. Palpus slender and long (fig. 310). Third palpal segment 30–40 μm



308–317. *Alluaudomyia succinea* sp. n., male; 308 — flagellum, MZW 2353/32; 309 — terminal flagellomeres, MZW 18225; 310 — palpus, 311 — tarsi of fore, middle and hind leg, 312 — wing, 313 — first radial cells, 314 — ventral view of genitalia, 315 — dorsal view of genitalia, 316 — lateral view of genitalia, 317 — lateral view of aedeagus, MZW 2353/32

long, without sensory pit. Scutum with long supra-alar and post-notal setae. Scutellum bearing 6 long setae. Fourth tarsomeres cordiform (fig. 311). TR(I) 2.0, TR(II) 2.4–2.6, TR(III) 2.4. Wing length 0.70–0.81 mm, CR 0.52–0.60. Both first radial cells present (figs. 312, 313). Membrane without microtrichia, macrotrichia on distal half of wing present. Vein M_2 with atrophied base.

Genitalia slightly broader than abdomen and rotated 90° (figs. 314–317). Sternite IX moderately long with distinct caudomedian excavation. Tergite IX long, tapering to tip with indistinct blunt apicolateral processes. Cerci slender and long, extending beyond caudal margin of tergite IX. Gonocoxite long and slender; gonostylus slender, simple and slightly curved distally. Aedeagus large with broad base; basal arch low, basal arms long and slender; caudomedian part with swollen, rounded apex bearing 2 strong subapical lateral hooks directed ventrally; 2 unprecisely shaped lateral sclerites fused with basal arms and reaching tip of aedeagus present. Parameres separated and long; distal part pointed, divergent and curved dorsally.

MATERIAL EXAMINED (8 ♂, 7 ♀)

Holotype — ♂, MZW 2353/32. Paratypes: MZW 6216, 1 ♂; 8958, 1 ♂; 18225, TG, 1 ♂.

MBI 143 (+ *Culicoides* 1 ♀), KÜHL, 1 ♀; MZW 7631, 1 ♀; 8862 b, 1 ♂; 11416, TG, 1 ♀; 13612 a (+ *Sciaridae* 1 ♀), 1 ♀; 16431, TG, 1 ♀; 17312, TG, 1 ♂; ZMC 39, C. V. HENNINGSEN, 1–5 1967, 1 ♀; 153, C. V. HENNINGSEN, 25–3 1961, 1 ♀; 176, C. V. HENNINGSEN, 1–1 1966, 1 ♂; 216, C. V. HENNINGSEN, 5–4 1966, 1 ♂.

2. ? *Alluaudomyia* sp. A
(Figs. 318–325)

DIAGNOSIS

Male of this species is characteristic in having wing membrane with distinct microtrichia and macrotrichia at wing tip, fourth tarsomeres subcylindrical, very short palpi and gonostylus with enlarged apex.

DESCRIPTION

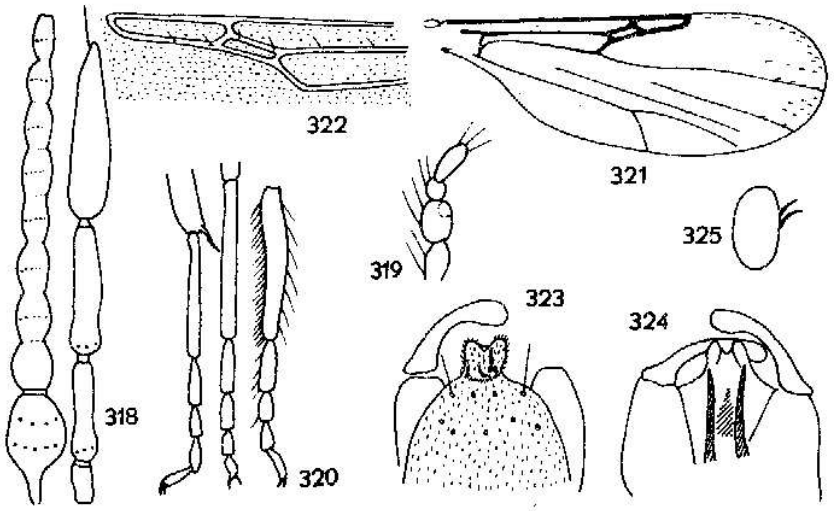
♀. Unknown.

♂. Body dark brown. Total length 0.9 mm. Flagellum length 424 μm, AR 0.94. Plume well developed. Proximal flagellomeres II–VIII or IX fused (fig. 318). First flagellomere without sensilla coeloconica. Palpus short (fig. 319). Third palpal segment ovoid with distinct sensory pit, 16–20 μm long. Scutum covered with sparse long setae. Scutellum with 4 long and 2 shorter setae. Legs slender. Fourth tarsomeres subcylindrical (fig. 320). Spur of fore tibia long. Claws very small. Tarsi without distinct spines. TR(I) 2.7–2.8, TR(II) 3.2–3.5, TR(III) 2.9–3.1. Wing length 0.62 mm, CR 0.60. Second radial cell 2.0 times longer than first one (figs. 321, 322). Microtrichia distinct, macrotrichia present at wing tip. Vein M_2 obsolete basally.

Genitalia small, not inverted (figs. 323–325). Sternite IX not visible. Tergite IX longer than gonocoxite with broad caudomedian projection of presumably of 2 submedian lobes (or cerci ?), apicolateral processes absent. Gonocoxite normal. Gonostylus with swollen rounded apex. Aedeagus not visible. Parameres long, separated, apices pointed and distally curved ventrally.

MATERIAL EXAMINED (1 ♂)

ZMC 86, C. V. HENNINGSEN, 9–3 1967, 1 ♂.



318–325. ? *Alluaudomyia* sp. A, male, ZMC 86; 318 — flagellum, 319 — palpus, 320 — tarsi of fore, middle and hind leg, 321 — wing, 322 — first radial cells, 323 — dorsal view of genitalia, 324 — ventral view of genitalia, 325 — lateral view of gonocoxite and parameres

DISCUSSION

This species supposedly does not belong to the genus *Alluaudomyia* since it has not only both first radial cells well developed, but also it has distinct microtrichia on wing membrane, fourth tarsomeres subcylindrical and very short palpi. It may be that this species belongs to the tribe *Ceratopogonini*, since sometimes sensilla coeloconica are difficult to discern, especially in males.

8. Genus *Stilobezzia* Kieffer, 1911

DIAGNOSIS

Eyes contiguous or separated. Flagellum usually long and slender composed of 13 free units. In female 5 distal and in male 3 distal flagellomeres elongated with rugose contour. In male plume well developed. Palpus slender, 5-segmented. Third palpal segment with sensory pit. Legs usually slender. Femora usually unarmed. Tarsi often with distinct ventral spines. Tarsomeres I and II of hind leg with palisade setae. Fourth tarsomeres cordiform. Fifth tarsomere of female sometimes with strong ventral spines. Female claws usually large and strongly unequal, simple and similar on all legs. Wing membrane covered with distinct microtrichia, macrotrichia often at wing tip present. Costa usually long. Both first radial cells usually well developed, first one small and rhomboidal, second one large. In some species only first radial cell present. Base of M_2 usually atrophied. Female genitalia not modified.

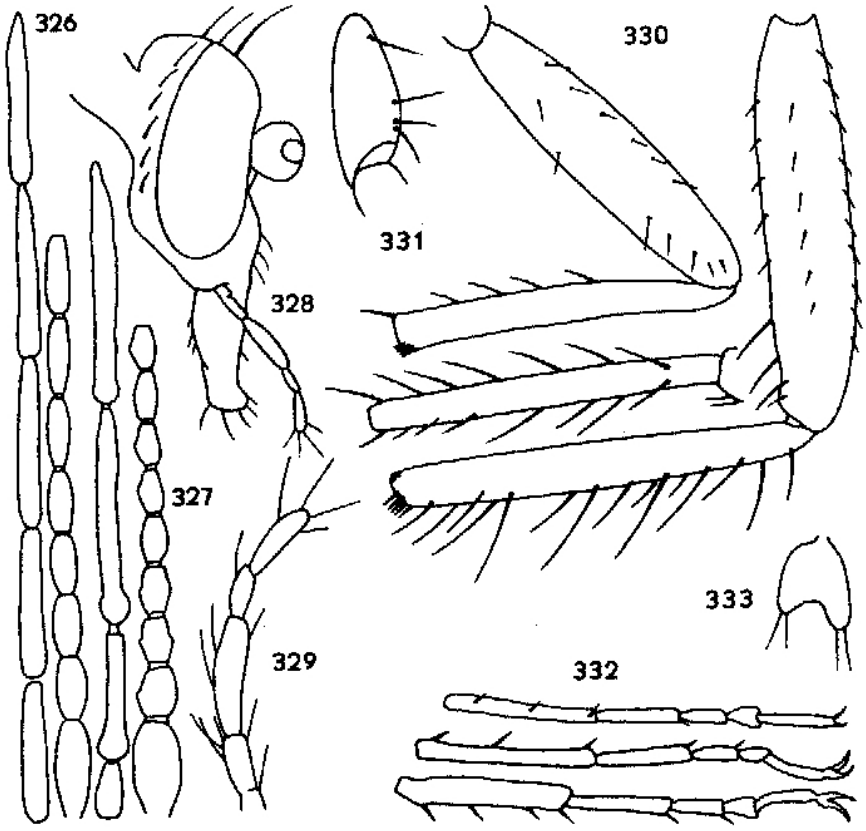
Male genitalia usually short and broad. Tergite IX usually rounded with distinct submedian lobes covered with setae. Aedeagus membranous usually with a pair of oblique strongly sclerotized lateral sclerites. Parameres separated, usually stout with apical slender projection.

Recent distribution and classification

Stilobezzia including more than 250 recent species (cf. Wirth et al., 1974) is distributed worldwide. Clastrier (1976) and Wirth and Grogan (1981) proposed not to use subgenera in the genus because of the apparent unnatural constitution of the subgenus *Neostilobezzia* Goetghebuer.

Fossils

Fossil *Stilobezzia* are known from Baltic amber and from Miocene impressions from Rott in West Germany. From Rott two species are



326–333. *Stilobezzia falcata* (Meunier); 326 — female flagellum, IMGPUG 5889; 327 — male flagellum, IMGPUG 7604; 328 — lateral view of female head, MZW 19191; 329 — female palpus, IMGPUG 5889; 330 — male femur and tibia of fore leg, tibia of middle leg and femur and tibia of hind leg, 331 — male coxa of fore leg, 332 — male tarsi of fore, middle and hind leg, IMGPUG 7604; 333 — fourth tarsomere of female fore leg, IMGPUG 5889

described: *S. veterana* (MEUNIER, 1920) and *S. goetghebueri* (STATZ, 1944). Unfortunately these species are based on single females and have only formal importance, since they are devoid of diagnostic characters.

Among the Baltic amber inclusions examined 29 specimens of the genus belonging to 6 more or less distinct species have been found. I do not propose new names for these because females predominate in the material and the males available for study usually have barely visible genitalia inappropriate for making informative descriptions with clear diagnoses.

Stilobezzia indetermined (2 ♂, 5 ♀)

IMGPUG Z 7715, 1 ♀, paralectotype of *Ceratopogon cothurnatulus* MEUNIER, 1904; MZW 469/112, 1 ♀; 4982, TG, 1 ♀; 10003, 1 ♂; 13598, 1 ♀; 17254, TG, 1 ♀; ZMC 93, C. V. HENNINGSEN, 3–5 1952, 1 ♂.

Key to Baltic amber species of *Stilobezzia*

1. Wing membrane without macrotrichia . . . . . 6. *S.* sp. E (♀)
—. Wing membrane with macrotrichia at tip 2
2. Basitarsi of all legs with 1–2 strong median spines . . . . . 1. *S. falcata* (MEUNIER) (♂, ♀)
—. Basitarsi of all legs without median spines 3
3. Second radial cell 2.6–2.8 times longer than first one 4
—. Second radial cell 1.7–2.2 times longer than first one 5
4. CR 0.81, wing length 2.01 mm . . . . . 3. *S.* sp. B (♀)
—. CR 0.71, wing length 1.45–1.50 mm . . . . . 4. *S.* sp. C (♀)
5. Second radial cell 1.7 times longer than first one. Wing length 0.80 mm. Scutellum with 4 long setae . . . . 5. *S.* sp. D (♀)
—. Second radial cell 2.0–2.2 times longer than first one. Wing length 1.26–1.52 mm. Scutellum with 6 long setae . . . 2. *S.* sp. A (♂, ♀)

1. *Stilobezzia falcata* (Meunier, 1904), comb. n.

(Figs. 326–340)

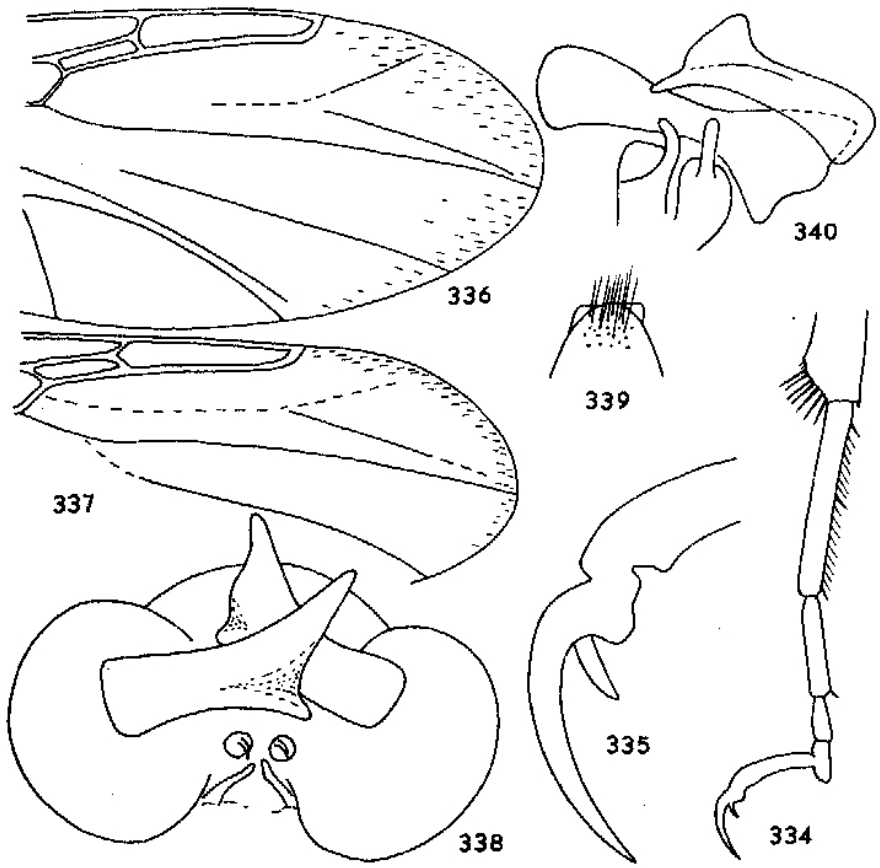
Ceratopogon falcatus MEUNIER, 1904: 233 (♀, Baltic amber).
Ceratolophus falcatus: KIEFFER, 1906: 1 (combination).
Ceratopogon spinosus MEUNIER, 1904: 234 (♂, Baltic amber), **syn. n.**
Palpomyia spinosa: KIEFFER, 1906: 1 (combination).

DIAGNOSIS

The species is characteristic in having macrotrichia at wing tip, all basitarsi with 1–2 strong median spines, legs with long and stout setae, and male genitalia with expanded and bicorned apex of gonostyli.

DESCRIPTION

♀. Body brown or dark brown. Total length 2.4–2.6 mm. Eyes separated. Flagellum length 1160–1370 μm, AR 1.26–1.40. Proximal flagellomeres elongated, cylindrical (fig. 326). Proboscis long (fig. 328). Palpus slender and long (fig. 329). Third palpal segment 104–116 μm long, sensory pit not visible. Scutum with stout and long postpronotal, prescutellar, supraalar setae. Scutellum with 8–10 long and several shorter setae. Legs moderately stout with strong setae including fore coxa. Tibial spur of fore leg stout and long. Tibial comb composed of 7–9 spines. Basitarsi with strong basal, apical and 1–2 median ventral spines. Fourth tarsomeres deeply cordate (figs. 333, 334). Claws long and strongly unequal (fig. 335). TR(I) 2.0–2.2, TR(II) 2.1, TR(III) 1.9–2.1. Wing length 1.81–2.00 mm, CR 0.75–0.77. First radial cell 2.1–2.3 times shorter than second one (fig. 336). Intercalary fork well visible. Microtrichia distinct, macrotrichia present along wing tip.



334–340. *Stilobezzia falcata* (MEUNIER); 334 — female tarsus of hind leg, 335 — female claws of hind leg, 336 — female wing, IMGPUG 5889; 337 — male wing, IMGPUG 4285; 338 — top view of male genitalia, ZMC 1; 339 — tergite IX of male, MBI 97; 340 — gonostyli and paramcres, MBI 97

♂. Body brown or dark brown. Total length 2.5–3.0 mm. Flagellum length 1068 µm, AR 1.32. Plume well developed, all flagellomeres separated (fig. 327). Third palpal segment 90–96 µm long, sensory pit absent. Scutellum with 8–10 long and several shorter setae. Legs moderately stout with distinct strong setae (figs. 330–332). Tibial comb with ca. 7 spines. Tibial spur of fore leg long. Basitarsi with 1–2 median ventral spines. Fourth tarsomeres cordiform. Claws with distinctly bifid apices. TR(I) 1.8, TR(II) 1.9–2.0, TR(III) 1.8–1.9. Wing length 1.54–2.37 mm, CR 0.73–0.77. Macrotrichia less abundant than in female (fig. 337). Second radial cell 2.0–2.1 times longer than first one.

Male genitalia large and stout, rotated, inverted or in normal position (figs. 338–340). Tergite IX not produced beyond gonocoxite with rounded and broad apex and short apicolateral lobes. Gonocoxite stout. Gonostylus stout, tip expanded into 2 blunt lobes. Aedeagus and parameres barely visible. Presumably aedeagus bears 2 lateral oblique sclerites. Parameres broad, each with finger-like or blade-like apical projection.

MATERIAL EXAMINED (7 ♂, 7 ♀)

Holotype female of *Ceratopogon falcatus*, IMGPUG Z 5889. Lectotype male of *Ceratopogon spinosus*, IMGPUG Z 7604. Paralectotypes of *C. spinosus*: IMGPUG Z 4285, 1 ♂; 6132 (+*Chironomidae* 1 ♀), 1 ♂. Present designations.

16178, TG, 1 ♂; 19191, TG, 1 ♀; 19934, 1 ♀; RSz 2, 1 ♀; ZMC 1, C. V. HENNINGSEN, 8–12 1954, 1 ♂; 143, C. V. HENNINGSEN, 26-2 1955, 1 ♀.

DISCUSSION

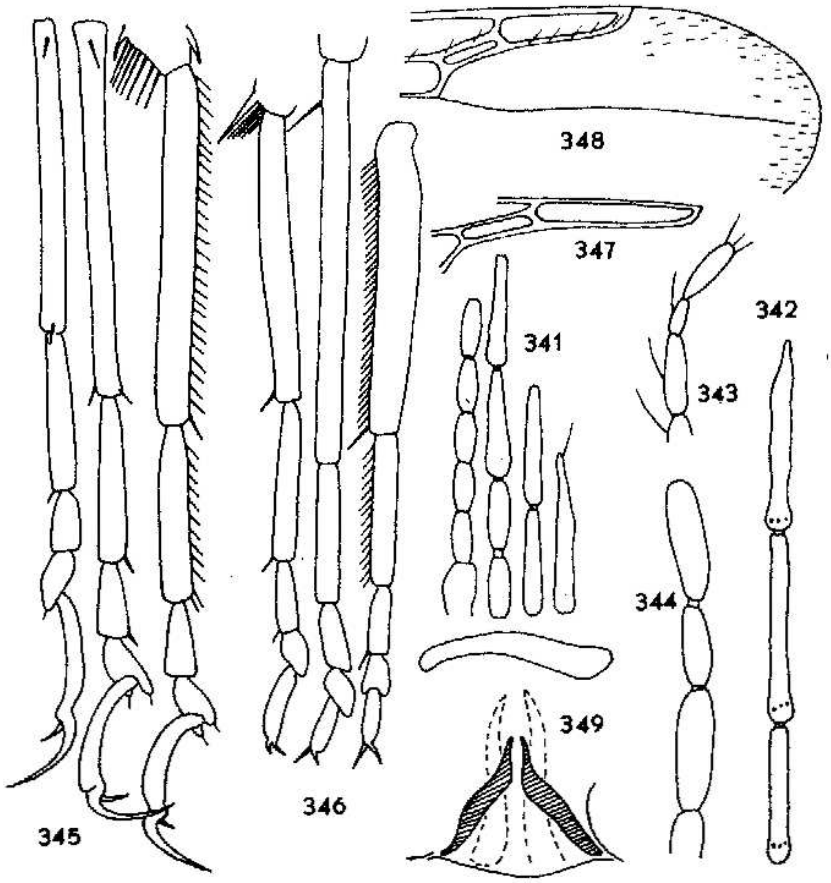
Stilobezzia falcata is the most common member of this genus in Baltic amber. This species belongs to the *calcaris* group as proposed TOKUNAGA and MURACHI (1959) for *S. calcaris* TOKUNAGA et MURACHI, *S. latiforceps* TOKUNAGA, *S. latiforceps setigera* TOKUNAGA, *S. tenuiforceps* TOKUNAGA et MURACHI, *S. truncata* TOKUNAGA, and *S. unidorsalis* TOKUNAGA restricted to the Micronesian Caroline Islands (Palau, Yap, Ponape) of Oriental region. Males of the group are characteristic in having gonostyli flattened and expanded at apex. Recent species of the group have a very long tibial spur on the fore leg which in *S. falcata* is normal. Micronesian species are all very similar differing mainly in details of male genitalia, so it may be that *S. falcata* from Baltic amber is a species complex.

It seems that this tropical group is of Euro-Asian origin (more probably Palaearctic than Oriental) and was widely distributed in Europe and northern Asia during Tertiary period where it became extinct. Relicts of this group apparently survived on isolated tropical islands.

2. *Stilobezzia* sp. A
(Figs. 341–349)

DIAGNOSIS

The species is distinguished by the following combination of characters: basitarsi without median spines, macrotrichia present at wing tip, second radial cell 2.0–2.2 times longer than first one, wing length 1.26–1.52 mm, CR 0.70–0.73, scutellum with 6 long setae.



341–349. *Stilobezzia* sp. A; 341 — female flagellum, MBI 167; 342 — male distal flagellomeres, ZMC 90; 343 — female palpus, ZMC 43; 344 — male palpus, ZMC 90; 345 — female tarsi of fore, middle and hind leg, MBI 167; 346 — male tarsi of fore, middle and hind leg, ZMC 90; 347 — first radial cells of female, ZMC 43; 348 — distal part of male wing, 349 — aedeagus, parameres and gonostylus, ZMC 90

DESCRIPTION

♀. Body brown, thorax darker. Total length 1.8 mm. Flagellum length 941 μm, AR 1.33. Proximal flagellomeres cylindrical (fig. 341). Proboscis long. Palpus slender (fig. 343). Third palpal segment 72 μm long, sensory pit not visible. Scutellum with 6 long setae. Tibial comb composed of 6 spines. Basitarsi without median spines, hind basitarsus without basal spine (fig. 345). Claws long and strongly unequal. TR(I) 1.9, TR(II) 2.2–2.3, TR(III) 2.0–2.1. Wing length 1.26–1.52 mm, CR 0.70–0.71. Second radial cell 2.0–2.1 times longer than first one (fig. 347). Macrotrichia present on distal part of wing.

♂. Similar to female with the usual sexual differences. Flagellum length 838 μm, AR 1.17. Distal flagellomeres as in fig. 342. Plume well developed. Palpus slender (fig. 344). Third palpal segment 52 μm long, sensory pit not visible. Scutellum with 6 long setae. Tarsi as in fig. 346. Tibial comb composed of 7 spines. TR(I) 1.8, TR(II) 2.9, TR(III) 2.1. Wing length 1.38 mm, CR 0.73. Second radial cell 2.2 times longer than first one. Macrotrichia present at wing tip (fig. 348).

Genitalia somewhat rotated, broader than tip of abdomen (fig. 349). Gonocoxite normal. Gonostylus slender, slightly curved, apex evenly rounded. Aedeagus with a pair of oblique lateral sclerites. Parameres separated, barely visible.

MATERIAL EXAMINED (1 ♂, 2 ♀)

MBI 167, KÜNOW, 1 ♀; ZMC 43, A. K. ANDERSEN, 28–3 1968, 1 ♀; 90, A. K. ANDERSEN, 28–3 1968 (+ *Brachypogon prominulus* 1 ♀), 1 ♂.

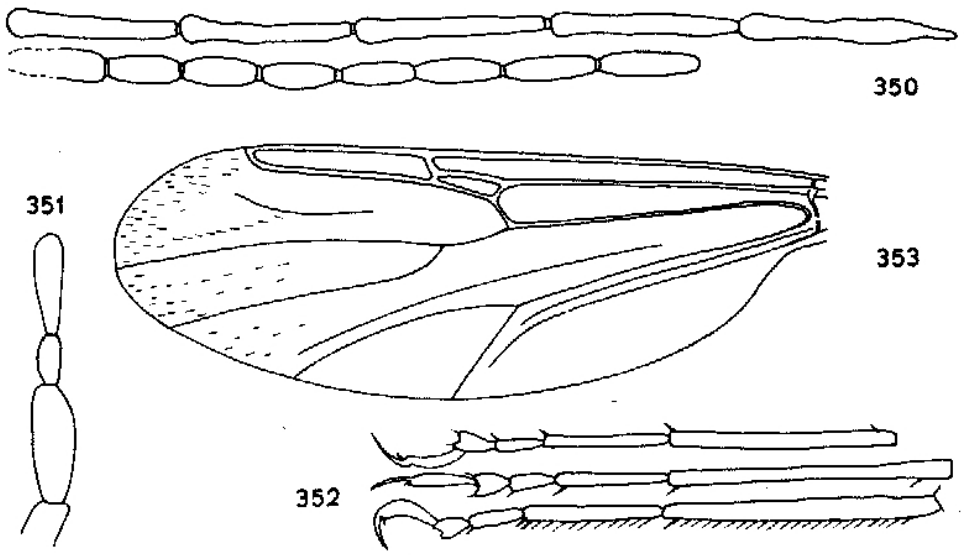
DISCUSSION

The species is a typical member of the subgenus *Neostilobezzia* common in many parts of the world including Central Europe. It may be that male and females do not belong to the same species.

3. *Stilobezzia* sp. B
(Figs. 350–353)

DIAGNOSIS

Female of the species is distinguished by the following combination of characters: wing membrane with macrotrichia distally, basitarsi without median spines, second radial cell 2.8 times longer than first one, CR 0.81, wing length 2.01 mm.



350–353. *Stilobezzia* sp. B, female, MBI 196; 350 — flagellum, 351 — palpus, 352 — tarsi of fore, middle and hind leg, 353 — wing

DESCRIPTION

♀. Body dark. Total length 2.4 mm. Flagellum length 1343 μm, AR ca. 1.38. Proximal flagellomeres cylindrical (fig. 350). Proboscis long. Palpus slender (fig. 351). Third palpal segment 96 μm long, sensory pit not visible. Scutellum presumably with 6 long setae. Legs slender. Basitarsi of fore and middle legs with basal and apical spines, of hind leg with apical spine only (fig. 352). Claws strongly unequal. TR(I) 1.9, TR(II) 2.5, TR(III) 1.9. Wing length 2.01 mm, CR 0.81. Second radial cell 2.8 times longer than first one (fig. 353). Macrotrichia present on distal part of wing.

♂. Unknown.

MATERIAL EXAMINED (1 ♀)

MBI 196, KŪNOW, 1 ♀ mounted in an artificial resin.

NOTE

The species is a typical member of the subgenus *Neostilobezzia* common in many parts of the world (see also above).

4. *Stilobezzia* sp. C
(Figs. 354–359)

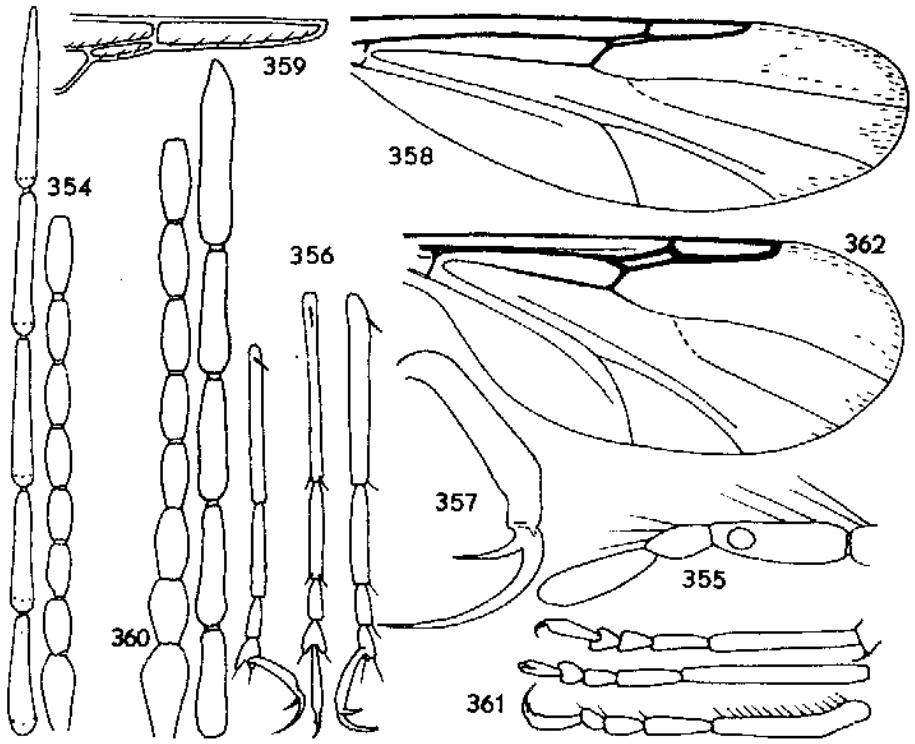
DIAGNOSIS

Female of the species is distinguished by the following combination of characters: wing membrane with macrotrichia distally, basitarsi without

median spines, second radial cell 2.6–2.8 times longer than first one, CR 0.71, wing length 1.45–1.50 mm.

DESCRIPTION

♀. Body dark brown. Total length 1.9 mm. Flagellum length 990 μm, AR 1.42. Proximal flagellomeres cylindrical (fig. 354). Proboscis long. Palpus slender (fig. 355). Third palpal segment 67–86 μm long, with distinct round sensory pit. Scutellum with 6 long and several shorter



354–362. *Stilobezzia* sp. C and *Stilobezzia* sp. D. *Stilobezzia* sp. C, female, MZW 13633 a (354–359): 354 — flagellum, 355 — palpus, 356 — tarsi of fore, middle and hind leg, 357 — claws of hind leg, 358 — wing, 359 — first radial cells; *Stilobezzia* sp. D, female, MZW 17936 (360–362): 360 — flagellum, 361 — tarsi of fore, middle and hind leg, 362 — wing

setae. Legs slender. Basitarsi with basal and apical spines; apical spine on fore leg not visible (fig. 356). Claws strongly unequal (fig. 357). TR(I) 1.7, TR(II) 2.0–2.2, TR(III) 1.9. Wing length 1.45–1.50 mm, CR 0.71. Second radial cell 2.6–2.8 times longer than first one (figs. 358, 359). Macrotrichia present at wing tip.

♂. Unknown.

MATERIAL EXAMINED (2 ♀)

MZW 7264, 1 ♀; 13633 a, 1 ♀.

NOTE

The species is a typical member of the subgenus *Neostilobezzia* (see above).

5. *Stilobezzia* sp. D
(Figs. 360–362)

DIAGNOSIS

Female of the species is distinguished by the following combination of characters: wing membrane with macrotrichia on distal margin, basitarsi without median spines, second radial cell 1.7 times longer than first one, wing length 0.80 mm, CR 0.73, scutellum with 4 long setae.

DESCRIPTION

♀. Body dark, scutum black, scutellum contrastly brown. Total length 1.1 mm. Flagellum length 553 μm, AR 1.12. Proximal flagellomeres cylindrical (fig. 360). Palpus barely visible. Scutellum with 4 long setae. Legs slender. Tarsi without distinct spines (fig. 361). Claws strongly unequal. TR(I) 2.6, TR(II) 3.0, TR(III) 2.5. Wing length 0.80 mm, CR 0.73. Second radial cell 1.7 times longer than first one. Macrotrichia present along wing tip (fig. 362).

♂. Unknown.

MATERIAL EXAMINED (1 ♀)

MZW 17936, TG, 1 ♀.

NOTE

The species is a typical member of the subgenus *Neostilobezzia* (see above).

6. *Stilobezzia* sp. E
(Figs. 363–365)

DIAGNOSIS

The species is characteristic in having the wing membrane without macrotrichia.

DESCRIPTION

♀. Body pale brown. Flagellum barely visible, AR ca. 1.24 (fig. 363). Palpus barely visible. Scutum with 2 rows of acrostichals and distinct dorsocentrals. Prescutal pits distinct. Scutellum bearing 4 long setae. Legs slender. Tarsi without median spines (fig. 364), hind tarsus barely visible. Claws strongly unequal. TR(I) 2.0, TR(II) 2.5. Wing length 1.08 mm, CR 0.72. Second radial cell 2.2 times longer than first one (fig. 365). Wing membrane with distinct microtrichia, macrotrichia absent.

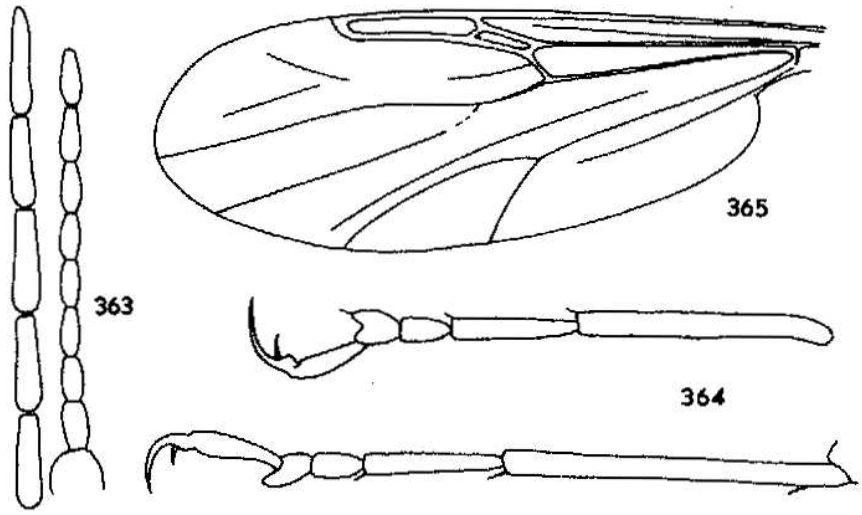
♂. Unknown.

MATERIAL EXAMINED (1 ♀)

MZW 14568, TG, 1 ♀.

DISCUSSION

The species belongs to the worldwide distributed subgenus *Stilobezzia* s. str. including more than 100 recent species, which are more numerous in the tropics and subtropics (DAS GUPTA and WIRTH, 1968). In southern and western Europe there are known 1–3 uncommon species that are occasionally recorded from more northern territories.

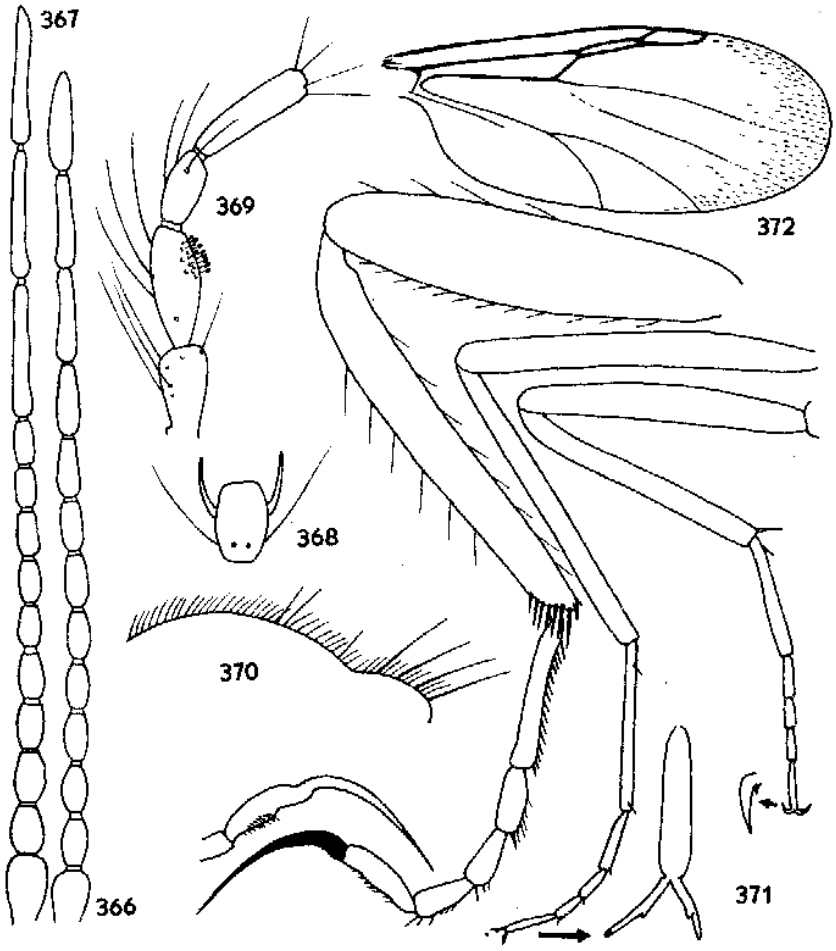


363–365. *Stilobezzia* sp. E, female, MZW 14568; 363 — flagellum, 364 — tarsi of fore and middle leg, 365 — wing

9. Genus *Monohelea* Kieffer, 1917

DIAGNOSIS

Stout midges. Eyes contiguous. Flagellum composed of 13 units. In male plume well developed, all flagellomeres free. Palpus 5-segmented. Third palpal segment with or without small sensory pit. Fore and middle legs slender. Hind leg often with femur and tibia more or less thickened; all femora unarmed. Tarsi usually with distinct spines. Fourth tarsomeres of fore and middle legs cylindrical, greatly elongated



366–372. *Monohelea clunipes* (LOEW); 366 — female flagellum, 367 — male flagellum, MBI 216; 368 — female fifth flagellomere, MZW 4998; 369 — female palpus, 370 — setae of female scutum, MZW 19211; 371 — female hind, middle and fore leg, 372 — female wing, MBI 216

on hind leg of female. Female claws of fore and middle legs small to moderately large, equal, with basal inner teeth; of hind leg with one claw very long, the other one absent or reduced to short basal barb. Male claws usually small and equal. Antepronotum small and hidden below postpronotum. Wing membrane covered with fine microtrichia, macro-

trichia restricted to tip or absent. Both first radial cells present. Second radial cell usually longer than first one. Base of M_2 often atrophied. Female abdomen without modifications. Male genitalia stout. Tergite IX with caudal margin truncate, rounded or bilobed. Aedeagus usually complicated, often with a pair of lateral sclerites and dorsomedian posterior lobes. Parameres variously shaped, moderately long, separated or fused.

Recent distribution and classification

The genus *Monohelea* is distributed worldwide including more than 120 recent species presently under revision by Wirth and Grogan (personal comm.) as to generic and subgeneric limits. The largest number of species of *Monohelea* is known from the Australian and Neotropical regions (Wirth, 1974; Debenham, 1979). In Europe there are known 5 species, of which the Holarctic *M.* (*Schizohelea*) *leucopeza* (Meigen) is most common.

Fossils

Fossil *Monohelea* are known only from the Eocene Baltic amber. In the material examined 27 specimens belonging to 3 distinct species have been found.

Key to Baltic amber species of *Monohelea*

Males

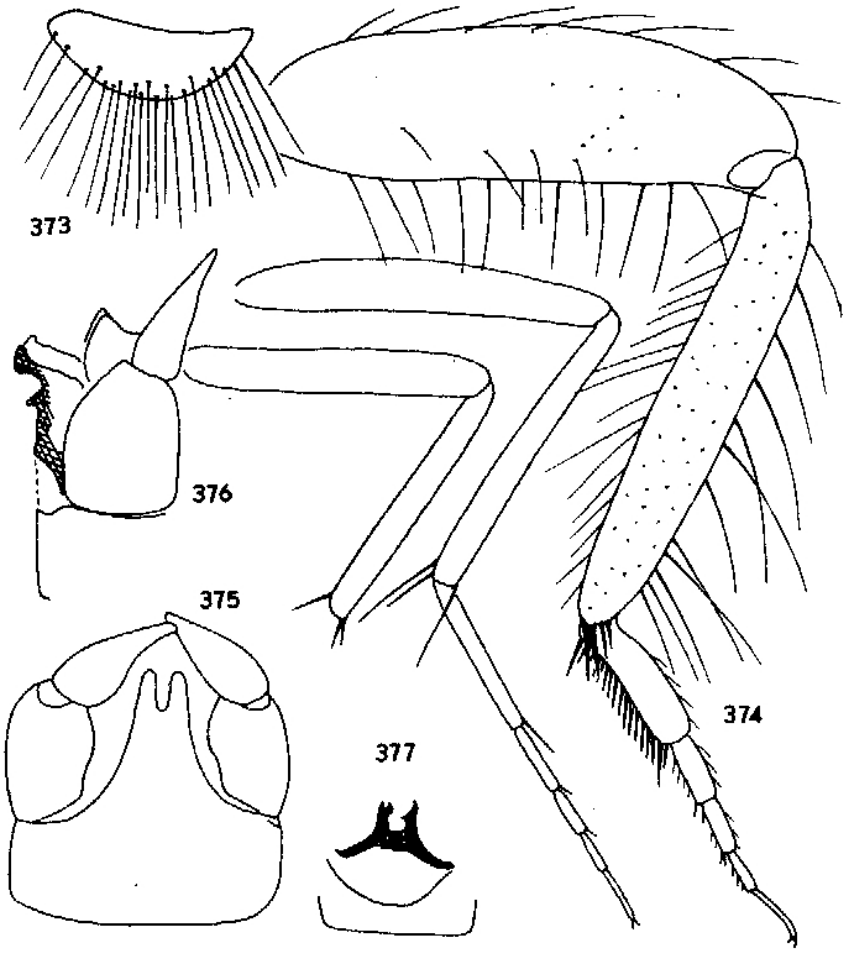
1. Hind femur with some ventral spine-like setae . . 3. *M.* sp. A
—. Hind femur without ventral spine-like setae 2
2. Hind femur greatly swollen. Wing length 1.3–1.4 mm. . . . . 1. *M. clunipes* (Loew)
—. Hind femur slightly swollen. Wing length 0.7 mm . . . . . 2. *M. baltica* sp. n.

1. *Monohelea clunipes* (Loew, 1850), comb. n.
(Figs. 366–377)

Ceratopogon clunipes Loew, 1850: 30 (Baltic amber); Meunier, 1904: 234 (♂, Baltic amber).

Diagnosis

The species is characteristic in having a greatly enlarged hind femur and tibia, the hind femur without ventral spine-like setae, and a long wing measuring 1.3–1.4 mm in male.



373–377. *Monohelea clunipes* (LOEW), male; 373 — scutellum, MBI 126; 374 — fore, middle and hind leg, MZW 17748; 375 — dorsal view of genitalia, MBI 126; 376 — lateral view of genitalia, MBI 180; 377 — aedeagus, MBI 126

DESCRIPTION

♀. Body brown, dark brown or black. Total length 1.6–2.3 mm. Flagellum length 650 μm, AR 0.96–1.22. Proximal flagellomeres cylindrical (fig. 366), each with a subapical pair of sensilla trichodea (fig. 368). Proboscis long. Palpus long (fig. 369). Third palpal segment moderately slender, 64 μm long, sensory pit absent, sensorium composed of scattered sensilla capitata. Scutum densely covered with short setae (fig. 370). Long prescutellars and supraalars present. Scutellum with more than 10 long and several shorter setae. Fore and middle legs slender, hind leg greatly thickened (fig. 371), setae and spines indistinct. Tibial comb composed of 7 spines. Fourth tarsomeres cylindrical. Claws of fore and middle legs short, equal, each with inner tooth. Hind leg with single very long claw, longer than fifth tarsomere. TR (I) 2.0–2.8, TR (II) 2.2–2.7, TR (III) 2.1–2.3. Wing length 1.06–1.48 mm, CR 0.65–0.70. Both first

radial cells long. Wing membrane with distinct microtrichia, macrotrichia present at wing tip (fig. 372).

♂. Similar to female but stouter and more hairy. Body brown, dark brown or black. Total length 1.8–2.4 mm. Flagellum length 709–762 μm, AR 0.95–1.00. Distal 3 flagellomeres elongated (fig. 367). Plume well developed. Proboscis long. Third palpal segment 60 μm long. Scutum with stronger setae than in female. Scutellum with numerous long setae (fig. 373). Fore and middle legs slender. Hind leg with greatly thickened femur, tibia and 3 first tarsomeres (fig. 374). Apices of fore and middle tibiae with long straight setae. Hind femur and tibia with numerous very long and strong setae. Tibial comb composed of very stout spines. Hind basitarsus enlarged, short, with thick palisade spine-like setae. Fourth tarsomeres cylindrical and slender. Fifth tarsomeres very slender. Claws small and equal on all legs. Wing length 1.26–1.42 mm, CR 0.65. Macrotrichia present at wing tip. Abdomen stout.

Genitalia inverted, stout and short (figs. 375–377). Sternite IX broad and short with shallow caudomedian excavation. Tergite IX tapering to narrow bilobed tip. Gonocoxite short. Gonostylus stout, gradually tapering from broad base to evenly pointed tip. Aedeagus barely visible, apparently with a pair of bifid distolateral extensions. Parameres not visible.

MATERIAL EXAMINED (9 ♂, 15 ♀)

Holotype — ♂, MBI 126, BERENDT "*Ceratopogon* ♂ sp. 13, *clunipes*, Original Dr B".

IMGPUG Z 6686, 1 ♂; IZPAN 41/73, 1 ♂; MBI 111, BERENDT, 1 ♀; 149, KÜHL (+*Psychodidae* 1 ♂, *Chironomidae* 1 ♂, *Sciaridae* 1 ♀), 1 ♀; 172, KÜNOW, 1 ♀; 176, KÜNOW, 1 ♀; 180, KÜNOW, 1 ♂; 183, KÜNOW, 1 ♀; 184, KÜNOW, 1 ♂; 201, KÜNOW, 1 ♀; 216, THOMAS, 1 ♂ 1 ♀ in copula; MZW 1135 a, 1 ♂ 2 ♀; 4998, TG, 1 ♀; 5590, TG, 1 ♂; 17478, TG, 1 ♂; 19211, TG, 1 ♀; 20009, TG, 1 ♀; ZMC 11, A. K. ANDERSEN, 28–3 1968, 1 ♀; 27, A. K. ANDERSEN, 28–3 1968, 1 ♀; 118, A. K. ANDERSEN, 28–3 1968, 1 ♀.

DISCUSSION

The single male in the collection of BERENDT at MBI labelled as *Ceratopogon clunipes* by LOEW is recognized here as the holotype of the species. One of two males determined by MEUNIER (1904) as *C. clunipes* in the collection at IMGPUG at present is described as *Fossihelea* sp. A.

In the recent fauna there are no species of *Monohelea* with such enlarged hind legs and setosed body of male. It may be that *M. clunipes* is a species complex.

2. *Monohelea baltica* sp. n.
(Figs. 378–382)

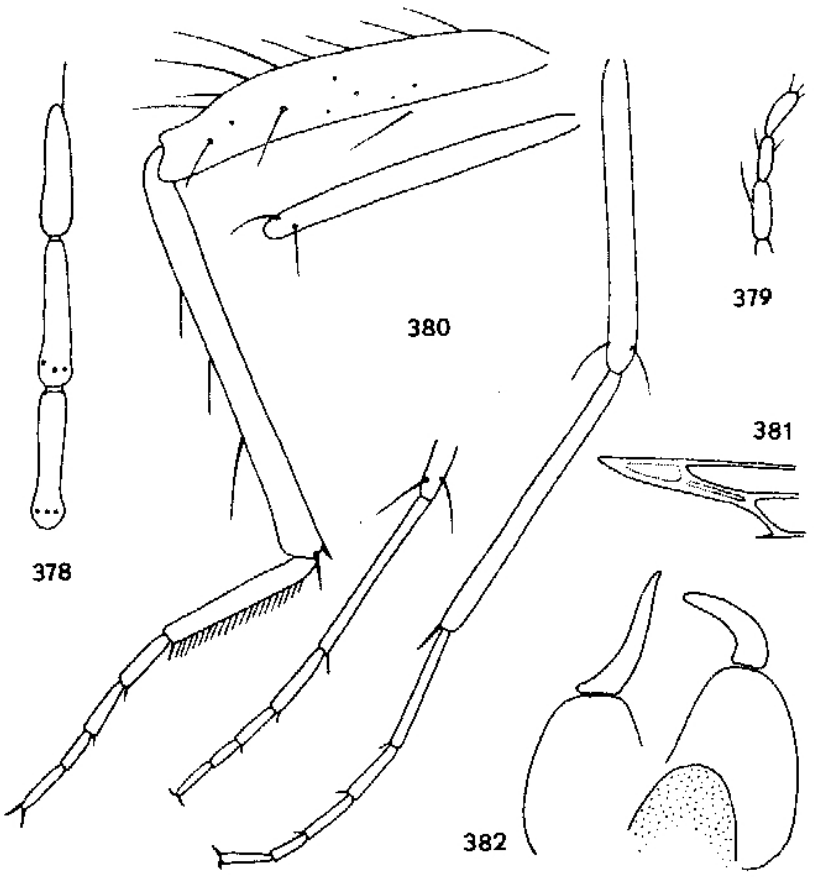
DIAGNOSIS

Male of this species is characteristic in having a relatively slender hind leg, long and slender hind tarsus, hind basitarsus without subbasal ventral spine, and wing length 0.71–0.74 mm.

DESCRIPTION

♀. Unknown.

♂. Body brown or black. Total length 0.8–1.0 mm. Flagellum length 432–445 μm, AR ca. 1.0. Distal flagellomeres as in fig. 378. Palpus slender (fig. 379). Third palpal segment cylindrical without sensory pit, 26 μm long. Scutum almost bare with long supraalars. Scutellum with about 8 long setae. Fore and middle legs slender (fig. 380). Fore and middle tibiae with long subapical setae. Spur of fore tibia long. Middle tibia with long subapical setae. Hind femur and tibia slightly enlarged,



378–382. *Monohelea baltica* sp. n., male, MZW 18161; 378 — distal flagellomeres, 379 — palpus, 380 — hind, middle and fore leg, 381 — first radial cells, 382 — genitalia

femur with strong setae, tibia with strong dorsal setae. Tibial comb composed of 5 spines. Tarsi slender. Hind basitarsus without subbasal ventral spine, apical spine distinct, palisade setae normal. Fourth tarsomeres cylindrical. TR(I) 2.1, TR(II) 2.5–2.6, TR(III) 2.5–2.6. Wing length 0.71–0.74 mm, CR 0.52. Wing membrane without microtrichia and macrotrichia, of brownish tint. First radial cells small, barely visible (fig. 381).

Genitalia not inverted, barely visible (fig. 382). Tergite IX with broad and blunt apex. Aedeagus barely visible, broad and short. Parameres not visible. Gonostylus slender, slightly curved and tapering to apex.

MATERIAL EXAMINED (2 ♂)

Holotype — ♂, MZW 18161, TG.

ZMC 92, A. K. ANDERSEN, 28–3 1968 (+*Aranei* 1), 1 ♂. This male is not recognized as paratype, since it is unnaturally swollen which was caused by gases from dacaying processes. One hind femur, both hind tibiae and the entire abdomen are enlarged.

NOTE

This species is probably a member of the subgenus *Schizohelea* KIEFFER.

3. *Monohelea* sp. A
(Figs. 383–388)

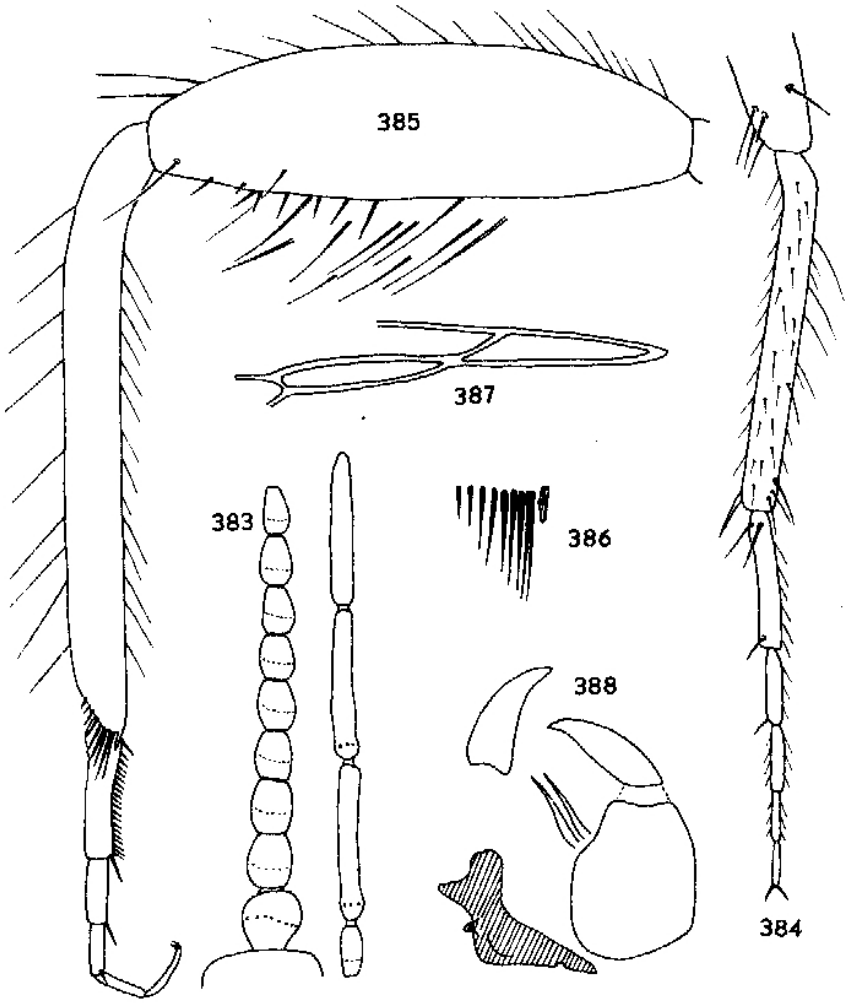
DIAGNOSIS

Male of the species is characteristic in having the hind femur armed on distal half with several spine-like setae.

DESCRIPTION

♀. Unknown.

♂. Body brown. Total length 2.3 mm. Eyes bare. Flagellum length 822 μm, AR 1.14. Proximal flagellomeres slightly elongated (fig. 383). Plume well developed. Palpus barely visible. Legs with numerous long and stout setae. Fore and middle legs slender. Hind femur and tibia strongly thickened, tarsus short. Hind femur with long spine-like setae on distal half (fig. 385). Tibial comb composed of 9 strong spines (fig. 386). Tarsi of fore and middle legs moderately slender (fig. 384). Fourth tarsomeres cylindrical. Claws small and equal with bifid apices. TR(I)



383–388. *Monohelea* sp. A, male, MBI THOMAS 489; 383 — flagellum, 384 — fore leg, 385 — hind leg, 386 — tibial comb, 387 — first radial cells, 388 — lateral view of genitalia

1.9. Wing length 1.75 mm, CR 0.67. Both first radial cells long and equal (fig. 387). Macrotrichia probably present at wing tip.

Genitalia inverted (fig. 388). Gonocoxite stout. Gonostylus stout, tapering slightly to pointed tip. Aedeagus barely visible. Parameres separated, distal portion slender and pointed.

MATERIAL EXAMINED (1 ♂)

MBI THOMAS 489, "*Tip. culiciformis*, *Ceratopogon spiniger*?", 1 ♂.

DISCUSSION

The species is somewhat intermediate between *Monohelea* and *Serromyia*. Its hind femur is swollen as in *Serromyia* but the ventral spines are more slender, like strong and short setae, and the hind tarsus is short and

stout as in *Monohelea clunipes*. It is worth noting that recent *Monohelea papuae* TOKUNAGA (TOKUNAGA, 1963; DEBENHAM, 1972) from New Guinea has legs covered with numerous short spine-like setae. However it may be that these ventral spines of *M.* sp. A are artifacts being only usual long setae impregnated with resin in their distal parts.

10. Genus *Serromyia* Meigen, 1818

DIAGNOSIS

Body moderately stout, nearly bare. Eyes contiguous or moderately separated. Antenna in both sexes with 13 flagellomeres. In male plume well developed and distal 3–4 flagellomeres elongated. Palpus slender, 5-segmented. Third palpal segment without sensory pit. Scutum covered with rows of small setae. Fore and middle legs usually slender, armed or unarmed with stronger spines or spine-like setae. Hind femur greatly swollen in both sexes and armed ventrally with numerous stout spines, hind tibia slender and more or less curved at base. Fourth tarsomeres of fore and middle legs cylindrical, subcylindrical to cordiform, of hind leg cylindrical. Female claws of fore and middle legs short and equal, each with inner tooth; of hind leg usually with a single long claw bearing a short basal barb, rarely short and equal. Wing membrane covered with microtrichia, macrotrichia sometimes present. Both first radial cells well developed.

Female abdomen stout, not modified. Male genitalia usually rotated or inverted, hidden below tip of abdomen. Sternite IX short. Tergite IX short and tapering to short apicolateral lobes. Gonocoxite short and stout. Gonostylus usually long and slender. Aedeagus short with broad basal arch, distal projection variously modified according to species. Parameres separated and usually variously modified.

RECENT DISTRIBUTION

To this well defined genus belong about 27 recent species recorded from all biogeographical regions except for the Neotropics. The largest number of species is found in Afrotropical region — 11 (DE MEILLON and WIRTH, 1983), and in Europe — 11 species. However the European species are poorly studied and the number of recent species is probably lower here. *Serromyia* seems to be quite recently evolved genus which originated in late Cretaceous when South America and Africa were separated, which may explain the recent distribution of the genus and its absence in the Neotropical region (see chapter VIII).

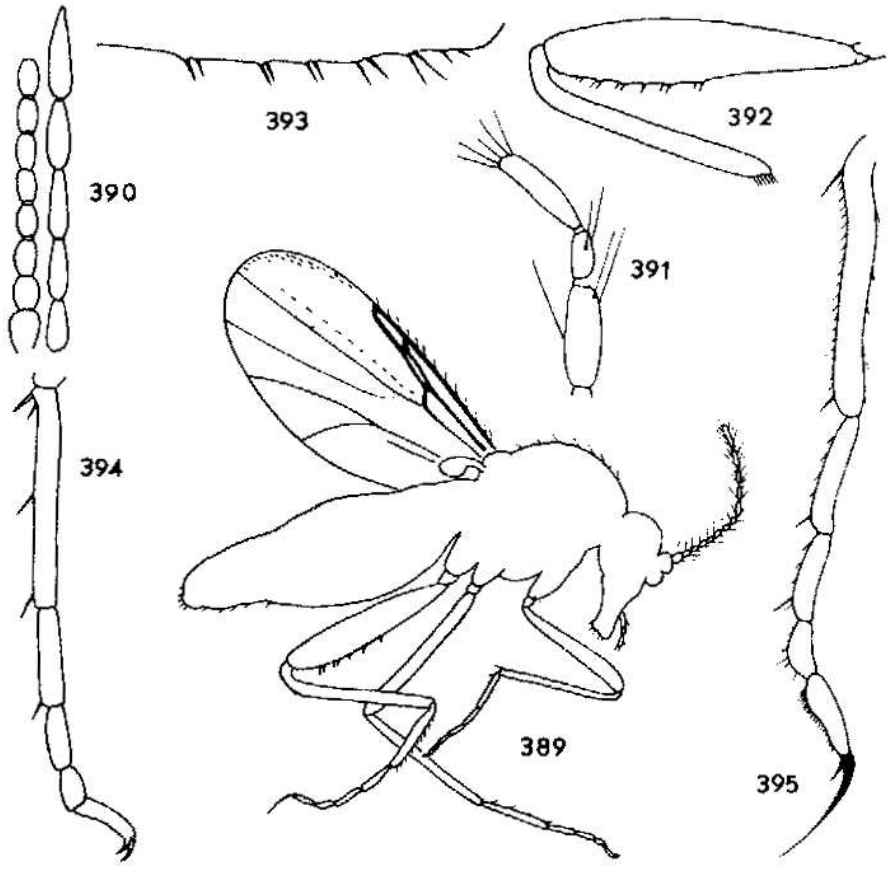
FOSSILS

Fossils of *Serromyia* are known only from Baltic amber and from Miocene impressions on rock from Rott in West Germany. STATZ (1944) found compressed in rock 4 females from Rott, and each specimen he described as distinct species: *S.* sp. (spines on hind femur not visible), *S. colorata*, *S. austera* and *S. spinosifemorata*. Long claws of the hind legs are visible only in *S. austera*. According to Dr. A. BORKENT of Biosystematics Research Institute, Ottawa (personal comm.) these named fossil species appear all to be the same and should be considered as one species.

Among the Baltic amber material examined 27 specimens belonging to 6 distinct species have been found. *Serromyia* in Baltic amber is much more common than today in Europe.

Serromyia indetermined (2 ♂, 9 ♀)

IMGPUG Z 5355, 1 ♀; 6662, 1 ♀; 6895, 1 ♀; all these specimens were determined by MEUNIER (1904) as *Ceratopogon spiniger*; MBI 181, KÜNOW, 1 ♀; 215, BERENDT, 1 ♂; MM 9, 1 ♀; MZW 4997, TG, 1 ♀; 5065, TG, 1 ♀; 9243, 1 ♀; 13278, TG, 1 ♀; ZMC 99, C. V. HENNINGSEN, 1–5 1967, 1 ♂.



389 – 395. *Serromyia polonica* sp. n., female, MZW 14977, RSz 4 (391): 389 — total habitus 390 — flagellum, 391 — palpus, 392 — hind femur and tibia, 393 — spines of hind femur 394 — tarsus of middle leg, 395 — tarsus of hind leg

Key to Baltic amber species of *Serromyia*

1. Females 2
—. Males 5
2. Claws of hind leg short and equal 3
—. Claws of hind leg long and strongly unequal 4
3. Hind femur 3.6–3.8 times as long as greatest width . . . . . 6. *S. anomalicornis* (LOEW)
—. Hind femur 5.3–6.5 times as long as greatest width . . . . . 5. *S. spinigera* (LOEW)
4. Wing length 1.48–1.56 mm. Hind femur 3.4–3.6 times as long as greatest width . . . . . 2. *S. succinea* sp. n.
—. Wing length 0.95–1.12 mm. Hind femur 5.0–5.1 times as long as greatest width . . . . . 1. *S. polonica* sp. n.
5. Femora of fore and middle legs without strong ventral spines 6
—. Femora of fore and middle legs armed with strong ventral spines 8
6. Second radial cell 1.4 times shorter than first one. Hind femur 5.7–5.8 times as long as greatest width . . . . . 3. *S.* sp. A
—. Second radial cell longer than first one 7
7. Hind femur 6.0 times as long as greatest width . . . . . 5. *S. spinigera* (LOEW)
—. Hind femur 4.0 times as long as greatest width . . . . . 6. *S. anomalicornis* (LOEW)
8. Second radial cell 1.1 times shorter than first one . . . 4. *S.* sp. B
—. Second radial cell 1.4 times longer than first one . . . . . 2. *S. succinea* sp. n.

1. *Serromyia polonica* sp. n.

(Figs. 389–395)

DIAGNOSIS

Female of the species is distinguished by the following combination of characters: wing length 0.95–1.12 mm, hind claws strongly unequal, hind femur 5.0–5.1 times as long as greatest width, and second radial cell slightly longer than first one.

DESCRIPTION

♀. Holotype. Body brown, thorax darker. Total habitus as in fig. 389. Total length 1.3 mm. Flagellum length 508 μm, AR 1.17. Proximal flagellomeres subcylindrical (fig. 390). Proboscis long. Palpus long and slender. Third palpal segment 37 μm long. Prescutal pits present. Fore

and middle legs slender, femora and tibiae unarmed (fig. 389), fourth tarsomeres subcylindrical (fig. 394). Hind femur moderately swollen, 5.0–5.1 times as long as greatest width, armed with 6–7 pairs of ventral spines (figs. 392, 393). Claws of hind leg strongly unequal (fig. 395). TR(II) 2.2, TR(III) 2.3. Wing length 0.95 mm, CR 0.64. Second radial cell slightly longer than first one (ca. 1.15 times). Macrotrichia present at wing tip, microtrichia not visible.

Another specimen provisionally determined as *S. polonica* is characterized as follows: AR 1.37. Scutellum with 8–9 long setae. Third palpal segment 48 μm long (fig. 391). Hind femur with 8–10 pairs of ventral spines. Wing length 1.12 mm, CR 0.68.

♂. Unknown.

MATERIAL EXAMINED (2 ♀)

Holotype — ♀, MZW 14977, TG. RSz 4, Gdańsk, 1 ♀.

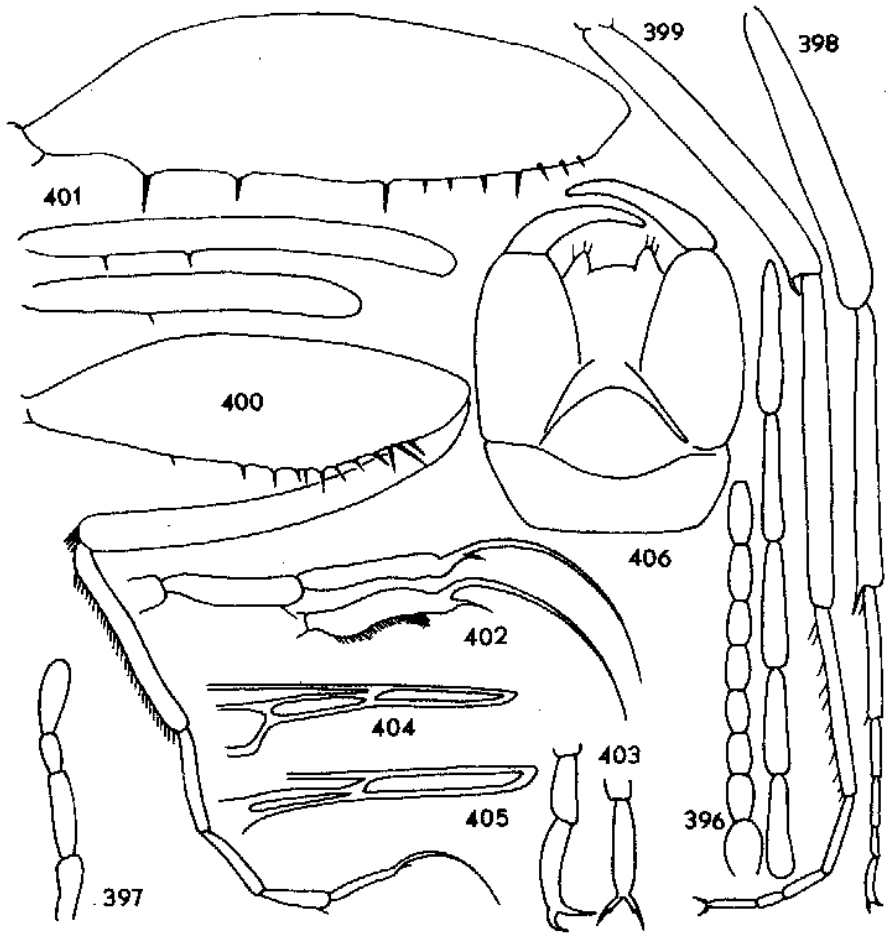
2. *Serromyia succinea* sp. n.
(Figs. 396–406)

DIAGNOSIS

The species is distinguished by the following combination of characters: wing length 1.5–1.7 mm, second radial cell 1.4–1.5 times longer than first one, hind femur 3.4–3.6 times as long as greatest width, fore and middle femora armed with ventral spines in male, hind claws very long and strongly unequal in female.

DESCRIPTION

♀. Body shining black. Eyes narrowly contiguous. Flagellum as in fig. 396, AR 1.31–1.54. Proboscis long. Palpus slender (fig. 397). Third palpal segment 75 μm long. Scutellum with 6 long and several shorter setae. Fore and middle legs slender and unarmed (figs. 398, 399). Fourth tarsomeres cylindrical. Basitarsus of middle leg with ca. 12 strong ventral spines. Claws of fore and middle legs short and equal, each with inner basal tooth (fig. 403). Hind femur distinctly swollen, 3.4–3.6 times as long as greatest width, armed with 11–12 pairs of strong ventral spines (fig. 400). Hind claws greatly unequal, longer claw distinctly longer than fifth tarsomere (fig. 402). TR(I) 2.3, TR(II) 2.4, TR(III) 2.1–2.2. Wing length 1.48–1.56 mm, CR 0.70–0.72. Second radial cell about 1.5 times longer than first one (fig. 405). Wing membrane with easily visible microtrichia, macrotrichia present at wing tip.



396-406. *Serromyia succinea* sp. n., MZW 11907, 13987; 396 — female flagellum, 397 — female palpus, 398 — female fore leg, 399 — female middle leg, 400 — female hind leg, 401 — fore, middle and hind femora of male, 402 — female claws of hind legs, 403 — female claws of fore and middle leg, 404 — first radial cells of male, 405 — first radial cells of female, 406 — male genitalia

♂. Body shining black. Fore femur armed with 1 ventral spine, middle femur with 2 ventral spines on basal half (fig. 401). Tibiae unarmed. Basitarsus of middle leg with distinct ventral spines. Hind femur 3.6 times as long as greatest width, armed with 10 pairs of strong spines. TR(I) 1.8, TR(II) 2.2, TR(III) 2.0. Wing length 1.72 mm, CR 0.70. Second radial cell 1.4 times longer than first one (fig. 404). Wing membrane with distinct microtrichia, some macrotrichia present at wing tip. Genitalia inverted, barely visible (fig. 406). Gonostylus slender, long and slightly curved.

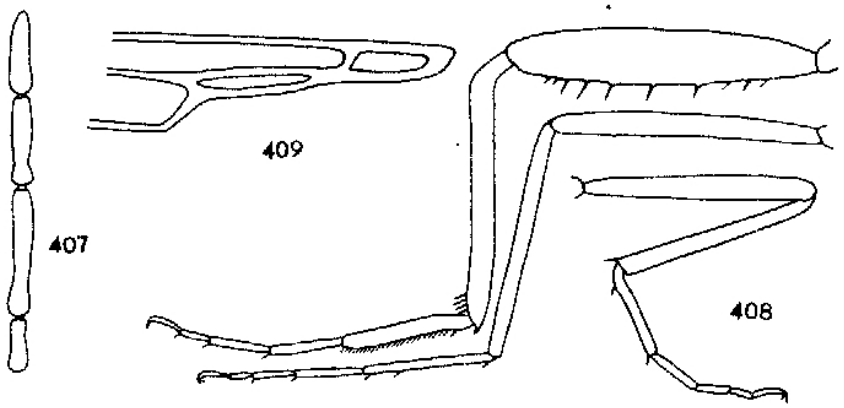
MATERIAL EXAMINED (1 ♂, 2 ♀)

Holotype — ♀, MZW 11907. Paratypes: MZW 11907, 1 ♂; 13987, TG (+*Chironomidae* 2 ♂), 1 ♀.

3. *Serromyia* sp. A
(Figs. 407–409)

DIAGNOSIS

Male of the species is characteristic in having second radial cell 1.4 times shorter than first one, wing length 1.12 mm, fore and middle femora unarmed, and the hind femur 5.7–5.8 times as long as greatest width.



407–409. *Serromyia* sp. A, male, MZW 14972; 407 — distal flagellomeres, 408 hind, middle and fore legs, 409 — first radial cells

DESCRIPTION

♀. Unknown.

♂. Body black, tarsi paler. Flagellum length 590 μm, AR 0.94. Last flagellomere distinctly shorter than preceding one (fig. 407). Fore and middle legs slender, femora unarmed (fig. 408). Hind femur slightly swollen, 5.7–5.8 times as long as greatest width, armed with 8–9 pairs of strong ventral spines. Fourth tarsomeres cylindrical. TR(I) 1.8, TR(II) 1.9, TR(III) 1.9. Wing length 1.12 mm, CR 0.58. Second radial cell 1.4 times shorter than first one (fig. 409). Genitalia inverted, barely visible. Gonostylus slender and long.

MATERIAL EXAMINED (1 ♂)

MZW 14972, TG, 1 ♂.

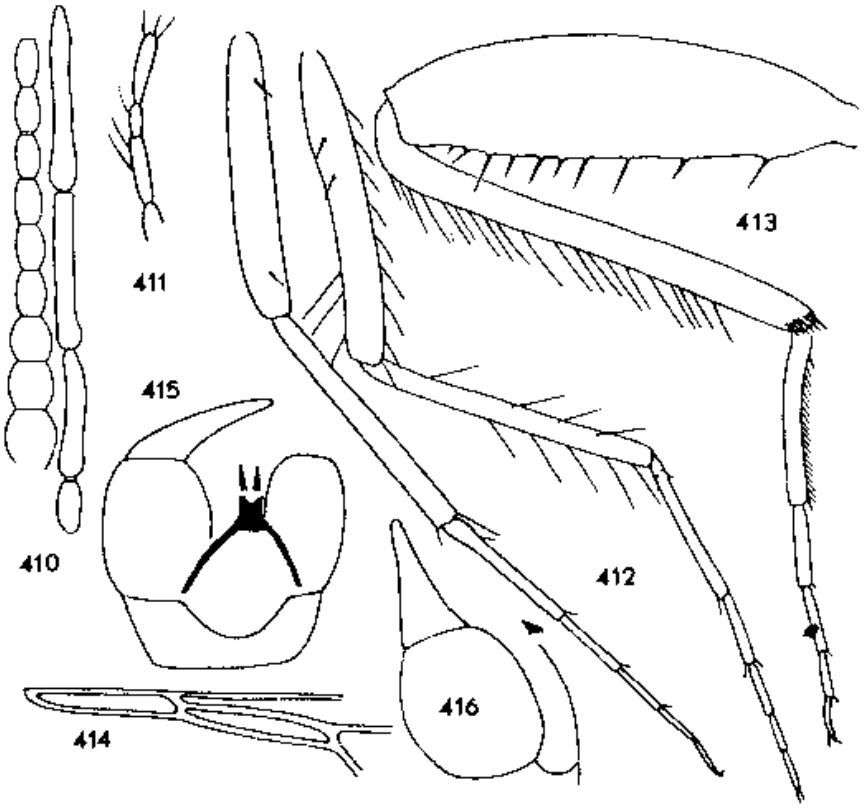
DISCUSSION

Male of *S.* sp. A is similar to the female of *S. polonica* **sp. n.**, however its second radial cell is distinctly shorter. In the genus *Serromyia* first radial cells are similar in both sexes.

4. *Serromyia* sp. B
(Figs. 410–416)

DIAGNOSIS

Male of the species is characteristic in having all legs with strong setae, all femora armed with ventral spines, hind femur 3.8 times as long as greatest width, genitalia not hidden below tip of abdomen.



410-416. *Serromyia* sp. B, male, MZW 16110; 410 — flagellum, 411 — palpus, 412 — fore and middle leg, 413 — hind leg, 414 — first radial cells, 415 — ventral view of genitalia, 416 lateral view of genitalia

DESCRIPTION

♀. Unknown.

♂. Body brown. Total length 1.9 mm. Flagellum length 784 μm, AR 1.24. Last flagellomere long (fig. 410). Palpus slender (fig. 411). Third palpal segment 60 μm long. Scutum with long and stout supraalar and postpronotal setae. Scutellum bearing 12 long and several shorter setae. Fore and middle legs slender (fig. 412), femora with some ventral and lateral spines and stout setae. Hind femur 3.8 times as long as greatest width, armed with 9–10 pairs of spines (fig. 413). Hind tibia with strong and long dorsal setae. Hind tarsus long and slender. Fourth tarsomeres

cylindrical. Tibial comb composed of 8 spines. TR(I) 2.0, TR(II) 2.2, TR(III) ca. 2.1. Wing length about 1.25 mm. Second radial cell slightly shorter than first one (fig. 414). Macrotrichia present at wing tip.

Genitalia inverted, not hidden below tip of abdomen and not curved ventrally (figs. 415, 416). Gonocoxite short and stout. Gonostylus stout, almost straight. Aedeagus with high basal arch; basal arms very long and nearly straight; tip bifid with divergent projections.

MATERIAL EXAMINED (1 ♂)

MZW 16110, TG, 1 ♂.

DISCUSSION

This male resembles *Monohelea* sp. A in having genitalia not hidden below tip of abdomen and strong setae on the thorax. However, it has a long and slender hind tarsus and femora of fore and middle legs are armed with some ventral and lateral spines. Such spiny male legs are found in the recent European *Serromyia femorata* (MEIGEN).

5. *Serromyia spinigera* (Loew, 1850)
(Figs. 417–427)

Ceratopogon spiniger LOEW, 1850: 30 (sex ?, Baltic amber).
Serromyia spinigera: KIEFFER, 1906: 2 (combination).
Ceratopogon elongatus MEUNIER, 1904: 231 (♀, Baltic amber), **syn. n.**

DIAGNOSIS

Large black species. Wing length 1.45–1.65 mm. Femora of fore and middle legs unarmed. Hind femur 5.3–6.5 times as long as greatest width. Female claws of hind leg short and equal.

DESCRIPTION

♀. Body black. Total length 2.3–2.8 mm. Flagellum length 779 μm long, AR 1.10 (fig. 417). Proximal flagellomeres as in fig. 418. Palpus slender, barely visible (fig. 420). Scutellum with some moderately long setae. Fore and middle legs slender, femora without spines (fig. 421). Hind femur clavate, moderately swollen, 5.3–6.5 times as long as greatest width (fig. 423, 424) bearing 7–10 ventral spines in 2 series on distal half. Fourth tarsomeres cylindrical. Hind claws short and equal (fig. 422). TR(I) 1.8–2.1, TR(II) 2.2, TR(III) 2.0–2.3. Second radial cell distinctly longer than first one (fig. 426). Macrotrichia present at wing tip.

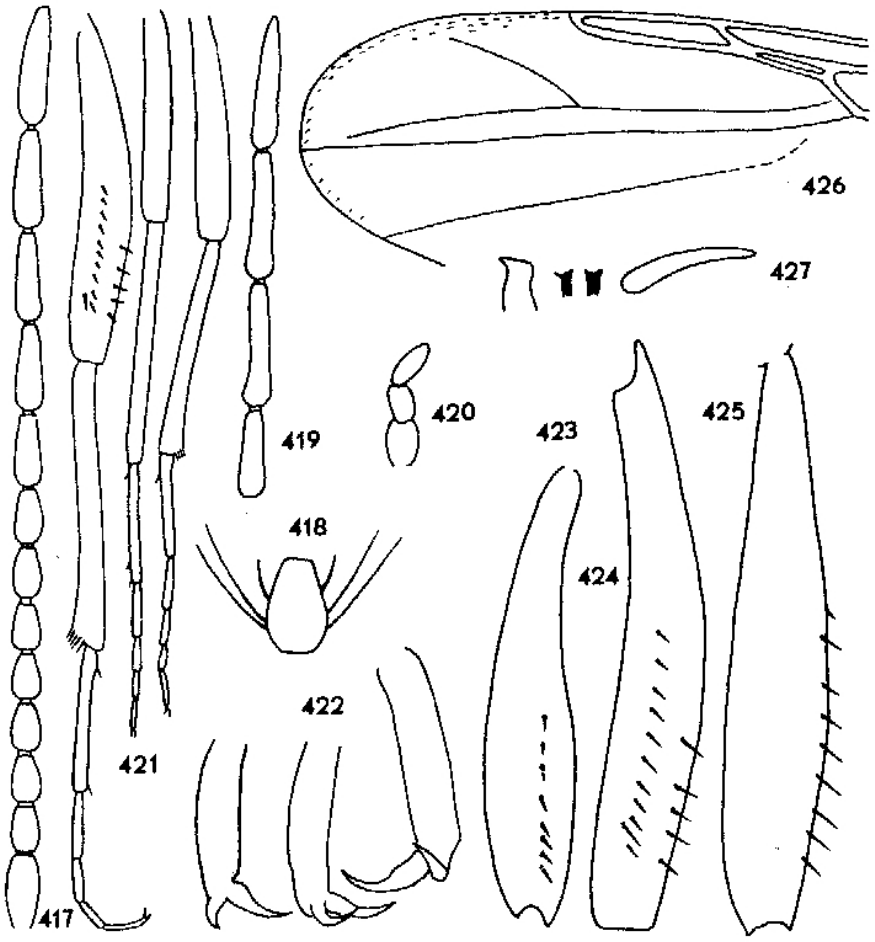
♂. Body black. Total length 2.5–2.8 mm. Flagellomere X relatively

long, about 2 times shorter than next one (fig. 419). AR ca. 0.82. Fore and middle legs slender, without stronger spines or setae. Hind femur 6.0 times as long as greatest width, clavate, armed with 7–8 ventral spines in 2 series on distal half (fig. 425). Fourth tarsomeres cylindrical. TR(I) 2.0, TR(II) 2.2–2.3, TR(III) 1.8–2.0. Wing length ca. 1.6 mm. Macrotrichia on wing membrane not visible.

Genitalia inverted and hidden below tip of abdomen (fig. 427). Gonostylus slender, shining. Tip of aedeagus in lateral view foot-shaped.

MATERIAL EXAMINED (2 ♂, 5 ♀)

Holotype — ♂ of *Ceratopogon spiniger* "*Ceratopogon* ♂ sp. 1 *spiniger*, Original Dr. B", MBI 116.



417–427. *Serromyia spinigera* (LOEW); 417 — female flagellum, 418 — fifth flagellomere of female, IMGPUG 4970; 419 — male distal flagellomeres, MBI 210; 420 — female palpus, IMGPUG 4970; 421 — female hind, middle and fore leg, MBI 107; 422 — female claws of fore, middle and hind leg, 423 — female hind femur, IMGPUG 4970; 424 — female hind femur, MBI 107; 425 — male hind femur, MBI 116; 426 — female wing, IMGPUG 4970; 427 — lateral and ventral view of aedeagus, gonostylus, MBI 116

Lectotype — ♀ of *C. elongatus*, IMGPUG Z 4970, present designation. Paralectotype — ♀ of *C. elongatus*, IMGPUG Z 5043 is barely visible, however it is distinctly smaller than *S. spinigera* with wing 1.27 mm long.

MBI 107, BERENDT, 1 ♀; 210, BERENDT, 1 ♂; MZW 7190, 1 ♀; 20282, 1 ♀.

DISCUSSION

Present examination of the types of *C. spiniger* and *C. elongatus* shows that these two species are synonymous. *Ceratopogon spiniger* s. MEUNIER (1904: 232) is misidentified, and 3 females determined by MEUNIER (IMGPUG Z 5355, 6662, 6895) are now included to indetermined *Serromyia* (see above). They are most similar to *S. succinea* **s p. n.**, however they are barely visible.

In the recent fauna there are four known species in which females have short and equal hind claws. They are: *S. albitarsis* KIEFFER (Germany), *S. micronyx* KIEFFER (Hungary), *S. nitens* GOETGHEBUER (West and Central Europe), and *S. crassifemorata* MALLOCH (eastern USA). It is possible that they may form a monophyletic group.

6. *Serromyia anomalicornis* (Loew, 1850), comb. n.
(Figs. 428–435)

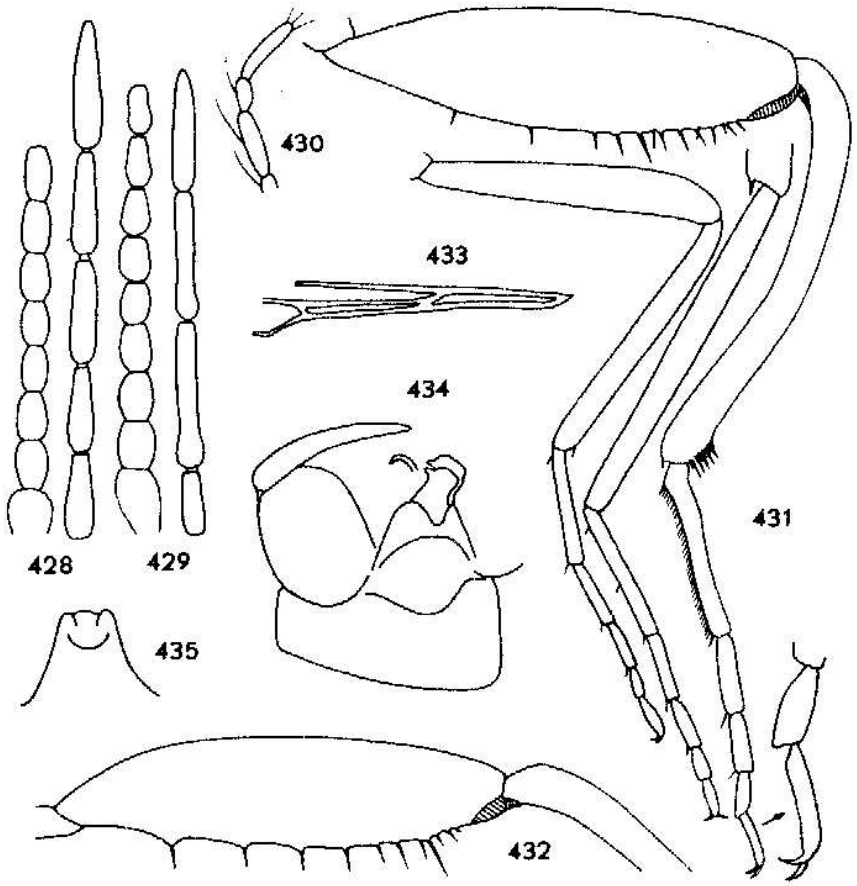
Ceratopogon anomalicornis LOEW, 1850: 30 (sex ?, Baltic amber).

DIAGNOSIS

This species is similar to *S. spinigera* but differs in having a stouter hind femur 3.6–4.0 times as long as greatest width and both first radial cells almost equal.

DESCRIPTION

♀. Body black. Total length 2.1 mm. Flagellum length 762 μm, AR 1.32 (fig. 428). Palpus slender. Third palpal segment 44 μm long. Thorax almost bare. Fore and middle legs slender and devoid of spines or strong setae. Hind femur distinctly swollen, 3.6–3.8 times as long as greatest width (fig. 431); with about 11 pairs of ventral spines. Fourth tarsomeres cylindrical. Claws of hind leg short and equal. TR(I) 1.9, TR(II) 2.2, TR(III) 2.2–2.3. Wing length 1.58 mm, CR 0.70. Second radial cell 1.1 times longer than first one (fig. 433). Macrotrichia present at wing tip.



428–435. *Serromyia anomalicornis* (LOEW), female MZW 5045, male MZW 18180; 428 — female flagellum, 429 — male flagellum, 430 male palpus, 431 — female fore, middle and hind leg, 432 — male hind femur, 433 — first radial cells of female, 434 — male genitalia, 435 — abdominal tergite IX of male

♂. Body black, legs dark brown. Total length 2.0 mm. Flagellum length 710 µm, AR 1.02. Flagellomere X short (fig. 429). Palpus slender (fig. 430). Third palpal segment 60 µm long. Fore and middle legs slender without spines or stronger setae. Hind femur swollen (fig. 432), 4.0 times as long as greatest width, with about 10 long ventral spines in 2 rows. Fourth tarsomeres cylindrical. TR(I) 1.8, TR(II) 2.0, TR(III) 2.0. Wing length about 1.40 mm, barely visible. Second radial cell slightly longer than first one.

Genitalia inverted, not hidden below tip of abdomen (figs. 434, 435). Gonostylus slender slightly curved, tip evenly pointed. Tergite IX distinctly tapering to apex.

MATERIAL EXAMINED (1 ♂, 1 ♀)

Neotype — ♀, MZW 5045, TG, present designation. MZW 18180, TG (+*Chironomidae* 1 ♀), 1 ♂.

Discussion

Type or types of *S. anomalicornis* are absent in the collections of Thomas and Berendt at MBI. Also Meunier (1904) did not find it in Königsberg. So this type was from the collection of Menge from Gdańsk (cf. Loew, 1864). However this collection is lost, and because of that I designate a neotype for this species. It is possible that the male described above does not belong to *S. anomalicornis*.

11. Genus *Mantohelea* gen. n.

Type-species *Ceratopogon lacus* Meunier, by present designation.

Diagnosis

The genus is characteristic in having fore femur greatly swollen and armed with strong ventral spines, long and single first radial cell and antepronotum well developed, collar-like.

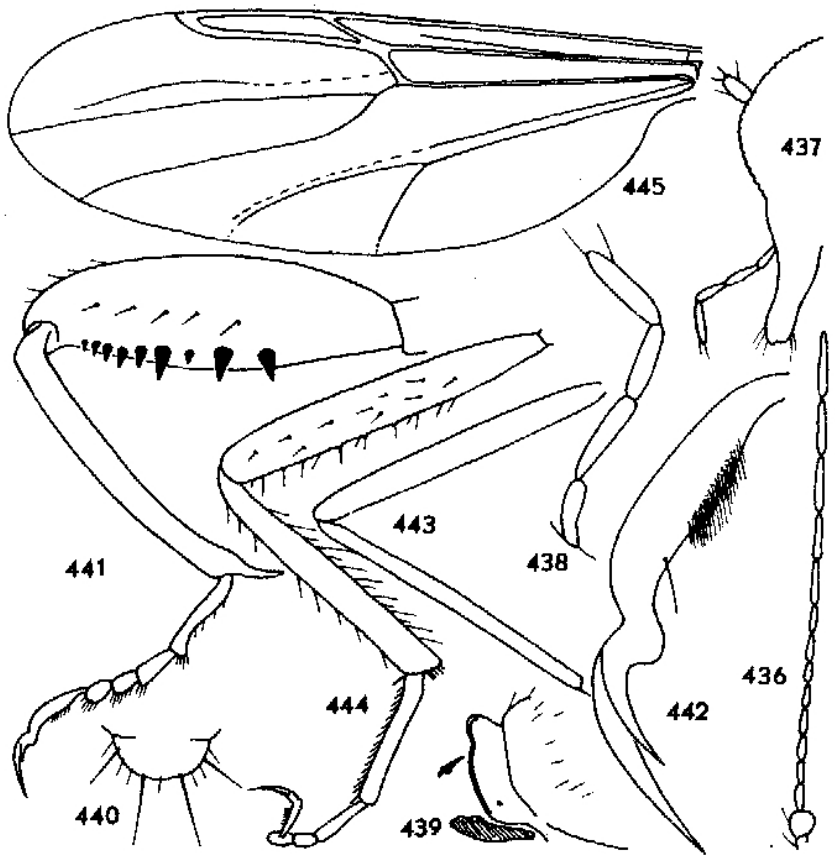
Description

Moderately large, stout midges. Only female known. Eyes narrowly separated. Antenna with 13 cylindrical flagellomeres. Sensilla coeloconica absent. Palpus long, 5-segmented. Third palpal segment cylindrical without sensory pit. Proboscis long. Antepronotum well developed, collar-like. Scutum without anterior tubercle, covered with short pubescence and long setae. Prescutal pits absent. Scutellum with 4 long and several shorter setae. Fore femur greatly swollen and armed ventrally with stout and short cone-like spines. Fore tibia somewhat arcuate, slender with apical prolongation. Middle leg slender, hind leg slightly enlarged. Hind femur with strong ventral and lateral setae. Fourth tarsomeres short, cordiform. Claws of all legs with outer claw long, inner claw shorter, without basal teeth. First radial cell single and long, CR 0.77–0.78. Media petiolate with short stem, base of M_2 easily visible. Wing membrane without distinct microtrichia, macrotrichia absent. Genitalia not modified. Cerci short.

Discussion

Mantohelea has a single first radial cell similar to the subgenus *Eukraiohelea* Ingram et Macfie of *Stilobezzia* and fore femur and tibia very similar to those of *Heteromyia* Say of the tribe *Heteromyiini*.

Mantohelea is apparently an extinct genus that includes 2 species from Baltic amber. In the material examined only 3 females of this genus have been found.



436–445. *Mantohelea lacus* (MEUNIER), female; 436 — flagellum, MZW 9598; 437 — head, 438 — palpus, IMGPUG 9551; 439 — antepronotum, 440 — scutellum, MZW 9598; 441 — fore leg, 442 — claws of fore leg, IMGPUG 9551; 443 — middle femur and tibia, 444 — hind leg, MZW 9598; 445 — wing, IMGPUG 9551

Key to Baltic amber species of *Mantohelea*

Females

1. Wing length 1.70–1.89 mm. Fourth palpal segment slightly shorter than third one. Hind femur with numerous spine-like setae . . . . . 1. *M. lacus* (MEUNIER)

—. Wing length 1.06 mm. Fourth palpal segment almost 2 times shorter than third one. Hind femur without spine-like setae . . . . . 2. *M. gedanica* sp. n.

1. *Mantohelea lacus* (Meunier, 1904), comb. n.
(Figs. 436–445)

Ceratopogon lacus MEUNIER, 1904: 232 (♀, Baltic amber).
Heteromyia lacus: KIEFFER, 1906: 2 (combination).

DIAGNOSIS

See key.

DESCRIPTION

♀. Body black or dark brown, scutum shining. Total length 2–3 mm. Flagellum length 1154 μm, AR 1.31. Scape small but easily visible; pedicel spherical, large; proximal 8 flagellomeres cylindrical, distal 5 more elongate (fig. 436). Eyes narrowly separated. Proboscis long (fig. 437). Palpus slender (fig. 438). Third palpal segment 74 μm long; sensory pit absent; fourth one slightly shorter — 67 μm. Antepronotum well developed, collar-like (fig. 439). Scutum with acrostichals, dorsocentrals and supraalar distinct setae. Scutellum with 4 long and several shorter setae (fig. 440). Fore femur greatly swollen and armed with stout 9 ventral cone-like spines and several strong lateral setae (fig. 441). Fore tibia arcuate with long curved prolongation or spur. Middle leg slender and unarmed (fig. 443). Hind leg stout, femur with ventral and lateral strong spine-like setae, hind tibia with long and strong dorsal and lateral setae (fig. 444). Fourth tarsomeres cordiform. Claws long simple, distinctly unequal, and similar on all legs (fig. 442). TR(I) 2.0. Wing length 1.70–1.89 mm, CR 0.78. First radial cell single and long (fig. 445). Media petiolate forking just beyond crossvein r-m. Membrane without macrotrichia, microtrichia not visible.

♂. Unknown.

MATERIAL EXAMINED (2 ♀)

Holotype — ♀, IMGPUG Z 9551. MZW 9598, 1 ♀. Female from MZW has preserved only proximal part of one wing.

2. *Mantohelea gedanica* sp. n.
(Figs. 446–450)

DIAGNOSIS

See key.

DESCRIPTION

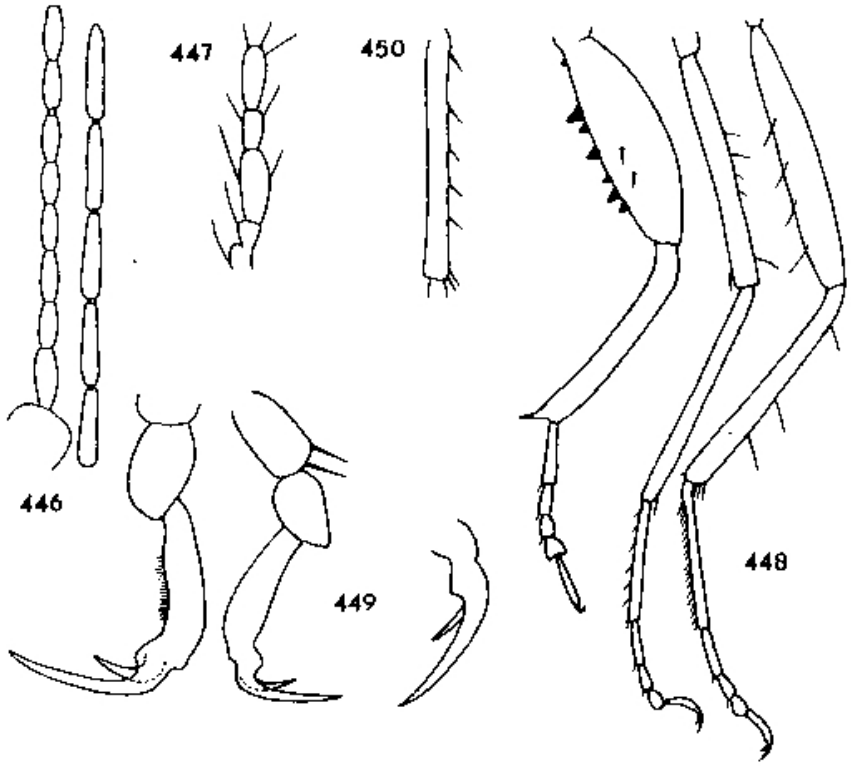
♀. Body brown. Total length 1.6 mm. Flagellum length 702 μm, AR 1.10. Proximal 8 flagellomeres cylindrical, distal 5 more elongate

(fig. 446). Proboscis long. Palpus slender (fig. 447). Third palpal segment 56 μm long, without sensory pit. Fourth palpal segment about half the length of third segment. Antepronotum well developed, collar-like. Scutum covered with short pubescence and normal fine setae. Scutellum with 4 long and several shorter setae. Prescutal pits not visible. Fore femur greatly swollen and armed with ca. 6 stout ventral cone-like spines and 2 lateral spine-like setae (fig. 448). Fore tibia somewhat arcuate, with moderately long and curved apical prolongation or spur. Middle leg slender, basitarsus with strong ventral spines (fig. 450). Hind femur and tibia slightly enlarged, tibia with 3 strong dorsal setae (fig. 448). Fourth tarsomeres short, cordiform. Claws long, greatly unequal, simple (fig. 449). TR(I) 2.1, TR(II) 2.7, TR(III) 3.1. Wing length 1.06 mm, CR 0.77. First radial cell single and long. Macrotrichia absent on wing membrane, microtrichia probably present.

♂. Unknown.

MATERIAL EXAMINED (1 ♀)

Holotype – ♀, MZW 10026.



446–450. *Mantohelea gedanica* sp. n., female, MZW 10026; 446 — flagellum, 447 — palpus, 448 fore, middle and hind leg, 449 claws of fore, middle and hind leg, 450 basitarsus of middle leg

12. Genus *Meunierohelea* gen. n.

Type-species *Meunierohelea nielseni* **sp. n.**, by present designation.

Diagnosis

This new genus is distinguished by the following combination of characters: first and second radial cells widely separated by anastomosed R_1 and R_{4+5} veins; male flagellum with 13–10 flagellomeres, proximal flagellomeres 2–10 or 2–7 more or less fused, plume well developed; legs slender and unarmed, fourth tarsomeres cylindrical; female claws short to moderately long, equal and simple on all legs.

Description

Small midges. Antenna of female composed of 13 flagellomeres, proximal units short, distal 5 elongated, all flagellomeres with long and strong verticils. In male number of flagellomeres 13 or 10, proximal flagellomeres 2–10 or 2–7 fused, distal 3 flagellomeres greatly elongated. Sensilla coeloconica absent. Palpus 5-segmented, third palpal segment without sensory pit. Proboscis moderately short.

Scutum shining without anterior tubercle, usually with sparse long setae. Prescutal pits present. Antepronotum small. Scutellum bearing 4–6 long setae. Legs slender and unarmed. Fifth tarsomeres cylindrical. Female claws similar on all legs, short to moderately long, equal and simple. Wing narrow without anal lobe, membrane without macrotrichia and usually with indistinct microtrichia. First and second radial cells well developed, narrow and widely separated by anastomosed R_1 and R_{4+5} (plus R_{2+3}) veins. CR 0.65–0.81. Intercalary veins well developed. Base of M_2 atrophied.

Female abdomen without modifications. Seminal capsule single. Male genitalia inverted, rotated or in normal position, short and broad. Sternite IX short and broad. Tergite IX long with distinct short apicolateral lobes. Gonostylus broad or slender, usually slightly bent. Aedeagus broad with distinct apical submedian lobes. Parameres separated, moderately long.

Discussion

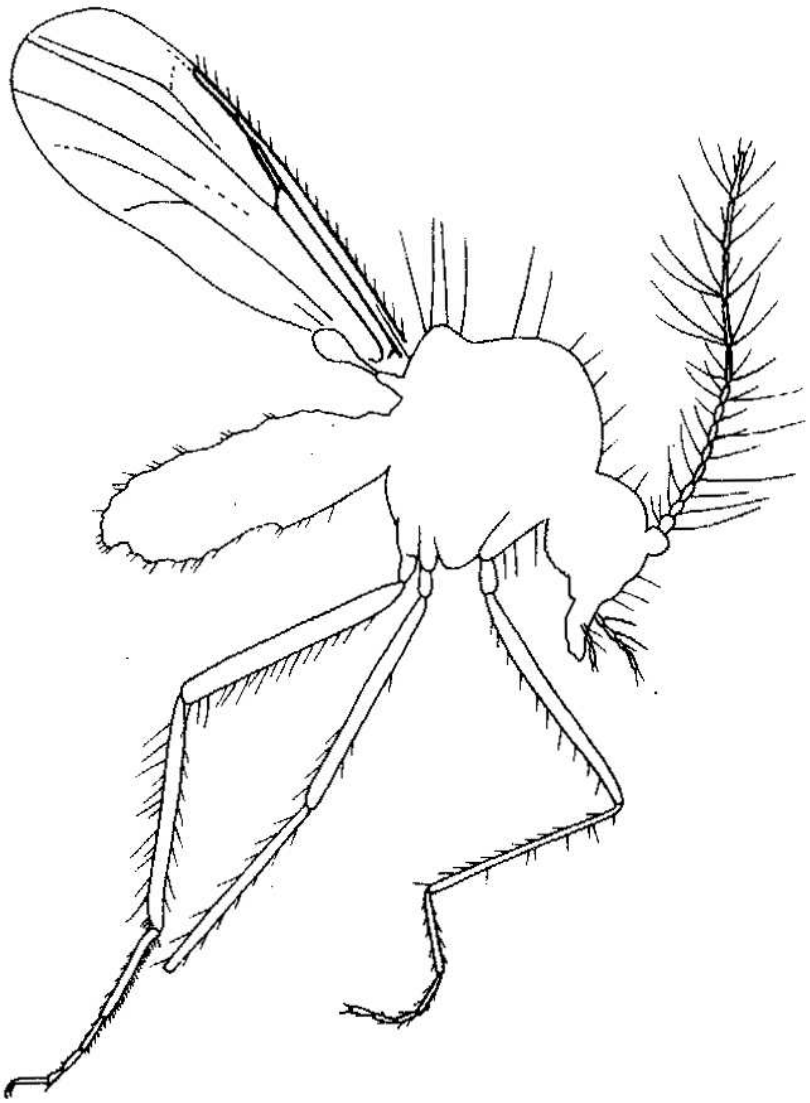
The systematic position of this extinct genus within the tribe is not clear as the wing venation of *Meunierohelea* is unique in the family. In the material examined 24 specimens of the genus belonging to 6 species have been found. However it may be that the number of species is higher or lower than herein described.

ETYMOLOGY

This genus is named for F. MEUNIER in recognition of his important contributions to the study of Baltic amber *Diptera* including *Ceratopogonidae*.

Meunierohelea indetermined (5 ♂)

MM 6, 1 ♂; MZW 9738, 1 ♂; ZMC 84, C. V. HENNINGSEN, 31–5 1961, 1 ♂; 98, C. V. HENNINGSEN, 3–5 1960, 1 ♂; 236, A. HENNINGSEN, 9–9 1974, 1 ♂.



451. *Meunierohelea nielseni* sp. n., total habitus of female, ZMC 111

Key to Baltic amber species of *Meunierohelea*

1. Males 2
—. Females 4

2. Flagellum with 10 recognizable flagellomeres. Gonostylus broad, not tapering to apex . . . . . 6. *M. wirthi* sp. n.
—. Flagellum with 13 recognizable flagellomeres. Gonostylus tapering to apex 3
3. CR 0.80 . . . . . 2. *M. gedanicola* sp. n.
—. CR 0.65–0.67 . . . . . 1. *M. nielseni* sp. n.
4. CR 0.79–0.81 5
—. CR 0.66–0.76 6
5. Palpus short. Claws 28 µm long . . . 2. *M. gedanicola* sp. n.
—. Palpus long. Claws 44–48 µm long . . . . . 3. *M.* sp. A
6. AR 1.08. CR 0.76. Seminal capsule large . . . . 4. *M.* sp. B
—. AR 1.32–1.57. CR 0.66–0.71. Seminal capsule small 7
7. Second radial cell 0.9–1.1 times as long as distance between tip of R_1 and base of first radial cell. CR 0.66–0.69 . . . 1. *M. nielseni* sp. n.
—. Second radial cell 1.3–1.4 times as long as distance between tip of R_1 and base of first radial cell. CR 0.71–0.73 . . . . 5. *M.* sp. C

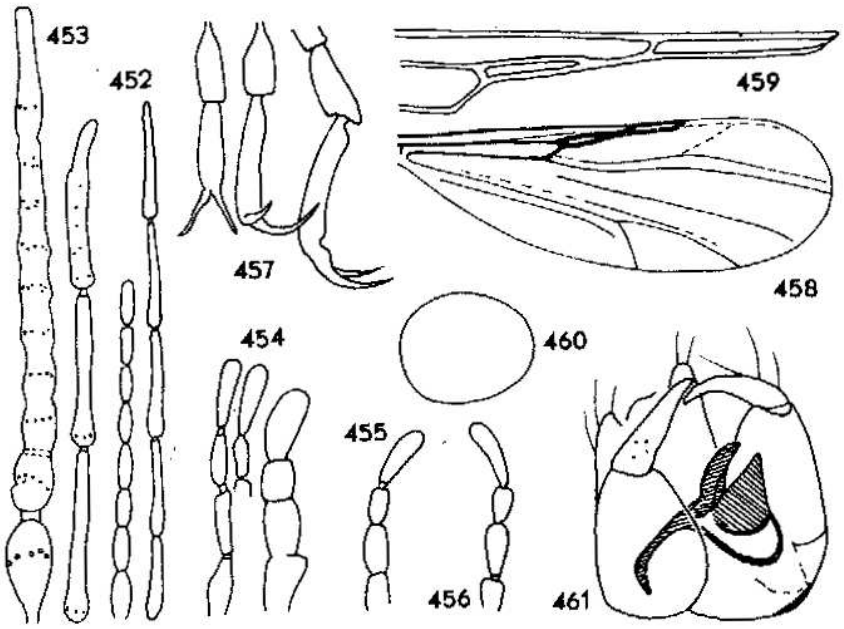
1. *Meunierohelea nielseni* sp. n.
(Figs. 451–472)

Diagnosis

This species is distinguished by the following combination of characters: CR 0.66–0.69, second radial cell 0.9–1.1 times as long as distance between tip of R_1 and base of first radial cell; setae of scutum strong; female claws slender, 20–32 µm long; seminal capsule almost spherical measuring 48 × 56 µm; flagellomere X of male long.

Description

♀. Body brown, dark brown or blackish. Total length 0.9–1.1 mm. Total habitus as in fig. 451. Flagellum length 534–675 µm, AR 1.43–1.57 (figs. 452, 463). Proximal 8 flagellomeres short and cylindrical, distal 5 flagellomeres greatly elongated. Proboscis moderately long. Palpus slender (figs. 454, 455, 464). Third palpal segment 20–28 µm long, without sensory pit. Scutum with long setae. Scutellum with only 6 long setae measuring 112–160 µm. Legs slender (fig. 451). Hind basitarsus somewhat curved at base, with distinct subbasal ventral spine and palisade setae in 2 series, second tarsomere also with 2 rows of palisade setae (fig. 466). Fourth tarsomeres cylindrical. Claws moderately long, slender, without basal inner teeth, 28–32 µm or 20–24 µm long (figs. 457, 467). TR(I) 2.0–2.7, TR(II) 2.4–2.7, TR(III) 2.5–2.8. Wing



452–461. *Meunierohelea nielseni* sp. n.; 452 — female flagellum, ZMC 17; 453 — male flagellum, ZMC 105; 454 — female palpi and male palpus, ZMC 111; 455 — female palpus, ZMC 117; 456 — female palpus, ZMC 17; 457 — female claws of fore, middle and hind leg, ZMC 111; 458 — male wing, ZMC 105; 459 — first radial cells of female, ZMC 17; 460 — seminal capsule, ZMC 132; 461 — male genitalia, ZMC 105

length 0.68–0.92 mm, CR 0.66–0.69. First radial cell plus anastomosed part of R_1 with R_{4+5} almost as long as second radial cell (figs. 459, 470). First radial cell 0.9–1.1 times as long as anastomosed veins. Intercalary veins readily visible. Vein M_2 long with atrophied base. Radial veins without setae. Seminal capsule almost spherical measuring 48 × 56 µm (fig. 460).

♂. Similar to female with the usual sexual differences. Body brown or dark brown. Flagellum length 508–560 µm, AR 1.17–1.31. Flagellomeres II–X fused, flagellomere X long (figs. 453, 462). First flagellomere with a single ring of long setae. Palpus short, as in figs. 454, 465. Tibial comb composed of 5 spines (fig. 469). Fourth tarsomeres cylindrical, claws small (fig. 468). TR(I) 1.9, TR(II) 2.2–2.5, TR(III) 2.3–2.5. Wing length 0.68–0.74 mm, CR 0.65–0.67. Venation as in fig. 458.

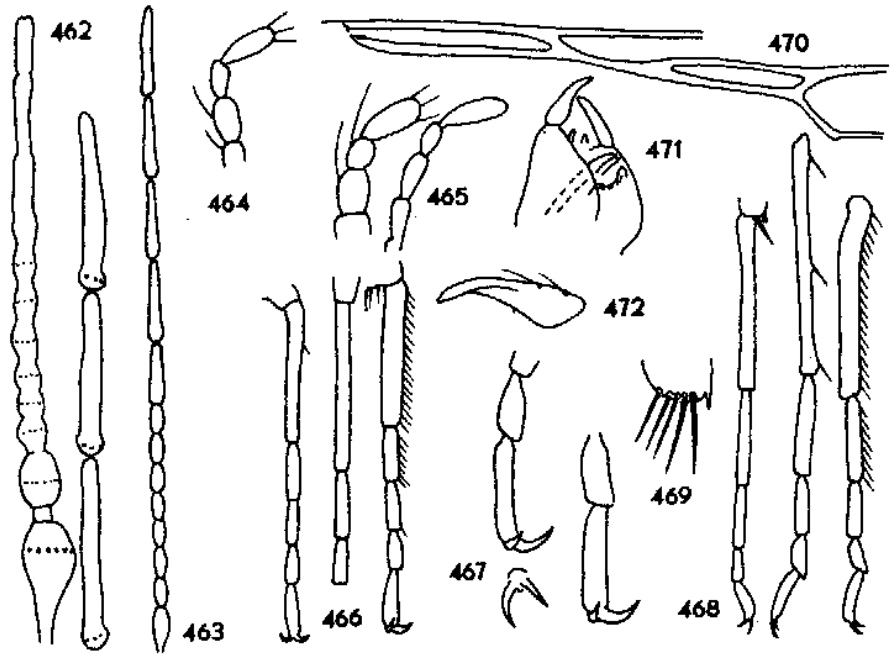
Genitalia inverted or in normal position, barely visible (figs. 461, 471, 472). Gonostylus moderately slender, slightly tapering distally and slightly curved. Aedeagus distinctly bilobed. Parameres separated, short, curved ventrally.

MATERIAL EXAMINED (3 ♂, 9 ♀)

Holotype — ♀, ZMC 17, Vesterhavet, S. NIELSEN, Skjddeler, Min. Mus. 1890, 108. Paratypes: ZMC 30, Vesterhavet, S. NIELSEN, Min. Mus.

1890, 108, 1 ♀; 105, C. V. HENNINGSEN, 22–6 1953, 1 ♂; 117, Vesterhavet, S. NIELSEN, Skjddeler, Min. Mus. 1890–108, 1 ♀.

MZW 14793, TG, 1 ♂; 19802, TG, 1 ♀; ZMC 35, C. V. HENNINGSEN, 3–5 1952, 1 ♀; 12, C. V. HENNINGSEN, 25–3 1961, 1 ♀; 31, Börge MORTENSEN, 1–9 1960, 1 ♀; 111, Nordjyllands Vestleyst, Guldsamed HENNINGSEN, Min. Mus. 1951–22, 1 ♂ 1 ♀; 132, Th. HANSEN, Mou, 16–1 1961, 1 ♀.



462–472. *Meunierohelea nielseni* sp. n., female MZW 19802, male MZW 14793; 462 — male flagellum, 463 — female flagellum, 464 — female palpus, 465 — male palpi, 466 — female tarsi of fore, middle and hind leg, 467 — female claws of middle and hind leg, 468 — male tarsi of fore, middle and hind leg, 469 — male tibial comb, 470 — female first radial cells, 471 — male genitalia, 472 — gonostylus

ETYMOLOGY

This species is named for S. NIELSEN, the collector of the holotype and two paratypes.

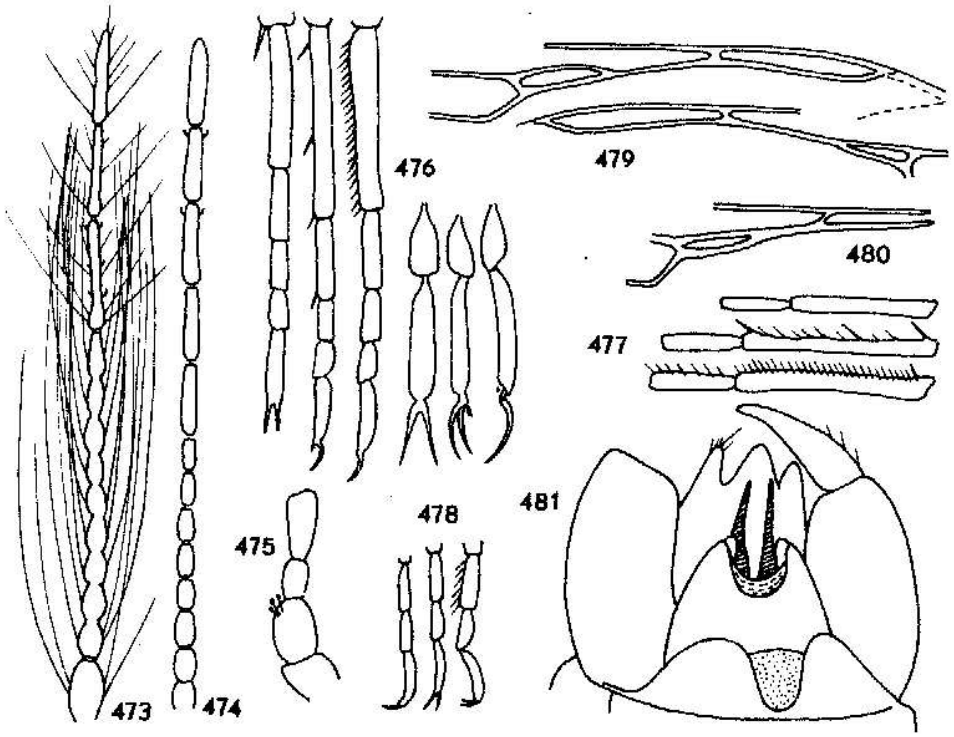
NOTE

It is worth noting that most specimens of this species are from the ZMC collection.

2. *Meunierohelea gedanicola* sp. n.
(Figs. 473–481)

DIAGNOSIS

The species is characterized by the following combination of characters: CR 0.81–0.81, scutum with short and fine setae first radial cell shorter than distance between both first radial cells, flagellomere X of male short.



473–481. *Meunierohelea gedanicola* sp. n., female MZW 5018, male MZW 11396; 473 — male flagellum, 474 — female flagellum, 475 — male palpus, 476 — female tarsi of fore, middle and hind leg, 477 — proximal tarsomeres of male, 478 — distal tarsomeres of male, 479 — female first radial cells, 480 — male first radial cells, 481 — male genitalia

DESCRIPTION

♀. Body brown. Total length 1.0 mm. Flagellum length 530 µm, AR ca. 1.32 (fig. 474). Palpus short, third palpal segment 16 µm long. Scutum with short indistinct setae. Scutellum apparently with 4 long setae. Legs slender. Tarsi as in fig. 476. Claws 28 µm long, slender, without basal inner teeth. TR(I) 2.1, TR(II) 2.4, TR(III) 2.3. Wing length 0.71 mm, CR 0.81. First radial cell short, much shorter than anastomosed veins R_1 and R_{4+5} (fig. 479). Second radial cell almost as first one plus

anastomosed veins. Microtrichia on wing membrane not visible. Radial veins without setae.

♂. Body brown. Total length 1.2 mm. Flagellum length 577 μm, AR 0.98. Proximal flagellomeres II–X fused (fig. 473). Palpus as in fig. 475. Third palpal segment 28 μm long, sensilla capitata readily visible at apex. Proboscis short. Scutum almost bare. Scutellum with 4 long setae. Legs slender. Tarsi as in figs. 477, 478. Tibial comb composed of 5 spines. Fourth tarsomeres cylindrical. Basitarsus of middle leg with 3 ventral spines. TR(I) 2.1, TR(II) 2.4, TR(III) 2.4. Wing length 0.72 mm, CR 0.80. First radial cell slightly shorter than distance between both first radial cells (fig. 480).

Genitalia rotated, short and broad (fig. 481). Sternite IX narrow, with deep caudomedian excavation. Gonocoxite slightly curved, extending past tergite IX. Gonostylus stout, almost straight, tapering slightly distally to broadly pointed tip. Aedeagus broad with deep U-shaped caudomedian excavation. Parameres long, straight, extending to tip of gonocoxites.

MATERIAL EXAMINED (1 ♂, 1 ♀)

Holotype — ♀, MZW 5018; TG. Paratype — ♂, MZW 11396, TG.

3. *Meunierohelea* sp. A
(Figs. 482–488)

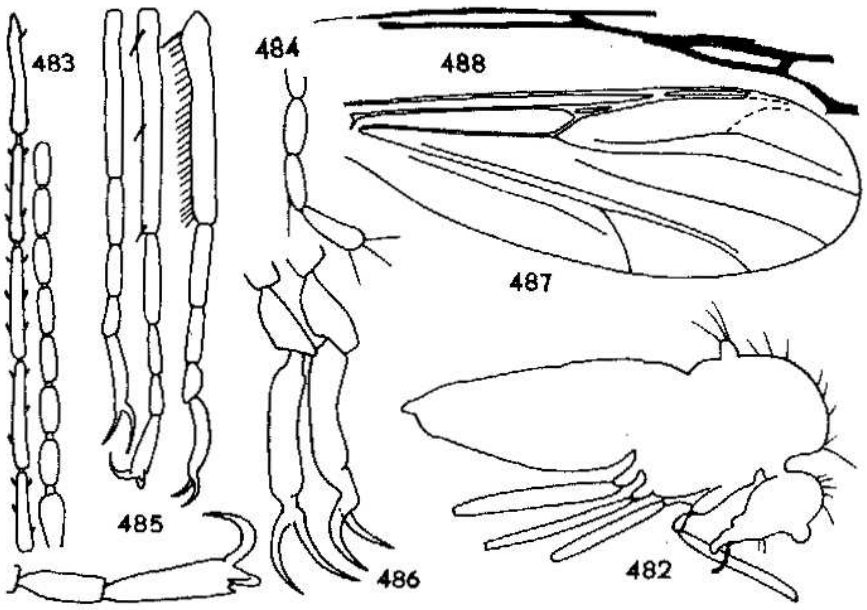
DIAGNOSIS

Female of the species is distinguished by having CR 0.79, long palpus and large claws measuring 44–48 μm.

DESCRIPTION

♀. Body brown. Total length 1.2 mm. Total habitus as in fig. 482. Flagellum length 742 μm, AR 1.23. Proximal flagellomeres cylindrical (fig. 483). All flagellomeres with strong, long verticils. Proboscis moderately long. Third palpal segment 32 μm, and fourth 24 μm long. Scutum with sparse long setae. Scutellum with 6 long setae measuring 140 μm, shorter setae absent. Tarsi as in fig. 485. Middle basitarsus with 3 strong ventral spines. Hind basitarsus with strong subbasal spine and palisade setae. Claws large, curved, without inner teeth, 44–48 μm long (fig. 486). Wing length 0.98 mm, CR 0.79 (fig. 487). First radial cell as long as distance between both first radial cells (fig. 488).

♂. Unknown.



482–488. *Meunierohelea* sp. A, female, ZMC 171; 482 — total habitus, 483 — flagellum, 484 — palpus, 485 — tarsi of fore, middle and hind leg, 486 — claws of fore, middle and hind leg, 487 — wing, 488 — first radial cells

MATERIAL EXAMINED (1 ♀)

ZMC 171, A. HENNINGSEN, 9–9 1974, 1 ♀.

4. *Meunierohelea* sp. B
(Figs. 489–494)

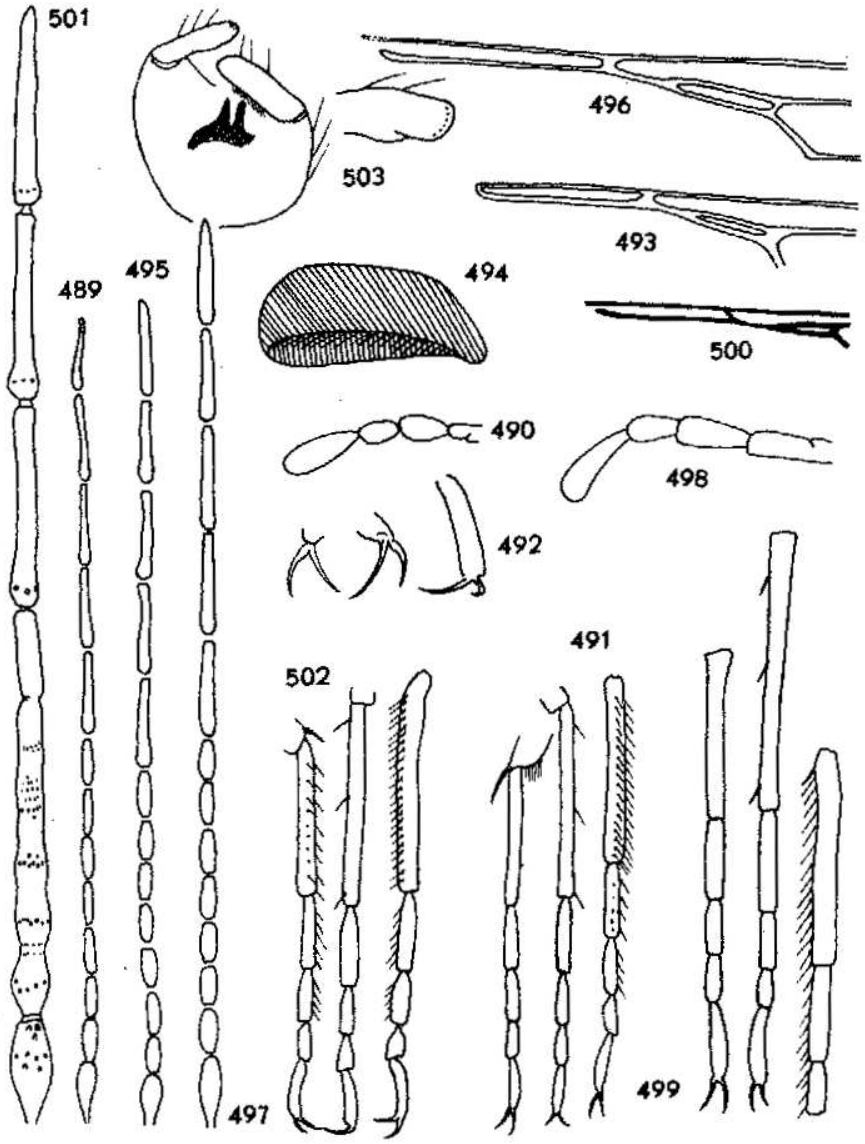
DIAGNOSIS

Female of this species is very similar to that of *M. nielseni* **sp. n.** but differs in having a large seminal capsule and CR 0.76.

DESCRIPTION

♀. Body brown. Total length 1.0 mm. Flagellum length 668 μm, AR 1.08. Proximal 8 flagellomeres cylindrical, distal 5 more elongate (fig. 489). Palpus as in fig. 490. Third palpal segment 22 μm long. Proboscis moderately long. Scutum with sparse long setae. Scutellum apparently with 6 long and several shorter setae. Tibial comb composed of 4 spines. Tarsi as in fig. 491. Claws slender, without basal inner teeth, 28–32 μm long (fig. 492). TR(I) 2.0, TR(II) 2.7, TR(III) 2.6. Wing length 0.71 mm, CR 0.76. First radial cell longer than distance between both first radial cells (fig. 493). One ovoid seminal capsule readily visible, length 100 μm (fig. 494).

♂. Unknown.



489–503. *Meunierohelea* sp. B, *Meunierohelea* sp. C, and *M. wirthi* sp. n. *Meunierohelea* sp. B, female, MZW 7292 (489–494): 489 — flagellum, 490 — palpus, 491 — tarsi of fore, middle and hind leg, 492 — claws, 493 — first radial cells, 494 — seminal capsule; *Meunierohelea* sp. C, female (495–500): 495 — flagellum, 496 — first radial cells, MZW 393 a; 497 — flagellum, 498 — palpus, 499 — tarsi of fore, middle and hind leg, 500 — first radial cells, MBI 120; *M. wirthi* sp. n., male, ZMC 225 (501–503): 501 — flagellum, 502 — tarsi, 503 genitalia

MATERIAL EXAMINED (1 ♀)

MZW 7292, 1 ♀.

5. *Meunierohelea* sp. C
(Figs. 495–500)

DIAGNOSIS

Female of this species is similar to *M. nielseni* **sp. n.**, but differs in having CR 0.71–0.73, long second radial cell which is 1.3–1.4 times longer than distance between tip of R_1 and base of first radial cell.

DESCRIPTION

♀. Body dark brown or black. Total length 0.9–1.1 mm. Eyes narrowly contiguous. Vertex with long setae. Flagellum length 675–757 μm, AR 1.32–1.37 (figs. 495, 497). Proboscis moderately long. Palpus slender and long (fig. 498). Third palpal segment 32 μm long. Scutellum with sparse long setae. Scutellum with 4–6 long setae measuring ca. 148 μm. Tarsi as in fig. 499. Claws slender, without basal inner teeth, 24 or 32 μm long. TR(I) 2.2, TR(II) 2.7–2.8, TR(III) 2.3–2.6. Wing length 0.84–0.93 mm, CR 0.71–0.73. Second radial cell about 1.3–1.4 times longer than distance between tip of R_1 and base of first radial cell (figs. 496, 500). Seminal capsule barely visible, nearly spherical, measuring 56 × 60 μm.

♂. Unknown.

MATERIAL EXAMINED (2 ♀)

MBI 120, BERENDT, "*Ceratopogon* ♀, sp. 5 *longicornis*, Orig. Dr B", 1 ♀; MZW 393 a (+*Psychodidae* 1), 1 ♀.

6. *Meunierohelea wirthi* sp. n.
(Figs. 501–503)

DIAGNOSIS

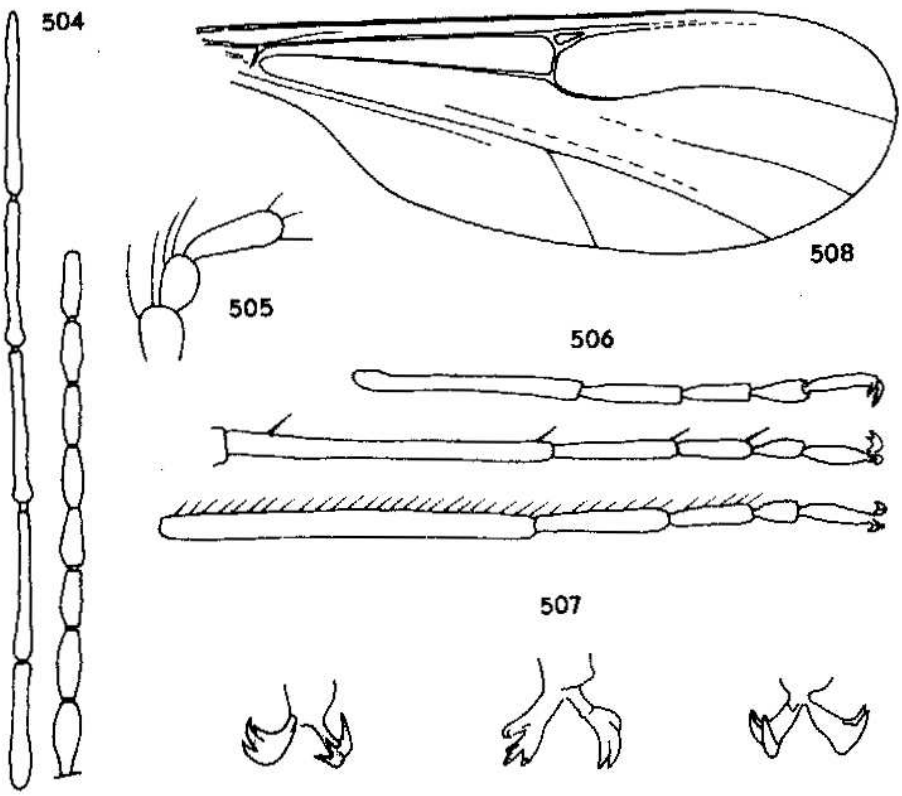
Male of this species is characteristic in having only 10 recognizable flagellomeres and very broad gonostyli.

DESCRIPTION

♀. Unknown.

♂. Body brown. Total length 0.9 mm. Flagellum length 512 μm, AR 1.61. Plume sparse. Flagellum composed of 10 recognizable flagellomeres (fig. 501). Proximal 7 flagellomeres fused. Distal 3 flagellomeres separate, long, with long, stout basal setae. Palpus barely visible. Scutum with sparse long strong setae. Scutellum with 4 long setae. Tarsi as in fig. 502. Claws small, about 20 μm long. Spur of fore tibia long. TR(I) 2.3, TR(II) 2.9, TR(III) 2.7. Wings ground during preparation, only basal portions visible. Wing membrane with microtrichia.

Genitalia rotated, barely visible (fig. 503). Gonostylus broad, with broad and blunt tip. Aedeagus broad with shallow basal arch, distal portion divided into 2 apices that are nearly parallel with broadly pointed tips.



504–508. *Wirthohelea trifida* sp. n., female, MZW 4457; 504 — flagellum, 505 — palpus, 506 — tarsi of fore, middle and hind leg, 507 — claws of fore, middle and hind leg, 508 — wing

MATERIAL EXAMINED (1 ♂)

Holotype — ♂, ZMC 225, C. V. HENNINGSEN, 1–8 1962.

ETYMOLOGY

This species is named for Dr. W. W. WIRTH of Gainesville, Florida, in recognition of his superb contributions to the study of the world *Ceratopogonidae*.

13. Genus *Wirthohelea* gen. n.

Type-species *Wirthohelea trifida* **sp. n.**, by present designation.

DIAGNOSIS

A genus of biting midges of the tribe *Stilobezziini* distinguished from all other ceratopogonid genera by the following combination of characters: claws of female moderately short with distinctly trifid tips. Wing with a small single first radial cell and a short, obsolete R_{4+5} not connecting with costa distally and extending only 0.6 of wing length; media petiolate, M_2 obsolete on base. Male unknown.

ETYMOLOGY

This genus is named for Dr. W. W. WIRTH of Gainesville, Florida, in recognition of his important contributions to the study of the world *Ceratopogonidae*.

NOTE

In the material examined only single female has been found.

1. *Wirthohelea trifida* sp. n.
(Figs. 504–508)

DESCRIPTION

♀. Body blackish brown. Total length 1.4 mm. Flagellum filamentous, proximal 8 flagellomeres cylindrical, distal 5 flagellomeres very long (fig. 504); length 1068 μm, AR 1.48. Sensilla coeloconica absent. Palpus 5-segmented; third palpal segment about 32 μm long, sensory pit not visible (fig. 505). Antepronotum indistinct. Scutum with sparse moderately long setae. Scutellum bearing 6 long setae. Legs slender, unarmed. Tibial comb composed of 5 spines. Fourth tarsomeres subcylindrical (fig. 506). Claws similar on all legs, short, equal, broad and distinctly trifid, without basal inner teeth (fig. 507). TR(I) 2.2, TR(II) 2.6, TR(III) 2.7. Wing length 1.11 mm. First radial cell small, second one absent, R_{4+5} obsolete distally, not connecting with costa and extending only ca. 0.6 of wing length (fig. 508). Wing membrane apparently without macrotrichia or microtrichia. Media petiolate, vein M_1 distinctly bent upward in mid portion, base of M_2 obsolete. Abdomen short with short cerci.

♂. Unknown.

MATERIAL EXAMINED (1 ♀)

Holotype — ♀, MZW 4457. One of the wings is broken off and lies near the body.

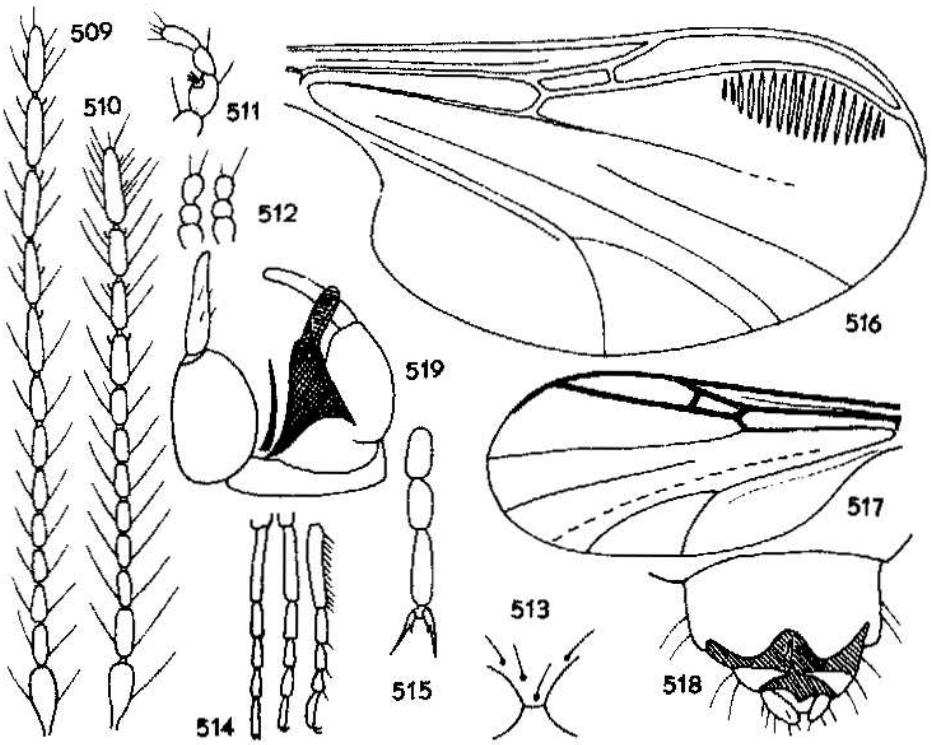
14. Genus *Eohelea* Petrunkevitch, 1957

Eohelea PETRUNKEVITCH, 1957: 208, type-species *E. stridulans* PETRUNKEVITCH, 1957 (=*Ceratopogon sinuosus* MEUNIER, 1904), by original designation; SZADZIEWSKI, 1985: 124 (diagnosis).

DIAGNOSIS

A genus of small extinct midges. Eyes separated. Female antenna with 13 cylindrical flagellomeres, the distal 5 elongated. Male antenna with 12 separate, cylindrical flagellomeres, the distal 4 elongated, last unit longest, plume not developed. Palpus short, 5-segmented. Third palpal segment ovoid with distinct sensory pit. Antepronotum small. Legs slender and unarmed. Fourth tarsomeres cylindrical or subcylindrical. Females claws short, equal, each with basal inner tooth. Wing broad in female, narrower in male. Membrane covered with microtrichia, macrotrichia absent. Second radial cell extending nearly to wing tip, costa prolonged almost to wing tip, in male radial cells slightly shorter. Vein R_{2+3} long. In anterodistal part of female cell r_{4+5} stridulating organ composed of ridges or honey-comb like cells present or absent. Vein M_1 atrophied distally when stridulatory organ present, base of M_2 atrophied. Intercalary veins in cell r_{4+5} absent.

Female abdomen with short cerci. Female genitalia not modified or with strongly developed gonapophyses VIII. Male genitalia small; tergite



509–519. *Eohelea sinuosa* (MEUNIER); 509 — female flagellum, 510 — male flagellum, 511 — female palpus, 512 — male palpi, 513 — eyes separation of female, 514 — female tarsi of fore, middle and hind leg, MZW 1884/1 a; 515 — female claws of fore leg, MZW 6940 b; 516 — female wing, MZW 7961; 517 — male wing, MZW 393 c; 518 — female genitalia, ZMC 61; 519 — male genitalia, MZW 393 c

IX moderately long with indistinct apicolateral setosed lobes. Aedeagus long with slender distal portion curved ventrally. Parameres separated, rod-like.

DISCUSSION

This unusual genus belong to the group of probably related genera including *Parastilobezzia* WIRTH et BLANTON, *Fittkauhelea* WIRTH et BLANTON, *Parabezzia* MALLOCH and *Paralluaudomyia* CLASTRIER which have elongated radial cells and costa prolonged to the wing tip.

It is worth noting that HENNIG (1973) recognized stridulatory organ of *Eohelea* as an artifact (see p. 10).

Eohelea is found also in the Miocene Saxonian amber from Bitterfeld (see *E. sinuosa*). In the Baltic amber material examined 50 specimens of the genus belonging to 4 distinct species have been found.

Key to Baltic amber species of *Eohelea*

Females

1. Stridulatory field present in anterodistal part of cell r_{4+5} just below the vein R_{4+5} 2
—. Wing without stridulatory organ 3
2. Stridulatory organ composed of 9–21 parallel ridges . . . . . 1. *E. sinuosa* (MEUNIER)
—. Stridulatory organ honey-comb like . . . . . 2. *E. petrunkevitchi* SZADZIEWSKI
3. Second radial cell narrow in distal part . . . 3. *E. grogani* sp. n.
—. Second radial cell broad in distal part . . . 4. *E. gedanica* sp. n.

1. *Eohelea sinuosa* (Meunier, 1904), comb. n.

(Figs. 509–519)

Ceratopogon sinuosus MEUNIER, 1904: 234 (♀, Baltic amber).
Ceratolophus sinuosus: KIEFFER, 1906: 1 (combination).
Johannsenomyia sinuosa: COCKERELL, 1919: 243 (combination).
Eohelea stridulans PETRUNKEVITCH, 1957: 208 (♀, Baltic amber); SZADZIEWSKI, 1984: 37 (♀, ♂, Baltic amber); SZADZIEWSKI, 1985: 124 (♀, ♂, Baltic amber), **syn. n.**
Eohelea sp. A indet. SZADZIEWSKI, 1985: 126 (♂, Baltic amber).
Eohelea sp. B indet. SZADZIEWSKI, 1985: 127 (♀, Baltic amber).

DIAGNOSIS

Female of the species is characteristic in having stridulatory organ composed of 9–21 parallel ridges forming an elliptic field in the cell r_{4+5}, and second radial cell narrow in distal part.

DESCRIPTION

♀. Body brown or black. Total length 1.1–1.3 mm. Flagellum length 424–485 μm, AR 0.91–0.95. Last flagellomere shorter than preceding one (fig. 509). All flagellomeres cylindrical. Palpus short (fig. 511). Third palpal segment with distinct sensory pit bearing sensilla capitata, length 24–28 μm. Eyes broadly separated (fig. 513). Scutellum with 4 long setae. Fourth tarsomeres cylindrical (fig. 514). Claws short, equal, each with basal inner tooth. Tibial comb composed of 4 spines. TR(I) 2.0–2.2, TR(II) 2.5–2.8, TR(III) 2.7–2.9. Wing length 0.71–0.95 mm. First radial cell short, second one long and narrow extending nearly to wing tip. Costa prolonged to wing tip. Distal portion of M_1 atrophied, base of M_2 lacking. In anterodistal portion of cell r_{4+5} just below the vein R_{4+5} is a readily visible elliptic stridulatory field composed of 9–21 ridges (fig. 516). Most common number of ridges 17–18. Stridulating apparatus composed of convex ridges formed by wing membrane. Genitalia not modified (fig. 518). Sternite VIII large with submedian caudal lobes. Sternite IX narrow, barely visible.

♂. Body brown or black. Total length 0.9–1.1 mm. Flagellum length 416–432 μm, AR 0.59–0.65. Flagellum composed of 12 separate flagellomeres. Plume not developed, each flagellomere with normal short verticils (fig. 510). Last flagellomere longest. Palpus as in fig. 512. Third palpal segment ovoid. Scutellum with 4 long setae. Fourth tarsomeres cylindrical or subcylindrical. TR(I) 2.0–2.3, TR(II) 2.4, TR(III) 2.2–2.5. Wing length 0.51–0.89 mm. Vein R_{4+5} straight, cells r_1 and r_{2+3} shorter than in female (fig. 517). Costa prolonged beyond tip of R_{4+5}, not quite reaching wing tip. Vein M_1 almost straight, readily visible from base to wing tip. Stridulating organ absent.

Genitalia in normal position or slightly rotated (fig. 519). Sternite IX with broad and shallow caudomedian excavation. Tergite IX short and broad. Gonostylus slender slightly tapering to somewhat curved tip. Aedeagus longer than gonocoxite with low basal arch, caudomedian projection long with rounded tip curved ventrally.

MATERIAL EXAMINED (7 ♂, 26 ♀)

Lectotype — ♀ of *C. sinuosus*, IMGPUG 5459 (+*Empididae* 1). Paralectotype – ♀ of *C. sinuosus*, IMGPUG 7972 (+ 1 ♂ *E. sinuosa* in the same amber piece not mentioned by MEUNIER in original description of the species). Present designation.

MBI 131, KÜHL, 1 ♀; 132, KÜHL (+*Dolichopodidae* 1 ♂, *Psychodidae* 1 ♀), 1 ♀; 199, KÜNOW (+*Aranei* 1), 1 ♀; 148, KÜHL (+*Mycetophilidae* 1 ♀), 1 ♀; MM 10, 1 ♂; MZW 393 c, 1 ♂; 1884/1 a, 1 ♂ 1 ♀; 2257, 1 ♀; 6553, 1 ♀; 6940 b, 1 ♀; 7961, 1 ♀; 14030, TG, 1 ♀; 18337, TG, 1 ♀; ZMC

55, C. V. HENNINGSEN, 12–4 1957, 1 ♀; 56, C. V. HENNINGSEN, 3–5 1960, 1 ♀; 57, A. K. ANDERSEN, 28–3 1968, 1 ♀; 58, A. K. ANDERSEN, 28–3 1968, 1 ♀; 59, as above, 1 ♀; 60, Libau, Kobmand TIDEMAND, Min. Mus. 1941–3, 1 ♀; 61, A. K. ANDERSEN, 28–3 1968, 1 ♀; 62, as above, 1 ♀; 64, C. V. HENNINGSEN, 16–1 1961, 1 ♀; 65, C. V. HENNINGSEN, 25–3 1961, 1 ♂; 66, C. V. HENNINGSEN, 1–7 1966, Ostpreussen, 1 ♂; 151, C. V. HENNINGSEN, 12–4 1957, 1 ♀; 196, A. HENNINGSEN, 9–9 1974, 1 ♀; 201, C. V. HENNINGSEN, 9–9 1974, 1 ♀.

NOTE

Among the specimens of *Ceratopogonidae* from the Miocene Saxonian amber from Bitterfeld in East Germany I have found 2 females of *E. sinuosa*.

2. *Eohelea petrunkevitchi* Szadziewski, 1984
(Figs. 520–525)

Eohelea petrunkevitchi SZADZIEWSKI, 1984: 39 (♀, Baltic amber); SZADZIEWSKI, 1985: 127 (♀, Baltic amber).

DIAGNOSIS

Female of this species is characteristic in having the stridulating organ honey-comb like.

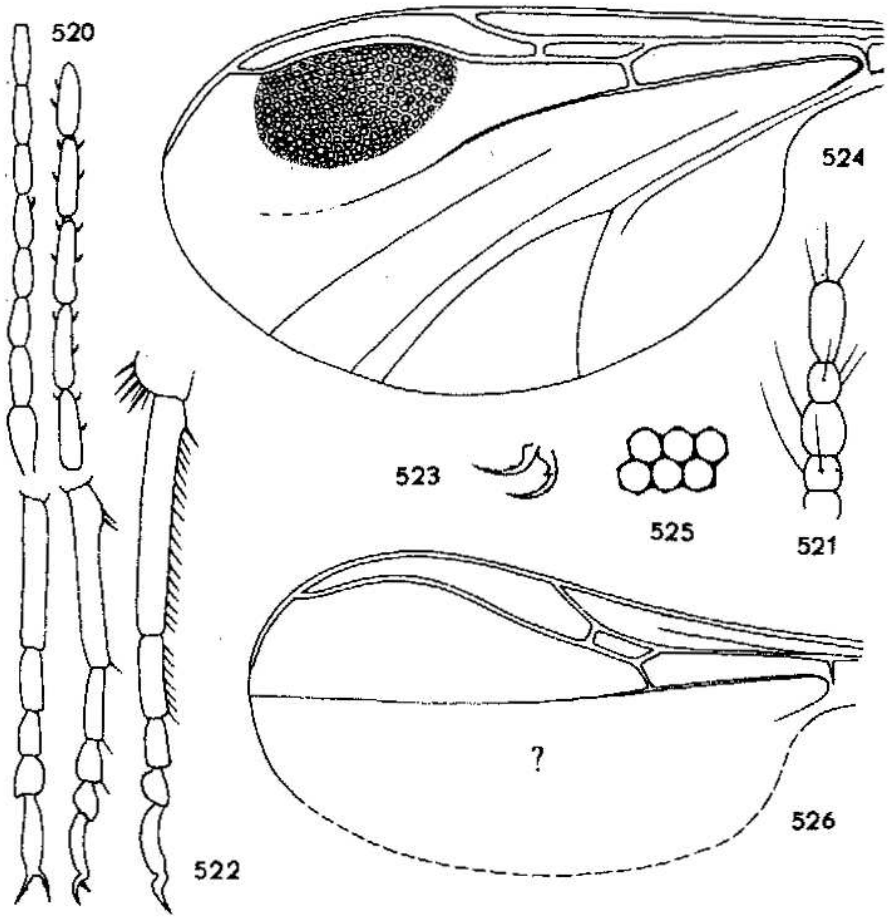
DESCRIPTION

♀. Body dark brown or black. Total length 1.5 mm. Flagellum length 589 μm, AR 0.88. Last flagellomere shorter than preceding one (fig. 520). Eyes separated. Palpus short (fig. 521). Third palpal segment about 10 μm long, sensory pit not visible. Scutum with distinct setae and short pubescence. Scutellum bearing 8 long setae. Tibial comb composed of 4 spines. Fourth tarsomeres subcylindrical (fig. 522). TR(I) 2.6–2.7, TR(II) 2.5–2.9, TR(III) 2.8–2.9. Wing length 0.92–0.98 mm (fig. 524). Second radial cell narrow and long extending nearly to wing tip, costa prolonged to wing tip. Stridulatory field ovoid, honey-comb like composed of round cells with bottoms convex on dorsal surface of wing (fig. 525). Vein M_1 strongly curved upward on distal portion which becomes obsolete, M_2 atrophied at base. Genitalia not modified.

♂. Unknown.

MATERIAL EXAMINED (3 ♀)

Holotype — ♀, MZW 13990, TG. MZW 2939, 1 ♀; ZMC 63, C. V. HENNINGSEN, 14–11 1959, 1 ♀.



520–526. *Eohelea petrunkevitchi* SZADZIEWSKI and *E. grogani* sp. n., females; *E. petrunkevitchi* (520–525): 520 — flagellum, 521 — palpus, MZW 13990; 522 — tarsi of fore, middle and hind leg, MZW 2939; 523 — claws of middle leg, 524 — wing, MZW 13990; 525 — "cells" of stridulatory field, ZMC 63; *E. grogani* sp. n., MZW 14831 (526): 526 — wing

3. *Eohelea grogani* sp. n.
(Fig. 526)

DIAGNOSIS

Female of this species is very similar to *E. sinuosa* but wing is devoid of stridulatory organ and vein M_1 is straight and not atrophied distally.

DESCRIPTION

♀. Body brown. Total length 1.4 mm. Scutum pollinosed and with fine setae and long supraalars. Scutellum with 4 fine long setae. Fourth tarsomeres subcylindrical. Claws short, equal, sharp, each with basal inner tooth. TR(II) 2.4, TR(III) 2.5. Wing length 0.91 mm. Anterior veins similar to *E. sinuosa* and *E. petrunkevitchi*, but stridulatory organ absent and vein M_1 straight and not reduced distally (fig. 526). Female genitalia not modified.

♂. Unknown.

MATERIAL EXAMINED (1 ♀)

Holotype — ♀, MZW 14831, TG.

ETYMOLOGY
(see p. 65)

4. *Eohelea gedanica* sp. n.
(Figs. 527–535)

DIAGNOSIS

Female of the species is distinguished by the following combination of characters: wing without stridulatory organ, second radial cell broad, vein M_1 almost straight and not atrophied distally, gonapophyses VIII very large. Male not differing from *E. sinuosa*.

DESCRIPTION

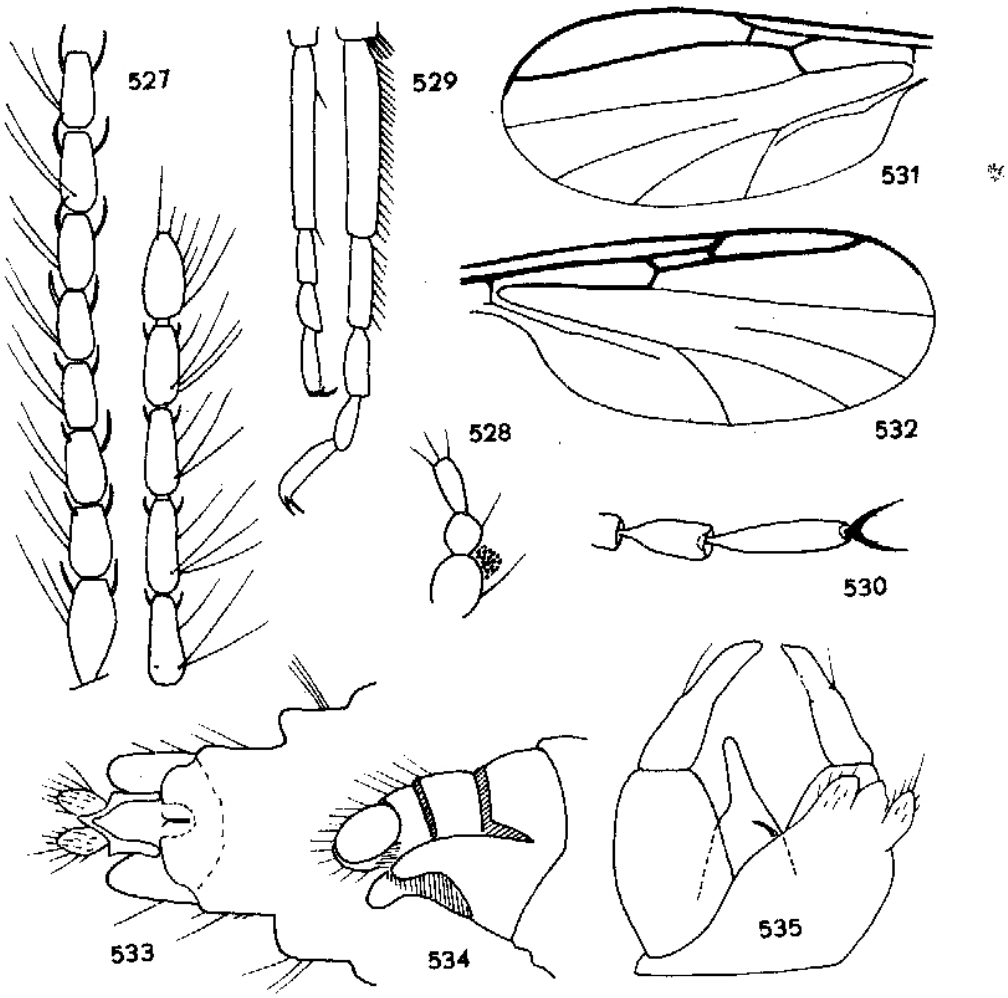
♀. Body brown or dark brown. Total length 1.4–1.6 mm. Flagellum length 444–478 μm, AR 0.72–0.82. Distal 5 flagellomeres only slightly longer than proximal 8 (fig. 527). Eyes broadly separated. Proboscis short. Palpus short (fig. 528). Third palpal segment 24 μm long, ovoid. Scutellum with 4 long and 2–5 shorter setae. Fourth tarsomeres cylindrical (fig. 529). Claws short, equal, each with basal inner tooth (fig. 530). TR(I) 2.1, TR(II) 2.2–2.5, TR(III) 2.2. Wing length 0.93–1.05 mm. Second radial cell extending almost to wing tip, in distal part broad (fig. 531). Costa extending to wing tip. Stridulatory organ absent. Vein M_1 readily visible from base to tip, almost straight. Vein M_2 with atrophied base. Membrane with distinct microtrichia, macrotrichia absent. Cerci short. Sternite VIII with long and broad lobe-shaped gonapophyses VIII reaching bases of cerci (figs. 533, 534).

♂. Body dark brown or black. Total length 1.1 mm. Antenna composed of 12 flagellomeres, plume absent. Last flagellomere longest. Third palpal segment short. Scutellum with 4 long and 4 shorter setae. Fourth tarsomeres cylindrical or subcylindrical. TR(I) 2.3, TR(II) 2.0, TR(III) 2.4. Wing length 0.74–0.76 mm. Venation as in *E. sinuosa* (fig. 532).

Genitalia inverted (fig. 535), not differing from those of *E. sinuosa*. Tergite IX strongly reclined.

MATERIAL EXAMINED (4 ♂, 9 ♀)

Holotype — ♀, MZW 7106. Paratypes: MZW 2145/96 a, b, 2 ♀ 4 ♂; 2613, 1 ♀; 3099 a, b, 2 ♀; 12259, 1 ♀; ZMC 125, C. V. HENNINGSEN, 1–1 1966, 1 ♀; 135, as above, 1 ♀.



527–535. *Eohelea gedanica* sp. n.; 527 — female flagellum, 528 — female palpus, 529 — female tarsi of middle and hind leg, MZW 7106; 530 — female claws of fore leg, MZW 2145/96 a; 531 — female wing, MZW 7106; 532 — male wing, MZW 2145/96 a; 533 — ventral view of female genitalia, MZW 2613; 534 — lateral view of female genitalia, MZW 12259; 535 — male genitalia, MZW 2145/96 a

15. Genus *Gedanohelea* gen. n.

Type-species *Gedanohelea loewi* **sp. n.**, by present designation.

DIAGNOSIS

Very small midges distinguished by the following combination of characters: antenna in both sexes with 13 flagellomeres, plume in male not developed, wing broad with broad anal lobe and with single, small radial cell, media petiolate, M_1 bowed upward distally and reaching wing margin distinctly anterad of wing tip, tarsi short, female claws long and single.

DESCRIPTION

Very small biting midges. Antenna composed of 13 cylindrical flagellomeres. In male plume not developed and all flagellomeres separated. Sensilla coeloconica absent. Proboscis short. Palpus short, 5-segmented. Third palpal segment spherical with distinct sensory pit bearing sensilla capitata. Eyes separated. Scutum with numerous setae and short pubescence. Prescutal pits present. Scutellum bearing 4 long setae. Antepronotum small, hidden below postpronotum. Wing broad with distinct anal lobe in both sexes. Membrane without macrotrichia, microtrichia indistinct. Radial cell very short and single. CR 0.47–0.55. M_1 and M_2 petiolate strongly divergent. M_1 bowed upward distally reaching wing margin distinctly anterad of wing tip. Costa rather not prolonged beyond radial cell. Legs slender and unarmed. Tarsi short. Fourth tarsomeres cordiform, fifth tarsomeres long and slender. Female claws single and long on all legs. Hind basitarsus with dense hair-like palisade setae. Female genitalia not modified, cerci short. Male genitalia not visible.

DISCUSSION

Gedanohelea is an extinct genus very similar to the recent Oriental genus *Camptopterohelea* WIRTH et HUBERT including 5 species from Philippines, Java (Indonesia), Malaysia and India (WIRTH and HUBERT, 1960; WIRTH and WADA, 1979; DAS GUPTA and SARKAR, 1982) (fig. 765). *Camptopterohelea* differs from *Gedanohelea* by the more reduced, 3-segmented palpi, by the more highly modified female wings: media and r-m crossvein absent, anterior part of wing with a large transverse area covered with dense and coarse microtrichia, and by the male flagellum composed of 11 flagellomeres.

In the material examined 5 females and 1 male of *Gedanohelea* have been found.

Key to Baltic amber species of *Gedanohelea*

Females

1. Veins M_1 and M_2 strongly divergent . . . . 3. *G. wirthi* sp. n.
—. Veins M_1 and M_2 slightly divergent 2
2. Fifth tarsomere of fore leg distinctly shorter than combined length of tarsomeres 2–4, claw almost as long as fifth tarsomere . . . . . 1. *G. loewi* sp. n.
—. Fifth tarsomere of fore leg as long as combined length of tarsomeres 2–4, claw shorter than fifth tarsomere . . . . 2. *G. succinea* sp. n.

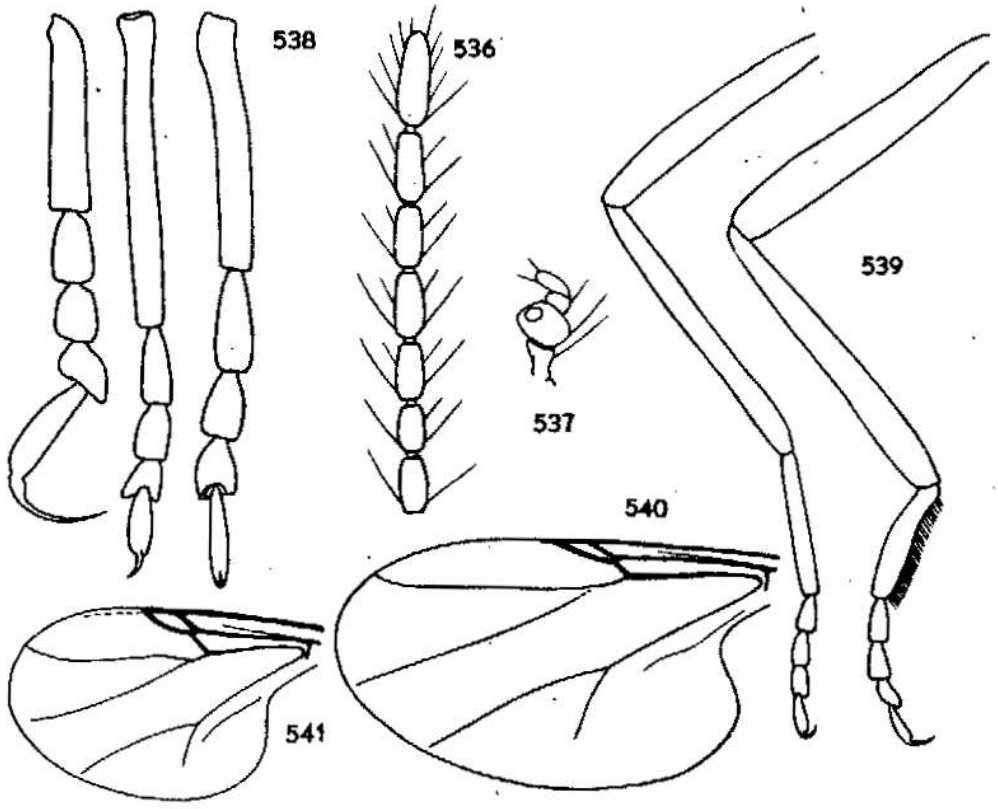
1. *Gedanohelea loewi* sp. n.
(Figs. 536–541)

DIAGNOSIS

Veins M_1 and M_2 weakly divergent in both sexes. Female claw of fore leg almost as long as fifth tarsomere and fifth tarsomere is distinctly shorter than combined lengths of tarsomeres 2–4; claws of middle and hind legs shorter.

DESCRIPTION

♀. Body dark brown. Total length 1.1 mm. Antenna with 13 cylindrical flagellomeres (fig. 536). Last flagellomere longest, measuring 44 μm. Distal 5 flagellomeres slightly longer than proximal units. Proboscis short. Palpus short, 5-segmented (fig. 537). Third palpal segment almost spherical with small, round sensory pit. Eyes separated. Scutellum with 4 long setae. Prescutal pits present. Legs slender (fig. 539). Hind basitarsus with dense hair-like palisade setae. Tarsomeres 2–4 short (fig. 538). Fourth tarsomeres cordiform or slightly subcylindrical on hind leg. Fifth tarsomeres long. Claws of all legs single. Claw



536–541. *Gedanohelea loewi* sp. n.; 536 — female distal flagellomeres, 537 — female palpus, MZW 7056 a; 538 — female tarsi of fore, middle and hind leg, MZW 10287; 539 — female middle and hind leg, 540 — female wing, 541 — male wing, MZW 7056 a

of fore leg almost as long as fifth tarsomere. Fifth tarsomere of fore leg shorter than combined lengths of tarsomeres 2–4. Claws of middle and hind legs shorter. TR(I) 2.8, TR(II) 3.9, TR(III) 2.5–3.1. Wing length 0.70–0.73 mm, CR 0.47–0.50. Veins M_1 and M_2 slightly divergent (fig. 540). Genitalia not modified, sternite VIII broad with distinct caudomedian notch.

♂. Body blackish brown. Antenna composed of 13 flagellomeres very similar to that of female. Plume absent. Last flagellomere 40 μm long. Prescutal pits visible. Scutellum bearing 4 long setae. Legs slender. Fourth tarsomeres slightly longer than in female, subcylindrical. Claws short and equal. TR(III) 2.5. Wing length 0.51 mm, CR about 0.55. Media slightly divergent (fig. 541). Genitalia barely visible.

MATERIAL EXAMINED (1 ♂, 3 ♀)

Holotype — ♀, MZW 10287. Paratypes: MZW 7056 a, 1 ♂ 1 ♀; 12460, 1 ♀.

ETYMOLOGY

This species is named for H. LOEW a prominent dipterist of XIX century who was the first to describe the Baltic amber biting midges.

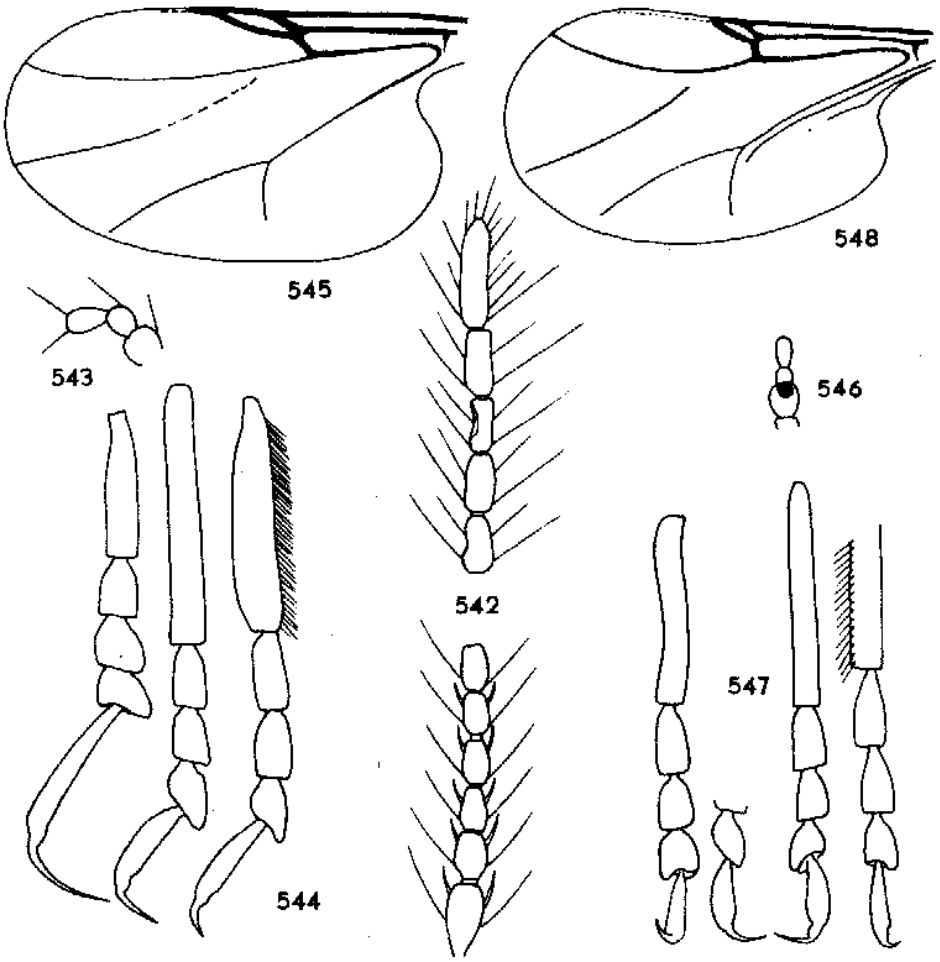
2. *Gedanohelea succinea* sp. n.
(Figs. 542–545)

DIAGNOSIS

Female of this species is similar to *G. loewi* **sp. n.** and differs only in having longer fifth tarsomere of fore leg which is as long as combined lengths of tarsomeres 2–4.

DESCRIPTION

♀. Body brown. Total length 1.2 mm. Flagellum as in fig. 542. Last flagellomere longest. Proboscis short. Palpus short (fig. 543). Eyes separated. Prescutal pits distinct. Scutellum with 4 long setae. Legs slender. Tarsi as in fig. 544. Hind basitarsus with dense hair-like palisade setae. Tarsomeres 2–4 short, fourth tarsomeres cordiform. Fifth tarsomere of fore leg long and slender, as long as combined lengths of tarsomeres 2-4, claw distinctly shorter than fifth tarsomere. Fifth tarsomeres of middle and hind legs shorter with shorter claw than those of fore leg. Wing length 0.76 mm, CR 0.52. Costa apparently not prolonged beyond



542–548. *Gedanohelea succinea* sp. n. and *G. wirthi* sp. n., females; *G. succinea* sp. n., MZW 20010 (542–545): 542 — flagellum, 543 — palpus, 544 — tarsi of fore, middle and hind leg, 545 — wing; *G. wirthi* sp. n., ZMC 133 (546–548): 546 — palpus, 547 — tarsi, 548 — wing

tip of vein R_{4+5} (fig. 545). M_1 and M_2 weakly divergent, base of M_2 broadly atrophied, distal portion of M_1 bowing slightly upward near wing margin.

♂. Unknown.

MATERIAL EXAMINED (1 ♀)

Holotype — ♀, MZW 20010, TG.

3. *Gedanohelea wirthi* sp. n.
(Figs. 546–548)

DIAGNOSIS

Female of this species is characteristic in having greatly divergent veins M_1 and M_2, vein M_1 bowing greatly upward distally, and claws of all legs short.

DESCRIPTION

♀. Body blackish brown. Total length 1.1 mm. Flagellum barely visible, last flagellomere longest. Proboscis short. Palpus short (fig. 546). Third palpal segment spherical with distinct sensory pit. Tarsi as in fig. 547. Fourth tarsomeres cordiform. Fifth tarsomeres and claws similar on all legs, short. TR(I) 2.7, TR(II) 3.5. Wing length 0.70 mm, CR 0.50. Veins M_1 and M_2 strongly divergent, M_1 bowed greatly upward distally (fig. 548). Costa not produced beyond tip of R_{4+5}.

♂. Unknown.

MATERIAL EXAMINED (1 ♀)

Holotype — ♀, ZMC 133, C. V. HENNINGSEN, 16–5 1956.

ETYMOLOGY

(see p. 159)

16. Genus *Ceratopalpomyia* gen. n.

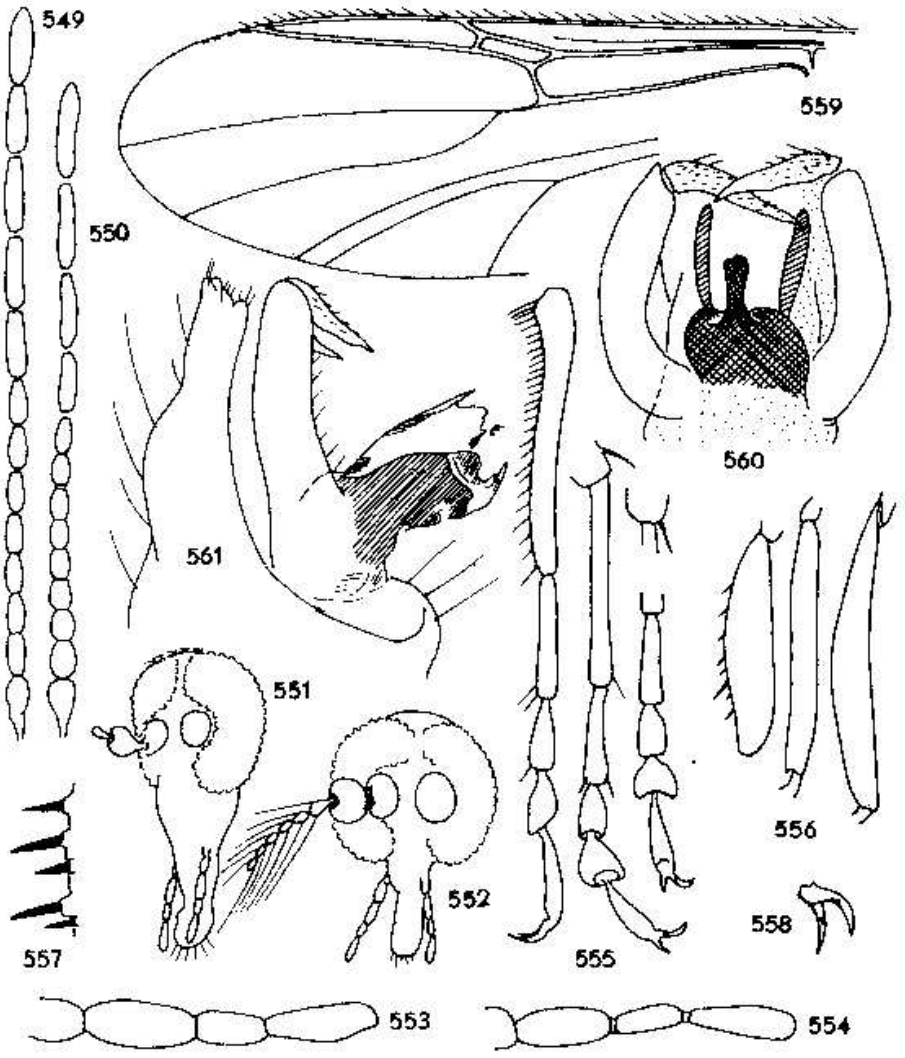
Type-species *Ceratopalpomyia eocenica* **sp. n.**, by present designation.

DIAGNOSIS

This genus is distinguished by the following combination of characters: wing with 2 first radial cells, media petiolate forking distally of r-m crossvein, fore femur enlarged and armed with strong ventral spines, female proboscis very long, male gonocoxites long and slender.

DESCRIPTION

Moderately large midges. Female eyes separated. Antenna moderately long, distal flagellomeres not distinctly elongated. In male distal 4 flagellomeres elongated, plume weakly developed. In both sexes antenna with 13 flagellomeres, sensilla coeloconica absent. Female proboscis very long, in male shorter. Palpus 5-segmented. Third palpal segment cylindrical, without sensory pit. Antepronotum small, hidden below postpronotum. Scutum without anterior spine or tubercle. Fore femur in both sexes enlarged and armed with at least 10 strong ventral spines. Fourth tarsomeres cordiform. Female claws short, equal, each with inner tooth, similar on all legs. Wing narrow. Costa long, first radial cell short, second one long. Media petiolate. Wing membrane with distinct microtrichia, macrotrichia absent. Female cerci short. Male



549–561. *Ceratopalpomyia eocenica* sp. n., ZMC 233; 549 — female flagellum, 550 — male flagellum, 551 — female head, 552 — male head, 553 — female palpus, 554 — male palpus, 555 — female tarsi of hind, middle and fore leg, 556 — female femora of fore, middle and hind leg, 557 — ventral spines of male fore femur, 558 — female claws of hind leg, 559 — female wing, 560 — ventral view of male genitalia, 561 — lateral view of male genitalia

genitalia rotated. Gonocoxite slender and long. Aedeagus with broad main body and long, slender caudomedian projection. Parameres widely separated, stout and long.

DISCUSSION

This new genus resembles the genus *Palpomyia* of the tribe *Palpomyiini* because of its spinose fore femur. However in *Palpomyia* the media is sessile, proboscis shorter, the aedeagus is usually broadly triangular and parameres are usually fused or only narrowly separated on their distal

portion. The wing venation of *Ceratopalpomyia* with its petiolate media is typical of the tribe *Stilobezziini.*

In the material examined only 2 specimens belonging to 1 species have been found.

1. *Ceratopalpomyia eocenica* sp. n.
(Figs. 549–561)

DESCRIPTION

♀. Body dark brown. Total length 1.6 mm. Eyes separated. Flagellum length 608 μm, AR 1.02. Distal 5 flagellomeres slightly longer than proximal 8 (fig. 549). Proboscis very long and stout (fig. 551). Third palpal segment 48 μm long, without sensory pit (fig. 553). Scutum covered with small and fine setae. Scutellum bearing ca. 10 long setae. Fore femur enlarged and armed with more than 10 strong ventral spines (fig. 556). Hind femur slightly enlarged and somewhat bent. Tibial spur of fore leg indistinct. Hind basitarsus distinctly bent at base, with numerous palisade setae (fig. 555). Fourth tarsomeres cordiform. Claws of all legs short, equal, each with basal inner tooth (fig. 558). TR(II) 2.2, TR(III) 2.3. Wing length 1.24 mm, CR 0.80. Second radial cell triangular and long (fig. 559). Costa not prolonged much beyond tip of R_{4+5}. M_2 not atrophied at base. Intercalary fork not visible. Membrane with distinct microtrichia, macrotrichia absent. Cerci short.

♂. Body blackish brown. Total length 1.6 mm. Flagellum length 594 μm, AR ca. 1.0. Distal 4 flagellomeres elongated (fig. 550). Plume sparse and short not reaching last flagellomere. Proboscis slender, moderately long (fig. 552). Palpus as in fig. 554. Third palpal segment 45 μm long. Fore femur armed with about 10 strong ventral spines (fig. 557). Tibial comb composed of 5 spines. TR(I) 1.8. Wing length 0.99 mm, CR 0.71.

Genitalia rotated 90° (figs. 560, 561). Sternite IX probably with broad and shallow caudomedian excavation. Tergite IX long, reaching tip of gonocoxite. Gonocoxite moderately curved proximally, straighter distally, very slender and long. Gonostylus slender, nearly straight with distinctly pointed tip. Aedeagus with main body broad and short bearing long finger-like apicomedian projection. Parameres widely separated, rod-like, long. Aedeagus and parameres strongly deflected ventrally.

MATERIAL EXAMINED (1 ♂, 1 ♀)

Holotype — ♀, ZMC 233, A. HENNINGSEN, 9–9 1974. Paratype — ♂, ZMC 233, together with the holotype.

Tribe *Heteromyiini* Wirth, 1962

Diagnosis

Usually large midges. Flagellum in both sexes with 13 flagellomeres. In male, plume developed and distal 4 flagellomeres elongated. Palpus slender, 5-segmented. Third palpal segment without sensory pit. Scutum with or without anterior spine or tubercle. Legs long and usually slender. Femora sometimes swollen and armed with strong ventral spines. Fourth tarsomeres cordiform or greatly elongated on hind leg. Fifth tarsomeres not armed with strong spines. Female claws usually unequal, at least on hind leg. If claws short and equal on all legs, then fifth tarsomere of fore leg inflated and broad. Wing membrane with distinct microtrichia, macrotrichia absent. Costa long. First radial cell single or both first and second radial cells present. Media barely to broadly sessile forking at level or proximal to crossvein r-m. Female abdomen without internal eversible glands or sclerotized gland rods. Male genitalia usually long and simple. Aedeagus more or less triangular, parameres separated.

Recent ecology, distribution and classification

The adult females are predaceous on *Chironomidae* and other small insects (Downes, 1978; Wirth and Grogan, 1979). In the tribe there are presently known 9 recent genera: *Neurohelea*, *Physohelea*, *Neurobezzia* Wirth et Ratanaworabhan (California, Seychelles), *Heteromyia* Say (South and North Americas), *Pellucidomyia* Macfie (Afrotropical, Neotropical, Australian regions), *Clinohelea* Kieffer (worldwide), *Ceratobezzia* Kieffer (Afrotropical, Neotropical), *Metahelea* Edwards (Oriental, Australian), and *Tetrabezzia* Kieffer (Oriental and Afrotropical regions). About 60 extant species are known in the tribe.

Fossils

The *Heteromyiini* are known as fossils only from Baltic amber. In the material examined 13 specimens belonging to the genera *Neurohelea* and *Physohelea* have been found.

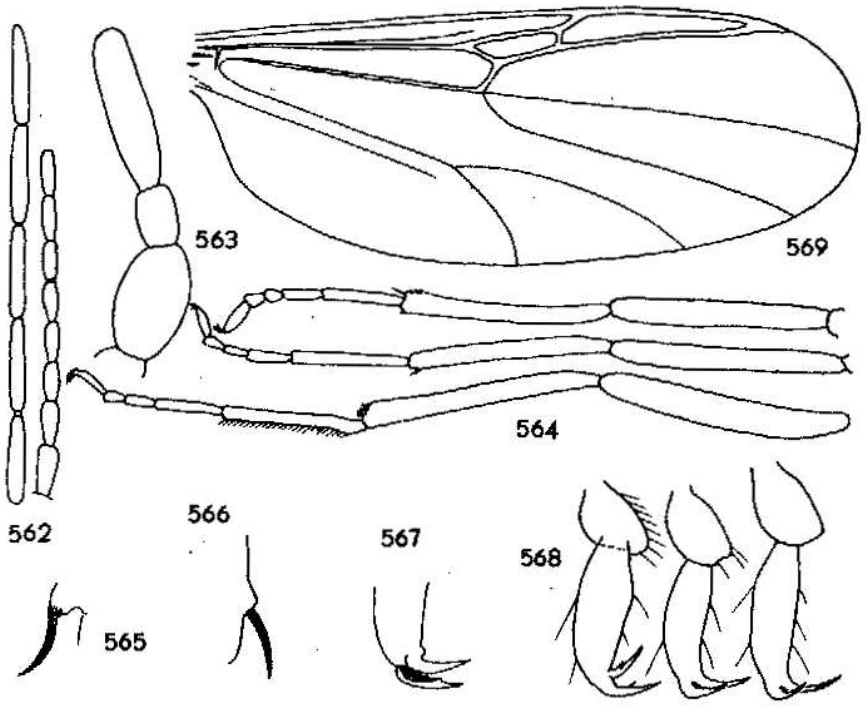
Key to Baltic amber genera of *Heteromyiini*

1. Fore femur without ventral spines. Fifth tarsomere of fore leg slightly swollen . . . . . *Neurohelea*
—. Fore femur with 4—5 ventral spines. Fifth tarsomere of fore leg elongated and greatly swollen . . . . . *Physohelea*

17. Genus *Neurohelea* Kieffer, 1925

DIAGNOSIS

Eyes separated. Male flagellum with sparse plume. Scutum without anterior spine or tubercle. All femora slender and unarmed. Fifth tarsomere of fore leg slightly swollen in both sexes. Female claws equal



562–569. *Neurohelea cothurnata* (MEUNIER), female, IMGPUG 6897, 8270; 562 — flagellum, 563 — palpus, 564 — fore, middle and hind leg, 565 — tibial spur of fore leg, 566 — preapical spine of middle tibia, 567 — claws of hind leg, 568 — claws of fore, middle and hind leg, 569 — wing

and similar on all legs, each with basal inner tooth. Wing moderately broad. First radial cells well developed. Costa produced beyond tip of R_{4+5}. Media barely sessile, forking at level of crossvein r-m.

RECENT DISTRIBUTION

There are presently 3 known recent species from Europe and North America: *N. luteitarsis* (MEIGEN) (West Europe: England, Belgium, Germany), *N. macroneura* (MALLOCH) (North America: Kansas, Texas, Illinois), and *N. nigra* WIRTH (North America: California, British Columbia, Oregon, Washington, Tennessee, Virginia, North Carolina and Georgia; WIRTH and GROGAN, 1979) (fig. 766).

FOSSILS

Fossil *Neurohelea* are known only from Baltic amber. In the material examined 8 females belonging to a single species have been found.

1. *Neurohelea cothurnata* (Meunier, 1904), comb. n.
(Figs. 562–569)

Ceratopogon cothurnatus MEUNIER, 1904: 231 (♀, Baltic amber).
Ceratopogon flagellus MEUNIER, 1904: 230 (♀, Baltic amber), **syn. n.**
Ceratolophus flagellus: KIEFFER, 1906: 1 (combination).

DESCRIPTION

♀. Body dark brown or blackish. Total length 1.5–2.0 mm. Flagellum length 683–846 μm, AR 1.12–1.43. Proximal 8 flagellomeres slightly elongated, distal 5 twice as long as proximal units (fig. 562). Last flagellomere slightly pointed with long apical seta. Proboscis moderately short. Third palpal segment 48–56 μm long (fig. 563). Scutum shining, covered with short sparse setae. Scutellum with 4 setae. Prescutal pits absent. Legs slender (fig. 564). Spur of fore tibia long and curved (fig. 565). Middle tibia with long preapical spine (fig. 566). Tibial comb composed of ca. 5 spines. Fourth tarsomeres cordiform. Fifth tarsomere of fore leg slightly swollen, of middle and hind legs slender (fig. 568). Claws short, equal, each with inner basal tooth (figs. 567, 568). TR(I) 2.0–2.2, TR(III) 2.1–2.2. Wing length 1.14–1.40 mm, CR 0.86–0.90 (fig. 569). Second radial cell twice as long as first one, costa produced slightly beyond R_{4+5}. Base of M_2 readily visible.

♂. Unknown.

MATERIAL EXAMINED (8 ♀)

Lectotype — ♀ of *C. cothurnatus*, IMGPUG Z 8270. Paralectotypes of *C. cothurnatus*: IMGPUG Z 5236, 1 ♀; 7715, 1 ♀. Present designations. Paralectotype female IMGPUG 7715 does not belong to *N. cothurnata* but to an undetermined species of the genus *Stilobezzia*. Holotype — ♀ of *C. flagellus*, IMGPUG Z 6897.

MBI 209, BERENDT, 1 ♀; MZW 16590, TG, 1 ♀; ZMC 77, C. V. HENNINGSEN, 1–4 1970, 1 ♀; 122, C. V. HENNINGSEN, 1–5 1967, 1 ♀; 239, A. HENNINGSEN, 9–9 1974, 1 ♀.

18. Genus *Physohelea* Grogan et Wirth, 1979

DIAGNOSIS

A genus very similar to *Neurohelea* differing in having the fore femur armed with 4–12 ventral spines and the fifth tarsomere of the fore leg greatly swollen and elongated. Male genitalia small.

RECENT DISTRIBUTION

Only 2 recent species described from females are known in the genus from Patagonia and South Chile (GROGAN and WIRTH, 1979 a) (fig. 766). *Physohelea* is a sister group of *Neurohelea*. This genus may be of Euro-North American origin which then may have migrated to South America and became extinct in the North Hemisphere (see chapter VIII).

FOSSILS

In the material examined 2 males and 3 females of a single species *P. obtusa* have been found. It is interesting that males of the genus are known only from Baltic amber. However, GROGAN (personal comm.) informs me that a new undescribed species and males of the genus were recently collected in southern South America by DOWNES and SPINELLI.

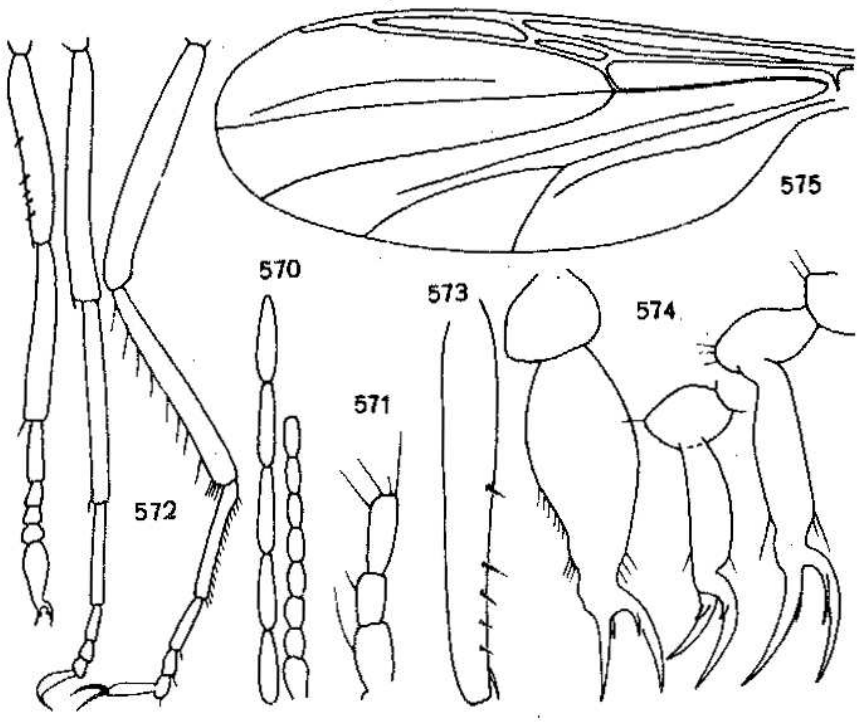
1. *Physohelea obtusa* (Meunier, 1904), comb. n.
(Figs. 570–583)

Ceratopogon obtusus MEUNIER, 1904: 235 (♂, Baltic amber).
? *C. cothurnatulus* MEUNIER, 1904: 231 (♀, Baltic amber), **syn. n.**

DESCRIPTION

♀. Body brown or dark brown. Total length 1.3–1.6 mm. Flagellum length 668–705 µm, AR 1.37–1.40. Proximal flagellomeres subcylindrical to slightly cylindrical bearing pair of long subapical sensilla trichodea (fig. 570). Distal 5 flagellomeres moderately long. Proboscis moderately long. Palpus as in fig. 571. Third palpal segment about 40 µm long, without sensory pit. Scutum shining, with sparse setae. Scutellum with 4 moderately long setae. Legs slender (fig. 572). Fore femur slender, armed with 5 moderately strong ventral spines on distal half. Fourth tarsomeres cordiform. Fifth tarsomere of fore leg elongated and strongly swollen (fig. 574), of middle and hind legs slender and shorter. Claws long, equal, each with distinct basal inner tooth, similar on all legs. Spur of fore tibia distinct and curved. TR(I) 2.1, TR(III) 2.3. Wing length 1.01–1.20 mm, CR 0.86–0.88. Media barely sessile, forking at r-m crossvein. Costa distinctly produced beyond tip of R_{4+5} (fig. 575).

♂. Body brown. Total length 1.2–1.4 mm. Flagellum length 599–616 µm, AR 1.02–1.13. Distal 4 flagellomeres more elongated than proximal ones. Plume sparse and short (fig. 576). Last flagellomere with pointed tip bearing long apical seta. Proboscis moderately short. Palpus as in fig. 577. Third palpal segment 30 µm long. Scutum shining, almost bare. Scutellum with 4 indistinct setae. Legs slender (fig. 578). Fore femur armed with 4–5 ventral spines on distal half (fig. 579). Tibial comb with 4 spines. Fourth tarsomeres cordiform. Fifth tarsomere of fore leg



570–575. *Physohelea obtusa* (MEUNIER), female, MZW 12249; 570 — flagellum, 571 — palpus, 572 — fore, middle and hind leg, 573 — fore femur, 574 — last two tarsomeres of fore, middle and hind leg, 575 — wing

elongated and greatly swollen, of middle and hind legs slender and short (fig. 580). Claws moderately short, equal and simple. TR(II) 2.4, TR(III) 2.1–2.5. Wing length 0.90 mm, CR 0.76 (fig. 581). Base of M_2 visible or not. Costa distinctly produced beyond tip of R_{4+5}.

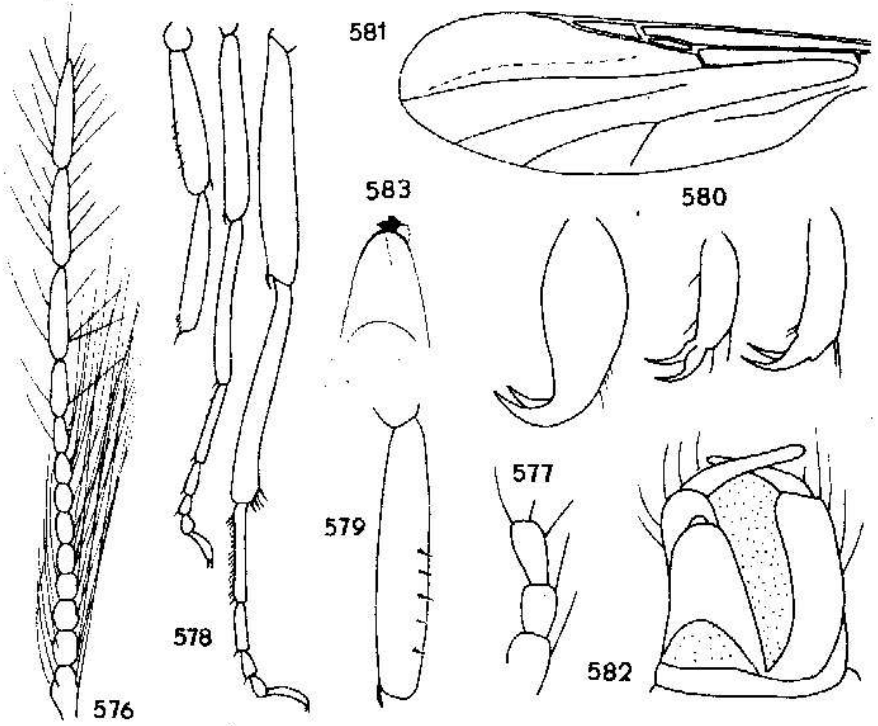
Male genitalia small, inverted or in normal position (figs. 582, 583). Sternite IX short, tergite IX barely visible. Gonocoxite slender, long, slightly curved. Gonostylus slender, nearly straight, tapering slightly distally to broadly rounded tip. Aedeagus with low basal arch, apex broadly rounded with short and indistinct apical projection. Parameres not visible.

MATERIAL EXAMINED (2 ♂, 3 ♀)

Holotype — ♂ of *C. obtusus*, IMGPUG Z 6505. MZW 1832/14 a, 1 ♂; 12249, 1 ♀; 16543, TG, 1 ♀; 19668, TG, 1 ♀.

DISCUSSION

I have not examined the types (2 females) of *Ceratopogon cothurnatulus* since Dr. S. RITZKOWSKI was not able to find them in the collection at IMGPUG (personal comm.). According to original description of this species it may be synonymous with *P. obtusa* "Cette espèce a beacoup de



576–583. *Physohelea obtusa* (MEUNIER), male; 576 — flagellum, 577 — palpus, 578 — legs, 579 — fore femur, 580 — fifth tarsomeres of fore, middle and hind leg, 581 — wing, 582 — genitalia, IMGPUG 6505; 583 — aedeagus, MZW 1832/14 a

ressemblance avec le *C. cothurnatus*. Elle en diffère principalement par le cubitus qui est un peu plus éloigné du bout de l'aile et par les crochets tarsaux qui sont longs et robustes".

Female of *P. obtusa* is distinctly smaller than the 2 known recent species *P. oeidactyla* (INGRAM et MACFIE) and *P. turgidipes* (INGRAM et MACFIE) which have wing 2.5–2.8 mm long (GROGAN and WIRTH, 1979 a).

Tribe *Palpomyiini* Enderlein, 1936

DIAGNOSIS

The *Palpomyiini* and *Stenoxenini* (the latter tribe is absent in Baltic amber) differ from all tribes of the *Ceratopogoninae* in having internal eversible glands and sclerotized gland rods in the female abdomen.

Eyes usually distinctly separated. Flagellum composed of 13 flagellomeres, sensilla coeloconica absent. Distal flagellomeres greatly elongated. In male, plume usually sparse, all flagellomeres separated. Proboscis short to moderately long. Palpus 5-segmented, usually long and slender. Third palpal segment without sensory pit. Antepronotum usually well developed, collar-like. Scutum with or without anterior spine or tubercle. Fore femur slender to greatly swollen, usually armed with strong ventral

spines. Middle and hind femora slender, often with some ventral spines on distal half. Fourth tarsomeres deeply cordiform to cylindrical. Fifth tarsomeres often armed with strong setae. Female claws moderately large or small, equal to subequal, usually similar on all legs, with or without inner teeth. In *Clastrieromyia* SPINELLI et GROGAN and in some *Palpomyia* the hind claws are distinctly elongated. Wing membrane with microtrichia, macrotrichia absent. One or two first radial cells present. Costa usually long, sometimes reaching nearly to wing tip, not produced beyond tip of R_{4+5}. Media sessile, vein M_2 usually forking proximal of crossvein r-m, in some groups at level of the crossvein. Male genitalia with prominent cerci fused with tergite IX. Gonocoxite simple or with prominent tubercle or lobe. Gonostylus usually well developed, slender and long to very short not articulated or totally reduced. Aedeagus usually distinct, triangular or conical. Parameres usually large, fused or narrowly separated.

RECENT ECOLOGY, DISTRIBUTION AND CLASSIFICATION

Females are predaceous on other insects. Larvae are predaceous and common in aquatic and semiaquatic habitats. There are known 6 genera: *Clastrieromyia* (4 spp., Neotropical), *Amerohelea* GROGAN et WIRTH (10 spp., Neotropical plus California to Texas in North America), *Bezzia* (ca. 250 spp., worldwide), *Pachyhelea* WIRTH (1 sp., Nearctic), *Palpomyia* (ca. 250 spp., worldwide) (WIRTH, 1962; WIRTH et al., 1974; GROGAN and WIRTH, 1979 b, 1981; WIRTH and GROGAN, 1982; SPINELLI and GROGAN, 1985).

FOSSILS

The oldest *Palpomyiini* are Eocene in age from Chinese amber (HONG, 1981) and from Baltic amber (present records). *Palpomyiini* have been found also in Oligocene and Miocene rocks. These fossils apparently all belong to the recent genera *Palpomyia* and *Bezzia*.

In the material examined only 5 specimens of *Palpomyia* and *Bezzia* have been found.

Key to Baltic amber genera of *Palpomyiini*

1. Radial cell single . . . . . *Bezzia*
—. First and second radial cells present . . . . . *Palpomyia*

19. Genus *Palpomyia* Meigen, 1818

Palpomyia MEIGEN, 1818: 82. Type-species *Ceratopogon flavipes* MEIGEN. GROGAN and WIRTH, 1979 b: 12 (= *Miopalpomyia, Neopalpomyia, Parapalpomyia*).

Miopalpomyia PIERCE, 1966: 95. Type-species *Miopalpomyia shilo* PIERCE (Miocene, California).

Neopalpomyia PIERCE, 1966: 95. Type-species *Neopalpomyia freyi* PIERCE (Miocene, California).

Parapalpomyia PIERCE, 1966: 97. Type-species *Parapalpomyia ryshkoffi* PIERCE (Miocene, California).

DIAGNOSIS

This genus is distinguished from other genera of the *Palpomyiini* by the following combination of characters: both first radial cells present, vein M_2 forking distinctly proximal of r-m crossvein. Fourth tarsomeres short and more or less cordiform on all legs, female claws short to moderately long, equal and similar on all legs, with or without basal inner teeth, hind claws rarely longer than fore and mid claws, fifth tarsomere unarmed or with 2 ventrolateral rows of strong setae. Parameres usually fused, gonostyli always well developed.

RECENT DISTRIBUTION AND CLASSIFICATION

Palpomyia is a worldwide distributed genus that includes about 250 recent species. Classification of the genus on a worldwide basis is poorly understood. GROGAN and WIRTH (1979 b) divided the North American species into 4 groups.

FOSSILS

Six fossil species previously have been described in the genus i.e. *P. unca* HONG, 1981 (♀, Eocene Chinese amber), *P. edwardsi* COCKERELL, 1921 (sex unknown, incomplete specimen from Oligocene rock impression, Isle of Wight in England), and *P. freyi* (PIERCE, 1966), *P. multispinosa* (PIERCE, 1966), *P. ryshkoffi* (PIERCE, 1966), *P. shilo* (PIERCE, 1966). The latter 4 species are described from pupae found in Miocene nodules in California.

It may be that *Johannsenomyia swinhoei* COCKERELL from Burmese amber is a member of the genus *Palpomyia* (see p. 26). The female of *P. unca* has quite long, rather unequal claws, and unarmed femora. I am not sure it is a member of *Palpomyia*, and Dr. HONG YOU-CHONG was not able to provide more information on this species. It may be that this species is a member of the tribe *Heteromyiini*.

This is the first record of the genus in Baltic amber. In the material investigated 3 specimens belonging to 3 different species of *Palpomyia* have been found.

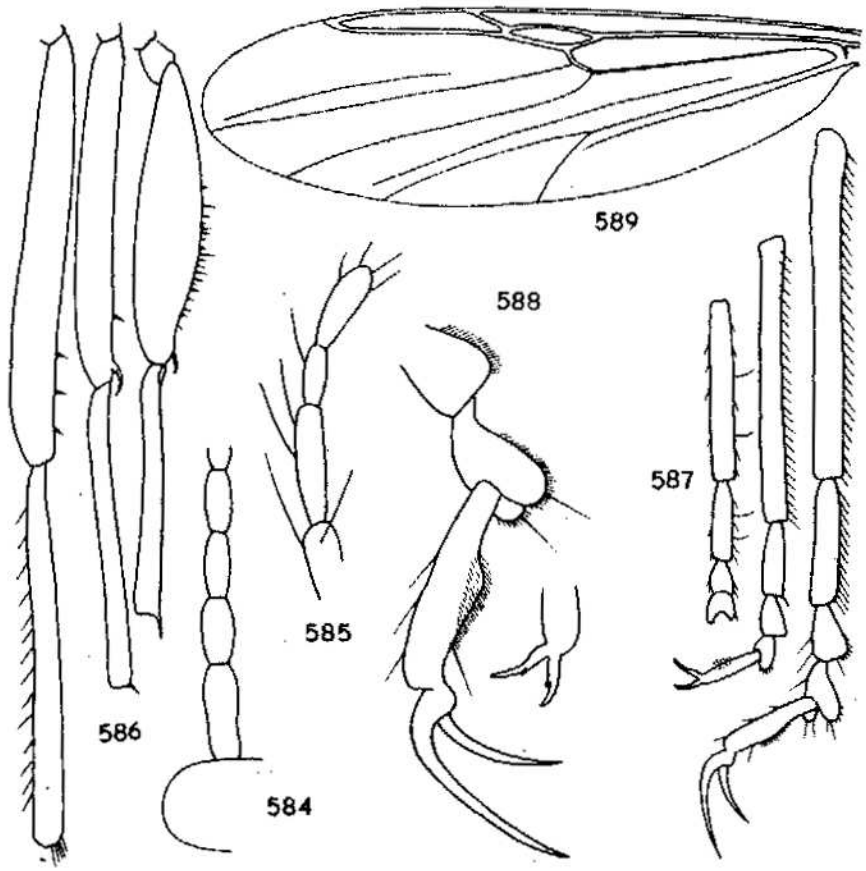
Key to Baltic amber species of *Palpomyia*

1. Only fore femur armed with ventral spines . . 3. *P. succinea* sp. n.
—. All femora armed with ventral spines 2
2. Female claws of hind leg long. Wing length 2.9 mm . . . . . 1. *P. jantari* sp. n.
—. Female claws of all legs short. Wing length 1.2 mm . . . . . 2. *P. riedeli* sp. n.

1. *Palpomyia jantari* sp. n.
(Figs. 584–589)

DIAGNOSIS

Female of this species is characteristic in having all femora armed with ventral spines, fore femur swollen, and claws of hind leg greatly elongated.



584–589. *Palpomyia jantari* sp. n., female, MZW 1325; 584 — proximal flagellomeres, 585 — palpus, 586 — femora and tibiae of hind, middle and fore leg, 587 — tarsi of fore, middle and hind leg, 588 — claws of hind and middle leg, 589 — wing

DESCRIPTION

♀. Body brown. Total length 3.3 mm. Flagellum incomplete, proximal flagellomeres cylindrical (fig. 584). Proboscis moderately long. Palpus slender and long (fig. 585). Third palpal segment 112 μm long. Scutum covered with fine pubescence and with some larger setae. Scutellum with several long setae. Legs as in figs. 586–588. Fore femur swollen and armed with 20 strong ventral spines arranged in 2 rows. Mid and hind femora slender; mid with 1 ventral spine, hind with 3 ventral spines. Hind basitarsus without subbasal ventral spine. Third and fourth tarsomeres short on all legs. Fourth tarsomeres bilobed, without stronger spines. Fifth tarsomere of fore legs missing. Fifth tarsomere of middle leg slender; claws short with inner tooth. Fifth tarsomere of hind leg with ventrolateral stronger seta, claws long, slightly unequal and without inner tooth. Tibial comb composed of 8 spines. Wing length 2.85 mm, CR 0.80. Costa not produced beyond tip of R_{4+5} (fig. 589). Second radial cell about 2 times longer than first one. Intercalary veins readily visible. Vein M_2 broadly sessile, forking distinctly proximal of base of M_1. Wing membrane covered with distinct microtrichia, macrotrichia absent. Anal lobe not developed. Abdomen filled with Canada balsam. Internal gland rods not visible. Cerci short, in dorsal view triangular.

♂. Unknown.

MATERIAL EXAMINED (1 ♀)

Holotype — ♀, MZW 1325.

DISCUSSION

Probably the species is a member of the *Palpomyia tibialis* group sensu GROGAN and WIRTH (1979 b). However the systematic position of this species is uncertain because it lacks an important fifth tarsomere of the fore leg. It is possible that it is a member of the tribe *Heteromyiini*.

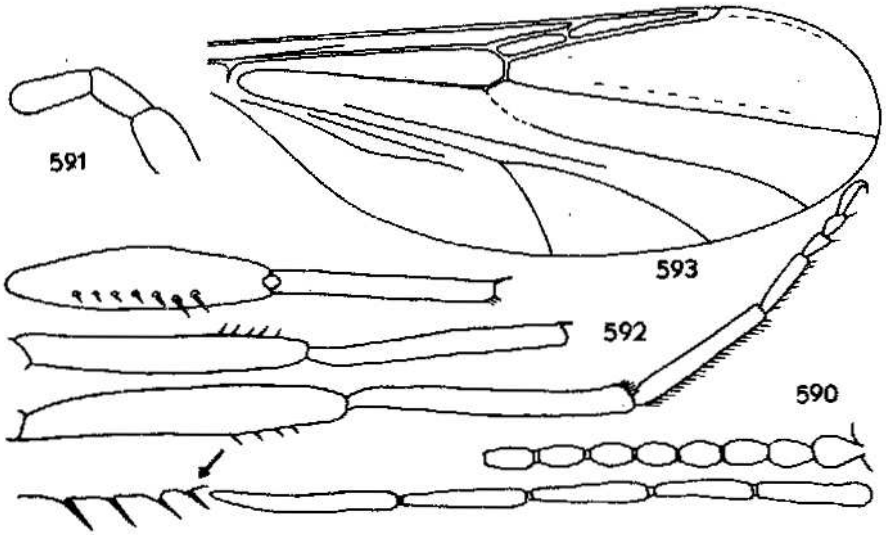
2. *Palpomyia riedeli* sp. n.
(Figs. 590–593)

DIAGNOSIS

Female of this species is characteristic in having all femora armed with ventral spines, claws of all legs short and scutum without anterior spine or tubercle.

DESCRIPTION

♀. Body black. Total length 1.9 mm. Eyes narrowly separated. Flagellum length 830 μm, AR 1.71. Distal 5 flagellomeres greatly elongated (fig. 590). Proboscis moderately short. Palpus rather short, length of fourth palpal segment ca. 32 μm (fig. 591). Antepronotum collar-like, small. Scutum shining without anterior spine or tubercle,



590–593. *Palpomyia riedeli* sp. n., female, IZPAN 53/76; 590 — flagellum, 591 — palpus, 592 — femora and tibiae of fore and middle leg, hind leg, 593 — wing

almost bare; 3 long supraalar setae present. Scutellum with 6 long and several shorter setae. Fore femur swollen and armed with 7–8 ventral spines (fig. 592). Mid and hind femora slender, with 4–5 ventral spines on distal half. Hind basitarsus without subbasal ventral spine. Fourth tarsomeres cordiform. Claws small and equal on all legs, each with basal inner tooth. Fifth tarsomeres without strong setae. TR(III) 2.4. Wing length 1.22 mm, CR 0.76. Vein M_2 forking distinctly proximal of r-m crossvein (fig. 593). Anal lobe not developed. Abdomen barely visible.

♂. Unknown.

MATERIAL EXAMINED (1 ♀)

Holotype — ♀, IZPAN 53/76.

ETYMOLOGY

This species is named for Professor Dr. A. RIEDEL of Institute of Zoology, Polish Acad. Sci., Warsaw, a curator of the collection of the Baltic amber inclusions.

DISCUSSION

This species is a member of a group *distincta* sensu GROGAN and WIRTH (1979 b). The female of *P. riedeli* is smaller than species of the *Palpomyia distincta* group from the Nearctic studied by GROGAN and WIRTH (l.c.).

3. *Palpomyia succinea* sp. n.
(Figs. 594–599)

DIAGNOSIS

Male of this species is characteristic in having only the fore femur armed with 6 ventral spines, scutum with anterior tubercle, and gonocoxite with a mesoventral distinct lobe.

DESCRIPTION

♀. Unknown.

♂. Body brown, thorax black. Total length 1.7 mm. Flagellum length 988 µm, AR 1.54 (fig. 594). Plume reaching middle of flagellomere XI. Proboscis moderately short. Palpus slender (fig. 595). Third palpal segment 60 µm, fourth 36 µm long. Scutum almost bare, with distinct anterior tubercle (fig. 596); 4 long supraalar setae present. Scutellum bearing 4 long and several shorter setae. Legs slender (fig. 597). All femora slender and long. Fourth tarsomeres rather cordiform (fig. 598). Claws small, equal, and with distinctly bifid apices. TR(II) 3.4, TR(III) 2.8. Wing length 1.28 mm, CR 0.73. Venation typical for the genus, base of M_2 barely visible.

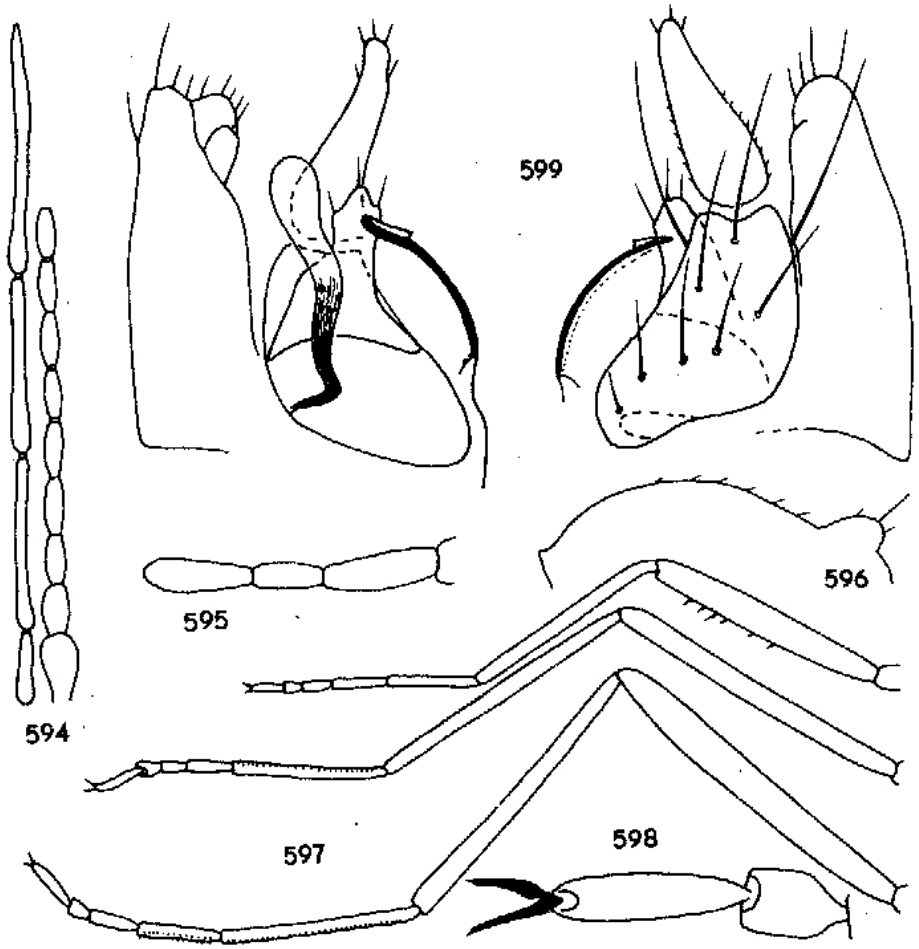
Genitalia inverted (fig. 599). Gonocoxite stout and short, with large mesoventral lobe extending to tip of gonocoxite. Gonostylus long and slender, slightly curved; tip moderately pointed. Aedeagus broad, triangular with distinct hastate tip. Parameres longer than aedeagus, fused, tip in lateral view enlarged and rather deeply bilobed or cleft.

MATERIAL EXAMINED (1 ♂)

Holotype — ♂, ZMC 235, Th. HANSEN, Mou, 16–1 1961. This specimen has ground tarsi of right legs and left gonocoxite.

DISCUSSION

This species is a typical member of the *distincta* group sensu GROGAN and WIRTH (1979 b). The group is common today in the Holarctic and includes about 50% of all species of *Palpomyia* in North America and presumably in the Palaearctic.



594–599. *Palpomyia succinea* sp. n., male, ZMC 235; 594 — flagellum, 595 — palpus, 596 — lateral view of scutum, 597 — fore, middle and hind legs, 598 — claws of hind leg, 599 — lateral views of genitalia

20. Genus *Bezzia* Kieffer, 1899

DIAGNOSIS

Bezzia is distinguished from the other genera of the tribe *Palpomyiini* by the following combination of characters: one radial cell. Fore femur usually slender and usually armed with ventral spines. Vein M_2 forking at level of crossvein r-m or proximal to it, base of M_2 usually barely visible. Male genitalia inverted, gonostyli always well developed. Claws of female short and equal on all legs, usually with basal inner teeth. Fourth tarsomeres cordiform.

RECENT DISTRIBUTION AND CLASSIFICATION

Bezzia is a worldwide distributed genus which includes about 250 recent species. This genus is divided into 2 subgenera *Bezzia* s. str. and *Homobezzia* MACFIE (REMM, 1974 b; WIRTH, 1983) well separated using male characters. Each of the subgenera includes more or less distinct species groups.

FOSSILS

STATZ (1944) described from Miocene rocks in Rott a single female of *Bezzia longipennis* with a question mark. Most probably this species does not belong to this genus because it has macrotrichia at wing tip "Makrotrichien auf den Adern und hauptsächlich am Apex." and the femora are unarmed.

This is the first record of fossil *Bezzia* in Baltic amber. In the material only 2 females of a single species have been found.

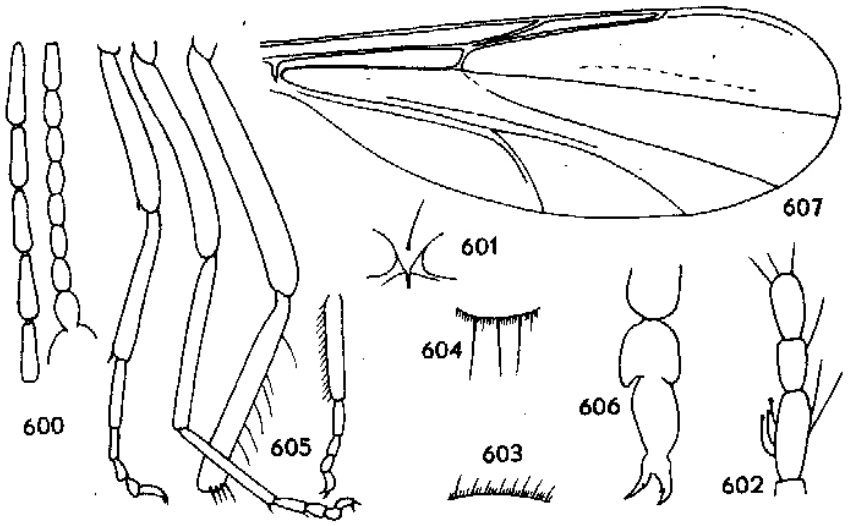
1. *Bezzia eocenica* sp. n.
(Figs. 600–607)

DIAGNOSIS

The species belongs to the subgenus *Bezzia* (*B.*) and to the Holarctic *bivittata* group sensu WIRTH and GROGAN, and is smaller than recent species of this group.

DESCRIPTION

♀. Body dark brown or black. Total length 1.5 mm. Flagellum length 531–534 μm, AR 1.03–1.15. Distal 5 flagellomeres moderately long (fig. 600). Eyes barely separated (fig. 601). Proboscis short. Palpus slender (fig. 602). Third palpal segment 40 μm long, sensilla capitata on inner surface readily visible. Scutum without anterior spine or tubercle,



600–607. *Bezzia eocenica* sp. n., female, MZW 16584; 600 — flagellum, 601 — vertex, 602 — palpus, 603 — setae of scutum, 604 — setae of scutellar tip, 605 — fore, middle and hind leg, 606 — claws of fore leg, 607 — wing

shining and uniformly covered with dense pubescence and sparse short, stout setae (fig. 603). Longer supraalar setae present. Scutellum bearing 6–8 stout and moderately long setae (fig. 604). Legs slender (fig. 605). Femora unarmed. Fourth tarsomeres cordiform. Claws short, equal and similar on all legs, each claw with inner tooth (fig. 606). TR(I) 2.4, TR(II) 3.6, TR(III) 3.0–3.2. Wing length 0.97–1.04 mm, CR 0.69–0.71. Wing membrane brownish with distinct microtrichia, macrotrichia absent. First radial cell single and slender. Vein M_2 forking at level of crossvein r-m (fig. 607). Abdomen barely visible.

♂. Unknown.

MATERIAL EXAMINED (2 ♀)

Holotype — ♀, MZW 16584, TG. Paratype — ♀, ZMC 13, A. K. ANDERSEN, 28–3 1968.

DISCUSSION

Among the Holarctic *Bezzia*, unarmed fore femora are characteristic for the species of the *bivittata* group (subg. *Bezzia*) and the *bicolor* group (subg. *Homobezzia*). Most probably *B. eocenica* **sp. n.** is a small species of the *bivittata* group sensu WIRTH and GROGAN (1983) of the subgenus *Bezzia* (*B.*) since the female of this species has scutum uniformly covered with short pubescence and longer setae than I have found in many recent species of this subgenus in my collection. In the subgenus *Homobezzia*, the scutum is covered only with abundant short hairs of the same length. However for final determination of the systematic position of *B. eocenica* male is necessary as I mentioned above.

3. Subfamily *Forcipomyiinae* Lenz, 1934

DIAGNOSIS

Eyes contiguous or narrowly separated. Female antenna composed of 13 flagellomeres or reduced to 11 and 9 in some species of *Forcipomyia*; usually distal 5, sometimes 6, flagellomeres elongated. In male plume always well developed and usually distal 4 flagellomeres elongated, proximal flagellomeres separated or fused; number of flagellomeres is reduced to 10 only in recent *Atrichopogon brevicornis* TOKUNAGA and *Forcipomyia eobreviflagellata* **sp. n.** Last flagellomere in both sexes always with distinct terminal papilla. Sensilla coeloconica absent. Palpus usually 5-segmented, often 2 distal segments incompletely or completely fused. Third palpal segment slender or swollen, with or without sensory

pit. Antepronotum small. Scutum without spine or tubercle, prescutal pits absent; its surface covered with long or very long erect or suberect unordered setae. Scutellum usually with numerous long setae. Legs more or less slender and unarmed, hairy. Tibia sometimes with lanceolate scales of diagnostic value. Basitarsi longer or shorter than second tarsomere. TR 0.2–3.2. Empodium well developed, usually as long as claws, broad and branching; in males of *Forcipomyia* (*Trichohelea*) and *F.*(*Phytohelea*) vestigial or absent. Claws distinct, slender and gently curved, simple; in male with bifid apices. Wing membrane densely covered with microtrichia and long macrotrichia; in many *Atrichopogon* macrotrichia absent or confined to wing tip. Costa short to distinctly elongated. First radial cell usually slit-like or absent, occasionally well developed. Veins M_1 and M_2 shortly petiolate, base of M_2 usually atrophied. Intercalary veins usually well developed.

Abdomen usually with short hairs, scales and with very long setae. Female cerci short. Male genitalia usually not inverted. Aedeagus usually shield-shaped. Parameres separated, fused or absent. Tergite IX short or long, often bearing lobe-shaped cerci at apex. Sternite IX usually distinct.

Recent ecology and classification

The larvae of *Forcipomyiinae* are terrestrial or semiaquatic often found under bark and among mosses. They feed on algae, plant debris or fungi (Downes and Wirth, 1981). Female adults of *Forcipomyia* (*Lasiohelea*) feed on mammals or amphibians. Other *Forcipomyiinae* feed on large insects such as moths, dragonflies, beetles, etc., on dead insects, pollen or nectar of flowers. Only 2 genera are known in the subfamily, i.e. *Forcipomyia* and *Atrichopogon*.

Fossils

The oldest *Forcipomyiinae* are known from late Cretaceous Canadian amber (*Forcipomyia*) and from the Eocene Baltic amber (*Forcipomyia* and *Atrichopogon*).

This subfamily is not common in Baltic amber. In the material investigated 176 specimens have been found, i.e. 15.9% of all biting midges. The genus *Forcipomyia* predominates because only a single specimen of *Atrichopogon* was found (table 3).

Key to Baltic amber genera of *Forcipomyiinae*

(from Downes and Wirth, 1981)

1. Microtrichia large and conspicuous. Macrotrichia when present scattered, suberect, not scale-like. Fringe of posterior wing margin

simple, consisting of a single row of alternating longer and shorter hairs . . . . . *Atrichopogon*

—. Microtrichia minute. Macrotrichia moderately abundant, sloping, often scale-like, covering most of wing. Fringe of posterior wing margin complex, not a single row of hairs . . . . *Forcipomyia*

21. Genus *Forcipomyia* Meigen, 1818

DIAGNOSIS

Body very hairy. Female antenna with 13 flagellomeres except for *F.*(*Phytohelea*) of *oligarthra* group with 9 units of flagellum and *F.*(*Blantonia*) with 11 units; distal 5 or 6 flagellomeres elongated. Male antenna with 13 flagellomeres, reduced to 10 units only in *F. eobreviflagellata* **sp. n.** Palpus usually 5-segmented, last 2 segments sometimes incompletely or totally fused. Scutum and scutellum usually covered with very long setae. Legs bearing numerous hairs, scales and long setae. Tibiae with or without lanceolate scales. TR 0.2–3.2. Empodia usually large and branching, in males of the subgenera *Trichohelea* and some species of *Phytohelea* vestigial or absent. Wing membrane covered with indistinct microtrichia and numerous long, often scale-like macrotrichia covering most of wing. Fringe of posterior wing margin complex. First radial cell usually slit-like or absent, second one long and narrow to short and broad. Intercalary veins usually well visible. CR 0.34–0.70.

Abdomen usually with very long setae. Parameres symmetrical and usually well developed or occasionally absent. Tergite IX in male genitalia usually short; apicolateral lobe-shaped processes often well developed, without taxonomic value.

RECENT DISTRIBUTION AND CLASSIFICATION

The genus *Forcipomyia* is distributed worldwide and common in all moist habitats. About 700 recent species are known in the genus which are classified into 20 more or less distinct subgenera.

FOSSILS

The oldest unnamed *Forcipomyia* is (or are) known from late Cretaceous Canadian amber (DOWNES and WIRTH, 1981). From this amber BOESEL (1937) described *Lasiohelea globosa* and *L. cretea*, however these species probably do not belong to the genus *Forcipomyia* (empodia and terminal papillae not indicated) but probably to subfamily *Ceratopogoninae* as suggested by REMM (1976). Long pedicellus of *L. cretea* is very

similar to that of *Protoculicoides depressus* (see p. 28) of the tribe *Culicoidini*.

In Baltic amber, *Forcipomyia* is quite common. In the material examined there were found 175 specimens belonging to 17 more or less distinct species.

In the genus *Forcipomyia* some subgenera are more distinct in the male sex while others in the female, and because of this the separation of the Baltic amber species into subgenera is very difficult. Despite the fact that some species described herein do not fit into or are distinctly different from known subgenera, new subgeneric names are not proposed here.

Forcipomyia indetermined (2 ♂, 38 ♀)

MBI 104, BERENDT (+*Sciaridae* 1 ♀), 1 ♀; 115, BERENDT, 1 ♂; 121, BERENDT, "*Ceratopogon eucerus*, Original Dr B", 1 ♀; 139, KÜHL, 1 ♀; 144, KÜHL, 1 ♀; 153, KÜNOW, 1 ♀; 169, KÜNOW, 1 ♀; 171, KÜNOW, 1 ♂; 182, KÜNOW, 1 ♀; 188, KÜNOW, 1 ♀; 191, KÜNOW, 1 ♀; 200, KÜNOW, 1 ♀; 205, KÜNOW, 1 ♀; 208, KÜNOW, 1 ♀; 211, KÜNOW, 1 ♀; MBI THOMAS 241, "*Ceratopogon eucerus* ?", 1 ♀; MZW 2127/A, 1 ♀; 4775, TG, 1 ♀; 4839, TG, 1 ♀; 7168, 1 ♀; 7184, 1 ♀; 7984, 1 ♀; 10172, 1 ♀; 12203, TG, 1 ♀; 12998, 1 ♀; 19286, TG, 1 ♀; 20272, TG (+*Hymenoptera* 1), 1 ♀; 20273, TG, 1 ♀; ZMC 5, C. V. HENNINGSEN, 16–1 1961, 1 ♀; 32, Udlandet, Min. Mus., 1 ♀; 46, C. V. HENNINGSEN, 25–3 1961, 1 ♀; 75, C. V. HENNINGSEN, 3–5 1960, 1 ♀; 78, C. V. HENNINGSEN, 21–11 1960, 1 ♀; 129, C. V. HENNINGSEN, Ostpreussen, 1–7 1966, 1 ♀; 141, Börge MORTENSEN, 1–9 1960, 1 ♀; 148, C. V. HENNINGSEN, 3–5 1960, 1 ♀; 157, A. Klarskov ANDERSEN, 3–5 1958, 1 ♀; 194, A. HENNINGSEN, 9–9 1974, 1 ♀; 237, A. HENNINGSEN, 9–9 1974, 1 ♀; MBI 197, KÜNOW, 1 ♀.

Key to Baltic amber species of *Forcipomyia*

1. TR(III) lower than 1.2 2
–. TR(III) higher than 1.7 9
2. TR(II and III) 0.2–0.3 . . . 9. *F.(F.) pseudomicrohelea* sp. n.
–. TR(II and III) 0.5–1.2 3
3. TR(II) 0.5 . . . . . 6. *F.(F.) eocostata* sp. n.
–. TR(II) 0.8–1.2 4
4. Large midge, wing length 1.75 mm . . . . . 8. *F.(F.)* sp. B
–. Small midges, wing length 0.83–1.22 mm 5
5. Empodia absent in male . . . . . 13. *F.(Trichohelea) eotrichoheleana* sp. n.
–. Empodia well developed in male 6

6. Wing with pattern formed by dense and sparse macrotrichia . . . . . 3. *F.(F.) lyneborgi* sp. n.
—. Wing uniformly covered with macrotrichia 7
7. Third palpal segment in female greatly swollen and short. Female AR 1.34–1.45 . . . . . 7. *F.(F.) turbinata* (MEUNIER)
—. Third palpal segment in female not greatly swollen. Female AR 0.77–0.95 8
8. Aedeagus short and broad with strongly sclerotized short triangular apical projection . . . . . 5. *F.(F.) gedanicola* sp. n.
—. Distal part of aedeagus weakly sclerotized . . . . . 4. *F.(F.) uncula* (MEUNIER)
9. Palpus 4-segmented, i.e. only 1 segment distal to third bearing sensory organ . . . . . 15. *F.*(subg.?) *krzeminskii* sp. n.
—. Palpus 5-segmented, i.e. 2 segments distal to third bearing sensory organ 10
10. Second radial cell very narrow and long, CR 0.64–0.70 11
—. Second radial cell short, if longer then broad 12
11. Female flagellomeres II–VII compressed and short. CR 0.70 . . . . . 1. *F.(Lasiohelea) succinea* sp. n.
—. Female flagellomeres II–VII not compressed, ovoid. CR 0.64 . . . . . 2. *F.(L.)* sp. A
12. Empodia absent in male . . . 14. *F.(Phytohelea) eophytoheleana* sp. n.
—. Empodia present in male 13
13. Male antenna with 10 flagellomeres . . . . . 17. *F.*(subg.?) *eobreviflagellata* sp. n.
—. Male antenna with 13 flagellomeres 14
14. Gonostylus in male genitalia with enlarged tip . . . . . 16. *F.*(subg.?) *kulickae* sp. n.
—. Gonostylus in male genitalia with slender tip 15
15. Aedeagus short, arch-shaped. Parameres present . . . . . 10. *F.(Euprojoannisia) piriformis* (MEUNIER)
—. Aedeagus long, shield-shaped. Parameres absent 16
16. Tip of aedeagus distinctly bilobed . . . 11. *F.(E.) berendti* sp. n.
—. Tip of aedeagus evenly pointed . . . 12. *F.(E.) henningseni* sp. n.

Subgenus *Lasiohelea* Kieffer, 1921

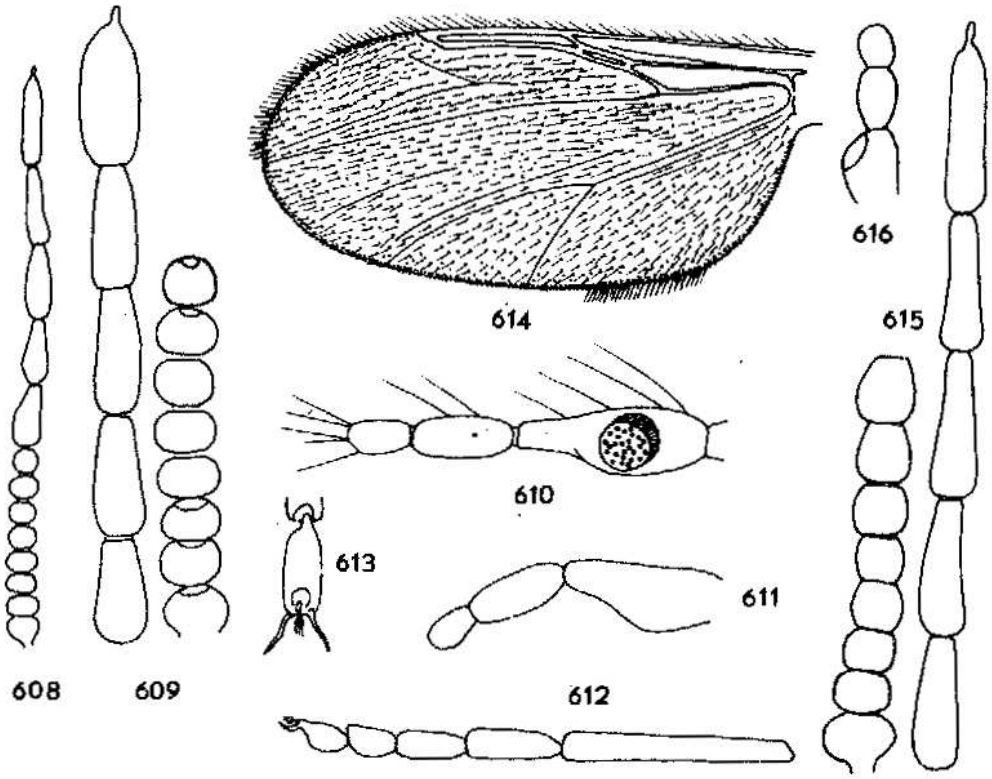
DIAGNOSIS

Antenna in both sexes with 13 flagellomeres. Proximal flagellomeres of female much shorter than distal 5, transverse to spherical or short cylindrical. Palpus 5-segmented. Third palpal segment more or less swollen with sensilla capitata scattered or enclosed in sensory pit.

Empodia always well developed in both sexes. TR(III) 1.0–3.0. Wing densely covered with suberect macrotrichia. Second radial cell long and narrow, first one slit-like and short. CR 0.54–0.70. Parameres in male genitalia absent. Apodemes of gonocoxites long and joined.

RECENT ECOLOGY AND DISTRIBUTION

Lasiohelea is a worldwide distributed subgenus including about 60 recent species. Only *F.(L.) velox* (WINNERTZ) occurs in Europe, a para-



608–616. *Forcipomyia* (*Lasiohelea*) *succinea* sp. n. and *Forcipomyia* (*L.*) sp. A, females; *F. succinea* sp. n. (608–614): 608 — flagellum, ZMC 185; 609 — flagellum, ZMC 188; 610 — palpus, ZMC 188; 611 — palpus, ZMC 185; 612 — tarsus of hind leg, 613 — claws of middle leg, ZMC 188; 614 — wing, ZMC 185; *Forcipomyia* sp. A, MZW 12654 (615, 616): 615 — flagellum, 616 — palpus

site of amphibians. The larvae were collected in moist or semiaquatic habitats among mosses, liverworts and algae, on rotting wood and in plant debris (DEBENHAM, 1983). Females take blood from mammals, man, and amphibians.

FOSSILS

This is the first record of fossil *Lasiohelea*. Two *Lasiohelea* species described by BOESEL (1937) from Canadian amber do not belong to the genus *Forcipomyia* (see p. 190).

In the material examined 9 females of the subgenus have been found.

F. (*Lasiohelea*) indetermined (6 ♀)

MM 1, 1 ♀; MZW 16375, TG, 1 ♀; 17967, TG, 1 ♀; ZMC 72, C. V. HENNINGSEN, 1–4 1970, 1 ♀; 189, C. V. HENNINGSEN, 11–10 1963, 1 ♀; 193, C. V. HENNINGSEN, 11–10 1963, 1 ♀.

1. *Forcipomyia* (*Lasiohelea*) *succinea* sp. n.
(Figs. 608–614)

DIAGNOSIS

Female of this species is characteristic in having proximal flagellomeres II–VII short and transverse, CR 0.70, TR(III) 2.5, fifth palpal segment short, proboscis long.

DESCRIPTION

♀. Body dark brown or black. Total length about 1.5 mm. Flagellum length about 460 μm, AR about 1.5–1.9. Distal 5 flagellomeres cylindrical, long; proximal flagellomeres II–VII short, transverse (figs. 608, 609). Proboscis long and slender. Palpus slender and long. Third palpal segment slightly enlarged on basal half, with distinct shallow and round sensory pit at middle (figs. 610, 611), length 88 μm. Fourth palpal segment long, fifth one short. Scutellum with numerous long setae. Legs slender. Empodia distinct. Claws relatively long, in dorsal view somewhat sinuate (fig. 613). TR(I) 2.6, TR(II) 2.7, TR(III) 2.5 (fig. 612). Wing length 0.87–0.97 mm, CR 0.70. Membrane densely covered with long, slender and appressed macrotrichia, microtrichia indistinct. Second radial cell very long and narrow, first one short, slit-like (fig. 614).

♂. Unknown.

MATERIAL EXAMINED (2 ♀)

Holotype — ♀, ZMC 188, A. HENNINGSEN, 9–9 1974 (+*Sciaridae* 1 ♂). Paratype — ♀, ZMC 185, J. FLANENSGAARD, 16–2 1966. The holotype has lost tip of abdomen and some tarsomeres, however it has palpus and flagellum better visible than the paratype which is complete.

2. *Forcipomyia* (*Lasiohelea*) sp. A
(Figs. 615, 616)

DIAGNOSIS

Female of this species differs from *F. succinea* in having very short proboscis, CR 0.64, all proximal flagellomeres spherical to slightly subcylindrical, and pit located at tip of third palpal segment. TR(III) 2.3.

DESCRIPTION

♀. Body brown, thorax darker. Total length 1.2 mm. Flagellum length 488 μm, AR 1.83. All proximal flagellomeres spherical, units VII, VIII slightly longer than broad (fig. 615). Proboscis very short. Palpus barely visible. Third palpal segment with pit located at tip. Fourth and fifth palpal segments relatively short (fig. 616). Scutum hairy. TR(I) 3.0, TR(II) ca. 2.6, TR(III) 2.3. Claws small. Wing length 0.74 mm, CR 0.64. Membrane covered with numerous, long and appressed macrotrichia, microtrichia indistinct. Second radial cell long and narrow, first one barely visible, presumably line-like.

♂. Unknown.

MATERIAL EXAMINED (1 ♀)

MZW 12654, 1 ♀.

Subgenus *Forcipomyia* Meigen, 1818

DIAGNOSIS

Proximal flagellomeres of female bottle-shaped or vasiform. Third palpal segment slender to greatly swollen, usually with distinct sensory pit. Fourth and fifth palpal segments always separated. Empodia well developed. TR(III) 0.3–1.3. Wing membrane densely covered with long macrotrichia, CR usually about 0.50. Both first radial cells short, first one usually slit-like. In male genitalia aedeagus usually shield-shaped; parameres always well developed, separated or fused at bases and attached to usually distinct apodemes of gonocoxites.

RECENT ECOLOGY, DISTRIBUTION AND CLASSIFICATION

The larvae of this subgenus live mainly in rotting wood. As far as it is known females do not take protein meal. Both sexes visit only flowers. *Forcipomyia* (*F.*) which includes most of the species described in the genus is worldwide distributed. Separation the species into groups on a world basis is still poorly developed. Some species groups are restricted to the Holarctic only.

FOSSILS

Fossil *Forcipomyia* (*F.*) are presently known only from Baltic amber. It is the most common subgenus in this resin including 96 specimens and 7 species.

Forcipomyia (*F.*) indetermined (12 ♂, 47 ♀)

MBI 106, BERENDT, 1 ♀; 110, BERENDT, 1 ♂; 112, BERENDT, 1 ♀; 170, KÜNOW, 1 ♀; 179, KÜNOW, 1 ♂; 206, KÜNOW, 1 ♀; MBI THOMAS 217, 1 ♂; THOMAS 266 "*Ceratopogon Heinei* ?", 1 ♀; MM 5, 1 ♀; MZW 1831/23 a, 2 ♂; 3623, 1 ♂; 4702, TG, 1 ♀; 4731, TG (+ *Chironomidae* 1 ♀), 1 ♀; 4875, TG (+ *Sciaridae* 1 ♀), 1 ♀; 5071, TG, 1 ♀; 7167, 1 ♀; 7259, 1 ♀; 7812, at *Culicoides speciosus*, 1 ♀; 8022, 1 ♀; 8359, 1 ♂; 8517, 1 ♀; 8903, 1 ♀; 10071, 1 ♂; 10231, 1 ♀; 11384, TG, 1 ♀; 11560, TG, 1 ♀; 12106, 1 ♀; 13199, TG, 1 ♀; 13292, TG, 1 ♀; 13988 b, TG, 1 ♀; 17278, TG, 1 ♀; 17499, TG, 1 ♀; 17541, TG, 1 ♀; 17672, TG, 1 ♀; 17951, TG, 2 ♀; 18990, TG, 1 ♀; 19300, TG, 1 ♀; 19932, 1 ♀; 20008, TG, 1 ♀; 20473, TG, 1 ♀; ZMC 10, Narskov Kóbm Salsóe, 21–10 1918, 1 ♀; 18, Dr. J. IPSEN nr 306, 1–6 1952, 1 ♀; 47, A. HENNINGSEN, 9–9 1974, 1 ♀; 80 a, C. V. HENNINGSEN, 11–10 1963 (+ *Collembola* 1), 1 ♀; 114, BÓRGE MORTENSEN, 21–3 1961, 1 ♀; 128, A. K. ANDERSEN, 28–3 1968, 1 ♀; 149, C. V. HENNINGSEN, 1–8 1962, 1 ♀; 154, BÓRGE MORTENSEN, 1–11 1964, 2 ♀; 159, C. V. HENNINGSEN, 1–7 1966, Ostpreussen, 1 ♀; 162, B. MORTENSEN, 11–7 1960, 1 ♂; 191, A. K. ANDERSEN, 28–3 1968, 1 ♂; 195, A. HENNINGSEN, 9–9 1974, 1 ♀; 215, A. HENNINGSEN, 9–9 1974, 1 ♀; 231, C. V. HENNINGSEN, 11–10 1963, 1 ♂; 244, A. HENNINGSEN, 9–9 1974 (+ *Ceratopogon* 1 ♀, *Dolichopodidae* 1 ♀), 1 ♂ 1 ♀.

3. *Forcipomyia* (*F.*) *lyneborgi* sp. n.

(Figs. 617–623)

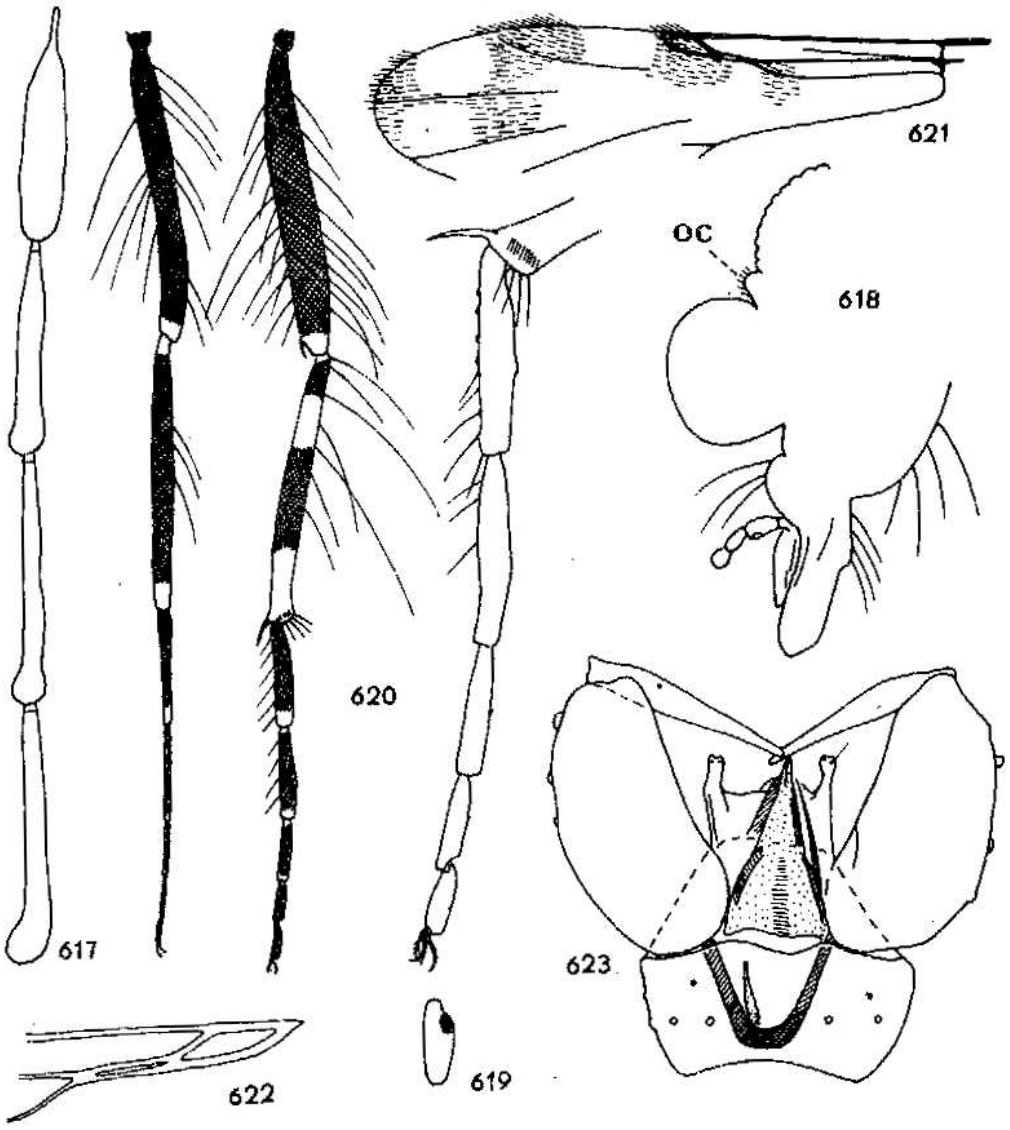
DIAGNOSIS

The species is characteristic in having wings with 2 anterior light spots formed by pale and sparse macrotrichia.

DESCRIPTION

♀. Unknown.

♂. Body blackish brown, legs with pale rings. Total length 1.9 mm. Flagellum length 812 μm, AR ca. 1.0; lengths of distal 4 flagellomeres as follows: 108–104–94–96 μm (fig. 617). Ocellar tubercles readily visible, proboscis long (fig. 618). Palpus barely visible. Third palpal segment rather slender with sensory pit located near apex (fig. 619). Legs with pale rings as in fig. 620. Empodia well developed. TR(I) 1.6, TR(II) 1.3, TR(III) 1.05. Wing length 1.06 mm, CR 0.50. Both first radial cells short (fig. 622). Wing membrane covered with long and flattened dark and pale macrotrichia forming dark patches and pale spots: 2 light spots in cell r_{4+5} and 1 in cell m_1 (fig. 621).



617–623. *Forcipomyia* (*F.*) *lyneborgi* sp. n., male, ZMC 15; 617 — distal flagellomeres, 618 — lateral view of head, 619 – third palpal segment, 620 — middle and hind leg, hind tarsus, 621 — wing, 622 — first radial cells, 623 — genitalia; oc — ocellar tubercle

Abdomen long and slender. Genitalia slightly rotated (fig. 623). Sternite IX probably with only slightly excavated caudomedian margin. Gonocoxite moderately stout. Gonostylus nearly straight, slender, gradually tapering to evenly pointed tip. Aedeagus barely visible, basal arch low. Dorsal apodemes of gonocoxites strongly sclerotized, long and fused. Parameres barely visible, probably reaching level of tip of apicolateral processes of tergite IX.

MATERIAL EXAMINED (1 ♂)

Holotype — ♂, ZMC 15, B. MORTENSEN, 23–2 1965.

ETYMOLOGY

This species is named for Dr. L. LYNEBORG of Zoologisk Museum in Copenhagen, a prominent dipterist and a curator of the amber collection.

DISCUSSION

I include *F. lyneborgi* **sp. n.** in the *cinctipes* group which is characteristic in having wings with marginal pale spots and including *F. cinctipes* (COQUILLETT), *F. macswaini* WIRTH, *F. townsendi* KNAB and some other species distributed in the Neotropic and from Mexico to Florida and from California to Washington (WIRTH, 1952, 1965). WIRTH (1952) supposed that *F. cinctipes* and *F. macswaini* are Neotropical faunal elements extending from Patagonia to the Sierra Nevada and the Rocky Mountains of western North America. However, this group was present in Europe during the Eocene which suggests it is of Euro-North American origin and then migrated to South America from North America like the genus *Physohelea*.

Larvae of the North American species have been found under pine bark and in decaying leaves (WIRTH, 1952).

4. *Forcipomyia* (*F.*) *uncula* (Meunier, 1904), comb. n.
(Figs. 624–631)

Ceratopogon unculus MEUNIER, 1904: 227 (♀, ♂, Baltic amber).

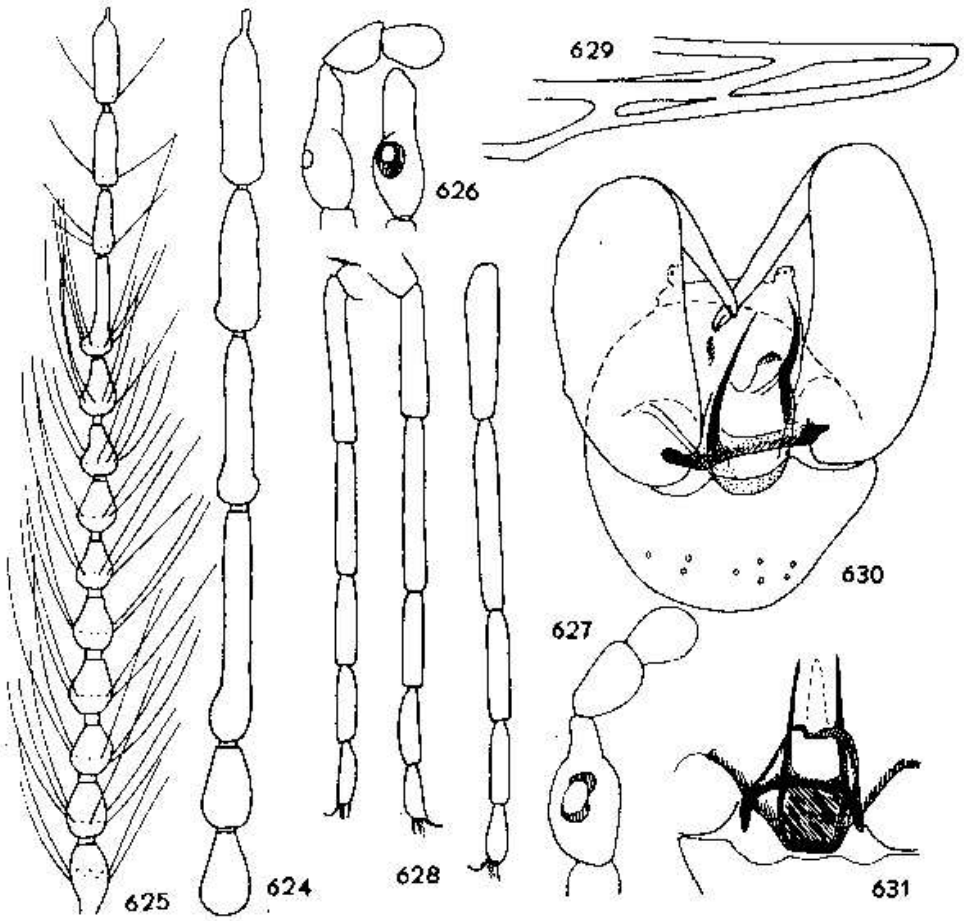
DIAGNOSIS

This species is a typical member of the subgenus distinguished from other fossil species by the following combination of characters: TR(III) 0.8–0.9. Third palpal segment moderately swollen. Gonostylus slender and straight. Aedeagus with weakly sclerotized distal portion. Flagellomere X 1.3–1.4 times longer than XI.

DESCRIPTION

♀. Body dark brown. Total length 1.6 mm. Proximal flagellomeres bottle-shaped, AR ca. 0.8. Third palpal segment moderately enlarged on proximal 2/3, sensory pit small (fig. 627). TR(I) 1.1, TR(II) 0.8, TR(III) 0.9. Wing length 0.87 mm. Membrane uniformly covered with macrotrichia.

♂. Body brown, dark brown or blackish. Total length 1.6–2.0 mm. Flagellum length 720–803 μm, AR 0.94–0.95. Flagellomere X 1.3–1.4 times longer than flagellomere XI (fig. 624). Third palpal segment



624–631. *Forcipomyia* (*F.*) *uncula* (MEUNIER); 624 — distal flagellomeres of male, IMGPUG 6650; 625 — flagellum of intersex with short plume, MZW 8715; 626 — male palpi, IMGPUG 6650; 627 — female palpus, MBI 220; 628 — male tarsi of fore, middle and hind leg, 629 — first radial cells of male, 630 — male genitalia, IMGPUG 6650; 631 — aedeagus and parameres, MZW 17953

enlarged slightly on basal half (fig. 626), length 66–80 μm. TR(I) 1.1–1.3, TR(II) 0.8–0.9, TR(III) 0.8 (fig. 628). Wing length 0.89–1.09 mm, CR 0.48–0.50. Membrane uniformly covered with macrotrichia. First radial cell short and narrow (fig. 629).

Genitalia (figs. 630, 631). Sternite IX without distinct caudomedian excavation. Gonocoxite moderately stout, simple. Gonostylus slender, straight. Aedeagus with low basal arch, distal portion weakly sclerotized. Parameres long, almost straight, broadly fused at bases, apices slender and pointed. Apodemes of gonocoxites long and distinctly sclerotized.

Intersex. All external characters typical for male except for flagellum which is intermediate between that of male and female (fig. 625): plume very short, proximal flagellomeres as in female, distal ones as in male, AR 0.62.

MATERIAL EXAMINED (19 ♂, 1 intersex, 1 ♀)

Lectotype — ♂ of *C. unculus*, IMGPUG Z 6650. Paralectotypes: IMGPUG Z 5057, 1 ♂; 5701, 1 ♂; 7458, 5 ♂; 6586, 1 ♂. Present designations. The paralectotype male IMGPUG Z 6586 originally described as "Var." belongs to the genus *Culicoides*. Only male syntypes were available for the present study.

MBI 102, BERENDT, 1 ♂; 137, KÜHL, 1 ♂; 218, THOMAS, 1 ♂; 220, THOMAS, 1 ♂ 1 ♀; MZW 1872/17, 1 ♂; 8917, intersex 1; 10307 (+*Mycetophilidae* 1 ♂), 1 ♂; 12746, 1 ♂; 17953, TG, 1 ♂; 19704, TG, 1 ♂; ZMC 91, A. K. ANDERSEN, 28–3 1968, 1 ♂.

NOTE

It is possible that *F. uncula* is a species complex.

5. *Forcipomyia* (*F.*) *gedanicola* sp. n.
(Figs. 632–642)

DIAGNOSIS

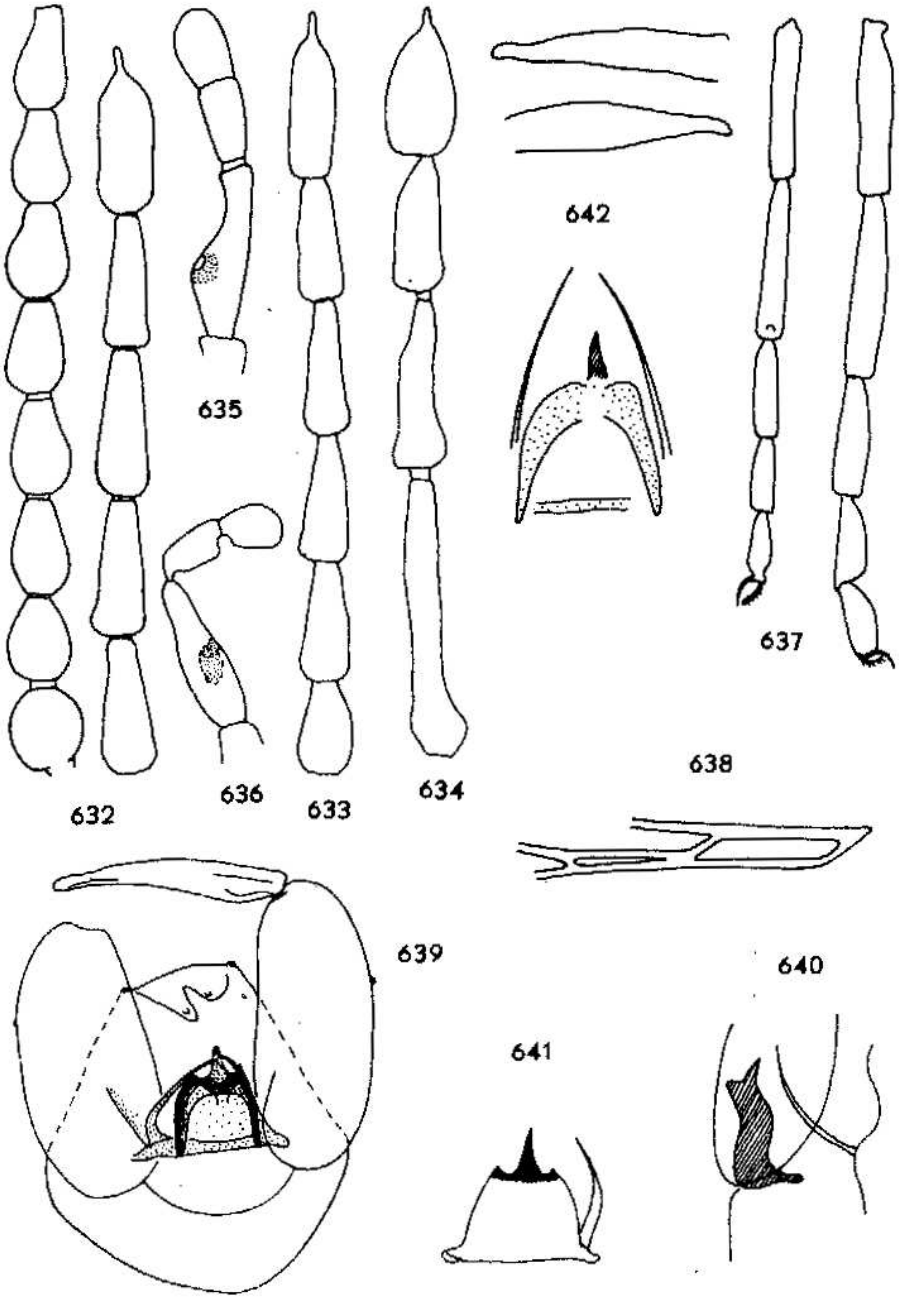
This species is similar to *F. uncula*. Males differ in having a short aedeagus bearing a short and triangular strongly sclerotized apical projection, apical third of gonostylus slender and slightly sinuous, flagellomere X 1.6–1.8 times longer than XI.

DESCRIPTION

♀. Body blackish brown. Total length 1.3 mm. Flagellum length 644 μm, AR 0.95 (fig. 632). Third palpal segment slightly swollen on basal half, length 76 μm, sensory pit small (fig. 635). TR(I) 1.1. Wing length 0.90 mm, CR 0.60. Membrane uniformly covered with macrotrichia. Second radial cell moderately long (fig. 638).

♂. Body brown or black. Total length 1.6–1.8 mm. Flagellum length 700–918 μm, AR 0.90–1.01. Flagellomere X 1.6–1.8 times longer than flagellomere XI (fig. 634). Third palpal segment slender, length 70–80 μm, sensory pit small (fig. 636). TR(I) 0.9–1.4, TR(II) 0.7–1.0, TR(III) 0.9–1.0 (fig. 637). Wing length 0.95–1.22 mm, CR 0.50–0.52. Membrane uniformly covered with macrotrichia. First radial cells small.

Genitalia (figs. 639–642). Sternite IX probably with shallow caudomedian excavation. Gonocoxite simple. Gonostylus distinctly slender and slightly sinuous on distal third. Aedeagus short, well sclerotized. Tip of aedeagus with short and triangular strongly sclerotized median projec-



632–642. *Forcipomyia* (*F.*) *gedanicola* sp. n.; 632 — female flagellum, RSz 1 c; 633 — distal flagellomeres of intersex, RSz 1 a; 634 — distal flagellomeres of male, MZW 10116; 635 — female palpus, RSz 1 c; 636 — male palpus, 637 — male tarsi of middle and hind leg, MZW 10116; 638 — first radial cells of male, RSz 1 b; 639 — male genitalia, MZW 10116; 640 — lateral view of aedeagus, 641 — aedeagus and paramere, MBI 213; 642 — gonostyli, aedeagus and parameres of intersex, RSz 1 c

tion and 2 lateral small horns. Parameres short and slender, broadly separated, at bases connected with distinct straigth bridge. Apodemes of gonocoxites rather short.

Intersex. Single specimen with female flagellum (fig. 633), and male genitalia (fig. 642).

MATERIAL EXAMINED (6 ♂, 1 intersex, 1 ♀)

Holotype — ♂, MZW 10116. Paratypes: MBI 213, BERENDT, 1 ♂; RSz 1 a,b,c, 1 intersex 1 ♂ 1 ♀; ZMC 94, Dr. IPSEN, Nr 284, 1 ♂; 108, A. K. ANDERSEN, 28–3 1968, 1 ♂. ZMC 107, C. V. HENNINGSEN, 28–5 1959, 1 ♂ does not belong to the type-series.

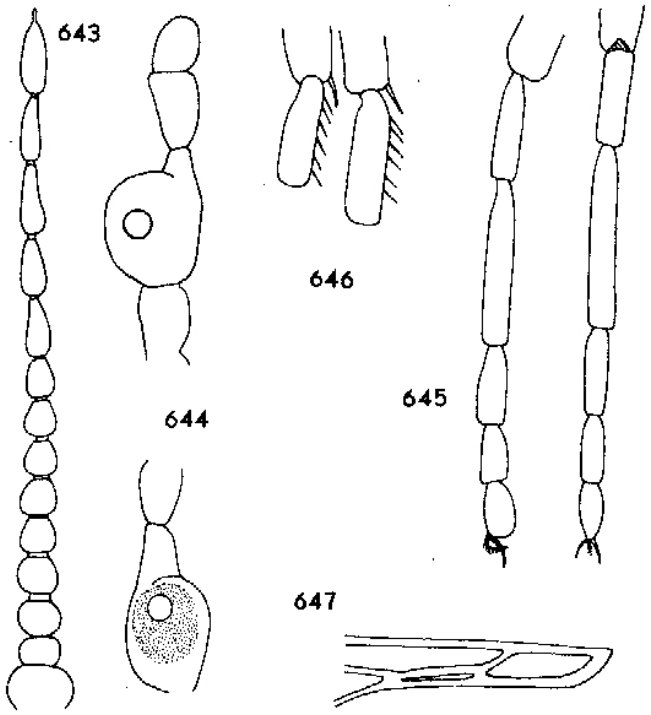
6. *Forcipomyia* (*F.*) *eocostata* sp. n.
(Figs. 643–647)

DIAGNOSIS

Female of this species is characteristic in having a greatly swollen third palpal segment, and TR(I and II) 0.5–0.6.

DESCRIPTION

♀. Body dark brown. Total length 1.4 mm. Flagellum length 529 µm, AR 1.11. Proximal flagellomeres short, spherical to slightly elongated (fig. 643). Third palpal segment greatly swollen on basal 2/3; sensory pit large with small opening (fig. 644). TR(I) 0.6, TR(II) 0.5. Hind basitarsus



643–647. *Forcipomyia* (*F.*) *eocostata* sp. n., female, MZW 8035; 643 — flagellum, 644 — palpi, 645 — tarsi of fore and middle leg, 646 — hind basitarsi, 647 — first radial cells

short (figs. 645, 646). Tibiae without lanceolate scales. Wing length 0.83 mm, CR 0.50. Second radial cell well developed, short (fig. 647).

♂. Unknown.

MATERIAL EXAMINED (1 ♀)

Holotype — ♀, MZW 8035.

DISCUSSION

This species is a typical member of the *costata* group (= *picea* sensu REMM, 1962 a) together with *F. turbinata* (see below). Female of the new species is close to *F. turbinata*, however it has a distinctly lower TR.

7. *Forcipomyia* (*F.*) *turbinata* (Meunier, 1904), comb. n.

(Figs. 648–651)

Ceratopogon turbinatus MEUNIER, 1904: 227 (♀, Baltic amber).
Culicoides turbinatus: KIEFFER, 1906: 1 (combination); ARNAUD, 1956: 148 (combination).

DIAGNOSIS

Females of this species are characteristic in having the third palpal segment greatly swollen, only slightly longer than width, and TR(III) 1.2.

DESCRIPTION

♀. Body dark brown. Total length 1.5–1.8 mm. Flagellum length 510–611 μm, AR 1.34–1.45. Proximal flagellomeres short (fig. 648). Almost entire third palpal segment greatly swollen, only apical portion slender, length 64–70 μm, sensory pit large (figs. 649, 650). Tibiae without lanceolate scales. TR(I) 1.3–1.4, TR(II) 1.1, TR(III) 1.2 (fig. 651). Wing length 0.83–1.03 mm, CR 0.50–0.51. Membrane uniformly covered with appressed macrotrichia. First radial cell narrow, second one short and relatively broad.

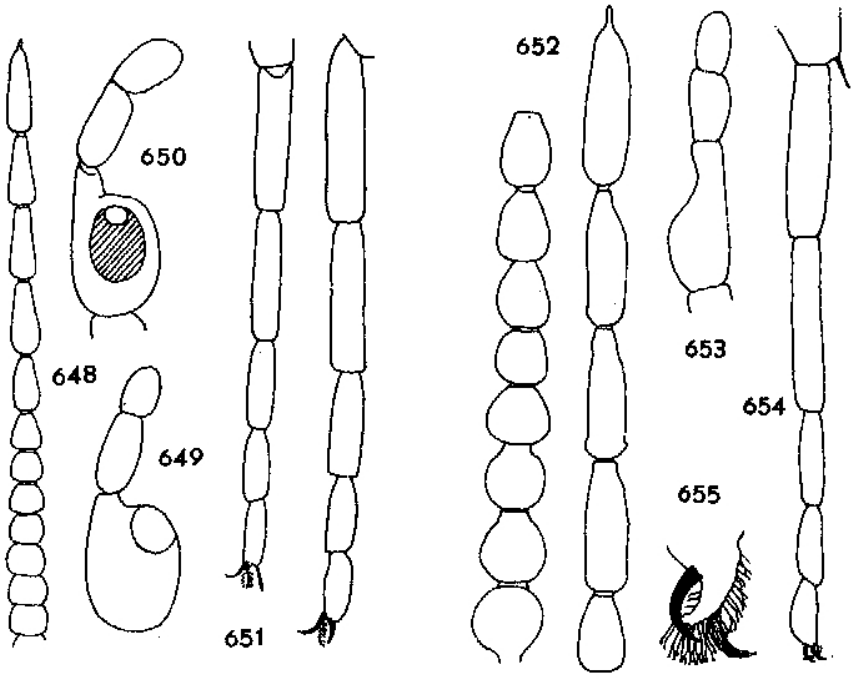
♂. Unknown.

MATERIAL EXAMINED (4 ♀)

Holotype — ♀, IMGPUG Z 5613. MBI THOMAS 211, "*Tip. culiciformia, Ceratopogon Heinei* ?", 1 ♀; MZW 1900, 1 ♀; 17734, TG, 1 ♀.

DISCUSSION

This species belongs to the *costata* group (= *picea* sensu REMM, 1962 a) including *F. eocostata* **sp. n.** described above and 5 recent species



648–655. *Forcipomyia* (*F.*) *turbinata* (MEUNIER) and *Forcipomyia* (*F.*) sp. B, females. *F. turbinata* (648–651): 648 — flagellum, 649 — palpus, IMGPUG 5613; 650 — palpus, MZW 17734; 651 — tarsi of middle and hind leg, IMGPUG 5613; *Forcipomyia* sp. B, ZMC 74 (652–655): 652 — flagellum, 653 — palpus, 654 — hind tarsus, 655 — empodium and claws of hind leg

occurring in Europe and North America. They are: *F. costata* (ZETTERSTEDT — Europe, *F. kaltenbachi* (WINNERTZ) — Europe, *F. hirtula* (ZETTERSTEDT) — Sweden, *F. simulata* WALLEY and *F. texana* (LONG) — North America (WIRTH, 1952; REMM, 1962 a; SZADZIEWSKI, 1986). Larvae of recent species live under the bark of logs and dead trees of a wide variety of plant families (REMM, 1962 a; WIRTH, 1975).

F. turbinata is distinctly smaller than recent species of the group.

8. *Forcipomyia* (*F.*) sp. B

(Figs. 652–655)

DIAGNOSIS

Female of this species is distinguished by the following combination of characters: wing long measuring 1.75 mm, TR(III) 1.0, and very short flagellomere IX that is unusual for the subgenus.

DESCRIPTION

♀. Body dark brown, scutum shining. Total length 2.9 mm. Flagellum length 1080 μm, AR 1.15. Flagellomere IX nearly twice as short as X

(fig. 652). Proboscis short. Third palpal segment enlarged on basal half, length 120 μm (fig. 653). Scutum covered with relatively short setae. Scutellum with long setae. Legs moderately slender. TR(II) ca. 1.0, TR(III) 1.0 (fig. 654). Empodia large (fig. 655). Wing length 1.75 mm, CR 0.51. Both first radial cells present. Membrane uniformly covered with macrotrichia. Abdomen stout.

♂. Unknown.

MATERIAL EXAMINED (1 ♀)

ZMC 74, C. V. HENNINGSEN, 8–7 1965, 1 ♀.

DISCUSSION

The very short flagellomere IX is unique in the genus *Forcipomyia*. I have not found in my collection or in the literature a species with a similar flagellum.

9. *Forcipomyia* (*F.*) *pseudomicrohelea* sp. n.
(Figs. 656–659)

DIAGNOSIS

Male of this species is characteristic in having CR 0.34, TR(III) 0.3, third palpal segment swollen only at the base and bearing small sensory pit, and distinctly sinuous gonostyli.

DESCRIPTION

♀. Unknown.

♂. Body dark brown, thorax darker. Total length 2.0 mm. Lengths of distal 4 flagellomeres as follows: 120–113–75–80 μm (fig. 656). Proboscis long and slender. Palpus slender (fig. 657). Third palpal segment 105 μm long, basal third weakly swollen, sensory pit small. Scutum covered with short and long setae. Scutellum with very long setae. Legs slender. Basitarsi very short (fig. 658). TR(II) 0.20, TR(III) 0.33–0.34. Wing length 1.10 mm, CR 0.34. Second radial cell very short, first one probably obsolete. Membrane uniformly covered with appressed macrotrichia.

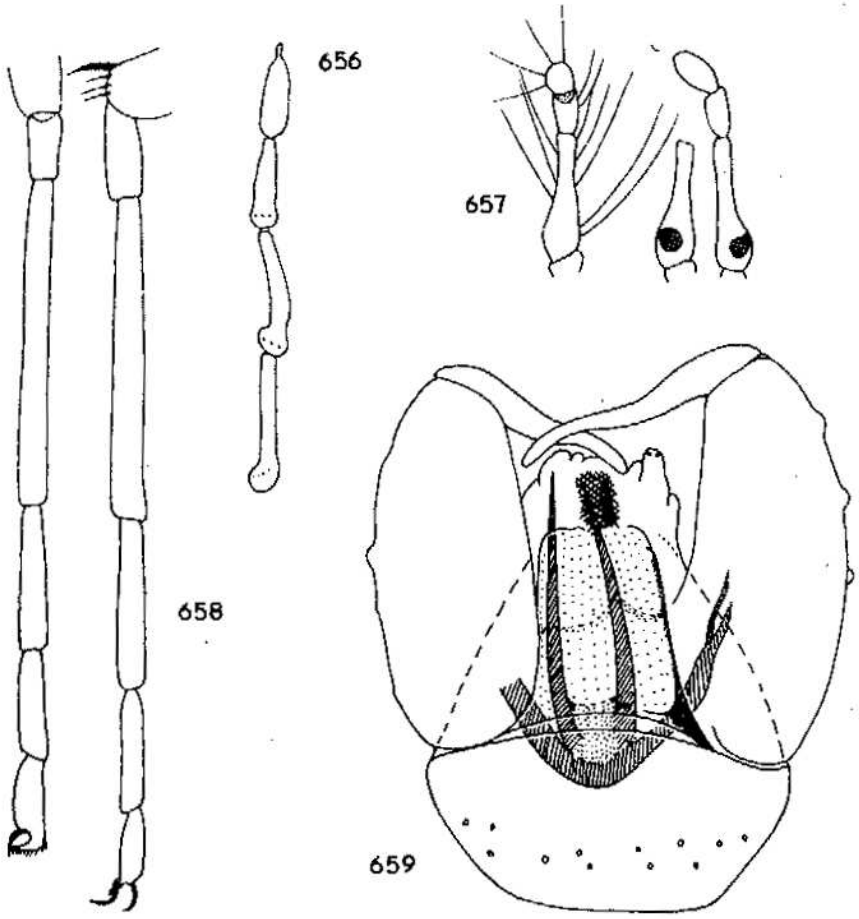
Genitalia (fig. 659). Sternite IX straight without caudomedian excavation. Gonocoxite long and slender. Gonostylus slender and distinctly sinuous. Aedeagus barely visible with low basal arch. Parameres long and slender with pointed apices and fused bases. Apodemes of gonocoxites distinct.

MATERIAL EXAMINED (1 ♂)

Holotype — ♂, MBI 136, KÜHL.

DISCUSSION

This species has very low TR index as in the subgenus *Microhelea* KIEFFER, however third palpal segment is swollen only at the base and flagellomere X is short as in the subgenus *Forcipomyia* (*F.*). In males of the subgenus *Microhelea* the third palpal segment is swollen at midpor-



656–659. *Forcipomyia* (*F.*) *pseudomicrohelea* sp. n., male, MBI 136; 656 — distal flagellomeres, 657 — palpi, 658 — tarsi of middle and hind leg, 659 — genitalia

tion, and the sensory pit is located at the middle or on the distal half of the segment (WIRTH, 1972). Such low TR and CR indices are unique for the subgenus *Forcipomyia* (*F.*). It may be that *F. pseudomicrohelea* **sp. n.** is a member of the *costata* group (see above).

Subgenus *Euprojoannisia* Bréthes, 1914

DIAGNOSIS

The flagellum in both sexes composed of 13 units. Proximal flagellomeres of female spherical, vasiform to subcylindrical; distal flagellomeres

usually slightly elongated. In male, flagellomere X longest, usually about 2 times longer than XI. Third palpal segment slender and long, usually swollen on basal half, sensory pit small or absent. Last 2 palpal segments usually incompletely fused. TR(III) 0.6–3.1. Empodia always present. Wing membrane uniformly covered with macrotrichia. CR 0.38–0.60. Both first radial cells usually small, first one present or obsolete. Aedeagus of variable shape, short or elongate, usually more or less triangular. Parameres usually absent. Apodemes of gonocoxites long and fused.

RECENT ECOLOGY AND DISTRIBUTION

The *Euprojoannisia* are common in moist sites of the world. Larvae live in semiaquatic habitats. Adults visit flowers (BYSTRAK and WIRTH, 1978).

FOSSILS

Fossil *Euprojoannisia* are known only from Baltic amber. In the material examined 20 specimens and 3 species of the subgenus have been found.

Forcipomyia (*Euprojoannisia*) indetermined (2 ♀)

MZW 7242 (+*Acarina* 1), 1 ♀; 12336 (+*Chironomidae* 1 ♂), 1 ♀.

10. *Forcipomyia* (*Euprojoannisia*) *piriformis* (Meunier, 1904), comb. n.

(Figs. 660–665)

Ceratopogon piriformis MEUNIER, 1904: 228 (♂, ♀, Baltic amber).

DIAGNOSIS

Males of this species are characteristic in having first radial cell and parameres well developed. TR(III) 2.2–2.7.

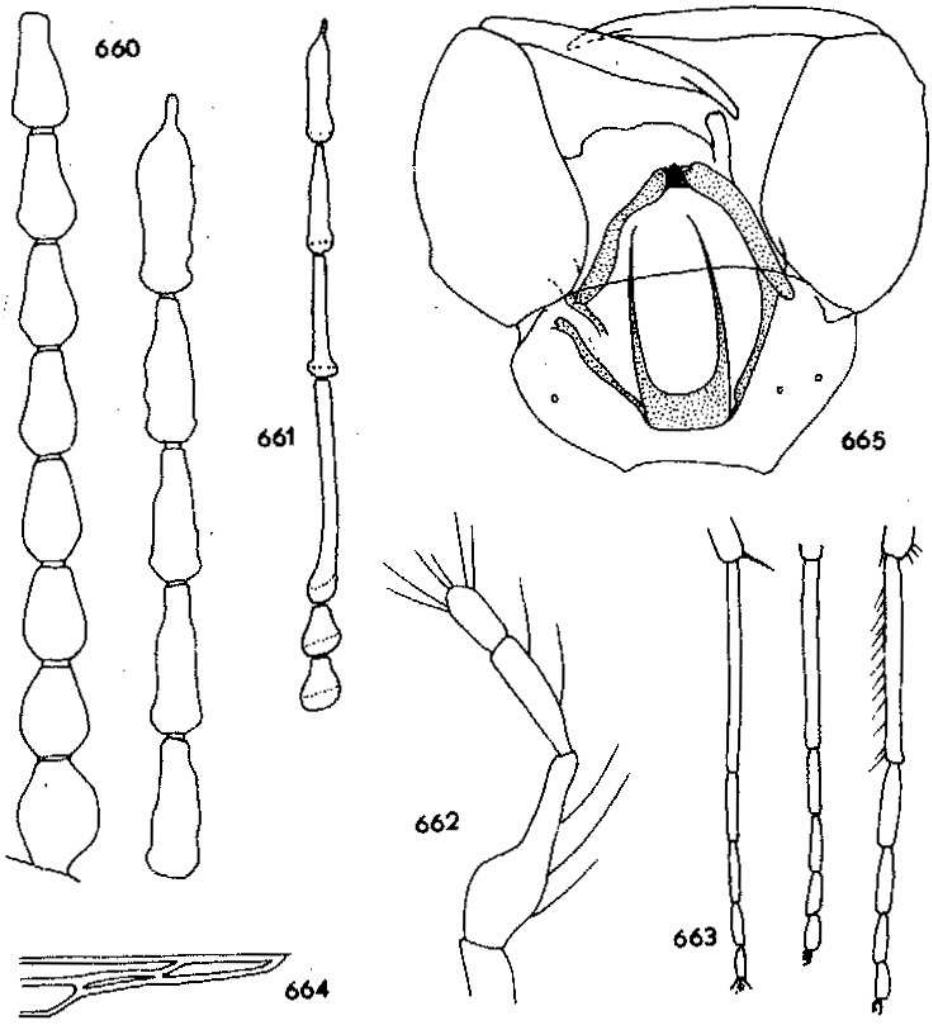
DESCRIPTION

♀. Body very hairy, dark brown to black. Total length 1.7–2.0 mm. Flagellum length 788–848 μm, AR 0.84–1.04 (fig. 660). Proximal flagellomeres relatively long. Proboscis long and slender. Palpus slender. Third palpal segment 76–94 μm long, basal half swollen, sensory pit not visible. Fourth and fifth palpal segments separated. Legs slender with long setae. Tibiae without lanceolate scales. TR(I) 2.4–2.8, TR(II) 2.5–2.8, TR(III) 2.2–2.7. Wing length 1.05–1.42 mm, CR 0.51–0.62. Second radial cell long and broad, first one narrow.

♂. Body dark brown to black with very long setae. Total length 2.2–2.8 mm. Flagellum length 825 μm (n = 1). Flagellomere X about 1.9 times longer than XI. Last 2 flagellomeres short (fig. 661). Proboscis long

and slender. Palpus slender and long (fig. 662). Third palpal segment distinctly swollen on basal half, sensory pit not visible, length 89–90 μm. Legs slender, bearing very long setae. Tarsi as in fig. 663. TR(I) 2.5–2.7, TR(II) 2.4–3.1, TR(III) 2.2–2.7. Wing length 1.05–1.52 mm, CR 0.50–0.57. First radial cell distinct, slit-like (fig. 664).

Male genitalia (fig. 665). Sternite IX barely visible. Tergite IX short. Gonocoxite broad. Gonostylus slender and long, tip distinctly tapered and slightly curved. Aedeagus broad and short with strongly sclerotized lateral and caudal margins, arch-shaped; at apex short cone-shaped median subapical projection present. Parameres well developed, moderately long and broadly fused at bases, apices slender and almost straight. Apodemes of gonocoxites long and slender, well sclerotized.



660–665. *Forcipomyia* (*Euprojoannisia*) *piriformis* (MEUNIER); 660 — female flagellum, IMGPUG 5998; 661 — distal flagellomeres of male, IMGPUG 6987; 662 — male palpus, 663 — male tarsi of fore, middle and hind leg, 664 — first radial cells of male, 665 — male genitalia, IMGPUG 8344

MATERIAL EXAMINED (5 ♂, 11 ♀)

Lectotype — ♂, IMGPUG Z 8344. Paralectotypes: IMGPUG Z 5998, 1 ♀; 6061 (+*Mycetophilidae* 1 ♂), 1 ♀; 6987, 1 ♂; 7089, 1 ♂; 7804, 1 ♂; 8827, 1 ♀. Present designations.

MBI 154, KÜNOW, 1 ♀; 202, KÜNOW, 1 ♂; MZW 14942, TG, 1 ♀; 16154, TG, 1 ♀; 19933, 1 ♀; ZMC 51, A. K. ANDERSEN, 28–3 1968, 1 ♀; 112, as above, 1 ♀; 178, A. HENNINGSEN, 9–9 1974, 1 ♀; 234, as above, 1 ♀.

DISCUSSION

F. piriformis has male genitalia with well developed parameres which are found only in 2 recent species of the subgenus, i.e *F. borealis* REMM (Lithuania, Caucasus — REMM, 1966, 1967; Poland — unpubl. data), and *F. pechumani* BYSTRAK et WIRTH (New York — BYSTRAK and WIRTH, 1978). Males of recent species are distinctly smaller (wing length 0.81–1.0 mm), and they have the last 2 palpal segments fused, second radial cell very small and first one obsolete.

It appears that the species mentioned above form a monophyletic group (*borealis* or *piriformis*) which occurs in Europe and in eastern North America at least since the Tertiary (fig. 768). Two recent species, now rarely recorded, are evidently relictal remains of this rather common group in Baltic amber.

11. *Forcipomyia* (*Euprojoannisia*) *berendti* sp. n.
(Figs. 666–670)

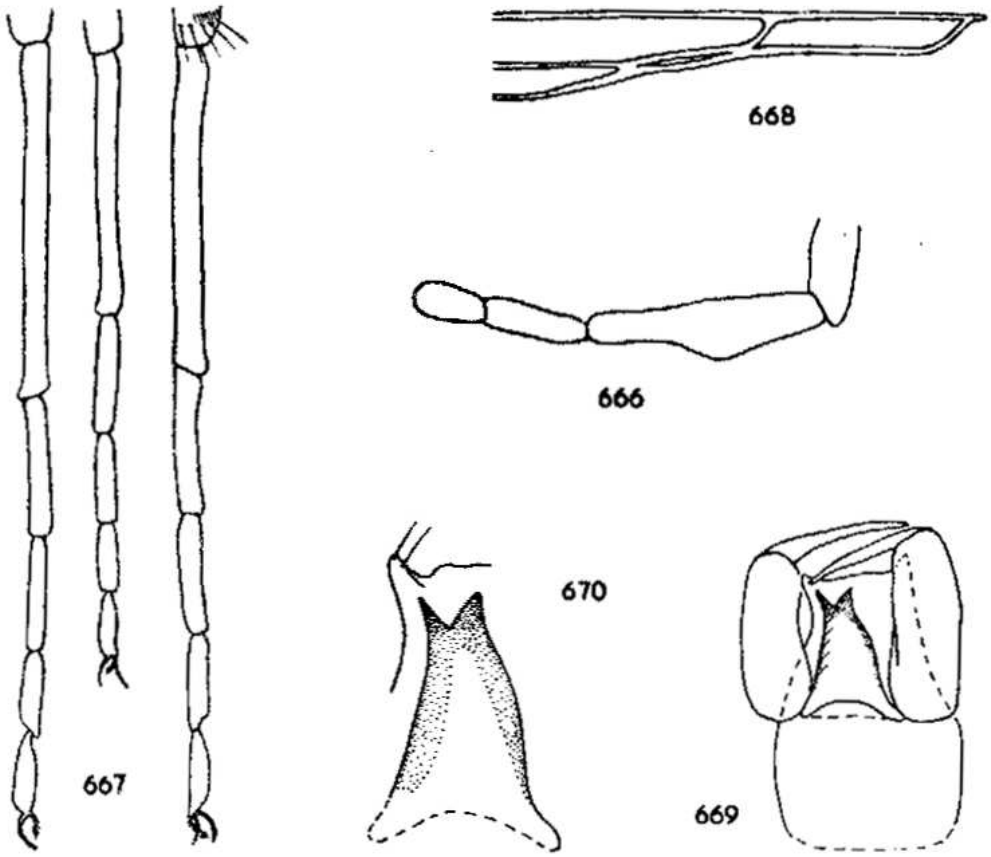
DIAGNOSIS

Male of the species is characterized by the following combination of characters: TR(III) 2.3. Second radial cell long and broad, first one slit-like. Parameres absent, aedeagus long with bilobed tip.

DESCRIPTION

♀. Unknown.

♂. Body very hairy, slender, black. Total length 2.0 mm. Flagellum barely visible. Proboscis long and slender. Palpus slender (fig. 666). Third palpal segment with enlarged basal half, sensory pit not visible, length 100 μm. Fourth and fifth palpal segments not fused. Tarsi as in fig. 667. TR(I) 2.6, TR(II) 2.3, TR(III) 2.3. Wing length 1.31 mm, CR 0.56. Second radial cell long and broad, first one short and slit-like (fig. 668).



666–670. *Forcipomyia* (*Euprojoannisia*) *berendti* sp. n., male, MBI 124; 666 — palpus, 667 — tarsi of fore, middle and hind leg, 668 — first radial cells, 669 — genitalia, 670 — aedeagus and apicolateral process of tergite IX

Genitalia (figs. 669, 670). Sternite IX barely visible. Tergite IX long and broad with short apicolateral processes. Gonocoxite slender. Gonostylus slender, almost straight, gradually tapering to tip. Aedeagus long, slightly tapering to short bilobed apex; basal arch low. Parameres absent. Apodemes of gonocoxites not visible.

MATERIAL EXAMINED (1 ♂)

Holotype — ♂, MBI 124, BERENDT, "*Ceratopogon* ♂, spec. 10, *scricpilosus*, Original Dr. B".

ETYMOLOGY

This species is named for the late physician Dr. G. C. BERENDT of old Gdańsk who studied insects in Baltic amber and made an extensive collection of inclusions.

DISCUSSION

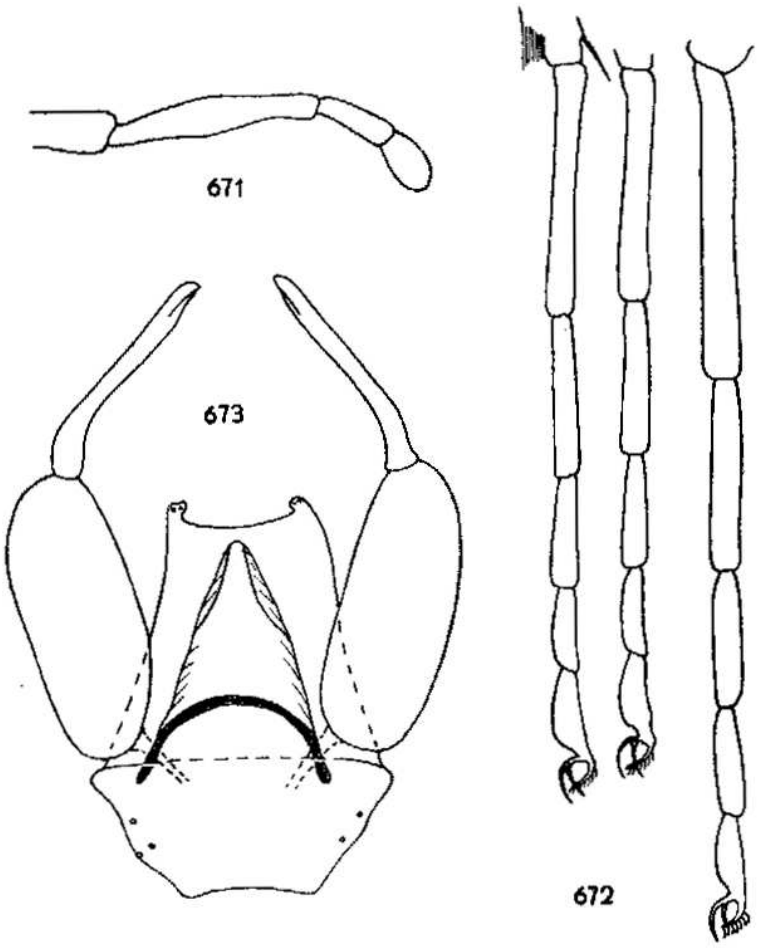
Male genitalia of *F. berendti* **sp. n.** are most similar to those of recent *F.*(*E.*) *fuscimana* (KIEFFER) from Oriental and Australian regions (TOKUN-

AGA and MURACHI, 1959; DEBENHAM and WIRTH, 1984). However the latter species has a more slender and bifid apex of aedeagus, lower TR, first radial cell obsolete, etc.

12. *Forcipomyia* (*Euprojoannisia*) *henningseni* sp. n.
(Figs. 671–673)

DIAGNOSIS

Male of this species is distinguished by the following combination of characters: TR(III) 1.7. Aedeagus long, triangular with evenly pointed tip. Parameres absent.



671–673. *Forcipomyia* (*Euprojoannisia*) *henningseni* sp. n., male, ZMC 67; 671 palpus, 672 tarsi of fore, middle and hind leg, 673 — genitalia

DECRIPTION

♀. Unknown.

♂. Body dark brown, thorax darker. Total length 1.9 mm. Flagellum barely visible. Proboscis long and slender. Palpus slender (fig. 671). Third

palpal segment slender, slightly swollen at the middle, sensory pit not visible, length 96 μm. Legs slender. TR(I) 1.6, TR(II) 1.5, TR(III) 1.7 (fig. 672). Wing length 1.26 mm, CR 0.57. Both first radial cells present.

Genitalia (fig. 673). Sternite IX presumably with straight caudal margin. Tergite IX long with short apicolateral processes. Gonocoxite slender, straight. Gonostylus slender not tapering at apex, slightly curved at base. Aedeagus weakly sclerotized, triangular, gradually tapering to evenly pointed barely visible tip, basal arch relatively high. Apodemes of gonocoxites barely visible.

MATERIAL EXAMINED (1 ♂)

Holotype — ♂, ZMC 67, A. HENNINGSEN, 9–9 1974.

ETYMOLOGY

This species is named for A. HENNINGSEN, a collector of the holotype.

DISCUSSION

This species is close to *F. berendti* **sp. n.** but it has a lower TR and aedeagus with evenly pointed tip. It seems that this species belongs to the *psilonota* group characterized by long triangular aedeagi which includes several species related to *F. psilonota* (KIEFFER) occurring in Africa, Australia and Oriental region (DESSART, 1963; DEBENHAM and WIRTH, 1984).

Subgenus *Trichohelea* Goetghebuer, 1920

DIAGNOSIS

Female proximal flagellomeres transverse to subspherical. Male antenna with 13 flagellomeres, X longest. Palpus 5-segmented. Third palpal segment slightly swollen, usually with well defined sensory pit. Fourth and fifth palpal segments not fused. Empodia of female well developed. Male empodia vestigial or absent. TR(III) 2.1–3.0 in recent species. CR 0.43–0.61. Wing membrane covered with slender decumbent macrotrichia. Second radial cell more or less short, first one slit-like. Gonostyli in male genitalia long and slender. Aedeagus usually with low, well sclerotized basal arch and short rounded posterior lobe bearing caudomedian peg-like process on dorsal side. Parameres short forming U-shaped structure, with broad clavate caudal lobes arising from articulation of gonocoxites and lateral ends of transverse connective of apodemal arch. Tergite IX in recent species not extending beyond apices of gonocoxites.

RECENT ECOLOGY AND DISTRIBUTION

Larvae breed in mosses and wet wood. Females are ectoparasites on other insects feeding on haemolymph mainly taken from wing veins of *Lepidoptera, Neuroptera, Megaloptera, Odonata, Diptera, Orthoptera, Coleoptera* (WIRTH and MESSERSCHMITH, 1971). Males visit flowers. This subgenus is distributed worldwide and includes more than 35 recent species.

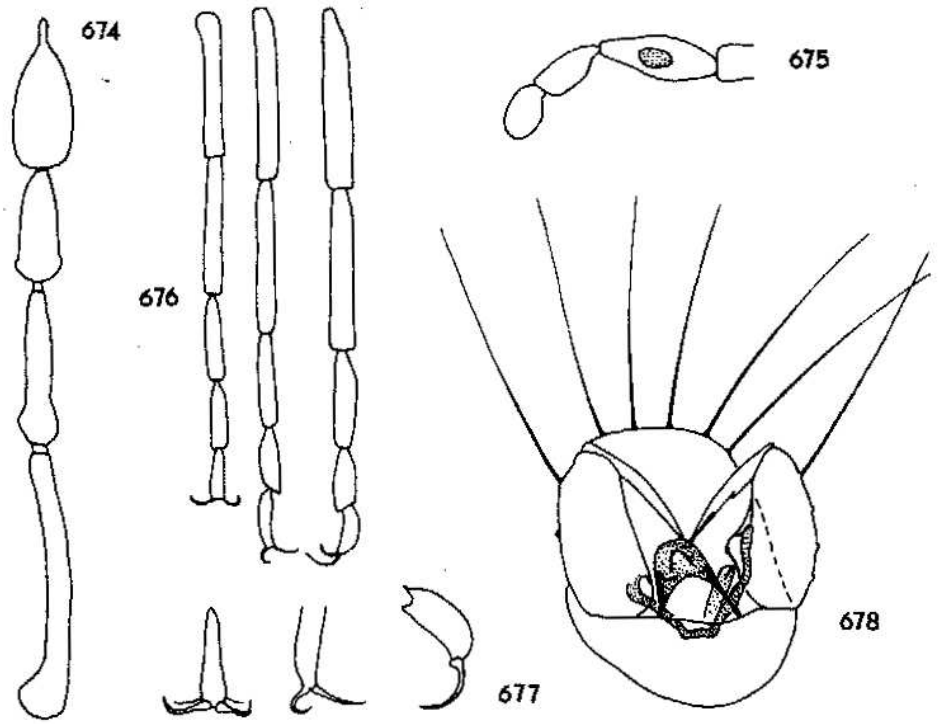
FOSSILS

This is the first record of fossil *Trichohelea*. Only a single male was found in the material examined.

13. *Forcipomyia* (*Trichohelea*) *eotrichoheleana* sp. n.
(Figs. 674–678)

DIAGNOSIS

Male of this species differs from recent species of the subgenus in having a low TR(1.0–1.1) and a long, broad tergite IX.



674–678. *Forcipomyia* (*Trichohelea*) *eotrichoheleana* sp. n., male, MBI 125; 674 — distal flagellomeres, 675 — palpus, 676 — tarsi of fore, middle and hind leg, 677 — claws of fore, middle and hind leg, 678 — genitalia

DESCRIPTION

♀. Unknown.

♂. Body slender dark brown, thorax darker. Total length 1.3 mm. Flagellum length 592 μm, AR 0.95. Lengths of distal 4 flagellomeres as follows: 112–68–48–62 μm (fig. 674). Proboscis moderately short. Palpus as in fig. 675. Third palpal segment slightly swollen with small well defined sensory pit at middle, length 52 μm. Claws slender and relatively long, empodia absent (fig. 677). TR(I) 1.0, TR(II) 1.1, TR(III) 1.1 (fig. 676). Wing length 0.83 mm, CR 0.53. First radial cell slit-like, second one narrow.

Genitalia small (fig. 678). Sternite IX barely visible. Tergite IX long and broad extending beyond apices of gonocoxites; caudal margin evenly rounded. Gonocoxite rather slender, broad basally. Gonostylus slender, gradually tapering to tip. Aedeagus short, barely visible; basal arch apparently high, caudomedian projection not extending beyond rounded and broad tip of aedeagus. Apodemes of gonocoxites and parameres forming U-shaped structure characteristic of the subgenus; caudal lobes of parameres barely visible, apparently short.

MATERIAL EXAMINED (1 ♂)

Holotype — ♂, MBI 125, BERENDT, "*Ceratopogon* ♂ sp. 11, *terminalis*, Original Dr. B" (+*Hymenoptera* 1).

DISCUSSION

It is possible that *F. eotrichoheleana* **sp. n.** does not belong to the subgenus *Trichohelea* because tarsal ratio is twice as low as in known recent species, and tergite IX is distinctly larger. Such a large and distally rounded tergite IX is similar to that of *F.* (*Blantonia*) *caribbea* WIRTH et DOW. However in subgenus *Blantonia* WIRTH et DOW (monotypic) fourth and fifth palpal segments are fused, TR(III) 2.7, and empodia in male are well developed (WIRTH and DOW, 1971).

Subgenus *Phytohelea* Remm, 1971

DIAGNOSIS

Male antenna with 13 flagellomeres; in female with 13 or 9 flagellomeres, proximal units compressed. Third palpal segment with well defined sensory pit. Last 2 palpal segments fused or separated. TR(III) 2.0–3.2. Empodia well developed in female; present, vestigial or absent in

male. Wing as in *Trichohelea*. Male genitalia with large shield-shaped aedeagus which usually has deep median incision or desclerotization dividing distal part into 2 submedian variously shaped lobes. Parameres in ventral view forming H-shaped structure.

RECENT ECOLOGY, DISTRIBUTION AND CLASSIFICATION

The larvae live submerged in water-filled leaf axils of various water-holding plants such as bromeliads in the tropics and subtropics (fig. 761). They feed on detritus. The subgenus includes 22 recent species classified in 3 groups: *comis*, *oligarthra* and *bromelicola* (DE MEILLON and WIRTH, 1979). Adults of most species, especially males, are very similar and because of this separation of the recent species is difficult, or even impossible in some cases.

FOSSILS

This is the first record of fossil *Phytohelea*. In the material examined only 2 males of a single species have been found.

14. *Forcipomyia* (*Phytohelea*) *eophytoheleana* sp. n.
(Figs. 679–686)

DIAGNOSIS

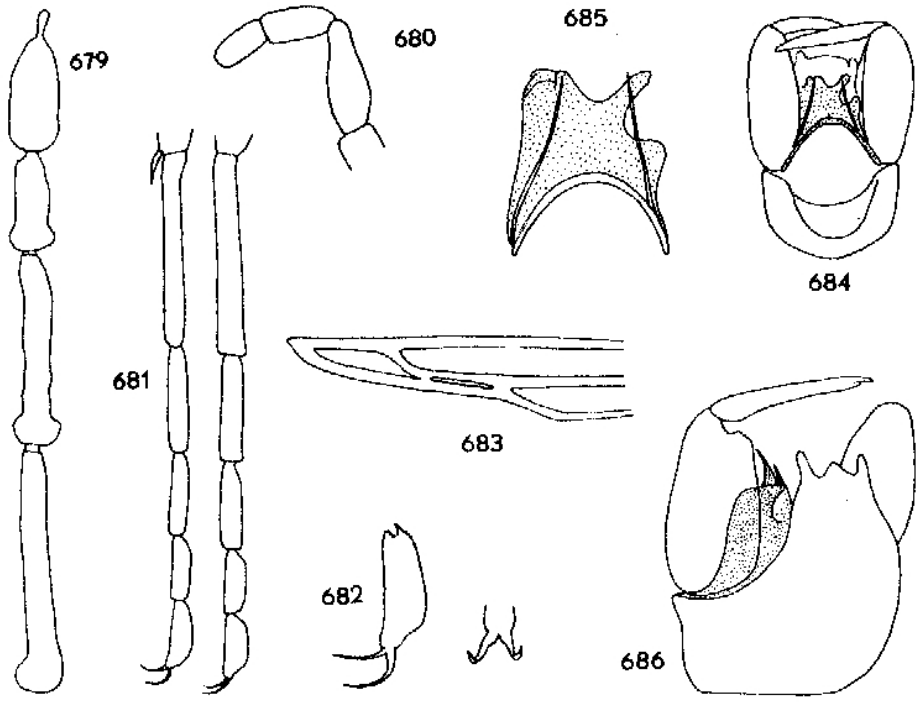
Males of this species are distinguished among the Baltic amber *Forcipomyia* by the following combination of characters: empodia absent, TR(I–III) 1.9–2.2. Aedeagus large.

DESCRIPTION

♀. Unknown.

♂. Body dark brown, thorax darker, scutum shining. Total length 1.4 mm. Flagellum length 638 μm, AR 0.93. Distal 4 flagellomeres as in fig. 679, with lengths as follows: 105–90–44–62 μm. Plume well developed. Proboscis moderately long. Third palpal segment slightly swollen, sensory pit not visible, length 52–72 μm. Fourth and fifth palpal segments separated (fig. 680). Empodia absent (fig. 682). TR(I) 1.9, TR(II) 2.0, TR(III) 2.2 (fig. 681). Wing length 0.70–0.85 mm, CR 0.50–0.55. Radial cells as in fig. 683.

Genitalia rotated or inverted (figs. 684–686). Sternite IX broad and



679–686. *Forcipomyia* (*Phytohelea*) *eophytoheleana* sp. n., male; 679 — distal flagellomeres, 680 palpus, 681 — tarsi of fore and middle leg, 682 — claws of fore and hind leg, 683 — first radial cells, 684 — ventral view of genitalia, 685 — aedeagus, MBI 212; 686 — lateral view of genitalia, ZMC 48

short with distinct caudomedian excavation. Tergite IX broad not extending to tips of gonocoxites, witch distinct apicolateral processes. Gonocoxite slender. Gonostylus slender, straight. Aedeagus broad and long with barely visible distal portion divided into lobes or pointed projections. Parameres not visible.

MATERIAL EXAMINED (2 ♂)

Holotype — ♂, MBI 212, BERENDT (+ *Cecidomyiidae*: *Heteropezini* 1 ♂; *Mycetophilidae* 1 ♂). Paratype — ♂, ZMC 48, C. V. HENNINGSEN, 3–5 1960.

DISCUSSION

I am not able to place this species in one of three groups distinguished by DE MEILLON and WIRTH (1979), or to compare it with known recent species. I hope that further materials which include females, allow this comparison.

Unknown subgenera

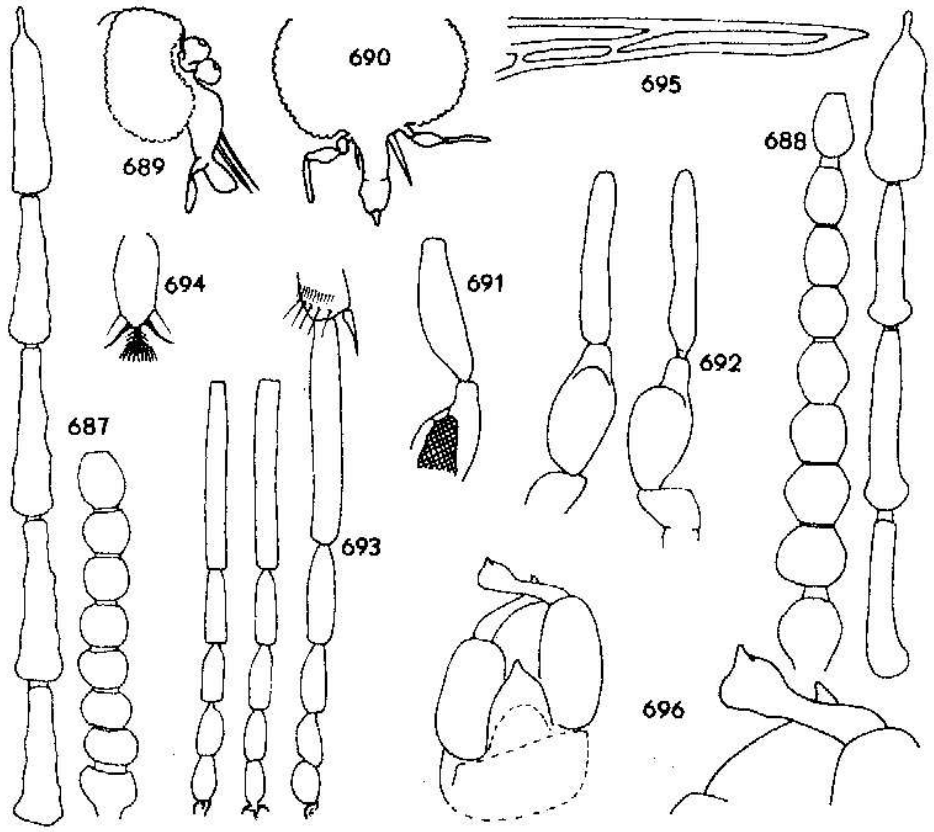
15. *Forcipomyia* (subg.?) *krzeminskii* sp. n.
(Figs. 687–696)

DIAGNOSIS

This species is characteristic in having the fourth and fifth palpal segments totally fused, TR(III) 2.1–2.2, gonostylus with expanded tip, and in the female proximal flagellomeres short, spherical, and AR 2.2.

DESCRIPTION

♀. Body dark brown. Total length 1.2–1.3 mm. Flagellum length 520–645 μm, AR 2.20–2.21. Proximal 7 flagellomeres spherical, short; flagellomere VIII slightly elongated, subcylindrical; distal 5 flagellomeres



687–696. *Forcipomyia krzeminskii* sp. n.; 687 — female flagellum, ZMC 186; 688 — male flagellum, MBI THOMAS 272; 689 — female head, ZMC 186; 690 — male head, MZW 8156; 691 — female palpus, ZMC 186; 692 — female palpi, MZW 8156; 693 — female tarsi of fore, middle and hind leg, ZMC 186; 694 — fifth tarsomere of female fore leg, MZW 9084; 695 — first radial cells of female, MZW 8156; 696 — male genitalia, MBI THOMAS 272

long, cylindrical (fig. 687). Proboscis long and slender, directed forwardly (fig. 689). Mandible with more than 30 distinct teeth. Third palpal segment short and distinctly swollen on basal 2/3 or more (figs. 691, 692), sensory pit deep with small rounded opening, length 64–80 μm. Fourth and fifth palpal segments totally fused, slender, length 72–80 μm. Legs slender. Tibial comb composed of 5 spines. Claws short with sharp apices, empodia well developed (fig. 694). TR(I) 2.5–2.6, TR(II) 2.3–2.4, TR(III) 2.1–2.2 (fig. 693). Wing length 0.81–0.92 mm, CR 0.58–0.59. Both first radial cells very narrow, first one short, second one very long (fig. 695). Wing membrane uniformly covered with decumbent macrotrichia.

♂. Similar to female with the usual sexual differences. Body length 1.3 mm. Flagellum length 518 μm, AR 1.14. Plume well developed. Flagellomere X shorter than XI. Lengths of distal 4 flagellomeres as follows: 70–84–64–72 μm (fig. 688). Proboscis long and slender (fig. 690). Third palpal segment 50 μm long. Fourth and fifth palpal segments totally fused, 56 μm long. Empodia well developed. TR(I) 2.5, TR(II) 2.3, TR(III) 2.1. Wing length 0.69 mm. First radial cells as in female.

Genitalia barely visible (fig. 696). Gonostylus with greatly expanded tip bearing distinct triangular dorsal projection. Aedeagus with evenly pointed triangular apex. Parameres not visible.

Material examined (1 ♂, 3 ♀)

Holotype — ♀, MZW 8156. Paratypes: MBI "Thomas 272, "*Tip. culiciform., Ceratopogon eucerus* ♂", 1 ♂; MZW 9084 (+ *Mycetophilidae* 2), 1 ♀; ZMC 186, C. V. Henningsen, 22–5 1969, 1–269, 1 ♀.

Etymology

This species is named for Dr. W. Krzemiński of Department of Systematic and Experimental Zoology, Polish Acad. Sci., Cracow, in recognition of his encouragements and help during the present study.

Discussion

This new species is related (or only superficially resembles) to the pantropical subgenus *Warmkea* Saunders but differs in having the third palpal segment distinctly enlarged with well developed sensory pit and an expanded tip of the gonostylus. In the subgenus *Warmkea* the third palpal segment is slender with scattered sensilla capitata over its surface and the gonostylus is always slender (Wirth and Soria, 1979). An expanded gonostylus tip is found in one species of the subgenus

Pedilohelea DE MEILLON et WIRTH and in some species of the subgenus *Lepidohelea* KIEFFER. However the latter two subgenera differ in many important characters from the new species (DESSART, 1963; WIRTH and RATANAWORABHAN, 1978; DE MEILLON and WIRTH, 1979).

16. *Forcipomyia* (subg.?) *kulickae* sp. n.
(Figs. 697–702)

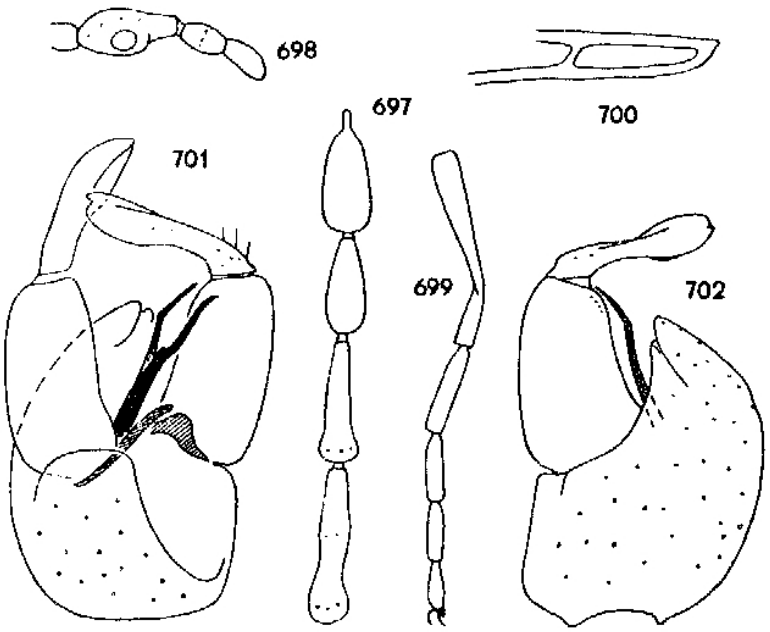
DIAGNOSIS

This species is characterised by having large male genitalia with long parameres, gonostyli with expanded tip, 5-segmented palpi, TR(III) 2.3, and well developed empodia.

DESCRIPTION

♀. Unknown.

♂. Body brown, thorax darker with very long and strong setae. Total length 0.9 mm. Flagellum composed of 13 units, length 448 μm, AR 0.91. Flagellomere X relatively short (fig. 697). Proboscis moderately long, slender. Palpus 5-segmented. Third palpal segment distinctly swollen on basal 2/3, sensory pit well developed, length 40 μm (fig. 698). Legs slender. Empodia well developed. TR(II) 2.2, TR(III) 2.3 (fig. 699). Wing length 0.67 mm, CR ca. 0.39. Second radial cell long, first one absent (fig. 700). Wing membrane covered with macrotrichia.



697–702. *Forcipomyia kulickae* sp. n., male, RSz 7; 697 — distal flagellomeres, 698 — palpus, 699 — hind tarsus, 700 — first radial cells, 701, 702 — genitalia

Genitalia very large, as long as half of abdomen (figs. 701, 702). Sternite IX with broad and deep caudomedian excavation. Tergite IX broad. Gonocoxite short, simple. Gonostylus distinctly enlarged on apical part. Aedeagus barely visible, short. Parameres very long, strongly sclerotized; basal portion stout and nearly straight, distal portion abruptly slender and curved ventrally, tips pointed.

MATERIAL EXAMINED (1 ♂)

Holotype — ♂, RSz 7. The holotype will be deposited in Department of Systematic and Experimental Zoology, Polish Acad. Sci., Cracow.

ETYMOLOGY

This species is named for M.Sc. R. KULICKA of Museum of the Earth, Polish Acad. Sci., Warsaw, a curator of the Baltic amber collection.

DISCUSSION

The combination of characters in the male of *F. kulickae* is unique in the genus. It has all of the important characters of the subgenus *Panhelea* REMM from western Palaearctic except for the shape of the second radial cell and male genitalia. In male of *Panhelea* the second radial cell is very small, genitalia are devoid of parameres, tergite IX with long and slender apicolateral processes, sternite IX is without caudomedian excavation, and apodemes of gonocoxites are extremely long. *F.(Panhelea) brevicubitus* GOETGHEBUER has rod-like projections of sternite IX which are unique in the genus (REMM and ŽOGOLEV, 1968; REMM, 1980).

17. *Forcipomyia* (subg.?) *eobreviflagellata* sp. n.
(Figs. 703–708)

DIAGNOSIS

Males of this species are characteristic in having flagellum composed of 10 units. TR(III) 1.9–2.1, empodia well developed.

DESCRIPTION

♀. Unknown.

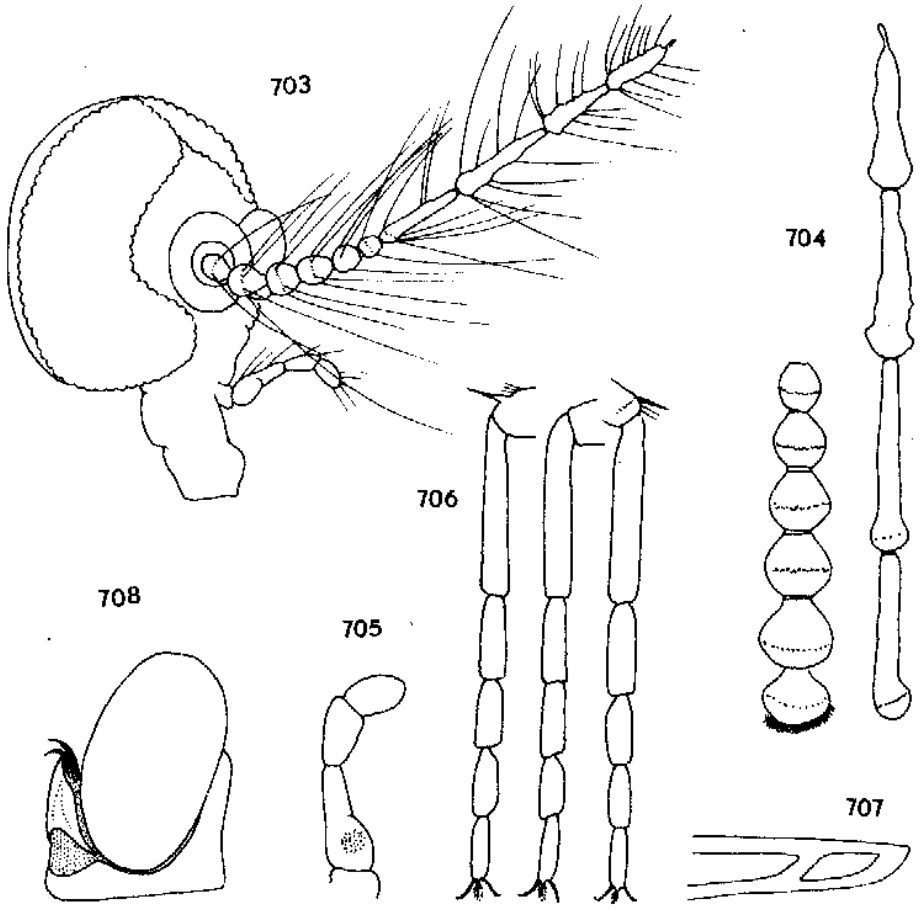
♂. Body black. Total length 1.1–1.2 mm. Flagellum composed of 10 units, proximal flagellomeres reduced from 9 to 6. Plume sparse

(fig. 703). Flagellomere X shorter than XI, lengths of distal 4 flagellomeres as follows: 72–88–80–76 μm, n = 1 (fig. 704). Proboscis moderately short (fig. 703). Palpus 5-segmented. Third palpal segment swollen on basal third, sensory pit small, length 44 μm (fig. 705). Legs moderately slender. Empodia distinct. TR(I) 2.2–2.4, TR(II) 1.8–2.1, TR(III) 1.9–2.1 (fig. 706). Wing length 0.67–0.71 mm, CR 0.38. Second radial cell small, first one absent (fig. 707). Wing membrane densely and uniformly covered with decumbent macrotrichia.

Male genitalia (fig. 708). Sternite IX barely visible, presumably with shallow caudomedian excavation. Tergite IX short. Gonocoxite broad. Gonostylus straight, gradually tapering to moderately slender tip. Aedeagus short and broad, triangular. Parameres barely visible, short.

MATERIAL EXAMINED (2 ♂)

Holotype — ♂, MZW 19242, TG, filled with Canada balsam. Paratype — ♂, together with the holotype, abdomen unnaturally swollen.



703–708. *Forcipomyia eobreviflagellata* sp. n., male, MZW 19242; 703 — head, 704 — flagellum, 705 — palpus, 706 — tarsi of fore, middle and hind leg, 707 — second radial cell, 708 — lateral view of genitalia

DISCUSSION

The subgeneric position of *F. eobreviflagellata* is unknown. The reduced number of male flagellomeres is unique in the genus. In the subfamily, only in *Atrichopogon brevicornis* TOKUNAGA is the male flagellum composed of 10 flagellomeres, however only the distal 3 units are elongated (TOKUNAGA and MURACHI, 1959).

22. Genus *Atrichopogon* Kieffer, 1906

DIAGNOSIS

Antenna in both sexes with 13 flagellomeres, except of male of *A. brevicornis* (see above). Female antenna with proximal flagellomeres transverse, spherical to slightly subcylindrical; distal 5 always long. Proboscis short to long, straight or curved. Palpus 5-segmented. Third palpal segment usually slender with usually small sensory pit. Scutum usually covered with fine short setae only. Scutellum bearing limited number of long setae of taxonomic value. Legs slender. Empodia always present. TR usually higher than 2.0. Wing membrane with well developed microtrichia; macrotrichia short, erect and sparse, often confined to wing tip or absent. Fringe of posterior wing margin simple, consisting of single row of alternating longer and shorter setae. Costa usually extending to 2/3 of wing length. Second radial cell long, first one short, often slit-like. Male genitalia without parameres. Aedeagus usually short and more or less trilobed.

RECENT ECOLOGY, DISTRIBUTION AND CLASSIFICATION

The larvae live on rotting wood, on stones in the rills, on partially submerged vegetation, in mosses, etc. They feed on algae and detritus. Adult females are parasites on larger insects feeding on their haemolymph or visit flowers for nectar or pollen. Males only visit flowers. The genus *Atrichopogon* including more than 350 recent species is distributed worldwide and common in moist habitats. The subgeneric classification of the genus is poorly understood on a world basis. Currently it is divided into the following subgenera: *Atrichopogon*, *Psilokempia* ENDERLEIN, *Meloehelea* WIRTH, *Dolichohelea* EDWARDS, *Rostropogon* REMM and *Psammopogon* REMM.

FOSSILS

Until now, a single fossil species, *Atrichopogon brunnescens*, has been described from Miocene rocks from Rott in West Germany by STATZ

(1944) (single female, wing length 1.3 mm). *Atrichopogon canadensis* Boesel is not member of the genus but it belongs to the tribes *Culicoidini* or *Ceratopogonini* (see p. 26).

This is the first record of *Atrichopogon* in Baltic amber. In the material examined only single female was found.

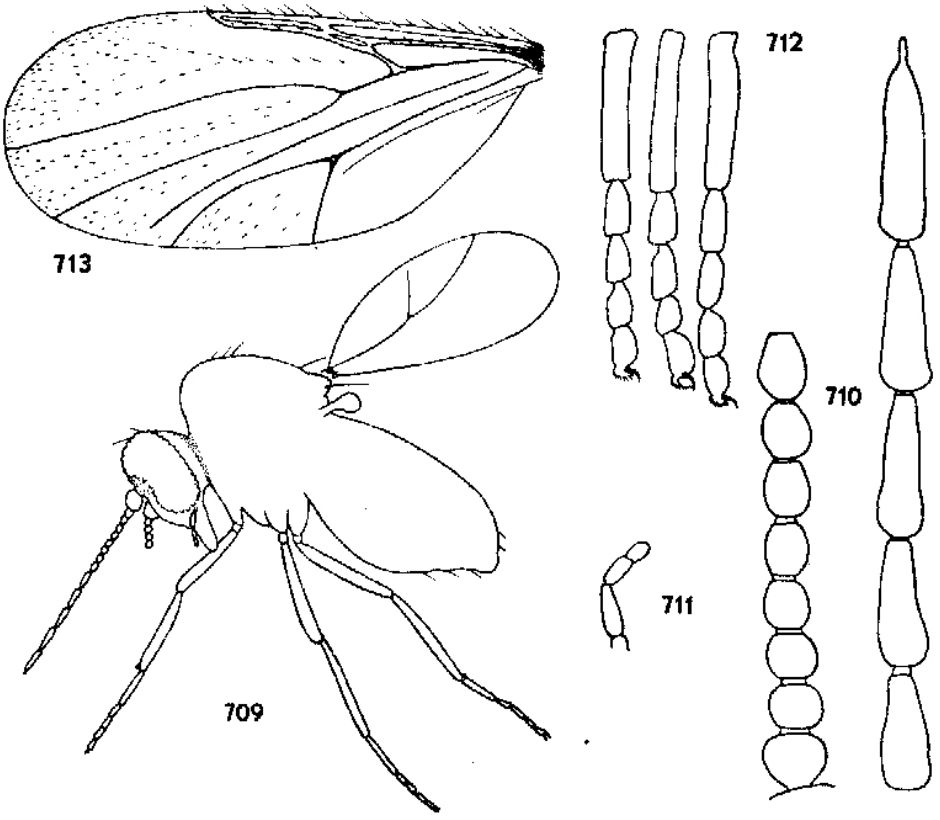
1. *Atrichopogon eocenicus* sp. n.
(Figs. 709–713)

Diagnosis

Female of this species is characteristic in having a very short wing measuring 0.77 mm and sparse macrotrichia restricted to the distal half of the wing.

Description

♀. Body dark and stout (fig. 709). Total length 1.1 mm. Flagellum length 563 μm, AR 1.64 (fig. 710). Proximal flagellomeres spherical to slightly elongated. Distal 5 flagellomeres long, cylindrical. Proboscis



709–713. *Atrichopogon eocenicus* sp. n., female, MZW 4834; 709 — total habitus, 710 — flagellum, 711 — palpus, 712 — tarsi of fore, middle and hind leg, 713 — wing

short, straight. Palpus barely visible (fig. 711). Third palpal segment ca. 40 μm long. Scutum covered with sparse and short setae. Scutellum bearing 4 long setae. Legs slender. Tarsi as in fig. 712. Claws small, empodia distinct. TR(I) 2.7, TR(II) 3.0, TR(III) 2.7. Wing length 0.77 mm, CR 0.62 (fig. 713). Membrane with distinct microtrichia and with suberect macrotrichja on distal half. Second radial cell ca. 2.9 times longer than first one. Intercalary veins well visible. Abdomen without special armature. Seminal capsule not visible.

♂. Unknown.

MATERIAL EXAMINED (1 ♀)

Holotype — ♀, MZW 4834, TG.

DISCUSSION

This species is most probably a member of the subgenus *Atrichopogon* (*A.*) and can be distinguished from the fossil *A. brunnescens* and recent Holarctic species by its small size.

4. Subfamily *Dasyheleinae* Lenz, 1934

The subfamily includes only the single genus *Dasyhelea*.

23. Genus *Dasyhelea* Kieffer, 1911

DIAGNOSIS

Eyes contiguous. Antenna in both sexes with 13 flagellomeres without sensilla coeloconica. Flagellomeres usually sculptured. Terminal flagellomere blunt, slightly pointed or with slender terminal stylet. Distal flagellomeres in female not markedly longer than proximal units. In male distal 4 flagellomeres elongated, plume well developed. Palpus 5-segmented, slender, usually basal 2 segments fused. Third palpal segment with scattered long and fine sensilla capitata on inner surface, sensory pit absent. Antepronotum indistinct, prescutal pits absent. Scutum usually with short setae. Legs slender, unarmed. Claws short, equal and simple. Empodia obsolete. Fourth tarsomeres cylindrical. TR usually higher than 2.0. Wing membrane with very fine microtrichia, macrotrichia usually abundant over all or part of wing. Costa usually extending to about middle of wing. First radial cell slit-like or absent, second one more or less small. Intercalary veins usually well visible. M_2 forking at or

distally of crossvein r-m, base usually atrophied. Squama often with fine hairs.

Female with 1–2 functional seminal capsules. Male genitalia inverted or not. Sternite IX usually produced to more or less cover the aedeagus. Tergite IX usually long and broad, with or without apicolateral processes. Aedeagus broad, usually with 2 submedian caudal processes. Parameres usually asymmetrical, with 2 basal arms articulating with gonocoxites and single long posterior projection.

Recent ecology, distribution and classification

The larvae of *Dasyhelea* are aquatic and semiaquatic. They have been usually collected in small and shallow bodies of water. Adults feed on honeydew or visit flowers for nectar (Waugh and Wirth, 1976). *Dasyhelea* is distributed worldwide and includes more than 400 recent species. Relationship of species, species groups or subgenera of the genus still remain poorly understood. Wirth (1952), Waugh and Wirth (1976) basing on the North American material divided the genus into species groups which generally correspond to the subgenera (*Sebessia* Remm, *Dicryptoscena* Enderlein, *Dasyhelea* s. str., *Pseudoculicoides* Malloch and *Prokempia* Kieffer (used by Remm (1962 b, 1979) in his studies of the Palaearctic *Dasyhelea*.

Fossils

Fossil *Dasyhelea* have been recorded in Miocene nodules from California (Palmer, 1957; Pierce, 1966). They are: *D. browneae* Pierce, *D. dara* Pierce, *D. judithae* Pierce, *D. kanakoffi* Pierce, *D. stenoceras* Palmer and *D. australis antiqua* Palmer (see chapter V). The latter species belongs to the subgenus *Sebessia* Remm or *cincta* group sensu Wirth including some recent species restricted to Europe, USA, and Chile and Patagonia in South America (Wirth, 1952; Remm, 1979; Szadziewski, 1986). *D. pallidihalter* Carter, Ingram et Macfie from Afrotropical region included to the group by Wirth (1952) does not belong to this subgenus because it has only single seminal capsule and asymmetrical parameres. It seems reasonable to treat *D. antiqua* Palmer **stat. n.** as a distinct fossil species than as a subspecies of the recent *D. australis* Wirth from the Juan Fernándes Islands in Chile. *D. antiqua* is described in all stages while the other species from Californian nodules are known only from pupae. It is interesting to note that the horseshoe-shaped eggs of this genus were isolated from the nodules (Pierce, 1966).

Dasyhelea tyrrelli Boesel from Canadian amber with only distal

3 flagellomeres of male antenna elongated does not belong to *Dasyhelea*, but to an unknown genus of the subfamily *Ceratopogoninae*.

This is the first record of fossil *Dasyhelea* in Baltic amber. In the material examined 18 specimens and 4 species have been found. It seems that all specimens from Baltic amber belong to one group. They have a well developed first radial cell and usually large second one. Most of recent species have totally reduced first radial cell and usually a very small second one. *Dasyhelea* from Baltic amber are relatively large as compared to "average" biting midge from this fossil resin, except for *D. gedanica* **sp. n.** which is small.

Dasyhelea indetermined (1 ♂, 7 ♀)

IZPAN 41/73, 1 ♀ at *Brachypogon balticus*; 53/76, 1 ♀; MZW 12159 a, 1 ♂; 12775, 1 ♀; 14039, TG, 1 ♀; 20006, TG, 1 ♀ at *Brachypogon prominulus*; ZMC 54, Th. HANSEN, Mou, 16–1 1961, 1 ♀; 168, A. HENNINGSEN, 9–9 1974, 1 ♀.

Key to Baltic amber species of *Dasyhelea*

Males

1. Apicolateral processes of tergite IX short and broad . . . . . 4. *D. stanislavi* sp. n.
—. Apicolateral processes of tergite IX long and slender 2
2. Second radial cell short. Wing length 0.70 mm . . . . . 1. *D. gedanica* sp. n.
—. Second radial cell long. Wing longer than 1.2 mm 3
3. Wing length 1.25–1.27 mm . . . . 2. *D. eodicryptoscenica* sp. n.
—. Wing length 1.68 mm . . . . . 3. *D.* sp. A

1. *Dasyhelea gedanica* sp. n.

(Figs. 714–720)

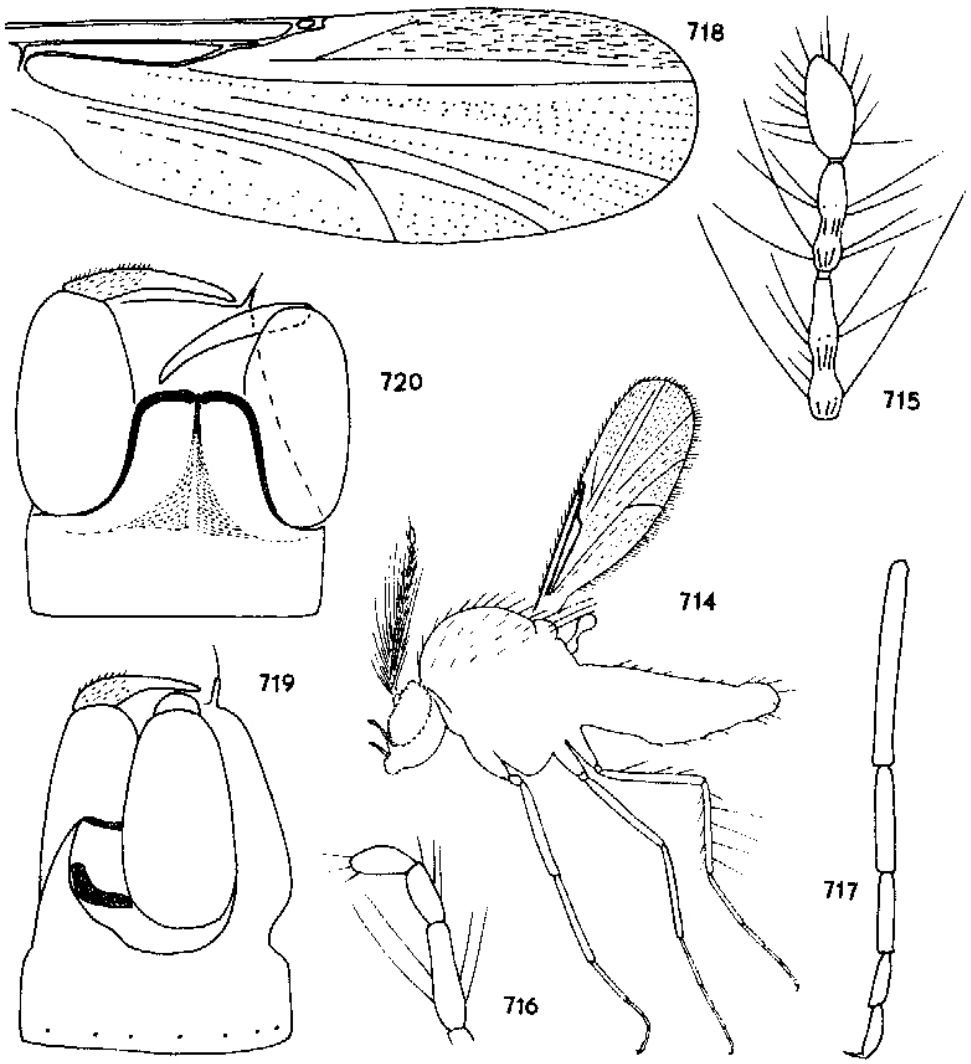
DIAGNOSIS

Male of this species is distinguished by the following combination of characters: wing length 0.70 mm, terminal flagellomere with rounded tip, tergite IX with distinct, slender and cylindrical apicolateral processes.

DESCRIPTION

♀. Unknown.

♂. Body black. Total length 1.1 mm. General habitus as in fig. 714. Flagellum length 500 μm, AR 0.87. Distal 4 flagellomeres elongated, lengths as follows: 62–64–52–48 μm. Terminal flagellomere short with



714–720. *Dasyhelea gedanica* sp. n., male, MZW 6133; 714 — total habitus, 715 — distal flagellomeres, 716 — palpus, 717 — hind tarsus, 718 — wing, 719 — lateral view of genitalia, 720 — ventral view of genitalia

evenly rounded tip (fig. 715). Palpus slender, barely visible (fig. 716). Third palpal segment ca. 48 μm long. Legs slender. Tibial comb composed of 6 spines. Claws with bifid apices. TR(I) 2.2, TR(II) 2.0, TR(III) 1.9 (fig. 717). Wing length 0.70 mm, CR 0.44. Membrane covered with macrotrichia, microtrichia not visible. First radial cell line-like; second one small, rounded with concave apex (fig. 718).

Genitalia not inverted (figs. 719, 720). Sternite IX greatly produced to cover aedeagus. Tergite IX long and broad with moderately long, slender and cylindrical apicolateral processes. Gonocoxite moderately stout. Gonostylus slender, slightly curved. Aedeagus and parameres not visible.

MATERIAL EXAMINED (1 ♂)

Holotype — ♂, MZW 16133, TG.

DISCUSSION

The subgeneric position of this species is not clear. It has both first radial cells as recent *Sebessia* and *Dicryptoscena*, apicolateral processes of tergite IX as *Dasyhelea* (*D.*), some *Pseudoculicoides* or *Prokempia*, and terminal flagellomere as *Pseudoculicoides* or *Prokempia*.

2. *Dasyhelea eodicryptoscenica* sp. n.
(Figs. 721–725)

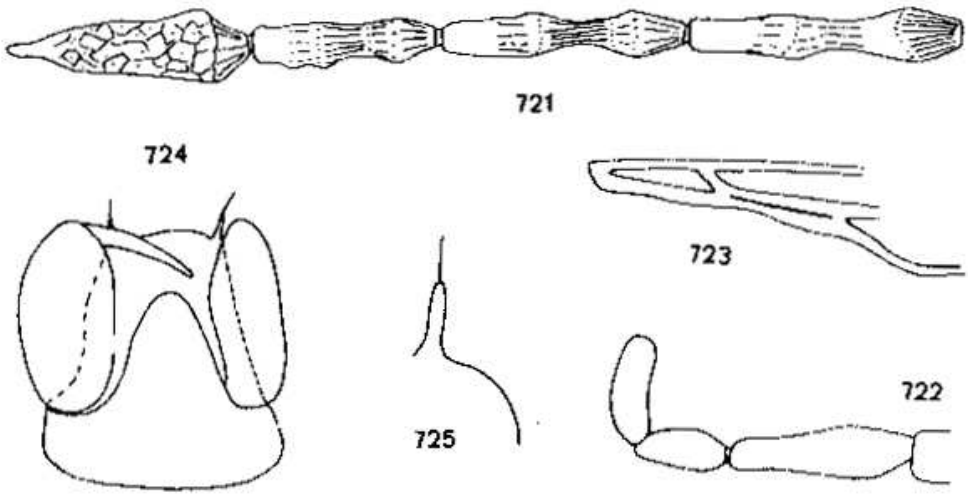
DIAGNOSIS

Males of this species are distinguished by the following combination of characters: wing length 1.25–1.27 mm. Last flagellomere long with slender terminal papilla. Tergite IX with long and slender apicolateral processes.

DESCRIPTION

♀. Body black, tarsi paler. Total length 1.9–2.0 mm. Terminal flagellomere with slender pointed papilla. AR ca. 1.0. Palpus long and slender; lengths of distal segments as follows: III — 80 μm, IV — 42 μm, V — 48 μm. TR(II) 2.1, TR(III) 2.0. Wing length 1.14–1.17 mm, CR 0.53–0.56. Both first radial cells present. First radial cell line-like, second one long and broad. Wing membrane densely covered with macrotrichia. Seminal capsules not visible.

♂. Body black, tarsi paler. Total length 1.9–2.1 mm. Lengths of distal 4 flagellomeres as follows: 112–120, 96–108, 80–96, 96–104 μm (fig. 721).



721–725. *Dasyhelea eodicryptoscenica* sp. n., male; 721 — distal flagellomeres, 722 — palpus, 723 — first radial cells, MBI 98; 724 — genitalia, MZW 9356; 725 — apicolateral process of tergite IX, MBI 98

Last flagellomere with distinct slender terminal papilla. Palpus as in fig. 722; lengths of distal segments as follows: III — 80–84 μm, IV — 40–44 μm, V — 48–52 μm. TR(I) 2.1, TR(II) 2.0–2.1, TR(III) 1.9–2.1. Wing length 1.25–1.27 mm, CR 0.49–0.56. Both first radial cells present. First radial cell line-like, second one long and broad with blunt tip (fig. 723). Macrotrichia abundant over almost entire wing membrane.

Genitalia inverted or not (figs. 724, 725). Sternite IX produced to cover aedeagus. Tergite IX long and broad with long, slender, cylindrical apicolateral processes. Gonocoxite moderately slender, slightly curved. Aedeagus and parameres not visible.

MATERIAL EXAMINED (3 ♂, 2 ♀)

Holotype -- ♂, MZW 9356. Paratypes: MBI 98 a, BERENDT (+ legs of *Ceratopogon* indet., 1 ♀), 1 ♂; MZW 8709 a, 1 ♂.

MBI THOMAS 245, "*Ceratopogon pilicornis* ♀", 1 ♀; MZW 5230, TG, 1 ♀.

DISCUSSION

This species has first radial cells and palpi as in the subgenus *Dicryptoscena* and *Sebessia*, long apicolateral processes of tergite IX in the male genitalia as *Dasyhelea* (*D.*) and terminal papilla of last flagellomere intermediate between *Dasyhelea* (*D.*) and *Dicryptoscena* or *Sebessia*.

3. *Dasyhelea* sp. A

DIAGNOSIS

Male of the species is close to *D. eodicryptoscenica* **sp. n.**, but is distinctly larger with wing length 1.68 mm.

DESCRIPTION

♀. Unknown.

♂. Body black. Total length 2.7 mm. Lengths of distal 4 flagellomeres as follows: 156–136–100–112 μm. Terminal flagellomere with slender pointed tip. Palpus slender and long. Lengths of distal palpal segments as follows: III — 112 μm, IV — 56 μm, V — 60 μm. TR(I) 2.4, TR(II) 2.0. Wing length 1.68 mm, CR 0.56. First radial cell slit-like, second one larger. Membrane covered with macrotrichia. Genitalia not inverted, barely visible. Tergite IX with long and slender apicolateral processes. Gonostylus slender, slightly curved.

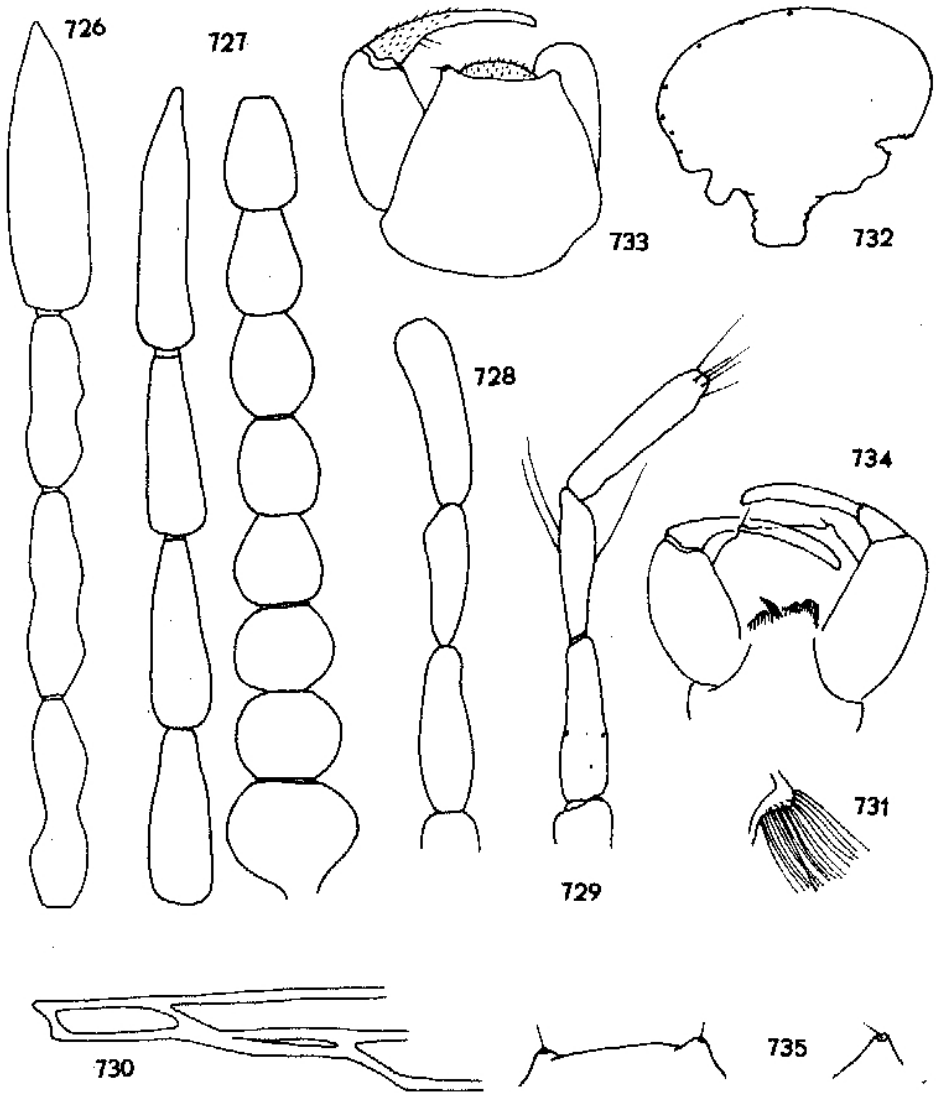
MATERIAL EXAMINED (1 ♂)

MBI 114, BERENDT, 1 ♂.

4. *Dasyhelea stanislavi* sp. n.
(Figs. 726–735)

DIAGNOSIS

Males of this species are distinguished by the following combination of characters: tergite IX with short and broad apicolateral processes, terminal flagellomere distinctly longer than flagellomere X.



726–735. *Dasyhelea stanislavi* sp. n.; 726 — distal flagellomeres of male, MZW 9617; 727 — female flagellum without flagellomere IX, 728 — female palpus, MZW 8862 a; 729 — male palpus, MZW 7647; 730 — first radial cells of male, 731 — wing squama of male with long hairs, MZW 9617; 732 — seminal capsule ?, MZW 8862 a; 733 dorsal view of male genitalia, MZW 9617; 734 — ventral view of male genitalia, MZW 9617; 735 — apicolateral processes of male tergite IX, MZW 7647, 9617

DESCRIPTION

♀. Body black. Total length 2.5 mm. Flagellum length 810 μm, AR 1.21 (fig. 727). Last flagellomere with slender pointed tip. Lengths of distal 5 flagellomeres as follows: 72–76–80–80–112 μm. Palpus slender and long (fig. 728). Last palpal segment longer than third one. Lengths of distal palpal segments as follows: III — 76 μm, IV — 60 μm, V — 88 μm. Wing length 1.42 mm, CR 0.56. Membrane covered with macrotrichia. First radial cell slit-like. Seminal capsule single and very large measuring 224 × 200 μm (fig. 732), however it may be an artifact.

♂. Body black. Total length 2.0–2.6 mm. Last flagellomere with pointed tip (fig. 726). Lengths of distal 4 flagellomeres as follows: 88–92–80–128 μm and 105–98–80–135 μm. Palpus slender and long (fig. 729). Last palpal segment very long. Lengths of distal palpal segments as follows: III — 76 μm, IV — 68 μm, V — 80 μm. TR(II) 1.8–2.0, TR(III) 2.0. Wing length 1.22–1.50 mm, CR 0.55. Membrane covered with distinct macrotrichia. First radial cell slit-like, second one long and broad with concave apex (fig. 730). Squama of wing with long hairs (fig. 731).

Genitalia rotated or not (figs. 733–735). Sternite IX barely visible. Tergite IX long and broad, with short and broad apicolateral processes. Gonostylus long, slender and slightly curved. Aedeagus and parameres barely visible.

MATERIAL EXAMINED (2 ♂, 1 ♀)

Holotype — ♂, MZW 9617. Paratype — ♂, MZW 7647. MZW 8862 a, 1 ♀ is not included to type-series.

ETYMOLOGY

This species is named for Dr. STANISŁAW PIĄTKOWSKI of Gdańsk University who indirectly made possible my work on the *Ceratopogonidae*.

NOTE

It seems that this species is a typical member of the subgenus *Dicryptoscena*.

5. Subfamily *Leptoconopinae* Noé, 1907

The subfamily includes only the single genus *Leptoconops*.

24. Genus *Leptoconops* Skuse, 1899

Diagnosis

Eyes widely separated in both sexes. Female antenna with 10–12 flagellomeres, first flagellomere swollen, terminal flagellomere long with evenly rounded tip, remaining units transverse, spherical to slightly elongated. Male antenna composed of 13 flagellomeres, plume well developed, usually only last flagellomere elongated. Sensilla coeloconica absent. Proboscis usually shorter than height of head. Palpus 4-segmented (primitive 4th and 5th segments fused). Third palpal segment swollen in female and bearing large sensory organ on inner surface. Scutum usually covered with sparse distinct setae. Prescutal pits well developed, each composed of 2–3 separate rounded membranous areas. Antepronotum indistinct. Scutellum bearing 4–6 strong setae. Legs usually slender. Femora unarmed. Tibial comb composed of 3–7 spines. TR about 1.5–2.0. Tarsomeres sometimes with strong ventral spines. Female claws similar on all legs, either simple or dentate with strong basal tooth. Male claws similar on all legs — both simple, or one simple but the other one with a long basal process; or dissimilar — on hind legs both claws simple but on fore and middle legs one claw with a long basal process. Empodia vestigial. Wing membrane covered with distinct microtrichia, macrotrichia absent. Costa short, usually ending before middle of wing. Intercalary veins conspicuous extending from MA to slightly before wing tip. Crossvein r-m absent. Median veins shifted caudally.

Female abdomen usually with long cerci. Male genitalia conspicuous. Sternite IX very narrow. Tergite IX usually with distinct apicolateral processes. Gonocoxite with prominent basal ventral lobe. Gonostylus tapering with subapical articulated blunt tooth. Aedeagus composed of 2 simple sclerotized rods fused distally with lateral projections. Parameres strongly sclerotized, each composed of 2 sclerites.

Recent ecology, distribution and classification

The larvae live in moist and usually saline soil of arid or desert areas and of coastal and inland beaches. They burrow in the soil feeding on the organic material found there. Adults are diurnal in activity. Females are hematophagous feeding on mammals and birds. Males visit flowers for nectar. Most species of the genus are present in the tropical and subtropical regions throughout the world, however there are species described from as far north as Hungary and Moscow district. To *Leptoconops* belong more than 90 recent species grouped in 6 subgenera. They are: *Styloconops* Kieffer, *Brachyconops* Wirth et Atchley,

Megaconops WIRTH et ATCHLEY, *Leptoconops* (*L.*), *Holoconops* KIEFFER and *Proleptoconops* CLASTRIER.

FOSSILS

Two undescribed specimens of the subfamily have been found in Cretaceous Siberian amber (KALUGINA, 1977), and *Leptoconops* was mentioned from Canadian amber (DOWNES and WIRTH, 1981).

This is the first record of *Leptoconops* in Baltic amber. In the material examined only 4 specimens of 1 species belonging to the subgenus *Leptoconops* have been found.

Subgenus *Leptoconops* Skuse, 1899

DIAGNOSIS

Female antenna with 12 flagellomeres. Frons bare, rarely with 1–2 setae. Vertex with a row of long setae. Third palpal segment with sensilla capitata scattered over inner surface or confined to a large open depression. Tarsi usually with strong spines only at apices of basitarsi. Female with long tapering cerci. Tergite IX in male genitalia with a pair of long digitiform apicolateral processes.

RECENT DISTRIBUTION

In this subgenus there are known 51 extent species distributed in the tropics and subtropics (fig. 760).

FOSSILS

These are the first described fossil *Leptoconops*. It is surprising that all 4 specimens of the genus were found only in the ZMC collection.

1. *Leptoconops* (*L.*) *succineus* sp. n.

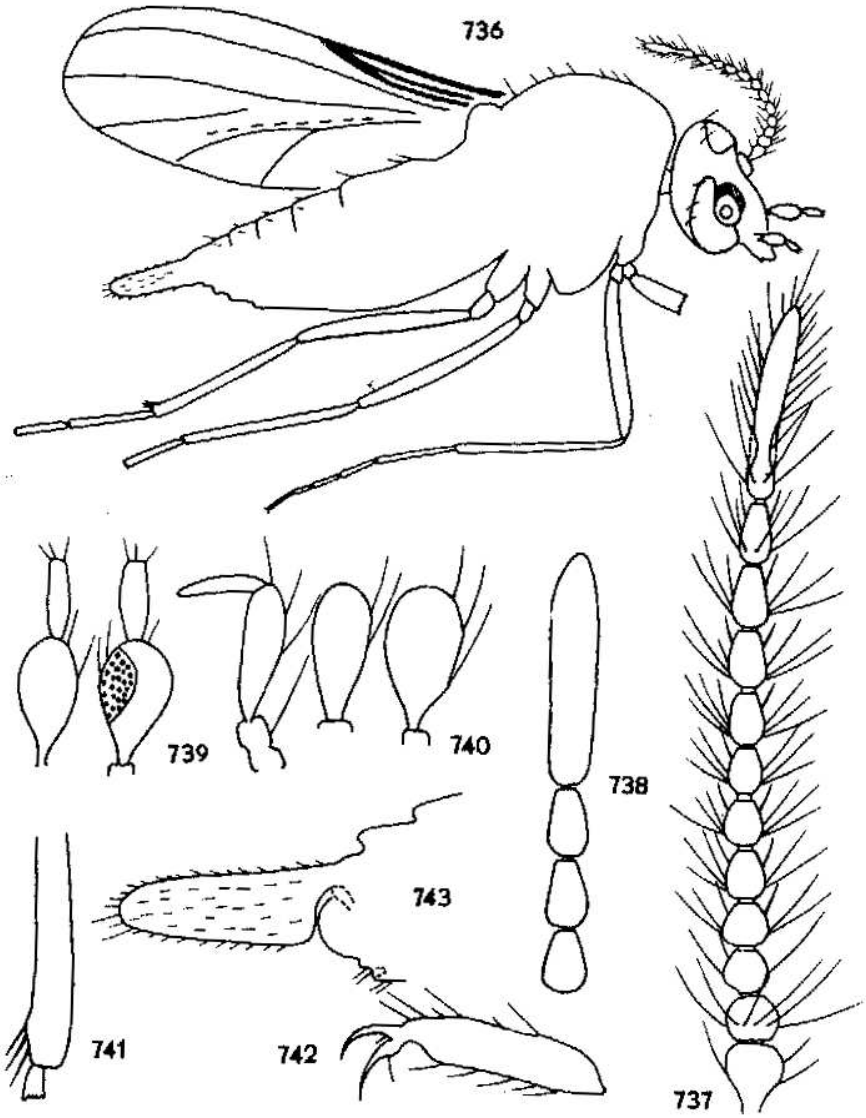
(Figs. 736–749)

DIAGNOSIS

The new species can be readily distinguished from recent species by its small size (wing length of female 0.7 mm, of male 1.0 mm), and by the elongated distal flagellomeres of the female.

DESCRIPTION

♀. Body blackish brown. General habitus as in fig. 736. Total length 1.1 mm. Eyes widely separated. Vertex with some long setae, frons

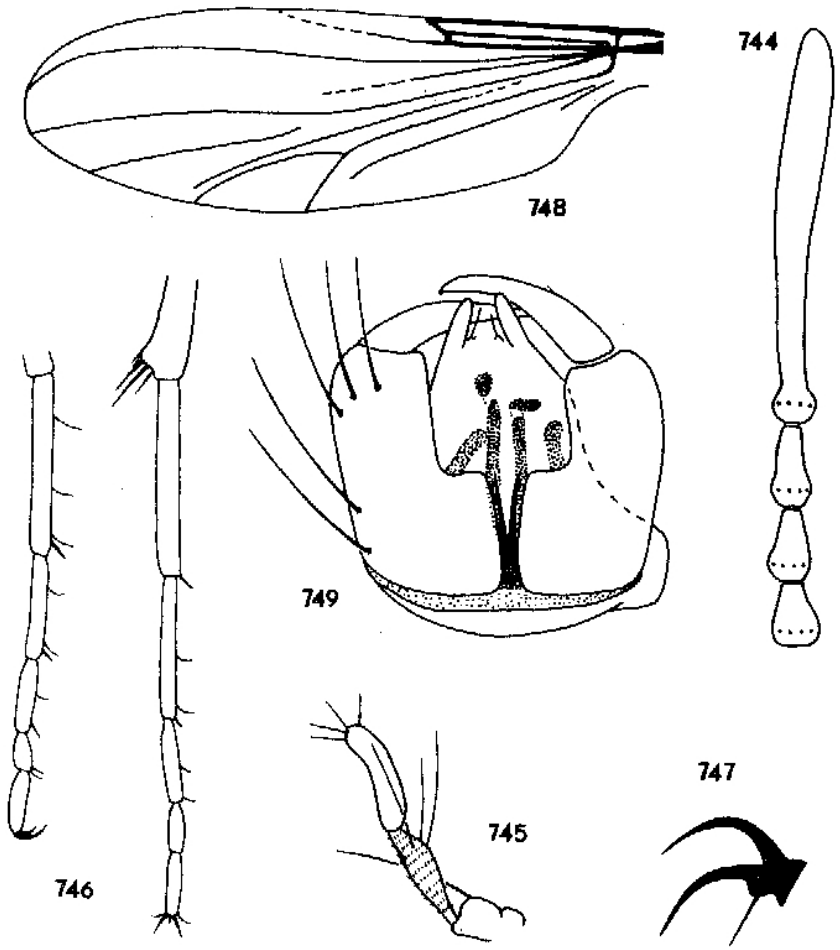


736–743. *Leptoconops* (*L.*) *succineus* sp. n., female; 736 — total habitus, 737 — flagellum, ZMC 252; 738 — distal flagellomeres, ZMC 251; 739 — palpi, ZMC 252; 740 — palpi, ZMC 251; 741 — tip of hind tibia, ZMC 251; 742 — claws of fore leg, ZMC 252; 743 — cercus, ZMC 251

bare, clypeus with 2 setae. Flagellum relatively long measuring 418 μm. Proximal flagellomeres II–V or VI more or less spherical, flagellomeres VII–XI slightly elongated. Terminal flagellomere 3.1–3.3 times longer than preceding one, length 86–96 μm (figs. 737, 738). Flagellomeres II–XI with long verticils, subapical sensilla trichodea present. Proboscis rather short, about half of head length. Palpus short (figs. 739, 740), last segment slender. Third palpal segment swollen with large open sensory depression on inner surface covered with sensilla capitata, length 48–64 μm. Scutum shining, finely dotted and densely covered with small hairs; a single row of short acrostichals and longer dorsocentrals present. Some larger supraalar setae readily visible. Prescutal pits each with

2 separated round areas. Scutellum bearing 2 long submedian and 2 shorter lateral setae. Tibial comb composed of 3 or 4 spines (fig. 741). Claws simple and equal on all legs, each with long seta at base (fig. 742). TR(I) 1.5–1.9, TR(III) 1.8. Wing length 0.67–0.73 mm, CR 0.41–0.43. Membrane covered with distinct microtrichia. Cerci 133–148 μm (fig. 743).

♂. Similar to female with the usual sexual differences. Body blackish brown, tarsi paler. Total length 1.5 mm. Eyes widely separated. Clypeus with 2 long setae. Flagellum length 544 μm, plume well developed. Terminal flagellomere 176 μm long, 4.8 times longer than preceding one (fig. 744). Proboscis longer than in female, about 0.8 of head length. Palpus slender (fig. 745). Third palpal segment 48 μm long, sensorium not visible. Scutum dotted and covered with short hairs. Prescutal pits invisible. Scutellum bearing 4 long setae. Tibial comb composed of 3 spines. Tarsi with indistinct apical spines (fig. 746). Claws similar on all legs, equal and simple, one claw with long basal seta (fig. 747). TR(II) 1.8, TR(III) 1.5. Wing length 1.0 mm (fig. 748).



744–749. *Leptoconops* (*L.*) *succineus* sp. n., male, ZMC 250; 744 — distal flagellomeres, 745 — palpus, 746 — tarsi of middle and hind leg, 747 — claws of middle leg, 748 — wing, 749 — genitalia

Male genitalia of typical shape of the subgenus (fig. 749). Aedeagus and parameres barely visible.

MATERIAL EXAMINED (1 ♂, 3 ♀)

Holotype — ♀, ZMC 252, C. V. HENNINGSEN, 1–2 1969, in a very small amber piece, distal tarsomeres of middle and hind legs lost. Paratypes: ZMC 250, C. V. HENNINGSEN, Nordgyllands Vestleyst., Min. Mus. 1951–26, 1 ♂; 251, C. V. HENNINGSEN, 1–2 1969, 2 ♀.

DISCUSSION

Females of *L. succineus* **sp. n.** have distinctly elongated flagellomeres VII–XI while most of the recent species have these flagellomeres transverse to spherical. Elongated flagellomeres VII–XI are found only in females of *L.(L.) longicornis* CARTER from western Australia, however it is a larger species (wing length of female 1.6–2.1 mm, of male 2.1–2.4 mm) (SMEE, 1966).

V. CHECKLIST OF THE FOSSIL *CERATOPOGONIDAE*

Fossil genera are marked with "+"

Subfamily *Ceratopogoninae*

Tribe *Culicoidini*

+ ***Atriculicoides*** REMM, 1976: 108

A. macrophtalmus REMM, 1976: 108 (♂, ♀, Siberian amber).
A. squamaticrus REMM, 1976: 110 (♀, Siberian amber).

Culicoides LATREILLE

C. abbreviatipennis STATZ, 1944: 142 (♀, Aquitanian, Rott).
? *C. abdominalis* STATZ, 1944: 145 (♀, Aquitanian, Rott).
? *C. atratulus* STATZ, 1944: 147 (♀, Aquitanian, Rott).
C. austerus STATZ, 1944: 144 (♀, Aquitanian, Rott).
C. balticus **sp. n.**
C. bicolor STATZ, 1944: 146 (♀, Aquitanian, Rott).
C. carri PIERCE, 1966: 91 (pupa, Miocene, California).
C. ceranowiczi **sp. n.**
C. dasyheleiformis **sp. n.**
C. elongatulus STATZ, 1944: 143 (♀, Aquitanian, Rott).
C. eoselficus **sp. n.**
C. filipalpis REMM, 1976: 111 (♀, Siberian amber).

C. fossilis PIERCE, 1966: 91 (pupa, Miocene, California).
C. gedanensis **sp. n.**
? *C. gracilior* STATZ, 1944: 143 (♀, Aquitanian, Rott).
C. jucundus STATZ, 1944: 147 (♀, Aquitanian, Rott).
C. kaluginae REMM, 1976: 110 (♀, Siberian amber).
C. laurae PIERCE, 1966: 91 (pupa, Miocene, California)
C. liliputanus STATZ, 1944: 142 (♀, Aquitanian, Rott).
C. megacanthus PALMER, 1957: 272 (pupa, Miocene, California).
C. miocenea PIERCE, 1966: 93 (pupa, Miocene, California).
C. obesus STATZ, 1944: 145 (♀, Aquitanian, Rott).
C. obscuratus STATZ, 1944: 144 (♀, Aquitanian, Rott).
C. prussicus **sp. n.**
C. speciosus (MEUNIER, 1904) — Baltic amber.
C. sphenostylus REMM, 1976: 112 (♂, ♀, Siberian amber).
C. succineus REMM, 1976: 113 (♂, ♀, Siberian amber).
C. succivarius **sp. n.**
C. tenuipennis STATZ, 1944: 147 (♀, Aquitanian, Rott).
C. spp. A-C — Baltic amber.

+ ***Protoculicoides*** BOESEL, 1937: 50

P. depressus BOESEL, 1937: 51 (♀, Canadian amber).

Tribe *Ceratopogonini*

Brachypogon KIEFFER

B. balticus **sp. n.**
B. eocenicus **sp. n.**
B. frigidus REMM, 1976: 115 (♂, ♀, *Ceratopogon*, Siberian amber).
B. gedanicus **sp. n.**
B. henningseni **sp. n.**
B. polonicus **sp. n.**
B. prominulus (MEUNIER, 1904) — Baltic amber.
B. sp. A — Baltic amber.

Ceratoculicoides WIRTH et RATANAWORABHAN

C. danicus **sp. n.**

Ceratopogon MEIGEN

C. aquilonius BOESEL, 1937: 49 (♀, Canadian amber).
C. ceranowiczi **sp. n.**

C. crypticus **sp. n.**
C. eminens MEUNIER, 1904 — Baltic amber.
C. forcipiformis MEUNIER, 1904 — Baltic amber.
C. gedanicus **sp. n.**
C. grogani **sp. n.**
C. hennigi **sp. n.**
C. macronyx REMM, 1976: 113 (♂, ♀, Siberian amber).
C. margaritae **sp. n.**
C. piotrowskii **sp. n.**
C. remmicolus **sp. n.**
C. ritzkowskii **sp. n.**
C. tertiaricus **sp. n.**
C. spp. A-C — Baltic amber.

+ *Fossihelea* gen. n.

F. gracilitarsis (MEUNIER, 1904) — Baltic amber.
F. sp. A — Baltic amber.

***Leptohelea* WIRTH et BLANTON**

L. taimyrica REMM, 1976: 115 (♂, *Baeohelea*, Siberian amber).

***Nannohelea* GROGAN et WIRTH**

N. eocenica **sp. n.**
N. grogani **sp. n.**

Tribe *Stilobezziini*

***Alluaudomyia* KIEFFER**

A. succinea **sp. n.**
? *A.* sp. A — Baltic amber

+ *Ceratopalpomyia* gen. n.

C. eocenica **sp. n.**

+ *Eohelea* PETRUNKEVITCH, 1957: 208

E. gedanica **sp. n.**
E. grogani **sp. n.**
E. petrunkevitchi SZADZIEWSKI, 1984 — Baltic amber.
E. sinuosa (MEUNIER, 1904) — Baltic and Saxonian ambers.

+ *Gedanohelea* gen. n.

G. loewi **sp. n.**
G. succinea **sp. n.**
G. wirthi **sp. n.**

+*Mantohelea* gen. n.

M. gedanica **sp. n.**
M. lacus (MEUNIER, 1904) — Baltic amber.

+ *Meunierohelea* gen. n.

M. gedanicola **sp. n.**
M. nielseni **sp. n.**
M. wirthi **sp. n.**
M. spp. A-C — Baltic amber.

Monohelea KIEFFER

M. baltica **sp. n.**
M. clunipes (LOEW, 1850) — Baltic amber.
M. sp. A — Baltic amber.

Serromyia MEIGEN

S. anomalicornis (LOEW, 1850) — Baltic amber.
S. austera STATZ, 1944: 150 (♀, Aquitanian, Rott).
S. colorata STATZ, 1944: 150 (♀, Aquitanian, Rott).
S. polonica **sp. n.**
S. spinigera (LOEW, 1850) — Baltic amber.
S. spinosifemorata STATZ, 1944: 151 (♀, Aquitanian, Rott).
S. succinea **sp. n.**
S. spp. A-B — Baltic amber.

Stilobezzia KIEFFER

S. falcata (MEUNIER, 1904) — Baltic amber.
S. goetghebueri STATZ, 1944: 148 (♀, Aquitanian, Rott).
S. veterana MEUNIER, 1920: 897 (♀, *Tetragoneura*, Aquitanian, Rott).
S. spp. A-E — Baltic amber.

+*Wirthohelea* gen. n.

W. trifida **sp. n.**

Tribe *Heteromyiini*

Neurohelea KIEFFER

N. cothurnata (MEUNIER, 1904) — Baltic amber.

Physohelea GROGAN et WIRTH

P. obtusa (MEUNIER, 1904) — Baltic amber.

Tribe *Palpomyiini*

Bezzia KIEFFER

B. eocenica **sp. n.**
? *B. longipennis* STATZ, 1944: 151 (♀, Aquitanian, Rott).

Palpomyia MEIGEN

P. edwardsi COCKERELL, 1921: 469 (sex?, Oligocene, England).
P. freyi PIERCE, 1966: 95 (pupa, *Neopalpomyia*, Miocene, California).
P. jantari **sp. n.**
P. multispinosa PIERCE, 1966: 97 (pupa, *Neopalpomyia*, Miocene, California).
P. riedeli **sp. n.**
P. ryshkoffi PIERCE, 1966: 98 (pupa, *Parapalpomyia*, Miocene, California).
P. shilo PIERCE, 1966: 95 (pupa, *Miopalpomia*, Miocene, California).
P. succinea **sp. n.**
P. unca HONG, 1981: 58 (♀, Chinese amber).

Unplaced species and genera of *Ceratopogoninae*

Atrichopogon canadensis BOESEL, 1937: 47 (♀, Canadian amber).
Dasyhelea tyrrelli BOESEL, 1937: 48 (♂, Canadian amber).
Johannsenomyia hotchkissae PIERCE, 1966: 94 (pupa, Miocene, California).
J. swinhoei COCKERELL, 1919: 249 (♂, Burmese amber).
Lasiohelea cretea BOESEL, 1937: 46 (♀, Canadian amber).
L. globosa BOESEL, 1937: 47 (♀, Canadian amber).
+*Neoculicoides* PIERCE, 1966: 93
N. jeanneae PIERCE, 1966: 94 (pupa, Miocene, California).
+ *Paraculicoides* PIERCE, 1966: 94
P. rouseae PIERCE, 1966: 94 (pupa, Miocene, California).

Subfamily *Forcipomyiinae*

Atrichopogon KIEFFER

A. brunnescens STATZ, 1944: 141 (♀, Aquitanian, Rott).
A. eocenicus **sp. n.**

Forcipomyia MEIGEN

F. berendti **sp. n.**
F. eobreviflagellata **sp. n.**
F. eocostata **sp. n.**
F. eophytoheleana **sp. n.**
F. eotrichoheleana **sp. n.**
F. gedanicola **sp. n.**
F. henningseni **sp. n.**
F. krzeminskii **sp. n.**
F. kulickae **sp. n.**
F. lyneborgi **sp. n.**
F. piriformis (MEUNIER, 1904) — Baltic amber.
F. pseudomicrohelea **sp. n.**
F. succinea **sp. n.**
F. turbinata (MEUNIER, 1904) — Baltic amber.
F. uncula (MEUNIER, 1904) — Baltic amber.
F. spp. A-B — Baltic amber.

Subfamily *Dasyheleinae*

Dasyhelea KIEFFER

D. antiqua PALMER, 1957: 266 (all stages, *D. australis antiqua*, Miocene, California), **stat. n.**
D. browneae PIERCE, 1966: 87 (pupa, Miocene, California).
D. dara PIERCE, 1966: 88 (pupa, Miocene, California).
D. eodicryptoscenica **sp. n.**
D. gedanica **sp. n.**
D. judithae PIERCE, 1966: 88 (pupa, Miocene, California).
D. kanakoffi PIERCE, 1966: 89 (pupa, Miocene, California).
D. stanislavi **sp. n.**
D. stenoceras PALMER, 1957: 271 (pupa, Miocene, California).
D. sp. A — Baltic amber.

Subfamily *Leptoconopinae*

Leptoconops Skuse

L. succineus **sp. n.**

Doubtful and unplaced *Ceratopogonidae*

Ceratopogon alpheus HEYDEN, 1870: 240 (♂, Aquitanian, Rott), type lost.
C. escheri GIEBEL, 1856: 252 (♂, Baltic amber), type lost.

"*Ceratopogon*" 16 spp. STATZ, 1944: 152–158 (imagines or pupae, Aquitanian, Rott).

\+ ***Pseudosimulium*** HANDLIRSCH, 1908: 631

P. humidum WESTWOOD, in BRODIE, 1845: 121 (*Simulium* ?, ♀, late Jurassic, Purbeck, England).

Nomina nuda (see p. 010)

Ceratopogon eucerus KEILBACH, 1982: 348.
C. heinei KEILBACH, 1982: 348.
C. longicornis KEILBACH, 1982: 348.
C. minimus KEILBACH, 1982: 348.
C. pectinatus KEILBACH, 1982: 348.
C. pilosus KEILBACH, 1982: 348.
C. terminalis KEILBACH, 1982: 349.
C. ungulatus KEILBACH, 1982: 349.
C. ungulinus KEILBACH, 1982: 349.

VI. AGE OF *CERATOPOGONIDAE*

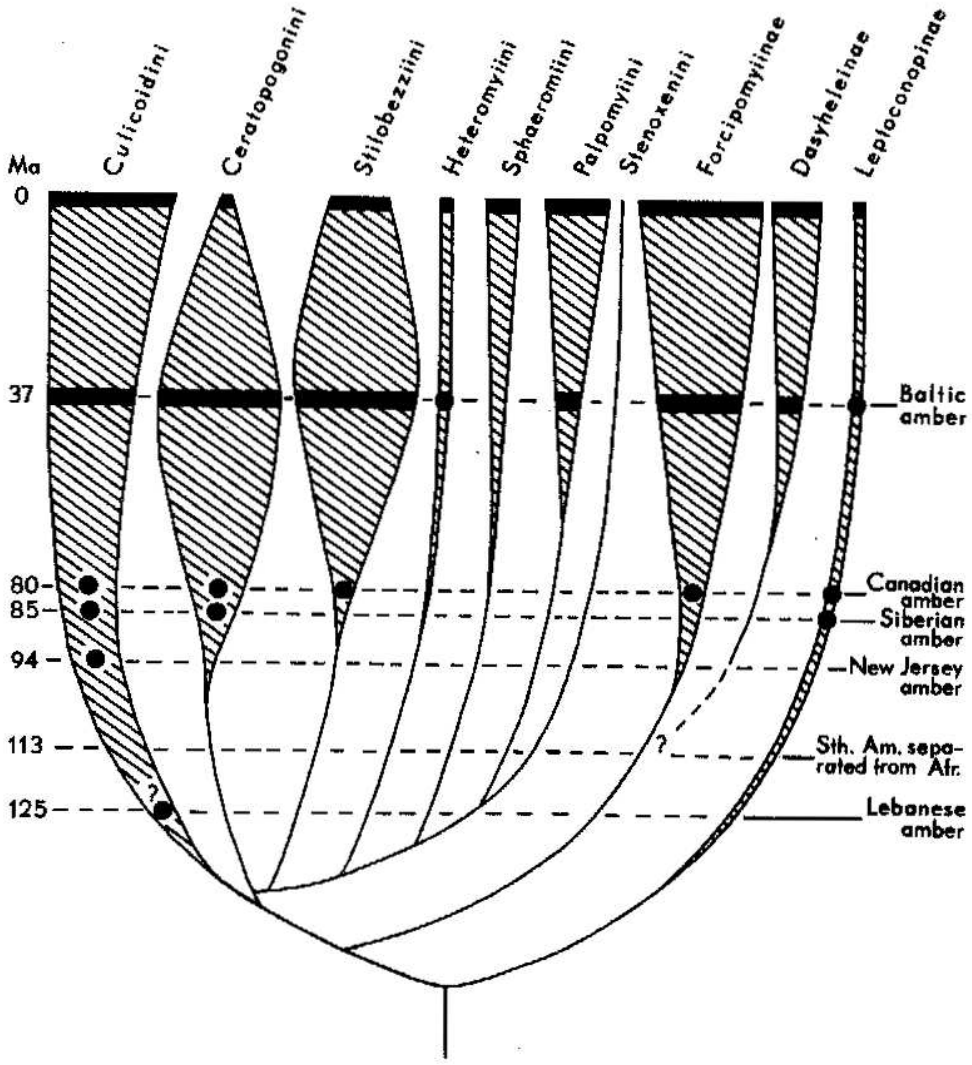
The oldest fossil *Diptera* are from the Fergana valley of Middle Asia and they are middle/late Triassic in age (KOVALEV, 1983), i.e. ca. 230 million years, but the relatively advanced conditions of these forms indicate that true ancestral *Diptera* existed as early as the Permian period ca. 250 Ma. The oldest *Culicomorpha* i.e. *Chaoboridae* are found in the early-middle Jurassic deposits of eastern Siberia (180–190 Ma). The oldest fossils of the superfamily *Chironomoidea* are as follows: *Chironomidae* — middle/late Jurassic, ca. 160 Ma, *Simuliidae* — early Cretaceous (KALUGINA, 1977).

The phylogenetic history of the *Ceratopogonidae* must go back at least to the late Jurassic, ca. 150 Ma, and their origin most probably was associated with the evolution of mammals which were found in the late Triassic ca. 210 Ma (KIELAN-JAWOROWSKA, 1970). The oldest fossil *Ceratopogonidae* are from early Cretaceous Lebanese amber, ca. 125–130 Ma (SCHLEE and DIETRICH, 1970) and are similar to *Austroconops* (WIRTH, personal comm.). A species of *Culicoides* is also known from late Cretaceous New Jersey amber, ca. 94 Ma (fig. 750). These fossils were both probably vertebrate blood-suckers.

Some genera of *Ceratopogonidae* exhibit an Africa — South America disjunction which may suggest their presence prior to their separation giving them a minimum age of early Cretaceous, ca. 113 million years. There are: *Echinohelea* MACFIE (*Ceratopogonini*), *Parabezzia* MALLOCH

(*Stilobezziini*), *Neurobezzia*, *Pellucidomyia*, *Ceratobezzia* (*Heteromyiini*), *Stenoxenus* (*Stenoxenini*). This indicates that all the tribes of subfamily *Ceratopogoninae* evolved before the early Cretaceous (fig. 750).

GAGNÉ (1981) found that the eastern Nearctic fauna of *Trichonta* WINNERTZ (*Diptera, Mycetophilidae*) is more similar to the European fauna than to the western Nearctic fauna, and he explained that this pattern of distribution was of middle Eocene age of the common species when North America had a land connection with Europe. Similarly GAGNÉ (1984) suggested that the widely distributed Holarctic *Semudobia skuhravae* ROSKAM (*Diptera, Cecidomyiidae*) living in birch catkins (many *Betula* spp.) is of Laurasian origin, and has remained unchanged for at least 50 million years when Europe lost its land connection with North America. Such a point of view however is singular since most biogeographers and paleontologists agree that more recent land bridges across the North Atlantic existed as a potential exchange faunal route. Also,



750. Supposed evolution of the *Ceratopogonidae*

natural dispersion of insects by island hopping or via wind currents is quite effective, especially when insects are very small as *Cecidomyiidae*. It is quite probable that *Diptera* capable of flight are not necessarily depend on complete land bridges as suggested by GAGNÉ (l.c.).

VÄISÄNEN (1984) on the basis of *Mycomyia* RONDANI (*Mycetophilidae*) put forward another hypothesis opposing GAGNÉ's model: "The faunal connections between Europe and North America have possibly been caused by human activity, transport with large amounts of soil and other material across the northern Atlantic". He suggested also (VÄISÄNEN, l.c.) that at the species level the faunal similarities between Europe and the eastern Nearctic are due to the large amount of species with circumpolar distributions and that the gaps in these ranges reflex only the lack of study and material.

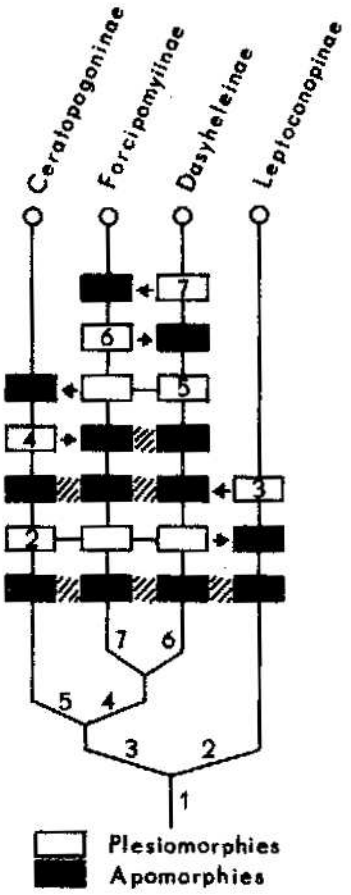
How long can species of insects remain unchanged is an interesting question subject to much speculation. ŽERICHIN and RASNICYN (1980) claim that the average age of recent species is about 5–7 million years. HENNIG (1966) found a specimen of *Muscidae* in Baltic amber that he was unable to separate from the recent *Fannia scalaris* (FABRICIUS). Hymenopterists claim that *Palaeomymar duisburgi* (STEIN) (*Mymarommidae, Chalcidoidea*), a parasite of insects eggs is still living species since the Baltic amber time (M.Sc. S. GŁOGOWSKI of Institute of Zoology, Polish Acad. Sci., Warsaw, personal comm.).

How long can ceratopogonid species live? Apparently the Baltic amber fauna is now extinct, or perhaps better that there is no evidence that any of these fossil species now is living. Females of *Eohelea sinuosa* with stridulating organ on the wings are common in Baltic amber and I have found them also in Miocene Saxonian amber. Therefore, at least this species existed from ca. 37 to 22 Ma, or about 15 million years.

VII. PHYLOGENY AND CLASSIFICATION OF THE FAMILY

I have attempted to delineate the cladogenesis of phylogenetic branching of the *Ceratopogonidae* subfamilies and tribes by means of a scheme of argumentation or theoretical diagram (figs. 751, 752). To simplify this scheme of argumentation, trends showing the same direction are grouped together. Numbers in the diagram refer to one or to several trends, however parallelisms are not indicated. According to SAETHER (1983) only synapomorphies and underlying synapomorphies (i.e. close parallelisms as a result of common inherited genetic factors causing incomplete synapomorphy) can show or indicate a genealogical relationship between two groups or taxa.

Among the *Ceratopogonidae*, parallel evolution caused by adaptations to a particular feeding behavior, independent reductionistic trends such as loss of macrotrichia on wing membrane, reductions in wing venation, and in the number of flagellomeres etc. are often found, and make difficult to determine cladogenesis. The decision as to whether



751. Scheme of argumentation delineating the cladogenesis of the subfamilies of the *Ceratopogonidae* by means of trends 2–7

a character is apomorphous or plesiomorphous, especially when an alternative character is not present in the entire group is always problematical, but the paleontological data may help in answering these questions.

The following trends sensu HIRVENOJA (1973) and SAETHER (1983, and other papers) are used (a — apomorphous, p — plesiomorphous):

Trend 1. Larva without pharyngeal apparatus (p); with pharyngeal apparatus unique among *Diptera* (a).

Note. The pharyngeal apparatus moving to and from causes the pharynx to function as a pump sucking the liquid contents from a prey. This unique synapomorphy suggests that the ancestral larvae were predaceous, which seems to be quite plausible ecologically since during the Mesozoic, inland waters were oligotrophic and poor in bacteria and

detritus (KALUGINA, 1977). Generally the oldest *Culicomorpha* were predaceous, and this type of feeding is retained by larvae of *Chaoboridae*, and among the oldest subfamilies of *Chironomidae* the *Tanypodinae* and *Podonominae*.

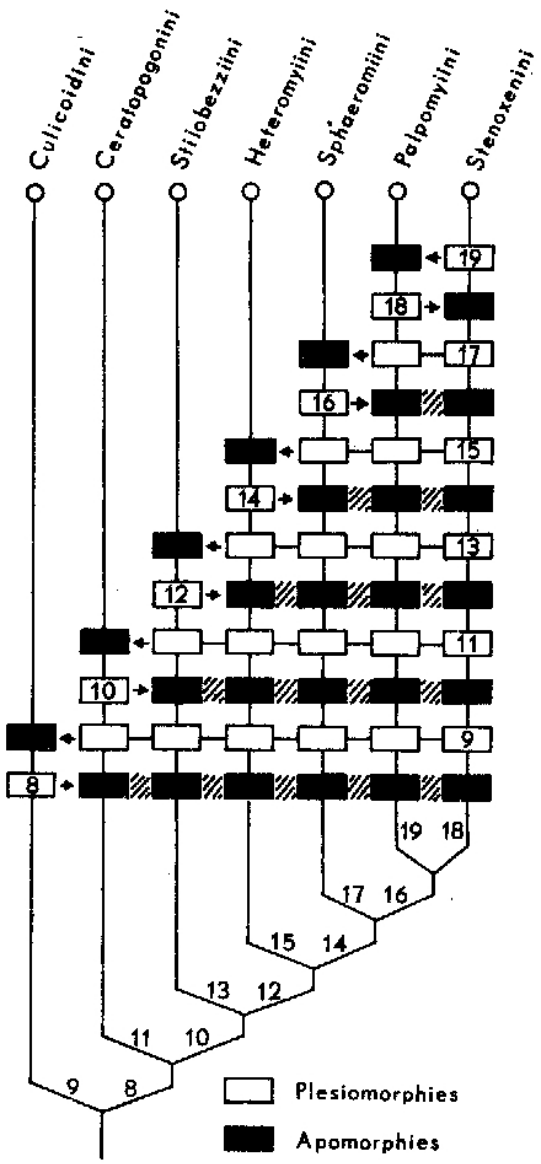
Trends 2. — Head capsule of larva well sclerotized (p); unsclerotized (a).
— Head of larva without additional internal sclerotized rods (p); with additional sclerotized internal rods (a).
— Female cerci short (p); female cerci long (a).
— Crossvein r-m present (p); absent (a).
— Number of female flagellomeres 13 (p); or reduced to 10–12 (a).
— Sternite X in female genitalia plate-shaped (p); or fork-shaped (a) (cf. SZADZIEWSKI, 1986).

Note. The unsclerotized larval head capsule is probably closely connected with the development of additional sclerotized internal rods, and both trends are possibly adaptations to life in arid and desert habitats, where they burrow in the soil, often following moisture downwards to great depths (WIRTH et al., 1977). It appears that this elastic head capsule is well adapted for pushing through sand. The long cerci of *Leptoconopinae* forming ovipositor are adapted for laying eggs deeper in the soil to protect them against dehydration in desert habitats.

Trends 3. — Gonostylus of male genitalia with articulated apical spine (p); without articulated apical spine (a).
— Eyes widely separated in both sexes (p); eyes narrowly separated to contiguous above the antennae (a).
— Only terminal flagellomere elongated in both sexes (p); in male 3–4, in female distal 5 flagellomeres elongate (a).
— Rudiments of gonocoxites IX in female genitalia present (p); or absent (a).

Note. The plesiomorphic *Chironomidae* and all *Simuliidae* have the male gonostylus with an articulated spine and the eyes widely separated (at least in females). Also, only the terminal flagellomere differs distinctly from the preceding ones.

Trends 4. — Larva prognathous (p); or more or less hypognathous (a).
— II–IV instar of larva without prolegs (p); with distinct prolegs (a).
— In male distal 3 flagellomeres elongate (p); or distal 4 flagellomeres elongate (a).
— Mandible of larva slender, hook-shaped (p); or mandible broad with 3 teeth (a).



752. Scheme of argumentation delineating the cladogenesis of the tribes of the *Ceratopogoninae* by means of trends 8–19

Note. Prolegs in larvae of the *Forcipomyiinae* + *Dasyheleinae* branch have most probably been developed secondarily as an adaptation to the terrestrial habitat and to non predaceous feeding on detritus, algae, etc. Absence of prolegs in *Leptoconopinae*, a sister group of all other ceratopogonids, is an evidence that the immediate ancestor of biting midges was without prolegs. It seems that anterior prolegs found in first instar larvae of some *Culicoides* (GLUCHOVA, 1979) have been developed independently and they may play certain role in leaving the chorion or may show distant relation with the other *Chironomoidea* bearing prolegs.

Trend 5. — In female genitalia rami fused, arch-shaped, notum sometimes present (p); rami rudimentary, usually separated, notum always absent (a).

Trends 6. — Egg oval to elongate (p); or horseshoe-shaped (a).
— Larva with anterior and posterior prolegs (p); or only with posterior prolegs (a).
— Flagellomeres not sculptured (p); or sculptured (a).
— Mandibles of adult well developed (p); or absent (a).

Trends 7. — Empodium indistinct or absent (p); or empodium well developed and branching (a).
— Antennae of larva located at anterior part of head capsule (p); or antennae shifted posteriorly to middle or more of the head capsule (a).
— Terminal flagellomere of adult with blunt or pointed apex (p); or with distinct apical papilla (a).
— Body segments of larva almost bare (p); or with conspicuous tubercles and setae (a).

Trends 8. — Proboscis of female with mandibles and maxillae armed with small and numerous teeth, blood-sucking type (p); proboscis of insectivorous type in which mandibles armed with small number of strong teeth and maxillae unarmed (a).
— Proteolytic enzymes in saliva absent (p); or proteolytic enzymes in saliva which break down the tissues of a prey to a liquid present (a) (DOWNES, 1978).
— Sensilla coeloconica usually numerous, on first and at least on some other flagellomeres (p); sensilla coeloconica absent or present only on first flagellomere (a
— Female claws equal and moderately short (p); or female claws long and equal, long and unequal, or very short and equal (a).

Note. It seems that sensilla coeloconica (hayline peg sunken in shallow pit bordered with a ring of dark setae) is a plesiomorphous character of *Culicoidini*, *Ceratopogonini* and the family as a whole. Sensilla coeloconica may function as infrared heat sensors and thereby serve for general orientation as well as chemical sensors (WIRTH and NAVAI, 1978). Similar ringed sensilla coeloconica also occur in some other nematocerous *Diptera* and *Lepidoptera*. These infrared sensory organs are of special functional importance in blood-sucking *Culicoidini* in seeking a warm-blood host (WIRTH and NAVAI, l.c.). JAMNBACK (1965) and BRAVERMAN and HULLEY (1979) correlated the number of sensilla coeloconica with host preference among *Culicoides* and found that species known to feed preferentially on large mammals had a small number of sensilla coeloconica, while those known to feed on birds had more sensilla coeloconica and more flagellomeres bearing sensilla coeloconica.

Sensilla coeloconica may be regarded as an important adaptation to crepuscular or night biting habits which are characteristic for *Culicoides*. These sensory organs may have been reduced not only in typically diurnal *Leptoconopinae* where they are apparently deeply set in flagellomeres, but also in other groups of predaceous, parasitic and flower-visiting midges seeking food sources during the late morning or late afternoon.

Sensilla coeloconica persist in only one tribe of the insectivorous *Ceratopogoninae*, the *Ceratopogonini*. These are usually restricted to the first flagellomere but are also present on flagellomeres 5–8 in *Macrurohelea thoracica* INGRAM et MACFIE and 2–4 in *Brachypogon* (*B.*) *fuscivenosus* (LUTZ) (GROGAN and WIRTH, 1980 b). In some genera included in this tribe i.e. *Nannohelea*, *Bothahelea* GROGAN et WIRTH and *Schizonyxhelea* CLASTRIER, sensilla basiconica are present instead of typical sensilla coeloconica. According to GROGAN and WIRTH (1983) in these genera the sensilla coeloconica have lost their surrounding ring of setae and the central peg became elongated into the sensilla basiconica.

Trends 9. — Parameres more or less stout, usually with stout tip (p); parameres usually with long, slender and curling tip (a).

— Tergite IX in male genitalia usually without pointed spicolateral processes, or tergite IX short and with pointed apicolateral processes (p); tergite IX usually long and bearing distinct, slender and pointed apicolateral processes (a).

— Cells with 4 pairs of chromosomes (p); or with 3 pairs of chromosomes (a).

Note. According to ISAEV (1983) *Culicoides* (*Culicoidini*) has 3 pairs of chromosomes ($2n = 6$) while insectivorous *Stilobezzia* (*Stilobezzini*), *Sphaeromias* (*Sphaeromiini*) and *Bezzia* (*Palpomyiini*) have 4 pairs. Also larvae of *Dasyhelea* (s.str.) sp. (*Dasyheleinae*) from Gdańsk examined in this respect by M.Sc. A. BURKIEWICZ of Gdańsk University have 4 pairs of chromosomes (unpubl. data). Then it may be that the tribe *Culicoidini* would have a good cytogenetical synapomorphy. However, further studies are needed to confirm this suggestion.

Trend 10. — First flagellomere with sensilla coeloconica or sensilla basiconica (p); or without sensilla coeloconica or basiconica (a).

Trend 11. — Eyes bare (p); or densely pubescent (a).

Trends 12. — Veins M_1 and M_2 petiolate (p); or sessille, forking at or proximally of the level crossvein r-m (a).

— Plume of male antenna normal (p); or plume somewhat to strongly reduced (a).

— Size of both sexes similar (p); or male distinctly smaller than female (a).
— Female does not devours the male during mating (p); or female devours the male during mating (a) (DOWNES, 1978).
— Abdominal tergites 1–2 separate (p); or fused (a).
— Frontoclypeus of larva well separated from genae by frontoclypeal and coronal sutures, head relatively short (p); frontoclypeus more or less distinctly fused with genae in proximal part of the head, head long and slender (a).
— Wing membrane with macrotrichia (p); or without macrotrichia (a).

Note. It is probable that the ancestors of *Ceratopogonidae* had bare wing membrane as in *Leptoconopinae* and *Simuliidae*. In branch 3 macrotrichia have been developed, and secondarily reduced in branch 12.

Trends 13. — Parameres simple, blunt and stout (p); or usually more complex (a).
— Aedeagus simple, triangular (p); or more complex (a).

Note. These trends are of rather formal importance.

Trend 14. — Fifth tarsomeres unarmed with strong setae or spines (p); or fifth tarsomeres with batonnets or strong setae on ventral surface (a).

Note. GROGAN and WIRTH (1979b) suggested that the strong setae found on ventral surface of the fifth tarsomeres in certain plesiomorphic *Palpomyia* indicate that they may be vestiges of batonnets of the *Sphaeromiini*.

Trend 15. — Fifth tarsomere of female fore leg not inflated (p); or more or less inflated (a) (GROGAN and WIRTH, 1979a).

Trend 16. — Female abdomen without internal eversible glands and sclerotized gland rods (p); or with internal eversible glands and sclerotized gland rods (a).

Trend 17. — Female sternite VIII without hair tufts (p); or with hair tufts near gonopore (a).

Trends 18. — Egg with simple rounded ends (p); or egg at one end with frilled subapical collar (a).
— Body normal, not flattened (p); or body unusually slender and flattened dorsally (a).

Trend 19. — Fore femur unarmed (p); or armed with strong ventral spines (a).

It is generally accepted that the *Leptoconopinae* with the single genus *Leptoconops* is a taxon somewhat apart in relation to "all other

Ceratopogonidae", however there are few doubts they are both sister groups. ZILAHI-SEBESS (1960), KRIVOŠEINA (1969), REMM (1975), DOWNES (1977) and GLUCHOVA (1977) gave *Leptoconops* family rank. I am in agreement with WIRTH et al. (1977) that *Leptoconops* is not distinctive enough from other *Ceratopogonidae* to warrant a distinct family level. It is worth noting that the position of the *Leptoconopinae* among the *Ceratopogonidae* is quite similar to that of the subfamily *Telmatogetinae* among the *Chironomidae*. WIRTH in his many papers recognized *Leptoconopinae* as more plesiomorphic in relation to other *Ceratopogonidae* and placed it as the first subfamily in his system. However it is evidently more apomorphic and because of that I place it as last subfamily in the present system.

Currently three different systems of classification of "all other" *Ceratopogonidae* or *Ceratopogonidae* sensu ZILAHI-SEBESS (1960) have been proposed:

1. The system developed by WIRTH and summerized by WIRTH et al. (1974) and ammended by WIRTH and GROGAN (1981) — *Forcipomyiinae*, *Dasyheleinae*, *Ceratopogoninae* (*Culicoidini*, *Ceratopogonini*, *Stilobezziini*, *Sphaeromiini*, *Heteromyiini*, *Palpomyiini* and *Stenoxenini*). DOWNES (1977) presented a phylogenetic diagram and recognized the feeding habit of *Forcipomyiinae* as the most plesiotypic for the family. He stated that the *Culicoidini* are the most plesiomorphic sister group of all other *Ceratopogoninae*, and suggested that the tribes *Ceratopogonini* and *Stilobezziini* are sister groups or perhaps just one group. CHAN and LEROUX (1971) suggested that *Atrichopogon* (*Forcipomyiinae*) is the living prototype of the family. However, this speculative point of view does not agree with the paleontogical findings since the oldest *Forcipomyia* has been recorded from late Cretaceous Canadian amber, and "the prototypic" *Atrichopogon* is known only from a single specimen in Baltic amber. Conversely, 175 specimens of *Forcipomyia* have been examined in the present study.

2. The system of REMM (1975) includes the following taxa: *Palpomyiinae* (*Stenoxenini*, *Sphaeromiini*, *Palpomyiini*, *Heteromyiini*), *Ceratopogoninae* (*Stilobezziini*, *Ceratopogonini*), *Forcipomyiinae* (*Dasyheleini*, *Forcipomyiini*). REMM recognized the insectivorous genera as most primitive for the family, united the blood-sucking *Culicoidini* and insectivorous *Ceratopogonini* into a single tribe, and recognized the subfamily *Forcipomyiinae* (incl. *Dasyheleinae*) as the most apomorphic in the family. He explained the lack of this most plesiomorphic *Palpomyiinae* in Cretaceous Siberian amber by their large size and peculiar behaviour (REMM, 1976). However, *Palpomyiinae* sensu REMM have been found only in younger Tertiary ambers and this is not in agreement with his speculative theory. It is most probable that *Ceratopogoninae* sensu REMM is not a monophyletic group.

3. The system of GLUCHOVA (1977, 1979) including *Palpomyiinae* sensu REMM, *Ceratopogoninae* (*Stilobezziini*, *Ceratopogonini*, *Culicoidini*), *Dasyheleinae* and *Forcipomyiinae* is based mainly on larvae. GLUCHOVA (1977) presented her doubts concerning the evolution of feeding habits and concluded that the phytophagous type of adult feeding is the most primitive in the family.

My own system presented here includes all taxa proposed by WIRTH and his co-workers, however the arrangement of subfamilies is almost totally inverted: *Ceratopogoninae* (*Culicoidini*, *Ceratopogonini*, *Stilobezziini*, *Heteromyiini*, *Sphaeromyiini*, *Palpomyiini*, *Stenoxenini*), *Forcipomyiinae*, *Dasyheleinae* and *Leptoconopinae*. I recognize the subfamily *Ceratopogoninae* and the tribe *Culicoidini* as the most plesiomorphic, and *Forcipomyiinae* + *Dasyheleinae* as the most apomorphic among these three subfamilies.

I regard the *Dasyheleinae*, in accordance with the fossil record, as the more apomorphic sister group of the more plesiomorphic *Forcipomyiinae*, and the genus *Atrichopogon* as the more apomorphic sister group of *Forcipomyia*.

Based upon symplesiomorphies, the *Culicoidini* may be the oldest and unspecialized tribe of blood-suckers in the family. In spite of this it is evidently a monophyletic group and I am not able to find true synapomorphies for this tribe. The synapomorphies used in the cladogram are rather of formal importance, and a reduced number of chromosomes which may be a good synapomorphy for *Culicoidini*, is presently poorly studied in the family. Also the monophyly of *Ceratopogonini*, *Stilobezziini* and *Sphaeromiini* + *Palpomyiini* + *Stenoxenini* is weakly founded. Even when the tribe *Stilobezziini* is included with the *Ceratopogonini* as suggested by DOWNES (1977) and WIRTH and GROGAN (personal comm.) still the tribe *Ceratopogonini* s.l. will be based only on symplesiomorphies. So further studies are needed to find synapomorphies for the above groups, which may result in a quite different system for the subfamily *Ceratopogoninae* in which all tribes fulfill the criteria of monophyly.

The absence of the tribes *Sphaeromiini* and *Stenoxenini* in Baltic amber may suggest that they are of Gondwana origin (see chapter VIII).

Lastly BORKENT, WIRTH and DYCE (personal comm.) are preparing a new interpretation of the phylogenetic placement of the monotypic genus *Austroconops*. According to BORKENT et al. (personal comm.) this genus may be a sister group of *Forcipomyiinae* + *Dasyheleinae* + *Ceratopogoninae*. It seems to me however, that it is not plesiomorphic but a hightly modified genus (see *Culicoidini*) of the subfamily *Ceratopogoninae*, with female genitalia typical for this subfamily. It may be that the

morphology of the unknown larva and pupa and further records of feeding habits will show more exactly the systematic position of this monotypic genus.

It seems that the *Ceratopogonidae* exhibited rapid evolution as 7 genera known only from Baltic amber became extinct during a relatively short period. It may be that the *Ceratopogonini* and *Stilobezziini* (fig. 750), and the family as a whole, flourished during the Tertiary and now play a less important role in recent entomofauna (see chapter IX). A good example illustrating extinction in the family is the Holarctic genus *Ceratopogon* represented in Baltic amber by 25.3% of all specimens. This genus is usually rare, inhabits the more northern parts of North Hemisphere and is often restricted to refugial isolated areas in mountains.

It is interesting to note the canalized reductionistic trends found in some groups. An example would be *Brachypogon* (*B.*) *balticus* presently described from Baltic amber which has macrotrichia on its wing membrane while recent species of the subgenus apparently have wings always bare. The Baltic amber *Alluaudomyia* has both first radial cells well developed and separated while all recent species have a single radial cell, or sometimes traces of the first radial cell present only. Tertiary *Nannohelea* has the last 2 palpal segments well developed and separated, while in all three recent species the last 2 palpal segments are fused into one very short segment. Also, all specimens of *Dasyhelea* now examined have a well developed first radial cell while most of the recent species have lost this cell.

VIII. ZOOGEOGRAPHIC RELATIONSHIPS

In order to understand the evolution and recent geographical distribution of *Ceratopogonidae* we should outline positions of the continents from the Triassic to the present. At the turn of Triassic and Jurassic, North America, Europe and Asia formed single mass land — Laurasia (figs. 753, 754). During the Cretaceous and Paleogene, the Tethys Sea still covered a considerable part of present-day Europe, west Asia and north Africa. It was connected with the boreal Siberian (or Russian) Sea along the Ural Mts. separating Fenno-Sarmatia from Katasia (figs. 758, 759). During the Paleogene there were numerous islands in the Tethys Sea which formed a complicated system of archipelagos. Frequent marine invasions and recessions often changed the configuration of islands, lands and seas, all the while the Tethys gradually became reduced in size. The Siberian Sea also gradually became more and more shallow and it disappeared during the late

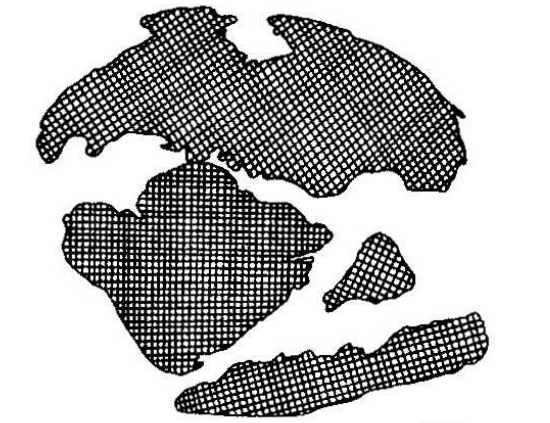
753. The continents at the turn of Triassic and Jurassic, ca. 210–200 Ma (after DIETZ and HOLDEN, 1970; from TROJAN, 1985)

Miocene and early Pliocene (10–5 Ma). During the Neogene, the Alps and Carpathians appeared, but by the end of that period the remains of the Tethys were transformed into Mediterranean and Pontocaspian seas (KOSTROWICKI, 1969).

The history of the North Atlantic region during Tertiary times is still poorly understood. The Atlantic Ocean formed by seafloor spreading which started in the Jurassic in the south. The North Atlantic opened about 50 Ma during the middle Eocene (THENIUS, 1977) when the DE GEER bridge between north Greenland and Norway (incl. Spitsbergen) was interrupted. During that time, Greenland was farther south than at present (JARDINE and MCKENZIE, 1972). MATTHEWS (1980) claims that the DE GEER bridge existed until 38 Ma (late Eocene) and was not breached during the 10 million years after the development of a sharp discontinuity of the North American and European mammalian faunas. The next bridge connected Greenland and the Faroe Islands along a line including Iceland, which originated 20 Ma (Miocene), and existed during the Tertiary to Miocene. However, this bridge was never more than a causeway to a chain of islands (MATTHEWS, 1980).

A land bridge probably connected Siberia and Alaska in the Beringian region for most of the Tertiary. During the Eocene its climatic conditions were such as to allow exchange of tropical and subtropical plants and animals (MATTHEWS, 1980).

From the early Cretaceous, Albian/Aptian ca. 113 Ma, Africa separated from South America, and Antarctica plus Australia. Australia separated from Antarctica during the middle Eocene ca. 43 Ma and moved northwards (fig. 756) (JARDINE and MCKENZIE, 1972). In the past 10 Ma this continent approached the Indonesian islands. Colonization of Antarctica during late Cretaceous and early Tertiary by mammals and insects was ecologically plausible. Antarctica was probably not glaciated



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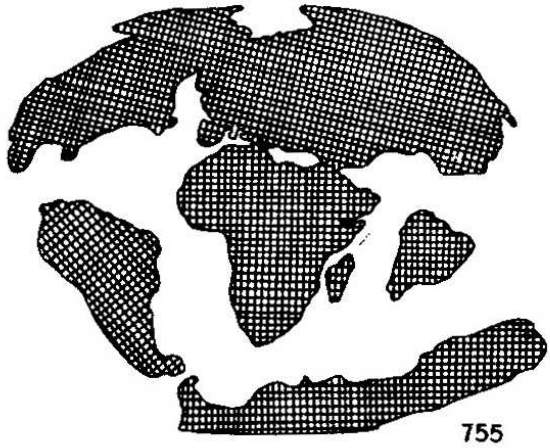

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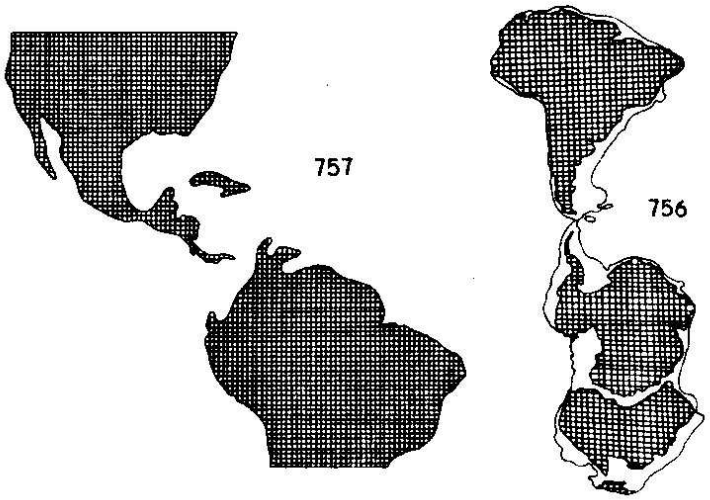
754, 755. The continents during early Cretaceous, ca. 135 Ma, fig. 754; and during early Tertiary, ca. 65 Ma, fig. 755 (after DIETZ and HOLDEN, 1970; from GAGNÉ, 1984)

during this period and the early Tertiary flora of Antarctica from Seymour Island, 64° S, indicates a cool temperate flora comparable with parts of New Zealand today (JARDINE and MCKENZIE, 1972).

During the Cretaceous and for much of the early Tertiary North and Middle America were separated from South America (fig. 757). The Panamanian Isthmus bridging this gap formed during the Pliocene only about 3 Ma (MATTHEWS, 1980). Prior to the Miocene volcanic islands existed along the present Cayman Ridge and other island chains allowing faunal exchange between both Americas.

In Baltic amber, the tribes *Stenoxenini* and *Sphaeromiini* are absent and this may suggest that they are of Gondwana origin. This is quite evident as concerns the *Stenoxenini* which includes the genera *Stenoxenus* COQUILLETT and *Paryphoconus* ENDERLEIN. *Stenoxenus* now occurs in Afrotropical, Oriental, Neotropical and in southern North America, and most probably was in existence prior to South America being separated from Africa. *Paryphoconus* is now distributed in South America and southern North America only. Both of these genera most probably



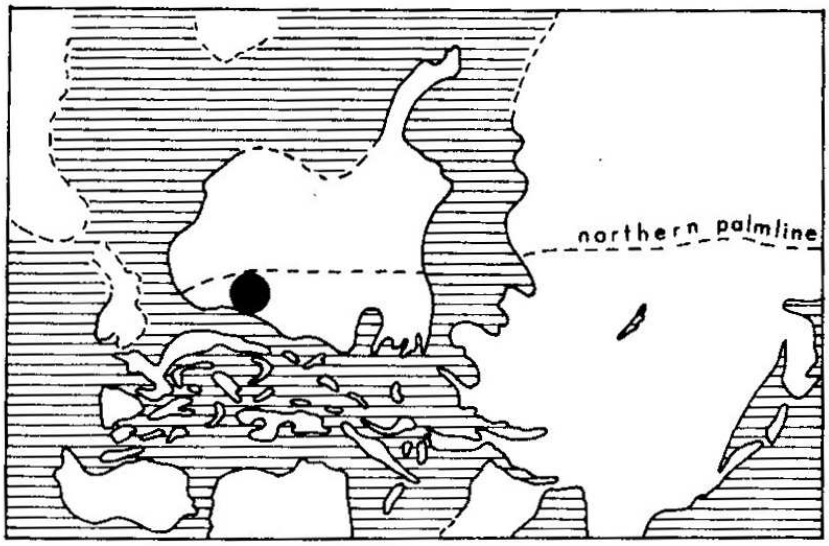
756, 757. 756 — South America, Antarctica and Australia during middle Eocene, ca. 45 Ma. The 2 km bathymetric contours of the continental edges are shown (after McKenzie and Sclater; from Jardine and McKenzie, 1972). 757 — Middle America during Miocene (after Thenius, 1977)

migrated from South to North America across the Panamanian Isthmus during late Tertiary or more recently when North America separated from Europe, which may explain their absence in Baltic amber.

A more complicated pattern of recent distribution is exhibited by the tribe *Sphaeromiini* which includes 19 extent genera, most of which are restricted to the Southern Hemisphere. *Johannsenomyia* Malloch and *Mallochohelea* Wirth are the only genera to exhibit worldwide distribution. The genera *Jenkinshelea* Macfie, *Nilobezzia* Kieffer, and *Sphaeromias* Curtis are known from all regions except for the Neotropical, and *Macropeza* Meigen is recorded from Africa, Oriental region, North America and Europe. If this tribe was absent in Europe during the Baltic amber period, then the genera now occurring there migrated to Europe from Africa and/or Asia during late Tertiary. Similarly those genera occurring in North America but absent in the Neotropics probably migrated there from Asia via Beringia. The cosmopolitan genera of the tribe were theoretically able to migrate to the Nearctic from South America, or across Beringia, or possibly from both directions.

It is interesting to note in the Baltic amber material the absence of such subgenera of *Culicoides* as *Culicoides* s. str., *Avaritia* Fox and *Monoculicoides* Khalaf which are very common now in Europe and in the Holarctic.

I have divided the genera, subgenera and species groups present in Baltic amber into three main groups depending on their recent and supposed original distribution when it was possible:



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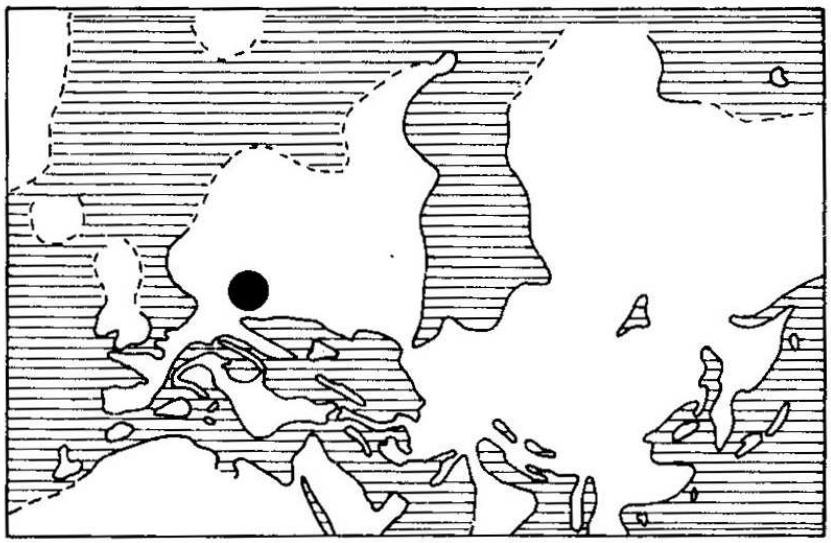

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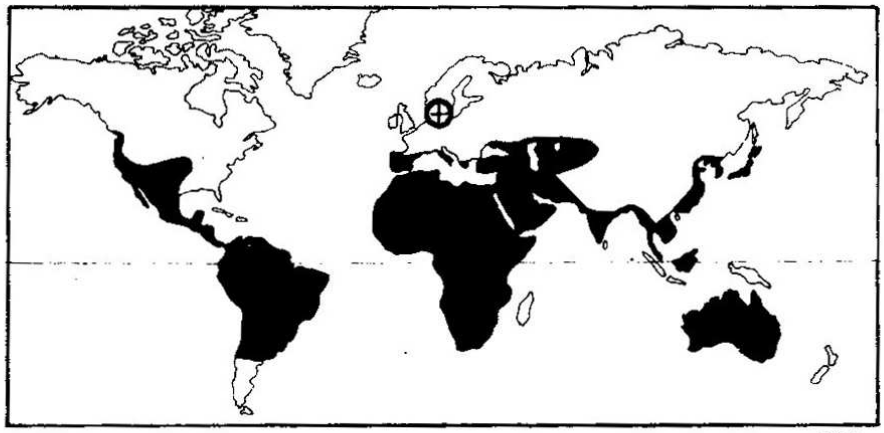
758, 759. Land contours of Europe during Tertiary; 758 — Eocene at the turn of Lutetian and Bartonian, ca. 44 Ma; 759 — Miocene, Aquitanian, ca. 22 Ma (from KOSTROWICKI, 1969). Solid circle — position of the Sambian Peninsula. Lands not hatched

I. Cosmopolitan: *Culicoides* (subg. *Oecacta*), *Alluaudomyia*, *Stilobezzia*, *Monohelea*, *Palpomyia*, *Bezzia*, *Forcipomyia* (s. str.), *F.* (*Euprojoannisia*), *Atrichopogon*, *Dasyhelea*. These groups usually include large numbers of recent species.

II. Pantropical: *Leptoconops* (*L.*) and *Forcipomyia* subg. *Phytohelea* (figs. 760, 761). Each of these subgenera is represented in Baltic amber by a single species. Also the pantropical *similis* group of the genus *Culicoides* is present in the Baltic amber material (*C. balticus* **sp. n.**). In the Palaearctic, the recent species of this group are distributed in the Mediterranean subregion, Middle Asia, Korea and Japan as for northward as Czechoslovakia. During the Tertiary, these groups occurred



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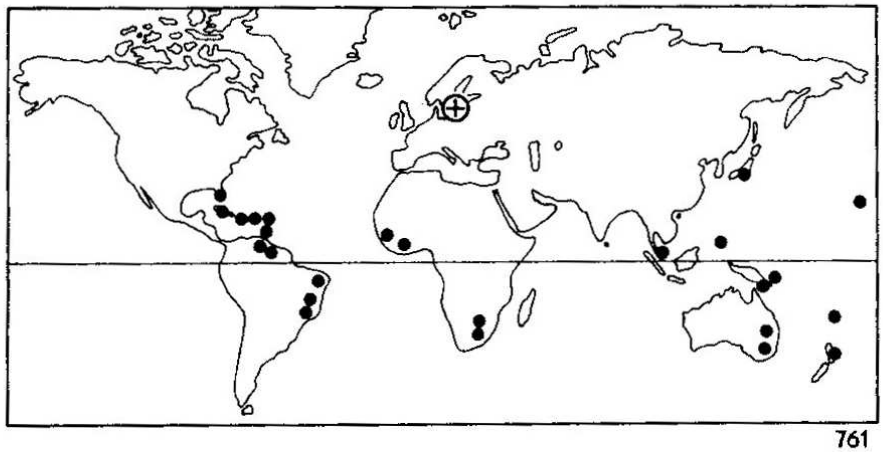

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760, 761. Generalized recent distribution of the pantropical subgenera present in Baltic amber (cross in circle); 760 — *Leptoconops* (*L.*), 761 — *Forcipomyia* (*Phytohelea*)

more northerly than now since during the Eocene the climate was warmer and allowed termites (*Isoptera*) and the dipteran family *Diopsidae* to exist (KEILBACH, 1982).

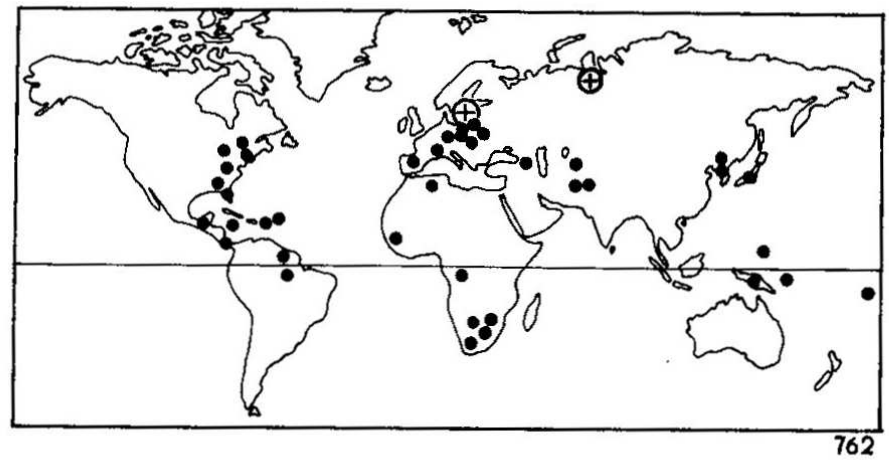
III. Laurasian. The groups included here are supposed to be of Laurasian origin. They now are:

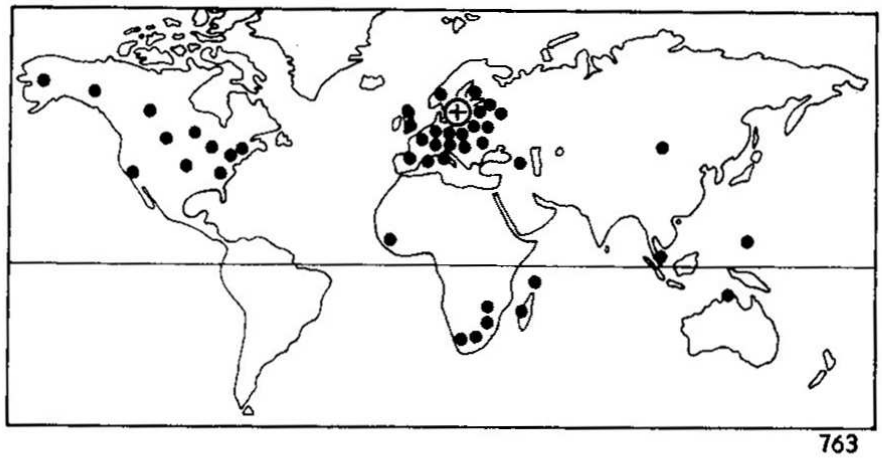
1. Almost cosmopolitan
2. Almost pantropical
3. Holarctic
4. Euro-North American
5. Neotropical and North American
6. Neotropical
7. East Palaearctic
8. Oriental
9. Extinct

Ad 1. I am inclined to believe that the genera *Brachypogon* and *Serromyia* originated in the Northern Hemisphere and dispersed from there to the southern continents. Both of these genera have quite similar

recent distribution (figs. 762, 763). *Brachypogon* (s.str.) (fig. 762) is distributed along the southern borders of the Palaearctic, eastern North America, Middle America, north of South America, Afrotropical region and in Australasian islands, while *B.* (*Isohelea*) is more wide distributed in the Holarctic. *Serromyia* (fig. 763) did not crossed Middle America southwards. It is worth noting that *Serromyia* is more common in Baltic amber than today in Poland and Europe. GROGAN (personal comm.) claims that *Brachypogon* (*Isohelea*) was present in late Cretaceous Siberian amber. If we add to the above that Africa in which both genera now are quite common was widely separated from Europe during late Cretaceous and early Tertiary then it may be suggested that Laurasia, or only Europe for *Serromyia*, was the centre of dispersion for these genera.

Ad 2. The relictal genus *Nannohelea* of almost pantropical distribution is evidently of Laurasian origin. There are 3 known recent species from Colombia, northern Africa, southern Europe and Australia (fig. 764). In Baltic amber this rare genus is represented by 2 distinct species. It may be suggested that this genus was common in Europe and in North

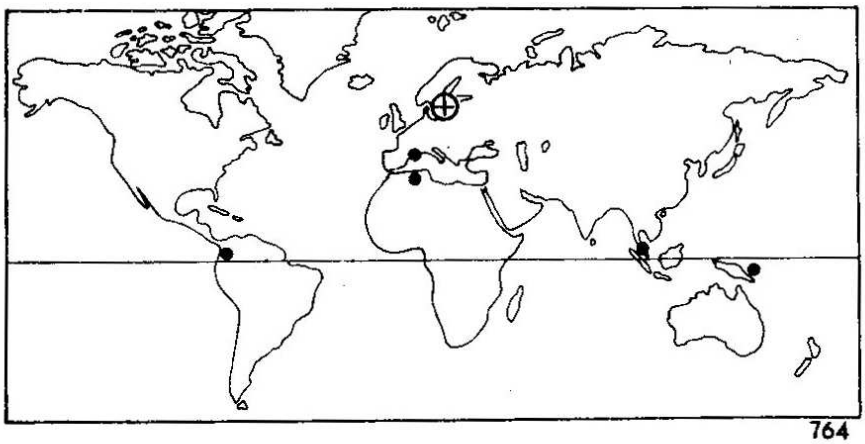




762, 763. Recent distribution of almost worldwide distributed genera which probably are of Laurasian origin; 762 — *Brachypogon* (*B.*), 763 — *Serromyia*; cross in circle — Baltic amber

America during the Tertiary. It probably migrated to South America from North America during Tertiary or more recent times when these continents were in more or less distinct contact, and to southern Europe and northern Africa during Miocene or later but its route to Australasia is unknown. It is inteesting that this genus survived on these quite new regions.

Ad 3. The genera *Ceratoculicoides* and *Ceratopogon* probably originated in the Holarctic and are still present there. *Ceratoculicoides* includes one species from Baltic amber and at least 4–5 recent species distributed along the east and west coasts of North America and along the southern borders of the Palaearctic (fig. 768). *Ceratopogon* existed in Laurasia at least from the late Cretaceous (fig. 767). In Baltic amber it is the predominant genus of the family, and apparently flourished during the Tertiary. Today *Ceratopogon* is restricted to refugial isolated stations in the mountains or other cooler parts of the Holarctic.



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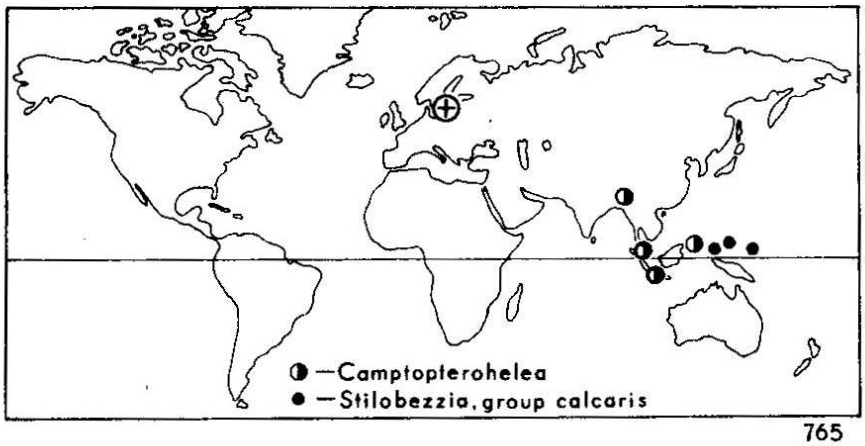

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764, 765. Recent distribution of tropical taxa of Laurasian origin; 764 — almost pantropical *Nannohelea* is found in Baltic amber (cross in circle); 765 — now Oriental *Stilobezzia calcaris* group is found in Baltic amber, while Oriental *Camptopterohelea* has in Baltic amber its sister fossil genus *Gedanohelea*

The genus *Macrurohelea* MACFIE which is probably the sister group of *Ceratopogon* as suggested GROGAN and WIRTH (1980b) is very interesting zoogeographically. This group occurs in southern South America (9 spp.), and in eastern Australia (3 spp.) (fig. 767) (GROGAN and WIRTH, 1980b; SPINELLI and GROGAN, 1984; GROGAN and WIRTH, 1985). It appears that *Macrurohelea* presents a comparable pattern of distribution similar to that of the recent genus *Paradasyhelea* MACFIE, and the families *Ironomyiidae* and *Sciadoceridae* (*Cyclorrhapha*). *Paradasyhelea* (6 spp.) occurs in North America, Patagonia, western Australia, New Zealand and the subantarctic Auckland Islands (WIRTH, 1981). *Ironomyiidae* are known from one recent species occurring in Tasmania and one fossil species from Canadian amber (HENNIG, 1973). *Sciadoceridae*, a fly family closely related to *Ironomyiidae*, are known from two recent species distributed in Australia, Tasmania, New Zealand, Chile and from a single fossil species recorded from Baltic amber (HENNIG, 1973). According to HENNIG (l.c.) "sciadocerids" described from Canadian amber by MCALPINE and MARTIN (1966) belong to the family *Phoridae*. The above examples demonstrate the existence of a former direct connection between South America and Australia across the Antarctic as suggested by HARRISON and MACKERRAS (HENNIG, 1968) and BRUNDIN (1966). According to JARDINE and MCKENZIE (1972) marsupials also reached Australia via the Antarctica.

Ad 4. Euro-North American recent distribution is exhibited by the genus *Neurohelea*, the *Forcipomyia* (*F.*) group *costata*, the *F.* (*Euprojoannisia*) group *borealis* and the *Serromyia* group *crassifemorata*, each of them represented by 1–2 species in Baltic amber.

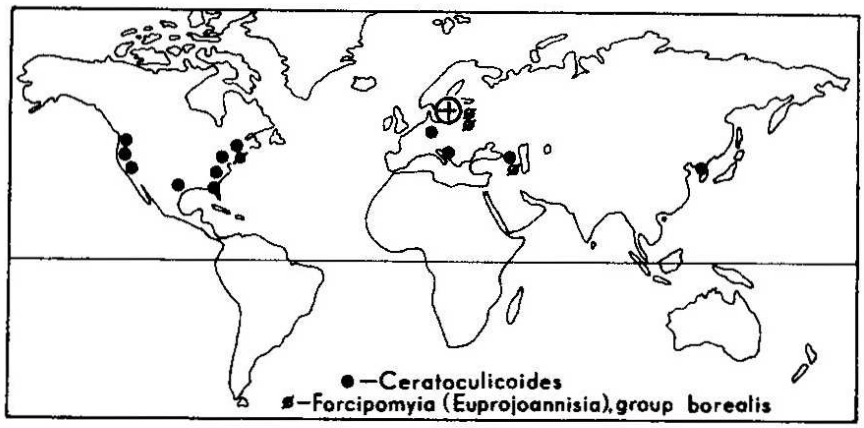
Neurohelea of the tribe *Heteromyiini* now occurs in west Europe (1 species) and in North America (2 species) (fig. 766). It is probable that this genus had a similar distribution during the early Tertiary, and that the western European species *N. luteitarsis* (MEIGEN) remains as evidence of a more widespread distribution of Tertiary *Neurohelea* in Europe. Probably *Neurobezzia* WIRTH et RATANAWORABHAN originally described from North America and subsequently placed by GROGAN and WIRTH (1979a) in the same phyletic branch as *Neurohelea* and *Physohelea* (see below) is of Gondwana origin, similarly as other genera of the tribe occurring in the Holarctic. This genus was recently recorded from the Seychelles Islands (CLASTRIER, 1983) off the east coast of Africa, and suggests that it may have reached North America from South America where it became extinct or is yet unknown.

The *Forcipomyia costata* group (see p. 203) includes *F. turbinata* and *F. eocostata* from Baltic amber and 5 recent species distributed in Europe (3) and in North America (2). The *F. borealis* group represented in Baltic

more than 100 years ago by LOEW (1864) "The European and the American *Dipterous* faunae always appear to me like two branches of the same stock, each having had a development of its own, very similar however to the development of the other... Are the amber *Diptera* preserved fragments of this common stock?". The answer to LOEW's question is a resounding "yes" based upon Baltic amber ceratopogonids.

Ad 5. Today in the southern parts of North America and South America occur species of the *Forcipomyia* (*F.*) *cinctipes* group, which is represented in Baltic amber by *F. lyneborgi* (p. 198).

Ad 6. Neotropical recent distribution is exhibited by the genus *Physohelea*, a sister group of *Neurohelea*. These genera probably existed during the Tertiary in Europe and North America. *Physohelea* however became extinct in Europe and North America, but migrated to South America where three recent species are known in Patagonia (fig. 766). A similar distribution is exhibited by the relictal genus *Merothrips* HOOD (*Thysanoptera*) recorded from Baltic amber and now occurring in the Neotropic (PESSON, 1951).



768. Recent distribution of Holarctic or Euro-North American taxa which most probably are of Euro-North American origin; cross in circle — Baltic amber

Ad 7. *Ceratopogon forcipiformis* from Baltic amber is close (or similar) to recent *C. gigaforceps* from the eastern Palaearctic (p. 60) and *C. gedanicus* to an undescribed recent species from North Korea (p. 75). Weak affinities of the Baltic amber fauna with the recent east Palaearctic fauna of *Ceratopogonidae* may suggests that during Tertiary, Europe was quite effectively isolated from east Asia (Katasia) by the Siberian Sea.

Ad 8. Recent Oriental distribution of the *Stilobezzia calcaris* group which includes the common in Baltic amber *S. falcata* and 6 recent species restricted to the Micronesian Caroline Islands (fig. 765). This group is probably of Euro-Katasian origin and it was widely distributed

in Europe and North Asia during the Tertiary period when it became extinct. Relicts of this group survived only on some tropical islands probably much more southward than they originally occurred.

A phylogenetic lineage leading to the Oriental region is exhibited by the genus *Gedanohelea* whose sister group is the recent genus *Camptoterohelea* which includes five species recorded from Philippines, Indonesia, Malaysia and India (fig. 765).

Ad 9. Certain fossil genera present in Baltic amber, i.e. *Fossihelea* **gen. n.**, *Mantohelea* **gen. n.**, *Meunierohelea* **gen. n.**, *Wirthohelea* **gen. n.**, *Eohelea* and *Ceratopalpomyia* **gen. n.** probably had European or Euro-North American (Translaurasian is less probable) distributions during the Tertiary. *Gedanohelea* **gen. n.** (see above) perhaps was distributed throughout Euro-Katasia. With the exception of *Gedanohelea*, which has its apparent sister group in the Oriental region, the other extinct genera do not show evident phylogenetic relationships to known recent or fossil genera.

IX. COMPOSITION AND ECOLOGY OF THE *CERATOPOGONIDAE* IN THE AMBER BEARING FOREST

The *Ceratopogonidae* in the Baltic amber bearing forest were quite common, probably much more common than in the recent fauna of the Middle European forest. Their rate among nematocerous *Diptera* enclosed in Baltic amber is from 6.9, 7.9 to 11% in three different large collections (KULICKA et al., 1985) while their rate among 10,404 specimens of *Nematocera* collected by means of yellow pan-traps in the deciduous forest near Warsaw is only 0.9% (materials of Institute of Zoology, Pol. Acad. Sci., from early spring to late autumn 1981, Klembów; unpubl. own data). It seems that the material obtained by yellow pan-traps is more or less comparable with that from the ambers. On the average there are 1.16 specimens of *Ceratopogonidae* per single amber piece. Usually a single piece of amber contains a single biting midge. Often two or three specimens are present together, occasionally five (IMGPUG 7458, *F. uncula*; ZMC 145, *B. prominulus*), six (MZW 2145/96, *E. gedanica*; MZW 5256, *B. prominulus*; MZW 9733, *C. speciosus*; MZW 18553 a,b,c,d, *Ceratopogonini* indet., *Culicoides* indet., *C. ceranowiczi*, *C. ritzkowskii*) or rarely nine (MZW 7812, *C. speciosus*, *F.* (*F.*) indet.).

Other arthropods are embedded together with the *Ceratopogonidae*, mainly nematocerous flies. They are: *Chironomidae* (most often), *Mycetophilidae* (*Diptera*, *Nematocera*), *Acarina* (*Arachnida*), *Sciaridae* (*Diptera*, *Nematocera*), *Dolichopodidae*, *Empididae* (*Diptera*, *Brachycera*),

Psychodidae (*Diptera, Nematocera*), *Aranei* (*Arachnida*), *Cecidomyiidae*, *Limoniidae* (*Diptera, Nematocera*), *Diptera Cyclorrhapha*, *Phoridae* (*Diptera, Muscomorpha*), *Hymenoptera*, *Collembola* and *Thysanoptera*.

In the material examined, males constitute 37.4% of all specimens which is the normal situation for recent biting midges. In the material collected by means of yellow pan-traps at Warsaw the rate of males is 41% while in emergence traps set over small brooks in West Germany it is 31% (HAVELKA, 1976). In Baltic amber more than 50% of males were found in the following genera: *Culicoides* — 64.8%, *Fossihelea* — 57.1%, and *Alluaudomyia* — 56.2% (table 3), which suggests they were trapped in the yet soft resin from male swarm aggregations which is normal in the recent *Culicoides* and many other genera during dusk. For example, in the amber piece MZW 7812, 6 males and 2 females, or in MZW 9733, only 6 males of *Culicoides speciosus* are present. Generally, males live shorter than females, and in some predaceous tribes they are consumed by females during copulation. Other groups may develop mating swarms, and still others may be less active than females which explain their lower numbers than females in amber or in material collected in the field.

The ceratopogonid fauna of the amber bearing forest was rich and diversified because the fossil ceratopogonids represent only a fragment of the amber forest fauna and is composed of 24 genera and 101 species. Whereas 27 genera are present in the recent fauna of the Palaearctic, 25 in Europe, 20 in Poland and 19 in Estonia. REMM (1979) found 186 species in Estonia, the result of more than 20 years of collecting.

More than half of species recorded now in Baltic amber are represented only by one or two specimens (43 spp. — 1, 14 spp. — 2 specimens). More common species are also present in the material, i.e.: 22 spp. (3–5 specimens), 8 spp. (6–8), 9 spp. (12–19), 3 spp. (21–33), and even *Culicoides speciosus* and *Brachypogon prominulus* are represented by 104–116 specimens. The latter two species comprise almost 20% of all ceratopogonids. However it may be that *C. speciosus* is a species complex.

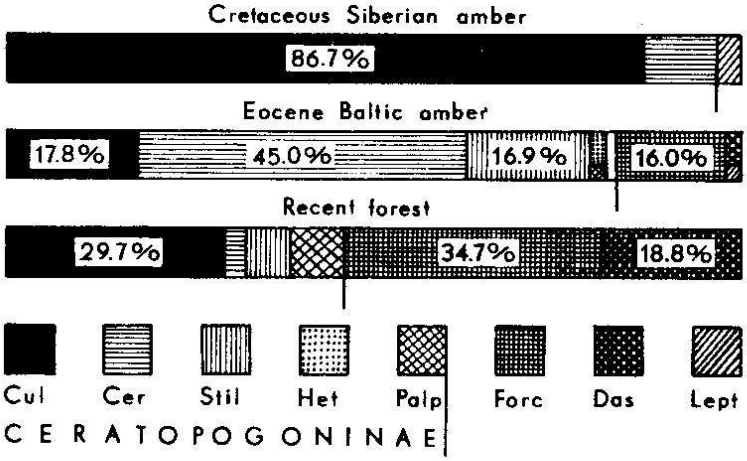
In the Baltic amber, the tribe *Ceratopogonini* predominates, comprising 45.0% of all specimens (table 3, fig. 769) while this tribe in the Polish recent forest is quite rare (3.0% and is apparently only represented by *Brachypogon* subg. *Isohelea*). The tribes *Culicoidini*, *Stilobezziini* and subfamily *Forcipomyiinae* take similar percentage rates in Baltic amber (16.0–17.8%). The tribe *Stilobezziini*, subfamilies *Forcipomyiinae* and *Dasyheleinae* are absent in Cretaceous Siberian amber (REMM, 1976) while the *Culicoidini* predominate. The diagrams presented on fig. 769 evidently show the decreasing importance of the subfamily *Ceratopogoninae* from the late Cretaceous to the present in the Northern Hemisphere

Table 3. Quantitative composition of the Baltic amber *Ceratopogonidae* (+ fossil genera)

Taxons	Total number	%	♀♀	♂♂	% ♂♂
1	2	3	4	5	6
Ceratopogoninae	905	82.05	559	346	38.23
Ceratopogoninae indet.	9		8	1	
Culicoidini (*Culicoides*)	196	17.77	69	127	64.80
Ceratopogonini	496	44.97	343	153	30.85
Indetermined	32		28	4	
Ceratopogon	279	25.30	186	93	33.33
Brachypogon	158	14.32	114	44	27.85
Nannohelea	12	1.09	8	4	33.33
Ceratoculicoides	1		1	—	
+ *Fossihelea*	14	1.27	6	8	57.14
Stilobezziini	186	16.86	124	62	33.33
Alluaudomyia	16	1.45	7	9	56.20
Stilobezzia	29	2.63	19	10	34.48
Monohelea	27	2.45	15	12	44.44
Serromyia	27	2.45	19	8	29.63
+ *Mantohelea*	3		3	—	
+ *Meunierohelea*	24	2.18	14	10	41.67
+ *Wirthohelea*	1		1	—	
+ *Eohelea*	50	4.53	39	11	22.00
+ *Gedanohelea*	6		5	1	
+ *Ceratopalpomyia*	2		1	1	
Indetermined	1		1	—	
Heteromyiini	13	1.18	11	2	15.38
Neurohelea	8		8	—	
Physohelea	5		3	2	
Palpomyiini	5	0.45	4	1	25.00
Palpomyia	3		2	1	
Bezzia	2		2	—	
Forcipomyiinae	176	15.96	119	57	32.39
Forcipomyia	175	15.87	118	57	32.57
Atrichopogon	1		1	—	
Dasyheleinae (*Dasyhelea*)	18	1.63	10	8	44.44
Leptoconopinae (*Leptoconops*)	4	0.36	3	1	25.00
Total	1103	100	691	412	37.35

forest habitats, and growing importance of the subfamilies *Forcipomyiinae* and *Dasyheleinae*. It is worth noting that the genus *Atrichopogon* is represented only by a single specimen in Baltic amber, while in yellow pan-trape its rate is 8% of all ceratopogonids.

The composition of the *Ceratopogonidae* fauna of the Baltic amber allows suggestions about the nature of the localities in which it flourished and in which the amber now enclosing it was formed.



769. Diagrams showing quantitative composition of the *Ceratopogonidae* of the North Hemisphere faunas from late Cretaceous (Siberian amber; REMM, 1976, KALUGINA, 1977) through late Eocene (Baltic amber) to recent time (deciduous forest near Warsaw, yellow pan-traps, unpubl. own data); Cer — *Ceratopogonini*, Cul — *Culicoidini*, Das — *Dasyheleinae*, Forc — *Forcipomyiinae*, Het — *Heteromyiini*, Lept — *Leptoconopinae*, Palp — *Palpomyiini*, Stil — *Stilobezziini*

The great prevalence of the subfamily *Ceratopogoninae*, both in the number of species and specimens, indicates that moist forests with semiaquatic and aquatic habitats were common. In these habitats live mainly the predaceous larvae of *Ceratopogoninae* and the larvae of *Dasyheleinae* which feed on algae and detritus. There were also tropical water-holding plants such as bromeliads, thus forming an appropriate habitat for *Forcipomyia* (*Phytohelea*) *eophytoheleana* where the larvae of this subgenus live submerged in the water-filled leaf axils.

The presence of numerous *Forcipomyia* which have terrestrial larvae feeding on plant debris, fungi is a testimony that this forest was rich in rotting wood. There were also, but not common, coastal or inland beaches in which the larvae of *Leptoconops succineus* (only 4 specimens recorded) lived.

By a comparison with the recent feeding habit of adults, the following food sources were probably present:

Mammals and birds were a source of protein for hematophagous

females of *Culicoides*, *Leptoconops* and *Forcipomyia* (*Lasiohelea*). The Baltic amber midges of the subgenus *Lasiohelea* may also have fed on amphibians as do some recent species. The hematophagous midges constitute about 19% of all *Ceratopogonidae* (incl. males) examined.

Insect prey and hosts were food sources for predatory females of all ceratopogonids of the subfamily *Ceratopogoninae* (except for *Culicoides*), and for the possibly parasitic *Forcipomyia eotrichoheleana* and *Atrichopogon eocenicus*. The biting midges feeding on insects in the amber bearing forest include 63.6% specimens examined (incl. males).

Flowers were visited by *Forcipomyia* (*F.*), *F.*(*Euprojoannisia*), and *Dasyhelea* which exclusively feed on nectar especially of *Apiaceae* (= *Umbelliferae*) flowers. They constitute about 12.1% of all *Ceratopogonidae* examined. Obviously other biting midges, of both sexes, visit flowers with easily accessible nectar.

X. RESULTS AND CONCLUSIONS

A taxonomic revision of the family *Ceratopogonidae* from Baltic amber is presented. A preparation of the amber inclusions including new experiences is described in detail. Among 1103 specimens enclosed in this fossil resin 101 species have been found. Redescriptions of 17 previously known species are presented and 23 unnamed and 61 named new species are described. These species belong to 24 genera, among them 6 are new.

The following new genera are described: *Fossihelea* (type-species *Ceratopogon gracilitarsis* MEUNIER), *Mantohelea* (type-species *C. lacus* MEUNIER), *Meunierohelea* (type-species *M. nielseni* **sp. n.**), *Wirthohelea* (type-species *W. trifida* **sp. n.**), *Gedanohelea* (type-species *G. loewi* **sp. n.**), and *Ceratopalpomyia* (type-species *C. eocenica* **sp. n.**).

The following new named species are described: *Culicoides dasyheleiformis*, *C. succivarius*, *C. balticus*, *C. eoselficus*, *C. ceranowiczi*, *C. gedanensis*, *C. prussicus*, *Ceratopogon hennigi*, *C. tertiaricus*, *C. grogani*, *C. crypticus*, *C. remmicolus*, *C. gedanicus*, *C. piotrowskii*, *C. ceranowiczi*, *C. ritzkowskii*, *C. margaritae*, *Brachypogon polonicus*, *B. henningseni*, *B. eocenicus*, *B. balticus*, *B. gedanicus*, *Nannohelea grogani*, *N. eocenica*, *Ceratoculicoides danicus*, *Alluaudomyia succinea*, *Monohelea baltica*, *Serromyia polonica*, *S. succinea*, *Mantohelea gedanica*, *Meunierohelea nielseni*, *M. gedanicola*, *M. wirthi*, *Wirthohelea trifida*, *Eohelea grogani*, *E. gedanica*, *Gedanohelea loewi*, *G. succinea*, *G. wirthi*, *Ceratopalpomyia eocenica*, *Palpomyia jantari*, *P. riedeli*, *P. succinea*, *Bezzia eocenica*, *Forcipomyia succinea*, *F. lyneborgi*, *F. gedanicola*, *F. eocostata*, *F. pseudomicrohelea*, *F. berendti*, *F. heningseni*, *F. eotrichoheleana*,

F. eophytoheleana, *F. krzeminskii*, *F. kulickae*, *F. eobreviflagellata*, *Atrichopogon eocenicus*, *Dasyhelea gedanica*, *D. eodicryptoscenica*, *D. stanislavi*, *Leptoconops succineus*.

Six new synonyms are proposed for the following species: *Ceratopogon forcipiformis* (= *C. defectus*), *Stilobezzia falcata* (= *C. spinosus*), *Serromyia spinigera* (= *C. elongatus*), *Eohelea sinuosa* (= *E. stridulans*), *Neurohelea cothurnata* (= *C. flagellus*), and *Physohelea obtusa* (= *? C. cothurnatulus*). A neotype is designated for *Ceratopogon anomalicornis* LOEW, and lectotypes are selected when necessary. Several new combinations are proposed. In addition to the extinct new genera some recent genera are recorded for the first time in the fossil material.

A checklist of all fossil biting midges is also provided. Nine nomina nuda introduced by KEILBACH (1982) are found. A new species status is proposed for subsp. *Dasyhelea australis antiqua* from the Miocene nodules, and *Baeohelea taimyrica* from Siberian amber is transferred to the genus *Leptohelea*.

Keys for the identification of subfamilies, tribes, genera and species, their composition, ecology and zoogeographical relationships are presented. On the basis of recent and fossil *Ceratopogonidae*, questions of systematics, phylogeny, evolution and zoogeography are discussed.

A phylogenetic history of the *Ceratopogonidae* must go back at least to the late Jurassic (ca. 150 Ma), and all tribes of the subfamily *Ceratopogoninae* evolved before the early Cretaceous. Some genera which exhibit an Africa-South America disjunction probably were present prior to their separation giving them a minimum age of early Cretaceous (ca. 113 million years). All species found in Baltic amber are recognized as extinct. An extinct species *Eohelea sinuosa* was found in Baltic and Saxonian ambers. Therefore, at least this species existed about 15 million years.

A reconstruction of the phylogeny of the subfamilies and tribes of *Ceratopogonidae* is presented. All taxa proposed by WIRTH and his co-workers are accepted, however the arrangement of subfamilies is almost totally inverted: *Ceratopogoninae*, *Forcipomyiinae*, *Dasyheleinae* and *Leptoconopinae*. The subfamily *Ceratopogoninae* and the tribe *Culicoidini* is recognized here as the most plesiomorphic, and *Forcipomyiinae* + *Dasyheleinae* as the most apomorphic among the latter three subfamilies. In accordance with the fossil findings *Dasyheleinae* is regarded as the more apomorphic sister group of the more plesiomorphic *Forcipomyiinae*, and the genus *Atrichopogon* as the more apomorphic sister genus of *Forcipomyia*.

It seems that the *Ceratopogonidae* exhibited rapid evolution as 7 genera known only from Baltic amber became extinct during a relative-

ly short period. It may be that the family as a whole flourished during the Tertiary, and now plays a less important role in recent entomofauna. A good example illustrating an extinction in the family is the Holarctic genus *Ceratopogon* represented in Baltic amber by 25.3% of all specimens and many species. This genus which is usually rare today, inhabits the more northern parts of the North Hemisphere and is often restricted to refugial isolated areas in mountains.

All subfamilies and tribes of the *Ceratopogonidae* have been found in the material studied except for the tribes *Stenoxenini* and *Sphaeromiini* which probably are of Gondwana origin. The genera, subgenera and species groups present in Baltic amber depending on their recent and supposed original distribution, when it was possible, are divided into the following main groups: I. Cosmopolitan, II. Pantropical, and III. Laurasian. The taxa included to the latter group are supposed to be of Laurasian origin. Now they are: 1. Almost cosmopolitan, 2. Almost pantropical, 3. Holarctic, 4. Euro-North American, 5. Neotropical and North American, 6. Neotropical, 7. East Palaearctic, 8. Oriental, 9. Extinct.

Weak affinities of the Baltic amber fauna with the recent east Palaearctic, Oriental and Afrotropical faunas on the one hand, and important affinities with Nearctic and Neotropical faunas on the other hand suggest that the Tertiary Europe was effectively isolated from east Asia by the Siberian Sea and from Africa by the Tethys Sea.

The *Ceratopogonidae* in the Baltic amber bearing forest were quite common, probably much more common than in the recent of the Middle European forest. The ceratopogonid fauna was also rich and diversified, both in the number of species and genera. A comparison of the quantitative composition of the family from the late Cretaceous Siberian amber, Baltic amber and from the recent deciduous forest near Warsaw evidently shows the decreasing importance of the subfamily *Ceratopogoninae* from the late Cretaceous to the present in the Northern Hemisphere forest habitats, and growing (quantitative) importance of the subfamilies *Forcipomyiinae* and *Dasyheleinae*.

The composition of the *Ceratopogonidae* fauna of the Baltic amber allows suggestions about the nature of the localities in which it flourished and in which the amber now enclosing it was formed. The great prevalence of the subfamily *Ceratopogoninae*, both in the number of species and specimens indicates that there were moist forests where semiaquatic and aquatic habitats were common. The presence of numerous *Forcipomyia* is a testimony that this forest was rich in rotting wood. There were tropical water-holding plants such as bromeliads. There were also, but not common, coastal or inland beaches in which the

larvae of *Leptoconops* succineus lived. Haematophagous biting midges which probably fed on mammals and birds constitute about 19% of all *Ceratopogonidae* examined (incl. males).

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XII. INDEX OF SCIENTIFIC NAMES