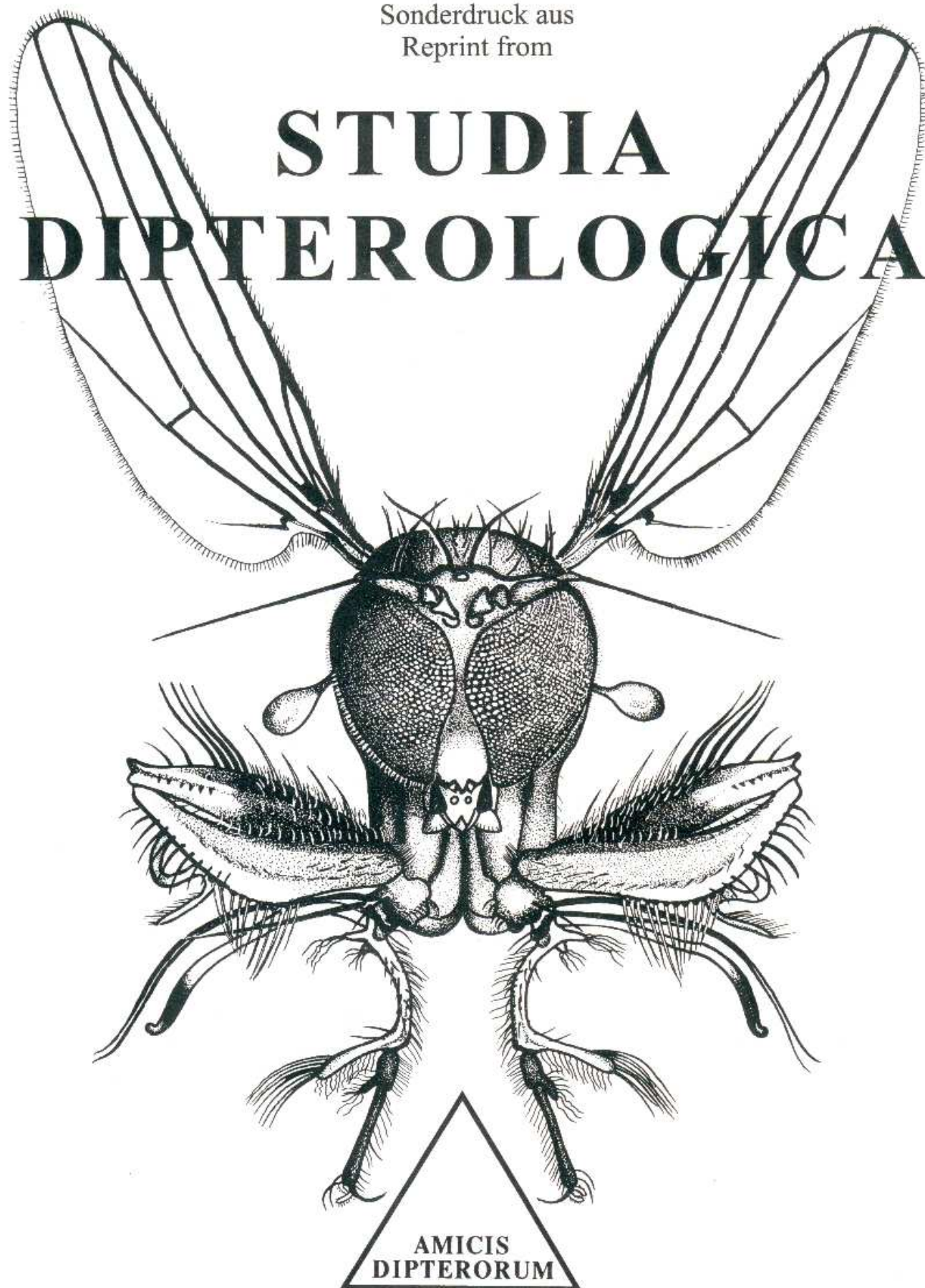


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# STUDIA DIPTEROLOGICA



Herausgegeben von Andreas Stark und Frank Menzel

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Das Titelbild zeigt die Frontalsicht eines Männchens von *Campsicnemus magius* (LOEW). Diese halophile Langbeinfliege (Dolichopodidae) kommt in den Binnensalzstellen um Halle (Saale) vor. Sie wurde von LOEW nach Tieren aus Sizilien (Syrakus) im Jahre 1845 in der Stettiner entomologischen Zeitung 6: 392-394 als *Medeterus magius* beschrieben. Hinsichtlich der Farbgebung und der Gestaltung der Beine weisen die Männchen dieser Spezies die prächtigste und komplizierteste Abwandlung im Vergleich aller einheimischen *Campsicnemus*-Arten auf. Sie versinnbildlicht also in besonderer Weise die Schönheit der Zweiflügler und ist deshalb von uns als Signet der Zeitschrift **Studia dipterologica** ausgewählt worden.

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# Biting midges from Lower Cretaceous amber of Lebanon and Upper Cretaceous Siberian amber of Taimyr (Diptera, Ceratopogonidae)

[Gnitzen aus unterkretazischem Bernstein des Libanon und oberkretazischen Bernstein  
der Taimyr Region in Sibirien (Diptera, Ceratopogonidae)]

by  
Ryszard SZADZIEWSKI

Gdynia (Poland)

## Abstract

Fossil biting midges from Lower Cretaceous Lebanese and Upper Cretaceous Siberian amber are described and illustrated. The material includes 30 specimens from Neocomian (125-130 Ma) Lebanese amber, 6 from Upper Cenomanian (91-92 Ma) Siberian amber and 97 specimens from Coniacian-Santonian (85-87.5 Ma) Siberian amber from Taimyr.

Five new fossil genera are described from Lower Cretaceous Lebanese amber (*Archiculicoides* gen. nov., *Lebanoculicoides* gen. nov., *Archiaustroconops* gen. nov., *Lebanoconops* gen. nov. and *Fossileptoconops* gen. nov.), and one from Upper Cretaceous Siberian amber (*Brachycretacea* gen. nov.). The following 18 new species are described: *Archiculicoides schleei* spec. nov., *Lebanoculicoides mesozoicus* spec. nov., *Protoculicoides succineus* spec. nov., *Austroconops cretaceous* spec. nov., *A. fossilis* spec. nov., *A. gondwanicus* spec. nov., *Lebanoconops lebanicus* spec. nov., *L. minutus* spec. nov., *L. wirthi* spec. nov., *Minyohelea schleei* spec. nov. and *Fossileptoconops lebanicus* spec. nov. from Lebanese amber and *Leptoconops sibiricus* spec. nov., *Austroconops sibiricus* spec. nov., *Atriculicoides dasyheleis* spec. nov., *Atriculicoides sibiricus* spec. nov., *A. taimyricus* spec. nov., *Peronehelea sibirica* spec. nov., *Washingtonhelea taimyrica* spec. nov. from Upper Cretaceous Siberian amber. *Atriculicoides squamiciliatus* REMM from Siberian amber is recognized as a new synonym of *A. macrophthalmus* REMM. The new tribe **Atriculicoidini** is placed in the subfamily Forcipomyiinae along with Forcipomyiini and Dasyheleini.

The Lebanese amber species are the oldest undoubted fossils in the family. The subfamily Austroconopinae was widely distributed in the northern hemisphere during the Cretaceous, where it became extinct at the end of the Mesozoic. At present only one "living fossil", *Austroconops mcmillani*, is known from Western Australia. Only one extant genus is known from the Lower Cretaceous (12.5% of the total fauna), while five extant genera are recorded from the Upper Cretaceous (41.7%).

The phylogeny of the family is discussed. The hypothesis that the blood sucking habit of females is plesiotypic for the family is supported. For the Diptera feeding on liquefied carbohydrates in both sexes is recognized as plesiotypic. Females feeding on proteins evolved within the order several times. Fossil materials are shown to be helpful in determining character polarity.

## Key words

Diptera, Ceratopogonidae, fossils, Cretaceous, Lebanese amber, Siberian amber.

## Zusammenfassung

Fossile Ceratopogoniden aus Bernstein der unteren Kreide des Libanon und der oberen Kreide Sibiriens werden beschrieben und abgebildet. Insgesamt beinhaltet das bearbeitete Material 30 Individuen aus dem libanesischen Bernstein des Neokom (125-130 Mio. a), 6 Individuen aus sibirischem Bernstein der Taimyr-Region aus dem Oberen Cenoman (91-92 Mio. a) und 97 Individuen aus dem Coniac-Santon (85-87,5 Mio. a).

Im Ergebnis der Untersuchungen werden 5 neue Gattungen aus dem libanesischen Bernstein (*Archiculicoides* gen. nov., *Lebanoculicoides* gen. nov., *Archiaustroconops* gen. nov., *Lebanoconops* gen. nov. und *Fossileptoconops* gen. nov.) und eine aus

dem Bernstein der Oberen Kreide Sibiriens beschrieben (*Brachycretacea* gen. nov.). Insgesamt schließen sie folgende 18 neue Arten ein: *Archiculicoides schleei* spec. nov., *Lebanoculicoides mesozoicus* spec. nov., *Protoculicoides succineus* spec. nov., *Austroconops cretaceous* spec. nov., *A. fossilis* spec. nov., *A. gondwanicus* spec. nov., *Lebanocconops lebanicus* spec. nov., *L. minutus* spec. nov., *L. wirthi* spec. nov., *Minyohelea schleei* spec. nov. und *Fossileptoconops lebanicus* spec. nov. aus Libanon-Bernstein und *Leptoconops sibiricus* spec. nov., *Austroconops sibiricus* spec. nov., *Atriculicoides dasyheleis* spec. nov., *A. sibiricus* spec. nov., *A. taimyricus* spec. nov., *Peronehelea sibirica* spec. nov., *Washingtonhelea taimyrica* spec. nov. aus oberkretazischem sibirischem Bernstein. *Atriculicoides squamiciliatus* REMM aus Bernstein sibirischer Herkunft wird als **syn.nov.** von *A. macrophthalmus* REMM aufgefaßt. Die **neue Tribus Atriculicoidini** wird gemeinsam mit den Forcipomyiini und Dasyheleini in der Unterfamilie Forcipomyiinae plaziert.

Die Inklusionen aus dem Libanon-Bernstein stellen die ältesten Fossilien dar, die sicher der Familie Ceratopogonidae zugeordnet werden können. Während der Kreidezeit war die Unterfamilie Austroconopinae auf der nördlichen Hemisphäre weit verbreitet und starb hier gegen Ende des Mesozoikums aus. In der Gegenwart kennt man mit *Austroconops mcmillani* nur eine Art aus West-Australien, die man deshalb als "Lebendes Fossil" bezeichnen kann. Nur eine Gattung mit rezenten Vertretern trat bereits in der Unteren Kreide auf und nimmt einen Anteil von 12,5% unter den Taxa gleichen Ranges ein. Dagegen reichen fünf Genera, die bereits in der Oberen Kreide entwickelt waren mit ihren Arten bis in die Gegenwart (41,7% aller Gattungen).

Die Phylogenie der Familie Ceratopogonidae wird diskutiert. Die Fossilien stützen die Hypothese, daß es sich beim Blutsaugen der Weibchen um eine plesiotypische Eigenschaft innerhalb der Familie handelt. Außerdem wird innerhalb der Dipteren die Aufnahme flüssiger Kohlehydrate durch Individuen beider Geschlechter als ursprüngliche Verhaltensweise angesehen. Es wird davon ausgegangen, daß sich die besondere Ernährungsweise der Weibchen, nämlich die Aufnahme von Proteinen, mehrfach in dieser Insektenordnung herausbildete. Wiederum wird gezeigt, daß Fossilien sehr hilfreich bei der Einschätzung sein können, ob Merkmale ursprünglich oder abgeleitet sind.

#### Stichwörter

Diptera, Ceratopogonidae, Fossilien, Kreide, Libanon-Bernstein, Sibirischer Bernstein

#### Introduction

The Ceratopogonidae is one of the best studied nematocerous families. There are presently known almost 5,000 species grouped in more than a hundred genera, with fossils representing almost 5% of these names. Especially well studied are Tertiary biting midges preserved as inclusions in Baltic amber (SZADZIEWSKI 1988), Saxonian amber (SZADZIEWSKI 1993) and Dominican amber (SZADZIEWSKI & GROGAN 1994). Biting midges are also relatively well preserved and common in Cretaceous ambers.

The oldest undoubtful biting midges are from Lower Cretaceous Lebanese amber, Neocomian, 125-130 Ma, collected at Jezzine (SCHLEE & DIETRICH 1970). Those specimens were examined by the late Dr. Willis W. WIRTH (personal comm.) during his visit to Stuttgart in 1975 but the results were not published. Subsequently the American Museum of Natural History in New York purchased from Aftim ACRA the Lebanese amber inclusions collected in the vicinity of Dar-el-Baidha (POINAR 1992). In this amber there are over a hundred biting midges (GRIMALDI, personal comm.).

Upper Cretaceous biting midges are known from Cenomanian amber from France, 95 Ma (SZADZIEWSKI & SCHLÜTER 1992), Cenomanian amber of New Jersey, 94 Ma (GROGAN & SZADZIEWSKI 1988), Upper Cenomanian amber of Western Taimyr, 91-92 Ma (KALUGINA 1991). Coniacian-Santonian inclusions of biting midges are recorded from Taimyr or Si-



berian amber at Yantardakh in Eastern Taimyr, 85-87.5 Ma (REMM 1976). The Campanian fossil biting midges are well known from Canadian amber, 71.3-83.5 Ma (BOESEL 1937, DOWNES & WIRTH 1981, BORKENT 1995).

Previous suggestions that *Simulidium priscum* WESTWOOD, 1854 from Jurassic Purbeck deposits was the oldest biting midge (GROGAN & SZADZIEWSKI 1988) representing a species of extant genus *Leptoconops* is incorrect. The species in question actually is of Lower Cretaceous age and is a member of the family Rhagionidae (ROSS et al., in prep.). SZADZIEWSKI (1990) suggested that a compression fossil from Lower Cretaceous deposits of Koonwarra in Australia named by JELL & DUNCAN (1986) as "Simuliid? indet. 2" might be a species of *Austroconops*. SCHLEE (1984) reported a male biting midge from Lower Cretaceous amber of Austria (120 Ma) and LANGENHEIM et al. mentioned a biting midge from the amber of Alaska of unprecised Cretaceous age (BORKENT 1995).

The main purpose of this paper is to describe and interpret the oldest biting midges from Lower Cretaceous Lebanese amber and to provide a revision of biting midges from Upper Cretaceous Siberian amber from the Taimyr, Russia.

### Materials and methods

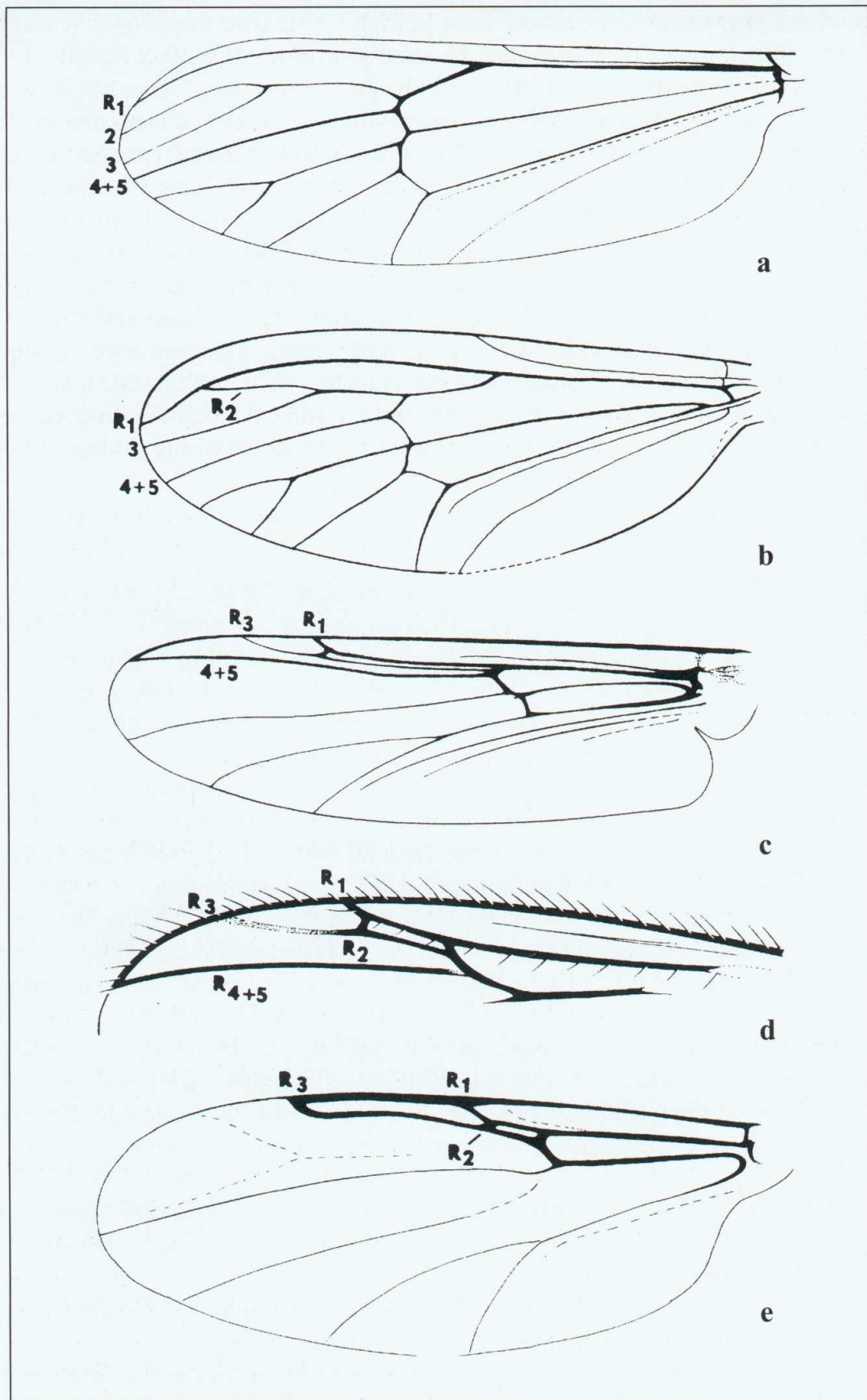
Special morphological terms and abbreviations used in the present paper follow those explained by DOWNES & WIRTH (1981) for extant and by SZADZIEWSKI (1988) for fossil biting midges. Male antennal ratio (AR) was obtained by dividing the combined lengths of the distal 4 flagellomeres by the combined lengths of proximal 9 flagellomeres. Length of the second tarsomere was measured excluding the basal portion hidden in the basitarsus which is usually invisible (SZADZIEWSKI 1988).

The nomenclature used for the radial sector of the wing differs in this paper. In that proposition (Fig. 1d) the transverse vein is  $R_2$  (as proposed by Edwards 1926;  $R_{2+3}$  in DOWNES & WIRTH 1981), while the next to  $R_1$  longitudinal radial vein is  $R_3$  [ $R_{4+5}$  of many authors,  $R_{2+3}$  of NIELSEN (1951)]. Within the Ceratopogonidae vein or veins  $R_{4,5}$  are usually greatly reduced, ignored and treated as false veins (DOWNES & WIRTH 1981). Only NIELSEN (1951) and LINDBERG (1964) recognized them as real veins. It is possible that the proposition by NIELSEN (1951) and LINDBERG (1964) to treat the transverse vein  $R_2$  as an additional vein  $r-r$  in the Ceratopogonidae and by KRZEMIŃSKI (1992) in other Diptera is correct. In the wing of *Lebanoculicoides mesozoicus* spec. nov. vein  $R_{4+5}$  is clearly visible and cannot be ignored or treated as a false vein (Fig. 1d). Within the infraorder Culicomorpha vein  $R_{4+5}$  is well developed in the Chironomidae (Fig. 1c), Thaumaleidae, Culicidae, Chaoboridae, Dixidae (Fig. 1 a, b), Corethrellidae, while in the Simuliidae it is reduced as it is in most biting midges.

Almost all drawings were made with a camera lucida, and all photographs were taken with an Olympus automatic exposure photomicrographic system PM-10AK. Detailed methods were described earlier by SZADZIEWSKI (1988).

Present study is based on 133 inclusions (30 from Lebanese amber, 6 from Cenomanian and 97 from Coniacian-Santonian Siberian amber).

Inclusions of biting midges in Lebanese amber were collected in the district of Jezzine by Dr. Dieter SCHLEE and his wife (Staatliches Museum für Naturkunde in Stuttgart) in 1968 and 1969. The age of the amber-bearing beds in Lebanon is Early Cretaceous (Neocomian, probably Hauterivian Stage), with the absolute age about 125-130 Ma (SCHLEE & DIETRICH 1970). The Lebanese amber specimens are housed in the Staatliches Museum für Naturkunde in Stuttgart, Rosenstein 1, D-7000 Stuttgart [SMNS].



**Fig. 1 (a-e):** Homology of wing veins in radial sector of Dixidae, Chironomidae and Ceratopogonidae; - **a:** *Dixa* MEIGEN (extant); - **b:** Lower Cretaceous Dixidae (from Dr. L. LUKASHEVICH of Paleontological Institute of Russian Acad. Sci.); - **c:** extant *Procladius* SKUSE, Chironomidae; - **d:** Lower Cretaceous *Lebanoculicoides mesozoicus* spec. nov.; - **e:** extant *Atrichopogon* KIEFFER, Ceratopogonidae.

Inclusions in Upper Cretaceous Siberian, or Taimyr, amber (retinite) were collected by the staff of the Paleontological Institute of Russian Academy of Sciences in Moscow, who organized expeditions to the Khatanga Basin in Eastern Taimyr in 1970 and 1971 (ZHERIKHIN & SUKACHEVA 1973, ZHERIKHIN 1978). The inclusions I studied were from deposits located at the Yantardakh site (series PIN 3130, 3311 and 3310) and are of Coniacian-Santonian Stage (85-87.5 Ma). Six inclusions of biting midges were from Upper Cenomanian (91-92 Ma) deposits located at Nizhnyaya Agapa River in Western Taimyr. They were collected by V. ZHERIKHIN and I. SUKACHEVA in 1973, series PIN 3426 (ZHERIKHIN 1978, personal comm.) According to ZHERIKHIN & SUKACHEVA (1973) the number of biting midges in Siberian amber was higher than 300. However, in the materials available only 97 specimens from Yantardakh and 6 from Nizhnyaya Agapa were present. I was not able to find further specimens in the Entomological Laboratory of Paleontological Institute in Moscow. Among unavailable materials were some types of species described by REMM and which were borrowed by Dr. V. GLUKHOVA of the Zoological Institute of the Russian Academy of Sciences, Petersburg.

Most of the Siberian amber specimens examined by REMM (1976) and KALUGINA (1991) and previously unstudied material were loaned from the Paleontological Institute of Russian Academy of Sciences in Moscow (abbr. PIN), Profsoyuznaya 123, 11764 Moscow. Three barely preserved specimens from Yantardakh (PIN 3311/435, 439, 441) were merely determined to the family level.

## Systematics

### Key to Cretaceous genera

- 1 Vein  $R_{4+5}$  well developed (Fig. 3 e) ..... ***Lebanoculicoides* gen. nov.** (Lower Cretaceous)
- Vein  $R_{4+5}$  absent or vestigial ..... **2**
- 2 Terminal flagellomere with apical stylet-like prolongation (Fig. 2 c) ..... ***Archiculicoides* gen. nov.** (Lower Cretaceous)
- Terminal flagellomere with rounded apex ..... **3**
- 3 Eyes broadly separate in both sexes (Fig. 18 b). Female cerci slightly to greatly elongate and tergite X with dorsal caudomedian excavation (Fig. 19 b, c). Palpus 4-segmented. Only 13th male flagellomere elongated (Fig. 21 a). Female antenna with 12-13 flagellomeres; terminal one elongated (Fig. 22 a). Leptoconopinae ..... **4**
- Eyes touching or more or less narrowly separate above antennae. Female cerci short and tergite X with straight caudal margin. Palpus 4-5 segmented. 1-4 distal male flagellomeres elongate. Female antenna with 13 flagellomeres, 1-5 distal ones elongate ..... **5**
- 4 Vein  $R_3$  not fused with  $R_7$ . Costa prolonged to wing apex. Female antenna with 13 flagellomeres, cerci slightly elongated (Figs. 18, 19).. ..... ***Fossileptoconops* gen. nov.** (Lower Cretaceous)
- Veins  $R_{2+3}$  fused with  $R_7$  into stigma. Costa short, ending at apex of stigma. Female antenna with 12 flagellomeres (Fig. 22), cerci greatly elongated..... ***Leptoconops* SKUSE** (Upper Cretaceous - Recent)
- 5 Tarsal ratio of hind leg 1.5-2.7 times lower than of fore and mid legs. Austroconopinae ..... **6**

-	Tarsal ratios of all legs similar .....	9
6	Vein $r-m$ more or less parallel to $R_1$ and $R_3$ (Figs. 8, 11) .....	
	..... <i>Austroconops</i> WIRTH et LEE (Lower Cretaceous - Recent)	
-	Vein $r-m$ transverse (= oblique) to $R_1$ and $R_3$ (Figs. 6 c, 14 d) .....	7
7	Vein $R_1$ long, cells $r_1$ and $r_2$ large (Fig. 6 c, f) .....	
	..... <i>Archiaustroconops</i> gen. nov. (Lower Cretaceous)	
-	Vein $R_1$ short, cells $r_1$ and $r_2$ obsolete (Fig. 14 d) .....	8
8	12th and 13th male flagellomeres elongated. Terminal palpal segment distinct (Fig. 14 a, b) .....	
	..... <i>Lebanconops</i> gen. nov. (Lower Cretaceous)	
-	Only 13th male flagellomere elongated. Terminal palpal segment very small (Fig. 17 a, b) .....	
	..... <i>Minyohelea</i> BORKENT (Lower - Upper Cretaceous)	
9	Palpus 4 segmented .....	10
-	Palpus 5 segmented .....	11
10	Vein $R_2$ absent, cells $r_1$ and $r_2$ confluent, short. Male antenna with 9 flagellomeres, wing membrane without macrotrichia (Fig. 35) .....	
	..... <i>Brachycretacea</i> gen. nov. (Upper Cretaceous)	
-	Vein $R_2$ present, cells $r_1$ and $r_2$ separated, long. Male antenna with 13 flagellomeres, wing membrane with macrotrichia .....	
	..... <i>Atriculicoides</i> REMM (part) (Upper Cretaceous)	
11	Cells $r_1$ and $r_2$ confluent .....	
	..... <i>Heleageron</i> BORKENT (Upper Cretaceous)	
-	Cells $r_1$ and $r_2$ separate, or only 1st radial cell present (=visible)(Figs. 4 d, 39 g) .....	12
12	Costa prolonged almost to wing apex. Radial cells large. Wing membrane without macrotrichia (Fig. 4 d). Female claws equal, simple .....	
	..... <i>Protoculicoides</i> BOESEL (Lower - Upper Cretaceous)	
-	Costa not prolonged to wing apex. Radial cells small to moderately large .....	13
13	Hind basitarsus without subbasal spine .....	14
-	Hind basitarsus with distinct subbasal spine (Fig. 38 d) .....	16
14	Wing membrane bare .....	
	..... <i>Adelohelea</i> BORKENT (Upper Cretaceous)	
-	Wing membrane with macrotrichia .....	15
15	Female claws with deeply bifid apices (Fig. 24 g). Male flagellomeres 10-13 elongate (Fig. 23 a), parameres fused into a single structure (Fig. 23 g-i) .....	
	..... <i>Atriculicoides</i> REMM (Upper Cretaceous)	
-	Female claws with simple or weakly bifid apices. Male flagellomeres 11-13 elongate and parameres double (Fig. 33 d) .....	
	..... <i>Culicoides</i> LATREILLE (Upper Cretaceous-Recent)	
16	Female claws short, equal, without basal teeth .....	
	..... <i>Washingtonhelea</i> BORKENT (Upper Cretaceous - Recent)	
-	Female claws modified, with basal tooth .....	17
17	Female claws similar on all legs, long, equal, each with basal tooth (Fig. 38 d, e) .....	
	..... <i>Ceratopogon</i> MEIGEN (Upper Cretaceous - Recent)	
-	Female claws short and equal on fore and mid legs, enlarged and unequal on hind leg .....	18
18	Claws of hind leg unequal, longer claw with 2 basal (inner and outer) teeth, shorter claw with inner tooth. Hind femur and tibia slightly enlarged .....	
	..... <i>Palaeobrachypogon</i> BORKENT (Upper Cretaceous)	



- Female claw of hind leg single, very long, armed with 1-2 short to long teeth (Fig. 43d-f). Hind femur and tibia distinctly enlarged (Fig. 40).....  
 ..... *Peronehelea* BORKENT (Upper Cretaceous)

**Basal lineages of the Ceratopogonidae**

Fossil genera placed here represent the basal lineages of biting midges and are not assigned to any subfamily of the Ceratopogonidae (Figs. 46, 47).

**Genus *Archiculicoides* gen. nov.**

Type-species *Archiculicoides schleei* spec. nov., present designation.

**Diagnosis:** male unknown. Female with wing membrane lacking macrotrichia, long costa and large second radial cell extending almost to wing apex, first flagellomere bearing sensilla coeloconica, terminal flagellomere with pointed apical prolongation. Lower Cretaceous.

**Discussion**

All characters found in the new species and genus are plesiotypic. The cylindrical apical prolongation on terminal flagellomere is a homoplastic character state present in Chaoboridae, Culicidae, Corethrellidae, and some Forcipomyiinae.

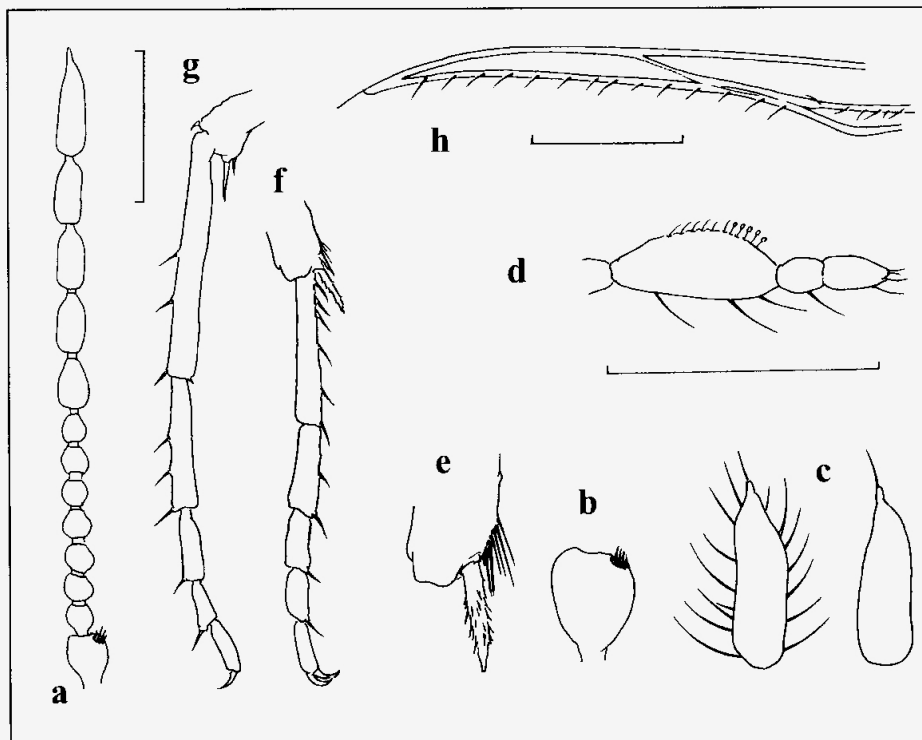
*Archiculicoides schleei* spec. nov. (Fig. 2 a-h)

**Diagnosis:** as for genus.

**Description:** ♂: unknown.

♀: body length 1.2 mm. **Head:** eyes rather narrowly separated. Antenna with 13 flagellomeres, length 413 µm, first flagellomere with 1 sensilla coeloconica (Fig. 2 a, b), flagellomeres 2-8 short, spherical, distal 5 elongate, cylindrical; terminal flagellomere

with slender apical prolongation (Fig. 2 a); AR 1.30. Proboscis moderately short. Palpus 5-segmented; 3rd palpal segment stout, 60 µm long, on inner surface with some capitate sensilla (Fig. 2 d).



**Fig. 2 (a-h):** *Archiculicoides schleei* spec. nov., female, SMNS C39/1. - a: flagellum; - b: first flagellomere; - c: apical flagellomere; - d: palpus; - e: tibial spur of fore leg; - f: tarsus of fore leg; - g: tarsus of hind leg; - h: radial cells. Scale bar = 0.1mm.

**Legs** unmodified, slender. Tibial spur of fore leg stout and long, covered with spines (Fig. 2 e). Tarsi with some distinct spines (Fig. 2 f, g). 4th tarsomeres cylindrical, claws similar on all legs, short, equal, simple. TR(I) 1.9, TR(III) 1.8. **Wing** barely visible. Length 0.65 mm. Costa reaching almost 0.9 of wing length. Both first radial cells present; second one large, much longer than first one (Fig. 2 h). Wing membrane bare. Veins  $R_1$  and  $R_3$  with long setae. **Abdomen**: cerci short.

**Material examined** (1 ♀): Holotype ♀, SMNS C39/1, Libanon-Bernstein, Unterkreide (Neocom), Nähe Jezzine (= near Jezzine), leg. D. SCHLEE, 1969.

### Genus *Lebanoculicoides* gen. nov.

Type-species *Lebanoculicoides mesozoicus* spec. nov., present designation.

**Diagnosis**: male unknown. Only Lower Cretaceous genus with bare wing membrane, well developed vein  $R_{4+5}$ ; costa extending to wing tip; proboscis long and palpus 5-segmented; legs unmodified with simple, equal claws.

### Discussion

The new genus has the most plesiotypic wing venation within the family with a well developed vein  $R_{4+5}$  and the radial sector arranged as in some Chironomidae. In some other extant and fossil biting midges vein  $R_{4+5}$  is visible as an indistinct fork while in *Leptoconops* it is simple. Formally *Lebanoculicoides* with the most plesiotypic wing venation would form a sister group to the rest of biting midges.

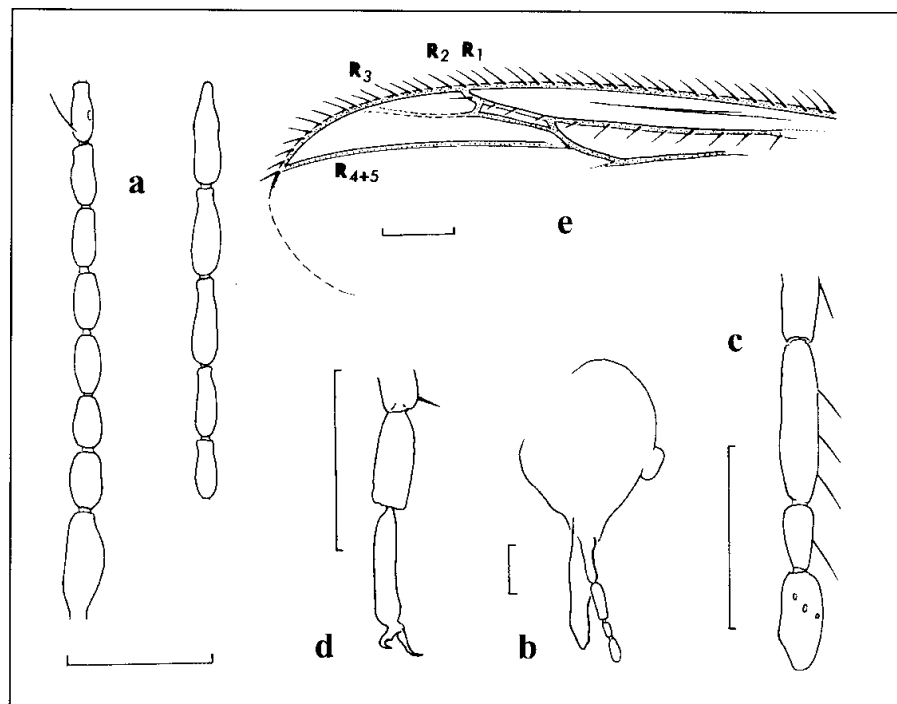
### *Lebanoculicoides mesozoicus* spec. nov. (Figs. 3 a-e, 48 a)

**Diagnosis**: as for genus.

**Description**: ♂: unknown.

♀: total habitus as in Fig. 48 a. Body length 1.5 mm. **Head**: eyes separation not visible. Proboscis as long as head height (Fig. 3 b). Antenna composed of 13 flagellomeres, length 690  $\mu$ m, AR 0.78; all flagellomeres cylindrical increasing in length from 2nd to 13th; sensilla coeloconica not visible (Fig. 3 a). Palpus long, 5-segmented; 3rd palpal segment slender, 84  $\mu$ m long, sensilla not visible (Fig. 3 c). **Thorax** barely visible. **Legs**: tibial spur of fore leg long and straight, first tarsomere of fore leg with distinct spines.

**Fig. 3 (a-e)**: *Lebanoculicoides mesozoicus* spec. nov., female, SMNS C32/33. - **a**: flagellum; - **b**: lateral aspect of head; - **c**: palpus; - **d**: distal tarsomeres of hind leg. Scale bar = 0.1 mm.



Hind basitarsus with strong palisade-like setae. 4th tarsomeres cylindrical. All claws similar, short, equal, simple (Fig. 3d). **Wing** obliquely situated in amber. Length 1.01 mm. Costa prolonged almost to wing apex (Fig. 3e).  $R_1$ ,  $R_2$  and  $R_3$  present,  $R_{4+5}$  terminating just before wing apex. Distal portion of  $R_3$  barely visible, however  $R_2$  is well developed. Wing membrane with distinct microtrichia, without macrotrichia. **Abdomen:** cerci short.

**Material examined** (1 ♀): Holotype ♀, SMNS C32/33, Libanon Bernstein, Unterkreide (Neocom), Nähe Jezzine, (= near Jezzine), leg. D. SCHLEE, 1969.

### Genus *Protoculicoides* BOESEL, 1937

Type-species *Protoculicoides depressus* BOESEL, 1937, by original designation. Canadian amber, Upper Cretaceous-Campanian.

**Diagnosis:** male unknown. Female wing membrane without macrotrichia, palpus 5-segmented, costa reaching almost wing tip, both first radial cells large, no traces of vein  $R_{4+5}$ , distal 4-5 flagellomeres elongate, sensilla coeloconica not visible on flagellum, legs unmodified with equal, simple claws and cylindrical 4th tarsomeres. Lower - Upper Cretaceous.

### Discussion

The male determined by BORKENT (1995) as *Protoculicoides depressus* with macrotrichia on wing membrane cannot be assigned to this genus because the associated female (holotype) lacks macrotrichia. Within all extant Ceratopogonidae the pattern is the opposite, i.e. if females have macrotrichia then males may have fewer or no macrotrichia on the wing membrane. The male determined by BORKENT likely is a member of the tribe Ceratopogonini (see phylogeny). This genus may not be monophyletic as it is based on symplesiomorphies.

BORKENT (l.c.) tentatively placed *Protoculicoides* in the subfamily Forcipomyiinae. According to his next suggested hypothesis it would represent the sister group to all Ceratopogonidae other than Leptoconopinae.

### Key to species of *Protoculicoides*

#### Females

- 1 Distal 5 flagellomeres elongate (Fig. 4 a) .....  
 ..... *P. succineus* spec. nov. (Lower Cretaceous)  
 - Distal 4 flagellomeres elongate .....  
 ..... *P. depressus* BOESEL (Upper Cretaceous Canadian amber)

*Protoculicoides succineus* spec. nov. (Figs. 4 a-e, 48 b)

**Diagnosis:** see key.

**Description:** ♂: unknown.

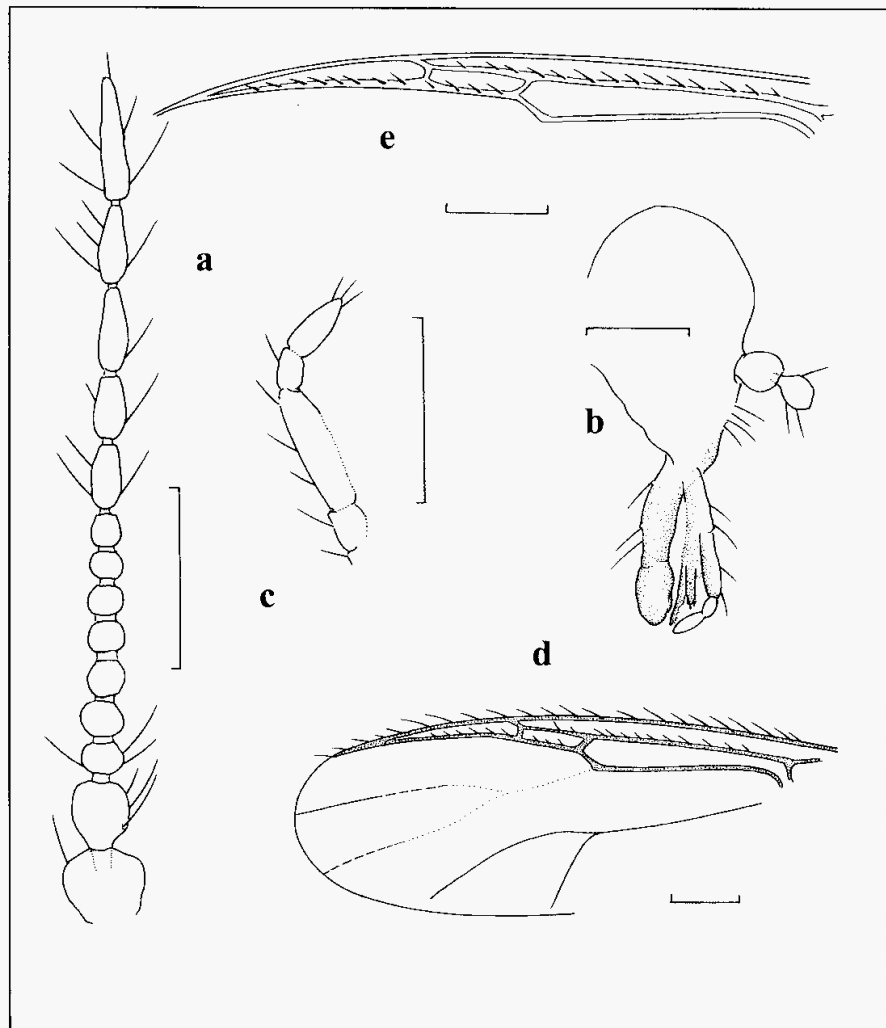
♀: body stout (Fig. 48 b). Total length 1.15 mm. **Head:** eyes touching or narrowly separated. Antenna composed of 13 flagellomeres, AR 1.25, distal 5 flagellomeres elongate (Fig. 4 a). Proboscis long (Fig. 4 b). Palpus 5 segmented; 3rd palpal segment cylindrical, 72 µm long; sensorium not visible (Fig. 4 c). **Thorax:** scutum with some strong setae. Humeral pits present, deep. Scutellum with 5 marginal strong bristles. Legs unmodified, barely visible. Fourth tarsomeres cylindrical; claws similar on all legs, short, equal, simple. **Wing** length 0.75 mm; wing membrane with distinct microtrichia, without macrotrichia; costa

long, somewhat prolonged beyond end of  $R_3$ , CR 0.92; both first radial cells well developed, second one 2.3 times longer than first one (Fig. 4 e). **Genitalia** not clearly visible. **Abdomen**: cerci short.

**Material examined** (1 ♀): Holotype ♀, SMNS C31/14, Libanon-Bernstein, Unterkreide (Neocom), Nähe Jezzine, leg. D. SCHLEE 1969.

### Discussion

The female of *Protoculicoides depressus* from Upper Cretaceous Canadian amber differs in having only 4 distal flagellomeres elongated and is distinctly larger with the wing length 1.72 mm and CR 0.87.



**Figs. 4 (a-e):** *Protoculicoides succineus* spec. nov., Lower Cretaceous, holotype female SMNS C31/14. - **a**: flagellum; - **b**: head; - **c**: palpus; - **d**: wing; - **e**: radial cells. Scale bar = 0.1 mm.

### Subfamily Austroconopinae BORKENT, WIRTH et DYCE, 1987

**Diagnosis:** wing membrane without macrotrichia. Palpus 4 (rarely 5) segmented, only one (rarely 2) segment distal to that bearing the sensory organ. Antenna with 13 flagellomeres; in female with no sharp difference in length between flagellomeres 8 and 9, flagellomeres gradually increasing in length from 2 to 13; in male flagellomere 1 with single whorl of plume setae, flagellomeres 12-13 or 13 elongated, 13 or 12-13 with a whorl of strong plume setae. Legs slender to moderately robust, unmodified, unarmed, with short setae; tibial spur usually present on fore and hind legs; hind tibial comb with 4-5 spines. Tarsal ratio of hind leg much lower (1.5-2.7 times) than of fore and mid legs. Fifth tarsomeres unarmed; claws small, equal, simple or each with subbasal tooth, apex of each claw bifid in male, simple in female; slender empodium present. Female with 2 large spermathecae plus vestigial third. Male genitalia with short to long tergite IX, with or without apicolateral processes. Gonostyli single or double. Parameres difficult to interpret in fossils. Immature stages unknown. Females of extant *Austroconops mcmillani* have been recorded biting humans.



## Discussion

WIRTH & LEE (1958) described females of *Austroconops mcmillani* as a new genus and species from western Australia. Almost 30 years later BORKENT et al. (1987) described the male of that species and proposed a new subfamily Austroconopinae. The latter authors in a detailed phylogenetic discussion showed that *A. mcmillani* represented an early lineage within the Ceratopogonidae.

SZADZIEWSKI (1990) reported for the first time fossils in the genus *Austroconops* from Upper Cretaceous amber of Taimyr and French amber. He suggested that a compression fossil from Lower Cretaceous deposits of Koonwarra in Australia named by JELL & DUNCAN (1986) as "Simuliid? indet. 2" may be a species of *Austroconops*.

Subsequently SZADZIEWSKI & SCHLÜTER (1992) described *Austroconops borkenti* based on an incomplete female from Cenomanian French amber (95 Ma) which was the first named fossil in the subfamily.

The present concept of the subfamily is expanded. In addition to the type genus *Austroconops*, there is now added *Archiaustroconops* gen. nov. which certainly is closely related to the type genus, *Lebanoconops* gen. nov., as well as *Minyohelea* BORKENT. The fossil genus and species *Minyohelea pumilis* was described by BORKENT (1995) from Campanian amber of Canada and placed within the Ceratopogonini. Two latter genera with greatly reduced wing venation, and peculiar genitalia in fact may represent an earlier lineage, as the synapomorphies may be homoplastic (convergence). Further materials and investigations, especially on male genitalia, are necessary to find the exact phylogenetic position of both genera. Synapomorphy proposed by BORKENT et al. (1987) for the Austroconopinae - posterior margin of scutellum forming nearly 90° angle - is not confirmed by the present study, as an elongated or rounded scutellum was found in other species. The Austroconopinae were widely distributed during the Cretaceous, probably throughout the world, but became extinct by the end of the Cretaceous (Fig. 5) except in Australia, where *A. mcmillani* remains extant as a "living fossil".

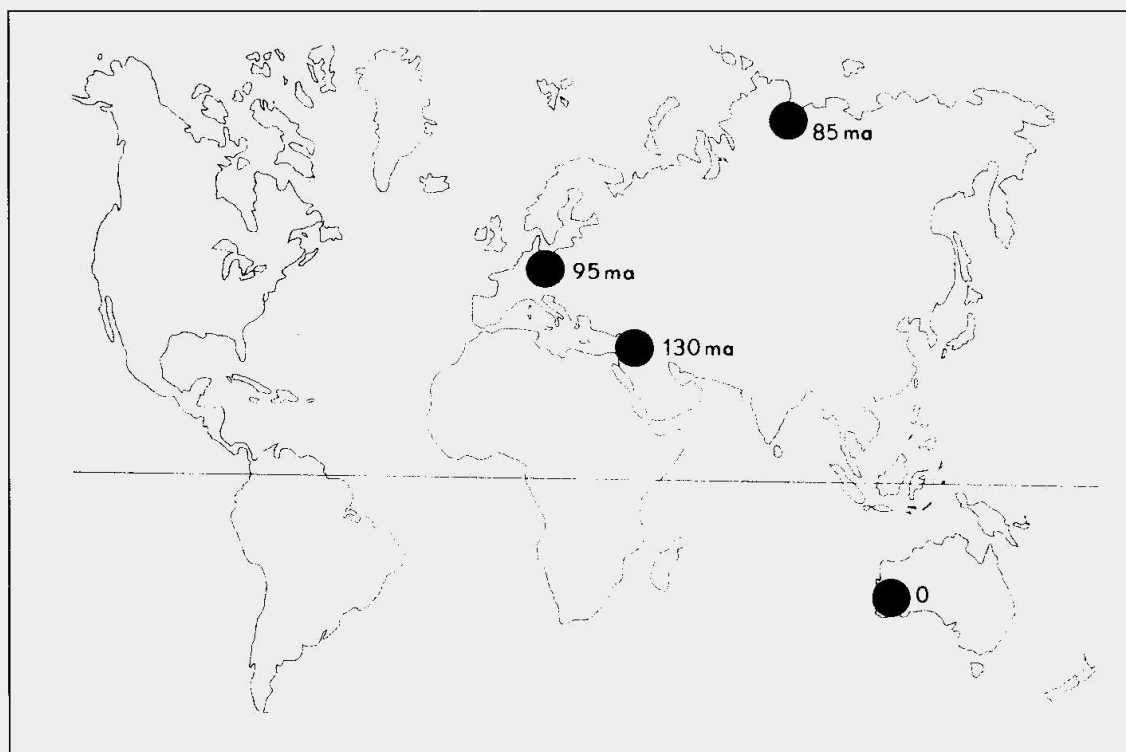


Fig. 5: Distribution of fossil and extant species of *Austroconops*. Abbr. ma = million years ago.

***Archiaustroconops* gen. nov.**Type-species *Archiaustroconops ceratiformis* spec. nov., present designation.

**Diagnosis:** only fossil Lower Cretaceous genus with transverse vein *r-m* oblique, both first radial cells large, costa long, ending at  $R_3$  in male or prolonged beyond  $R_3$  in female. Two terminal flagellomeres in male elongate with enlarged bases, and subbasal constriction. Palpus 4-segmented. Tergite IX in male genitalia elongated and with apicolateral processes. Tarsal ratio of hind leg distinctly lower than that of fore and mid legs and claws short, equal and simple in both sexes.

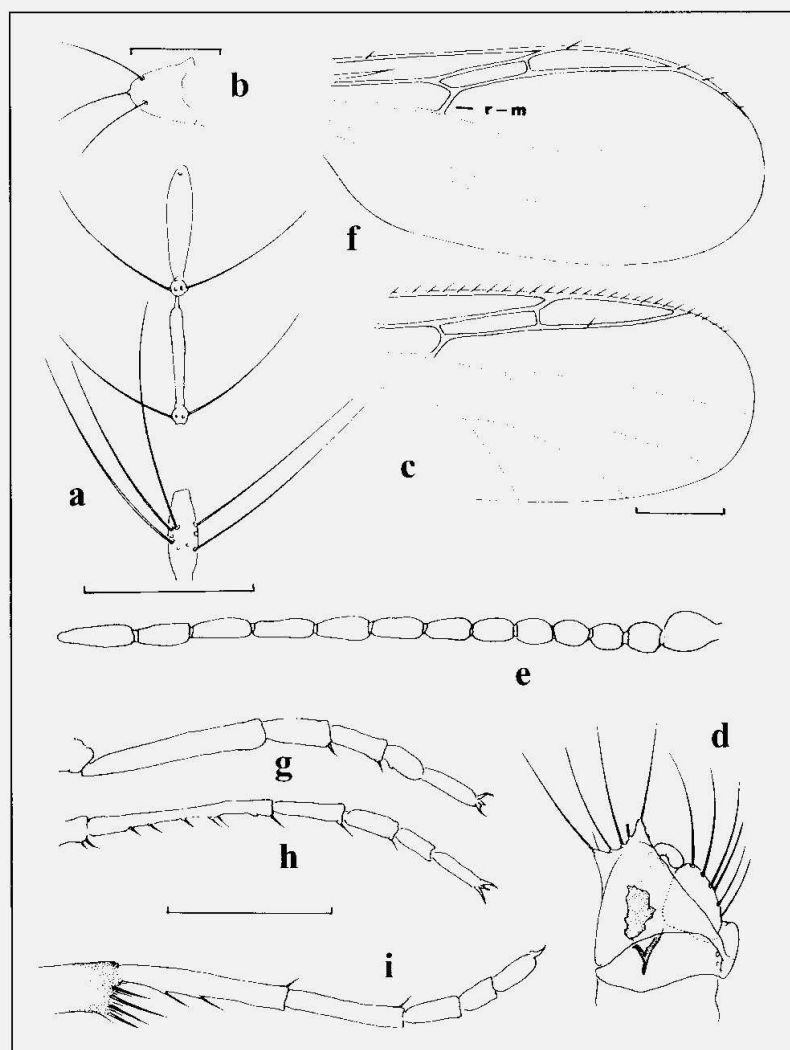
**Discussion**

Males having 2 terminal flagellomeres elongate with a subbasal constriction, parameres orally directed, and both sexes having 4 segmented palpi, tarsal ratio of hind leg distinctly lower than of fore and mid legs are similar to those of *Austroconops*. The wing venation with an oblique transverse vein *r-m* certainly represents a plesiotypic condition.

***Archiaustroconops ceratiformis* spec. nov. (Fig. 6 a-i)**

**Diagnosis:** As for genus.

**Description:** ♂: body slightly deformed in the amber, length 1.1 mm. **Head:** proboscis moderately long, somewhat bent forward. Palpus 4-segmented, barely visible. Flagellum with 13 flagellomeres. First flagellomere with long setae not arranged in ring (whorl) or rings; two terminal flagellomeres elongate, 12th 72  $\mu\text{m}$  and 13th 80  $\mu\text{m}$  long; both terminal flagellomeres with basal enlargement bearing some strong setae (Fig. 6 a). **Thorax:** scutellum with 2 submedian and 1 median marginal strong setae (Fig. 6 b). **Legs** slender. Fore tibia with slender spur, hind tibia probably without distinct tibial spur. Tibial comb barely visible. Fourth tarsomeres cylindrical. Claws short, equal, simple, empodium indistinct. TR(I) 2.3, TR(II) 2.4, TR(III) 1.5. **Wing** length 0.71 mm. Costa ending at  $R_3$ . Both



**Fig. 6 (a-i):** *Archiaustroconops ceratiformis* spec. nov., Lower Cretaceous, holotype male SMNS C2, paratype female SMNS C63/9. - **a:** first and distal male flagellomeres; - **b:** male scutellum; - **c:** male wing; - **d:** laterodorsal aspect of male genitalia; - **e:** female flagellum; - **f:** female wing; - **g-i:** female tarsi of fore, mid and hind legs. Scale bar = 0.1 mm.

first radial cells large, second one slightly larger than first (Fig. 6 c). Vein *r-m* oblique. Media petiolate. Wing membrane covered with distinct microtrichia. **Abdomen** slender. **Genitalia** slightly rotated, slightly broader than preceding segments. Tergite IX much longer than gonocoxite (Fig. 6 d); distinct apicolateral processes clearly visible. Sternite IX barely visible. Gonocoxite short, stout. Gonostylus barely visible, short, slender and simple. Aedeagus not visible. V-like structure, probably parameres, visible between bases of gonocoxites.

♀: body stout, length 1.0 mm. **Head** with eyes narrowly separated. Proboscis moderately long with apex bent anteriorly. Palpus 4-segmented; 3rd palpal segment somewhat swollen, 4th slender. Flagellum (Fig. 6 e) about 390 µm long, composed of 13 flagellomeres. Flagellomeres 2-13 gradually increasing in length. Sensilla on first flagellomere barely visible. **Thorax** robust. Scutellum with 2 submedian and 1 median marginal setae. **Legs** moderately stout. Tibial spur of hind leg weakly developed or absent. Tibial comb composed of 4 spines, with second one longest (Fig. 6 i). Fourth tarsomeres cylindrical, claws small, equal, simple (Fig. 6 g-i). TR(I) 2.5, TR(II) 2.5, TR(III) 1.5. **Wing** length 0.56-0.58 mm. Both radial cells well developed. Costa prolonged beyond  $R_3$  almost to wing apex. Media petiolate. Vein *r-m* transverse (Fig. 5 f). Wing membrane covered with distinct microtrichia, macrotrichia absent. **Abdomen** stout with short cerci.

**Material examined** (1♂, 2♀): Holotype ♂, SMNS C2, Nähe Jezzine, leg. D. SCHLEE 1969, Lebanese amber, Lower Cretaceous (Neocomian). In the same amber piece 1 female of *Austroconops* indet., 1 Psocoptera and 1 Homoptera. Paratype ♀, SMNS C63/9, Nähe Jezzine, leg. D. SCHLEE, 1969, other data as above. Not included in the type series 1♀, SMNS C 20/9, same data as above.

### Genus *Austroconops* WIRTH et LEE, 1958

*Austroconops* WIRTH et LEE, 1958: 337. Type-species *Austroconops mcmillani* WIRTH et LEE, by original designation.

**Diagnosis:** wing with vein *r-m* parallel to  $R_1$ , forming almost straight line with vein  $R_3$ . Male antenna with 2 groups of sensilla trichodea on flagellomere 1, flagellomeres 12 and 13 elongate, each with subbasal constriction. Male genitalia short and broad; 9th tergite short to long, slightly bilobed apically. Gonocoxite short to long. Gonostylus single, variously shaped, with or without subapical spine. Aedeagus short. Parameres fused basally, short.

### Key to fossil and extant species of *Austroconops*

#### Males

- 1 Genitalia elongated; gonocoxite and gonostylus long and slender; gonocoxite bearing long recurved seta ventrally at midlength; gonostylus ventrally swollen at midlength; tergite IX very short (Fig. 8 e) ..... *A. cretaceous spec. nov.* (Lebanese amber)
- Genitalia short and broad; gonocoxite and gonostylus short, gonocoxite without recurved seta at ventral midlength; gonostylus not swollen at midlength; tergite IX long ..... 2
- 2 Claws armed with basal inner tooth (Fig. 10 g) ..... *A. gondwanicus spec. nov.* (Lebanese amber)
- Claws simple ..... 3
- 3 Tibial spur of hind leg indistinct; tarsi armed with strong spine-like setae; outer spine of hind tibial comb stout (Fig. 9 c) ..... *A. fossilis spec. nov.* (Lebanese amber)

- Tibial spur of hind leg long and stout (Fig. 12 c); tarsi unarmed with strong spine-like setae; outer spine of hind tibial comb slender ..... 4
- 4 Hind tibial spur straight; gonostylus tapering to slender apex .....  
..... *A. mcmillani* WIRTH et LEE (extant, Western Australia)
- Hind tibial spur curved; gonostylus broad, not tapering to apex .....  
..... *A. sibiricus* spec. nov. (fossil, Siberian amber)

#### Females

- 1 Third palpal segment slender, 3.0 times as long as greatest width .....  
..... *A. borkenti* SZADZIEWSKI et SCHLÜTER (French amber)
- Third palpal segment stout, 2.2 times as long as greatest width .....  
..... *A. mcmillani* WIRTH et LEE (extant, Western Australia)

#### *Austroconops* indet. (3 ♂♂, 5 ♀♀)

Lower Cretaceous Lebanese amber, Neocomian, near Jezzine, SMNS. C17/15, 1 ♂ [male genitalia as in Fig. 7, costa prolonged beyond tip of  $R_3$ , claws simple, TR(III) 1.6; by mistake this specimen was ground]. C32/17, leg. D. SCHLEE, 1969, 1 ♂ [costa prolonged beyond  $R_3$ , claws simple, flagellum typical of the genus,  $r-m$  parallel to  $R_3$ ]. C53/3, leg. D. SCHLEE, 1969, 1 ♂ [costa ending at  $R_3$ , claws simple, palpus 4-segmented,  $r-m$  forming a straight line with  $R_3$ , genitalia barely visible]. B4/3, leg. D. & H.-B. SCHLEE, 1968, 1 ♀ [eyes narrowly separate, wing venation almost invisible, palpus 4-segmented, 3rd palpal segment probably with deep sensory pit, mandibles not visible, lacinia with distinct spines]. B11/1, leg. D. & H.-B. SCHLEE, 1968, 1 ♀ [wing venation not visible, length 0.59 mm; palpus 4-segmented, claws simple, TR(II) 2.0, TR(III) 1.3]. C2, leg. D. SCHLEE 1969, 1 ♀ together with holotype male of *Archiaustroconops ceratiformis* spec. nov. described above plus 1 Psocoptera and 1 Homoptera [total habitus (Fig. 48 d), wing venation (Fig. 48 e)]. C 25, leg. D. SCHLEE, 1969, 1 ♀ [eyes fused or narrowly separate, wing length 0.58 mm, costa prolonged beyond end of  $R_3$ , vein  $r-m$  forming a straight line with  $R_3$ , legs slender, TR(II) 2.5, TR(III) 1.4]. C 31/42, leg. D. SCHLEE, 1969, 1 ♀ [eyes touching or narrowly separate, proboscis straight, 3rd palpal segment stout, 4th slender, legs, wing and abdomen incomplete; flagellum 284  $\mu$ m long, flagellomeres 2-13 gradually increasing in length].

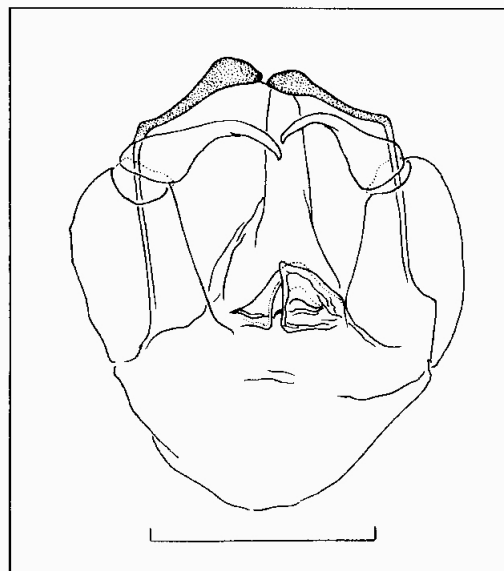


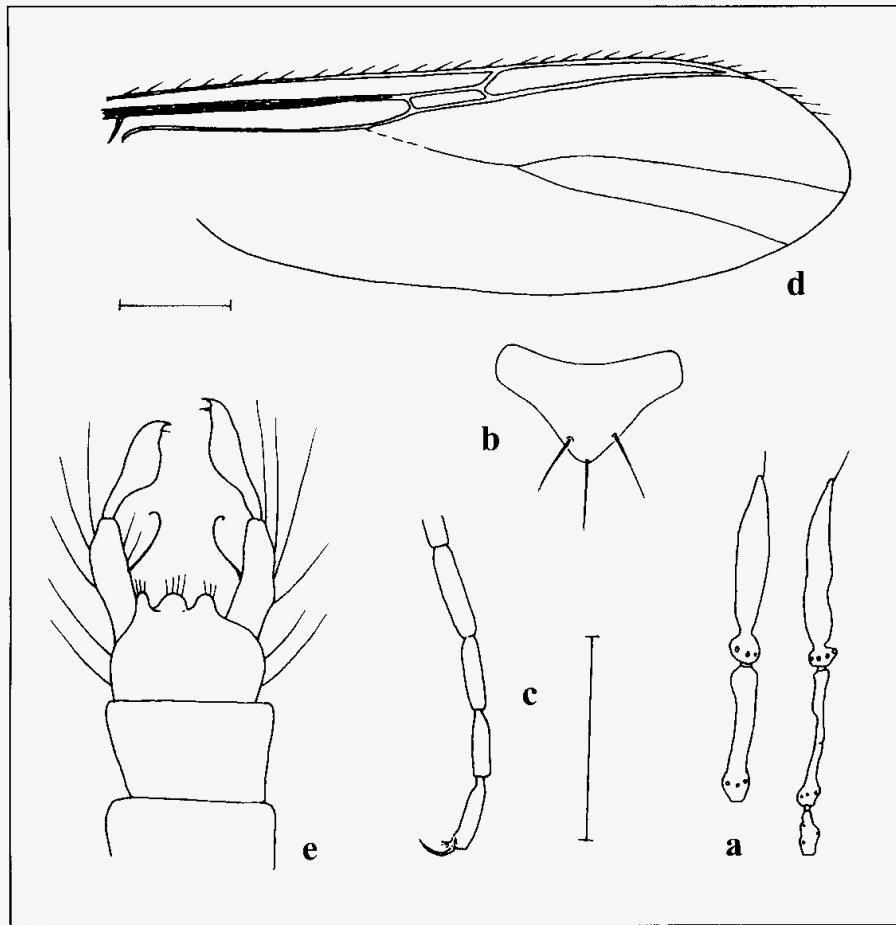
Fig. 7: Male genitalia of *Austroconops* indet., Lower Cretaceous, SMNS C17/15 (ground by mistake). Scale bar = 0.1 mm.

#### *Austroconops cretaceous* spec. nov. (Fig. 8 a-e)

**Diagnosis:** males with simple claws, flagellomere 13, 1.4 times longer than 12, tibial spurs slender, gonostylus long and ventrally swollen at midlength, and gonocoxite slender and bearing long recurved seta ventrally at midlength.



**Description:** ♂: very small slender midge, with total length 1.0 mm. **Head:** flagellum with well developed sparse plume, length about 0.5 mm. Flagellomere 13 with distinct subbasal constriction; flagellomere 12 without distinct subbasal constriction (Fig. 8 a);



length of flagellomere 13, 92  $\mu\text{m}$ ; of 12, 68  $\mu\text{m}$ ; flagellomere 13, 1.35 times longer than 12; flagellomeres 2-11 short, gradually increasing in length. First flagellomere probably with some sensilla trichodea, but only one short seta hardly detectable; single whorl of plume setae. Proboscis very short, bent forward.

**Fig. 8 (a-e):** *Austroconops cretaceous* spec. nov., holotype male, SMNS C31/18. - a: distal flagellomeres; - b: scutellum; - c: tarsomeres 2-5 of mid leg; - d: wing; - e: dorsal aspect of genitalia. Scale bar = 0.1 mm. Scutellum outside of scale.

Palpus 4 segmented. **Thorax** distinctly convex on anterior portion. Scutellum with relatively well pointed apex bearing 2 caudolateral and 1 caudomedian seta (Fig. 8 b). **Legs** slender. Hind tibial spur not visible, absent or indistinct; tibial spur of fore leg slender, straight; tibial comb barely visible, normal. Tarsi without distinct spine-like setae. Fourth tarsomeres cylindrical. Claws elongate, simple, equal (Fig. 8 c). Empodium not discernible. TR(I) 3.1; TR(II) 2.7; TR(III) 1.5. **Wing** length 0.66 mm, CR 0.87. Two radial cells present (Fig. 8 d), second radial cell about 3 times longer than first. Media with short petiole, less than half the length of distal forked portion. Vein *r-m* forming an indistinct angle with radial veins; cubital, anal veins not visible. Wing membrane with distinct microtrichia, macrotrichia absent. **Genitalia** (Fig. 8 e) not inverted or rotated. Sternite IX not visible; tergite IX short and broad, apparently with short, blunt apicolateral processes. Gonocoxite long, slender, with long, stout recurved seta on medial surface at midlength; gonostylus long, swollen on ventral surface at midlength, with pointed apex bearing distinct spine. Parameres and aedeagus not visible.

♀: unknown.

**Material examined** (1 ♂): Holotype ♂, Lebanese amber, Lower Cretaceous, C31/18 (SMNS). In the same amber piece is another male of *Austroconops* described below as *A. gondwanicus* spec. nov., one Mycetophilidae, flagellum of Cecidomyiidae (subfamily Porricondyliinae) and one probable Homoptera.

## Discussion

Male genitalia of the new species are distinctly different from those of extant *A. mcmillani* and fossil *A. sibiricus* described below, the only other species with clearly visible genitalia. In the new species the gonocoxites and gonostyli are long and slender, and the gonocoxites bear unique seta-like inner structure. It has also unusually shaped scutellum which resembles in some way the tripartite scutellum found in the family Culicidae. Within the Ceratopogonidae a similar scutellum shape is found in *Archiaustroconops* described above.

### *Austroconops fossilis* spec. nov. (Fig. 9 a-c)

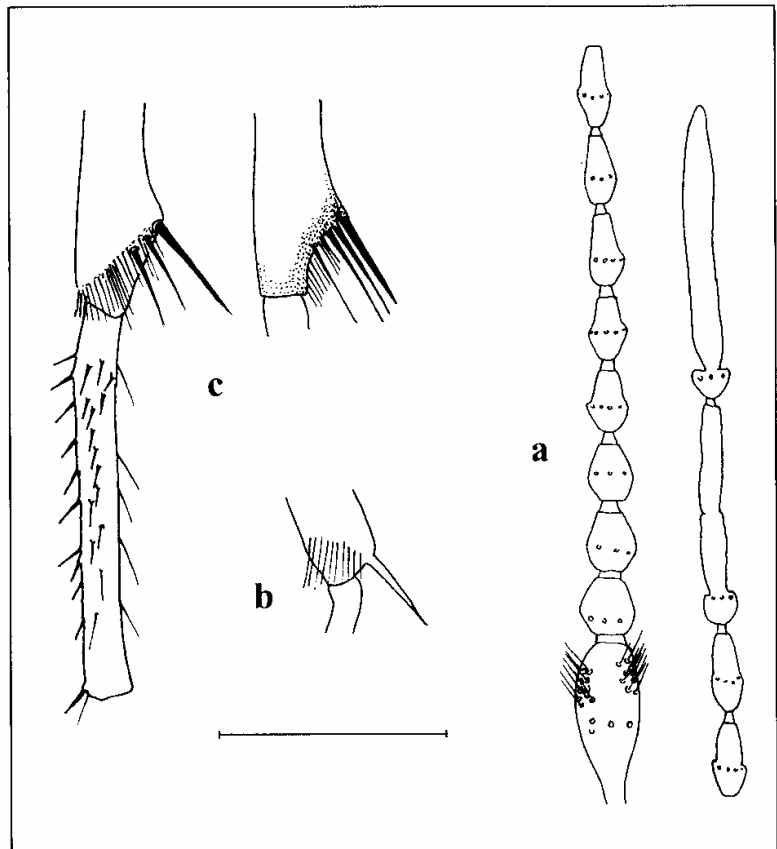
**Diagnosis:** male with simple claws, tarsi with distinct spine-like setae, and tibial comb with strong outer spine, apex of hind tibia without distinct spur.

**Description:** ♂: incomplete specimen lacking wings and genitalia. Total length about 1.3 mm. **Head:** proboscis short, bent forward. Antenna with flagellum 639 µm long, plume sparse; first flagellomere with 2 groups of sensilla trichodea well visible; proximal flagellomeres short, gradually elongated from 2 to 11. Flagellomeres 12 and 13 each with subbasal constriction (Fig. 9a); length of flagellomere 13th, 126 µm; of 12th, 98 µm; terminal flagellomere 1.3 times longer than preceding one. Palpus barely visible. **Legs** slender. Tibial spur of fore leg long, slender and straight (Fig. 9b), tibial spur of hind leg absent or greatly reduced, tibial comb composed of 3-4 spines, outer spine distinctly stouter (Fig. 9c). Tarsomeres of all legs with distinct apical spines, basitarsi with some spine-like setae (Fig. 9c), fourth tarsomeres cylindrical. Claws short, equal, simple, bent at midlength.

♀: unknown.

**Material examined** (1♂): Holotype ♂, Lebanese amber, Lower Cretaceous, SMNS C 31/34.

**Fig. 9 (a-c):** *Austroconops fossilis* spec. nov., holotype male, SMNS C31/34. - a: flagellum; - b: tip of fore tibia; - c: tibial comb and first tarsomere of hind leg. Scale bar = 0.1 mm.

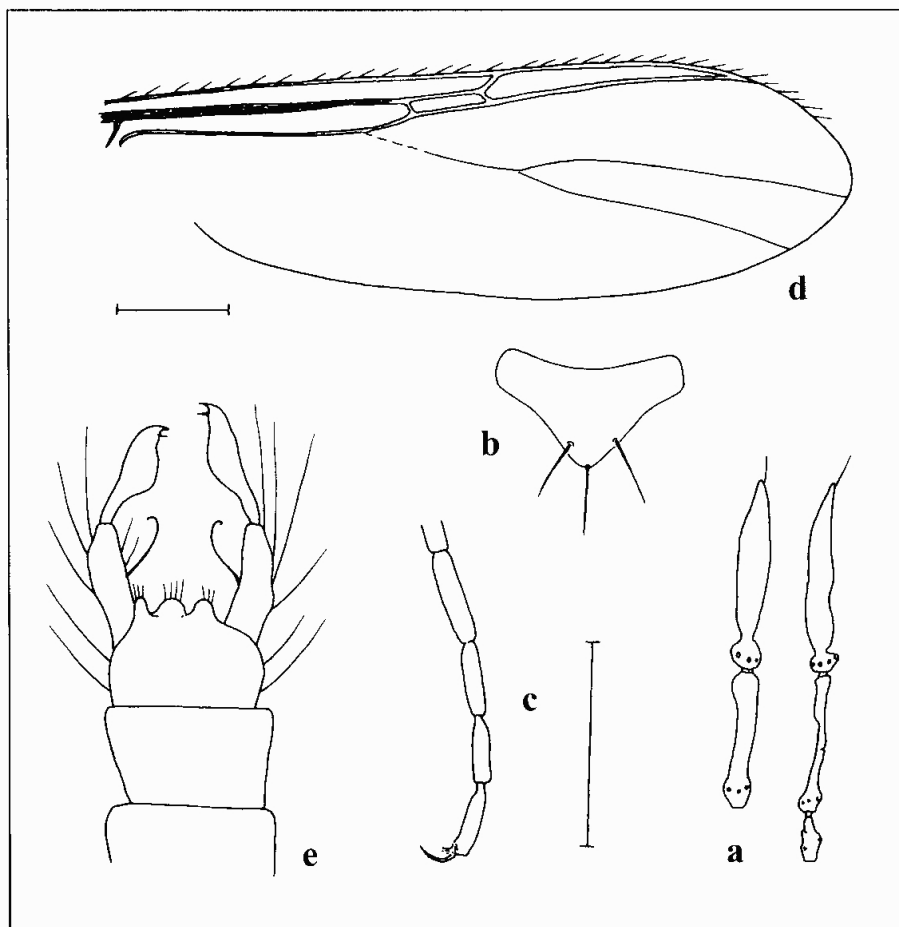


### *Austroconops gondwanicus* spec. nov. (Fig. 10 a-h)

**Diagnosis:** palpi 5-segmented. Male claws with greatly enlarged basal inner tooth.

**Description:** ♂: holotype; incomplete, abdomen and wings absent. Body fragmented in amber. **Head:** proboscis and palpi barely visible. Length of flagellomeres 12 (100 µm), 13 (104 µm); 13 with subbasal constriction, 12 without one (Fig. 10 a). **Thorax:** Pleura

**Description:** ♂: very small slender midge, with total length 1.0 mm. **Head:** flagellum with well developed sparse plume, length about 0.5 mm. Flagellomere 13 with distinct subbasal constriction; flagellomere 12 without distinct subbasal constriction (Fig. 8 a);



length of flagellomere 13, 92  $\mu\text{m}$ ; of 12, 68  $\mu\text{m}$ ; flagellomere 13, 1.35 times longer than 12; flagellomeres 2-11 short, gradually increasing in length. First flagellomere probably with some sensilla trichodea, but only one short seta hardly detectable; single whorl of plume setae. Proboscis very short, bent forward.

**Fig. 8 (a-e):** *Austroconops cretaceous* spec. nov., holotype male, SMNS C31/18. - a: distal flagellomeres; - b: scutellum; - c: tarsomeres 2-5 of mid leg; - d: wing; - e: dorsal aspect of genitalia. Scale bar = 0.1 mm. Scutellum outside of scale.

Palpus 4 segmented. **Thorax** distinctly convex on anterior portion. Scutellum with relatively well pointed apex bearing 2 caudolateral and 1 caudomedian seta (Fig. 8 b). **Legs** slender. Hind tibial spur not visible, absent or indistinct; tibial spur of fore leg slender, straight; tibial comb barely visible, normal. Tarsi without distinct spine-like setae. Fourth tarsomeres cylindrical. Claws elongate, simple, equal (Fig. 8 c). Empodium not discernible. TR(I) 3.1; TR(II) 2.7; TR(III) 1.5. **Wing** length 0.66 mm, CR 0.87. Two radial cells present (Fig. 8 d), second radial cell about 3 times longer than first. Media with short petiole, less than half the length of distal forked portion. Vein *r-m* forming an indistinct angle with radial veins; cubital, anal veins not visible. Wing membrane with distinct microtrichia, macrotrichia absent. **Genitalia** (Fig. 8 e) not inverted or rotated. Sternite IX not visible; tergite IX short and broad, apparently with short, blunt apicolateral processes. Gonocoxite long, slender, with long, stout recurved seta on medial surface at midlength; gonostylus long, swollen on ventral surface at midlength, with pointed apex bearing distinct spine. Parameres and aedeagus not visible.

♀: unknown.

**Material examined** (1♂): Holotype ♂, Lebanese amber, Lower Cretaceous, C31/18 (SMNS). In the same amber piece is another male of *Austroconops* described below as *A. gondwanicus* spec. nov., one Mycetophilidae, flagellum of Cecidomyiidae (subfamily Porricondylinae) and one probable Homoptera.

without setae. Scutellum with rounded apex. **Legs** slender (Fig. 10 d). Tibial spur of fore leg slender, sinuate (Fig. 10 e); tibia of midleg with spur-like seta (Fig. 10 f); hind tibial spur not visible, probably greatly reduced; tibial comb barely visible. Hind basitarsus without palisade setae. Fourth tarsomeres cylindrical. Claws short, equal, each with broad inner tooth (Fig. 10 g). TR(I) 3.0; TR(II) 2.7; TR(III) 1.6.

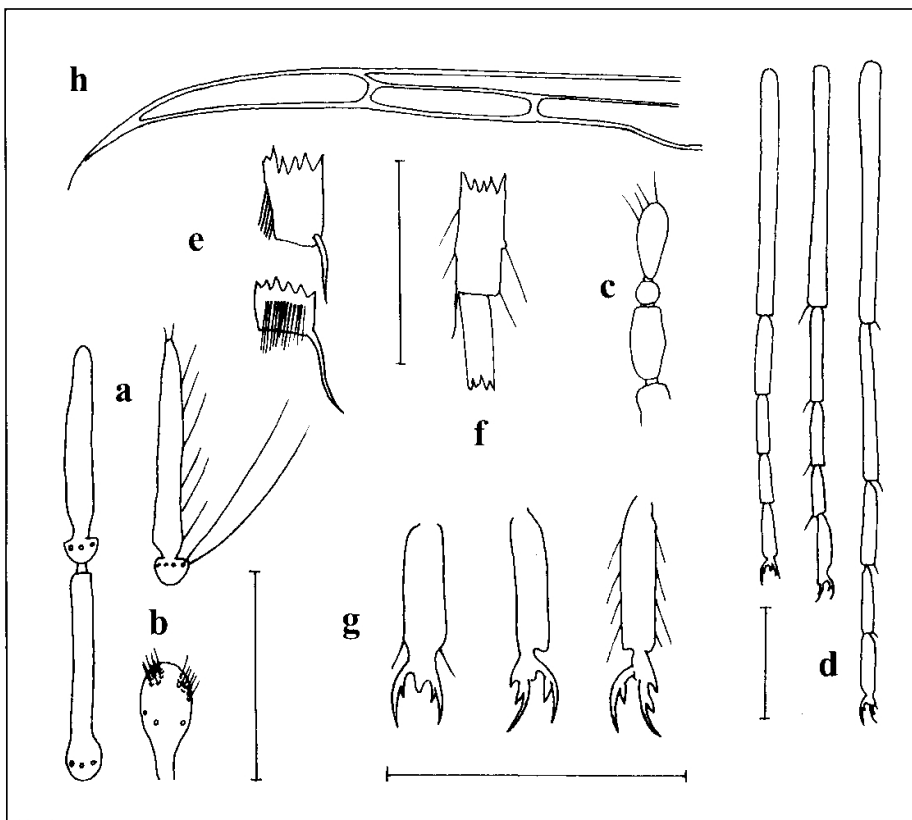
Paratype C 10/25: barely visible. **Head**: Length of flagellum 510  $\mu\text{m}$ ; flagellomere 13 with distinct subbasal constriction, length 116  $\mu\text{m}$ ; first flagellomere with two groups of sensilla trichodea (Fig. 10 b). **Legs**: Claws small, equal, each with basal inner tooth. TR(I) 2.8; TR(III) 1.4. **Genitalia** barely visible; gonocoxite moderately long, rather slender; gonostylus cylindrical.

Paratype C 17/15: specimen fragmented in amber. **Head**: antennae absent. Palpus 5-segmented (Fig. 10 c). 4th palpal segment very short. Anterior anepisternum bare with evenly rounded posterior margin. Mid tibia with distinct spur. TR(I) 2.8, TR(II) 2.7, TR(III) 1.4. **Wings** well preserved, length 0.95 mm. Costa prolonged beyond end of  $R_3$  and reaching almost wing tip (Fig. 10 h). **Genitalia** relatively large. Gonostylus simple, C-shaped.

♀: unknown.

**Material examined** (4 ♂♂): holotype ♂, Lebanese amber, Lower Cretaceous, Neocomian, SMNS C31/18, together with *Austroconops cretaceous* described above. Paratypes: C 10/25, 1 ♂, same data as the holotype; C 17/15, near Jezzine, leg. D. SCHLEE, 1969, 1 ♂ (+ 1 wing of *Lebanconops* indet., ground by mistake). Not included

in the type series 1 ♂, SMNS C 23, near Jezzine, leg. D. SCHLEE, 1969 [barely visible, body length 0.9 mm, claws toothed, terminal flagellomere probably pointed, wing length about 0.75 mm, costa prolonged beyond  $R_3$ ; genitalia barely visible, smaller than in specimens from type series].



**Fig. 10 (a-h):** *Austroconops gondwanicus* spec. nov., male; holotype SMNS C 31/18 (a, d-g), paratype SMNSC 10/25 (b), paratype SMNSC 17/15 (c, h). - a: distal flagellomeres; - b: first and last flagellomere; - c: palpus; - d: tarsi of fore, mid and hind legs; - e: tibial spur of fore legs; - f: apex of mid tibia; - g: claws of fore, mid and hind legs; - h: radial cells. Scale bar = 0.1 mm.

## Discussion

The specimens with toothed claws identified as *A. gondwanicus* may in fact represent more than one species. Palps were visible only in one specimen. I consider the 5-segmented palp as a secondary reversion to the plesiotypic state. A similar reversion was found in the Ceratopogonini genus *Nannohelea* WIRTH et GROGAN, whose extant species have palpal segments 4 and 5 fused while some Tertiary fossil midges have separated segments (SZADZIEWSKI 1988).



*Austroconops sibiricus* spec. nov. (Figs. 11, 12 a-f, 49 g)

**Diagnosis:** males with flagellomere 13 1.8 times longer than flagellomere 12, large tibial spurs, tibial comb with slender spines, simple claws, and stout, short gonostyli.

**Description:** ♂: body length about 1.5 mm. Total habitus as in Figs. 11, 49 g. **Head:** Flagellomeres 12 and 13 with subbasal constriction; length of 12, 72-80 µm; of 13, 132-140 µm. Flagellomere 13, 1.75-1.83 times longer than 12 (Fig. 12 a). Plume well developed. Flagellomeres 2-11 short, gradually elongated. Sensory setae on first flagellomere not visible. Proboscis bent forward, relatively short. Palpus 4-segmented; third palpal segment slender (Fig. 12 b), length 53 or 60 µm, with some sensilla capitata discernible; fourth palpal segment 44-48 µm long. **Thorax:** scutellum bearing 2 lateral and 2 submedian setae; tip rounded. **Legs** slender, unarmed; fore tibia with relatively long, almost straight spur; hind tibia with stout, dis-

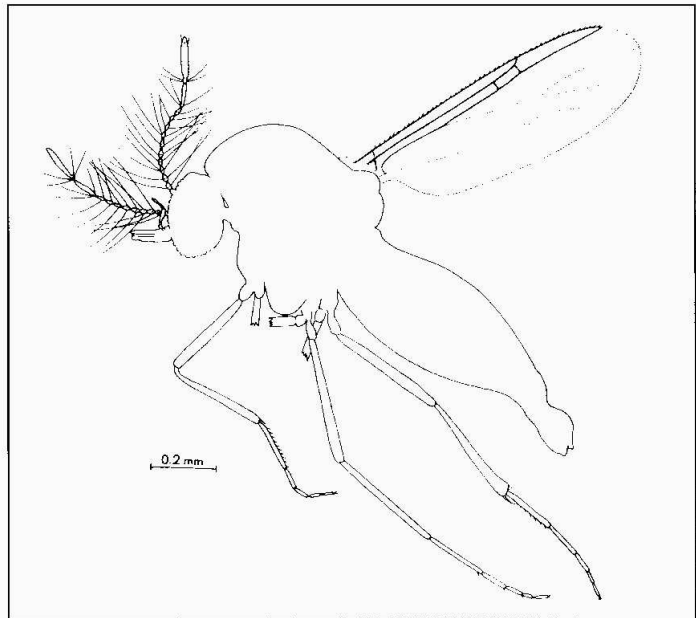


Fig. 11: *Austroconops sibiricus* spec. nov. Lateral aspect of male holotype, PIN 3130/136.

tinctly curved spur (Fig. 12 c); tibial comb composed of 5 indistinct spines. Palisade-like setae present on basitarsus of hind leg; fourth tarsomeres cylindrical. Claws short, equal, simple, sharply bent on distal third (Fig. 12d); tip of each claw bifid. Empodium not discernible. TR(I) 2.1-2.3, TR(II) 2.5, TR(III) 1.5. **Wing** length 0.94 mm, CR about 0.91. Two radial cells present, second about 3 times longer than first (Figs. 11, 12 e). Media faint with long petiole, of almost same length as distal forked portion. Anal angle broad (Fig. 11). Fringe of posterior wing margin composed of simple row of alternating long and short setae. Wing membrane covered with microtrichia, macrotrichia absent. **Genitalia** inverted, broad and short (Fig. 12 f). Sternite IX not visible. Tergite IX relatively long, with almost straight caudal margin and without apicolateral processes. Gonocoxite stout and broad, as long as gonostylus; gonostylus stout, with broad distal portion, armed with apical spine. Aedeagus and parameres not visible.

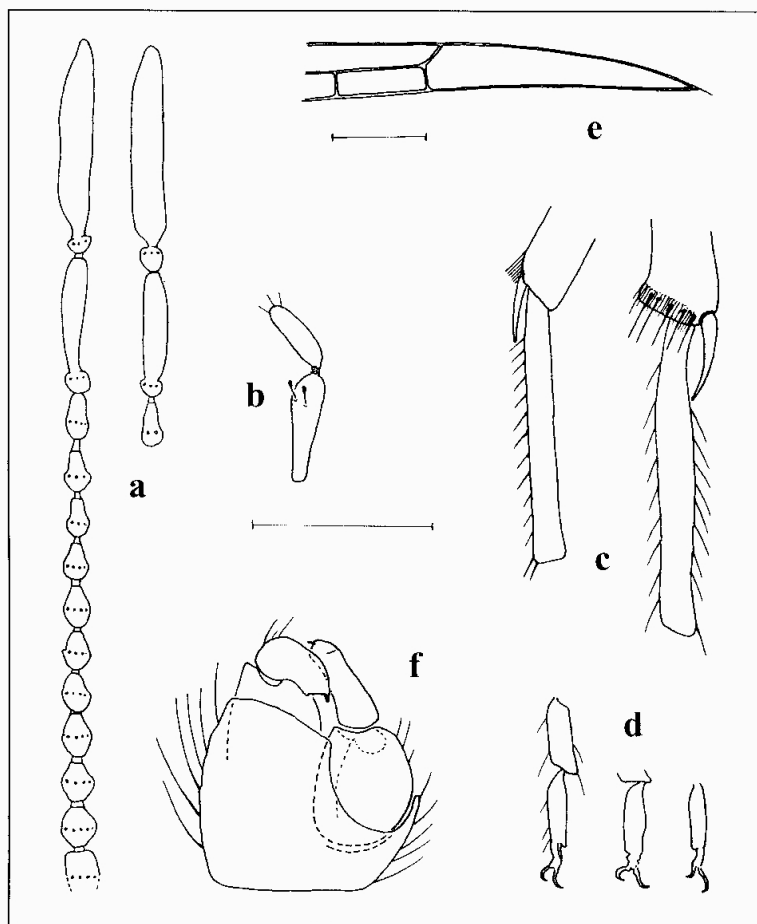
♀: unknown.

**Material examined** (2♂♂): holotype ♂, PIN 3130/136, in almost perfect condition. Paratype ♂, PIN 3311/427, incomplete specimen without wings, genitalia and scutellum. Siberian amber from Taimyr, Upper Cretaceous, Coniacian-Santonian, Yandardakh.

*Lebanoconops* gen. nov.

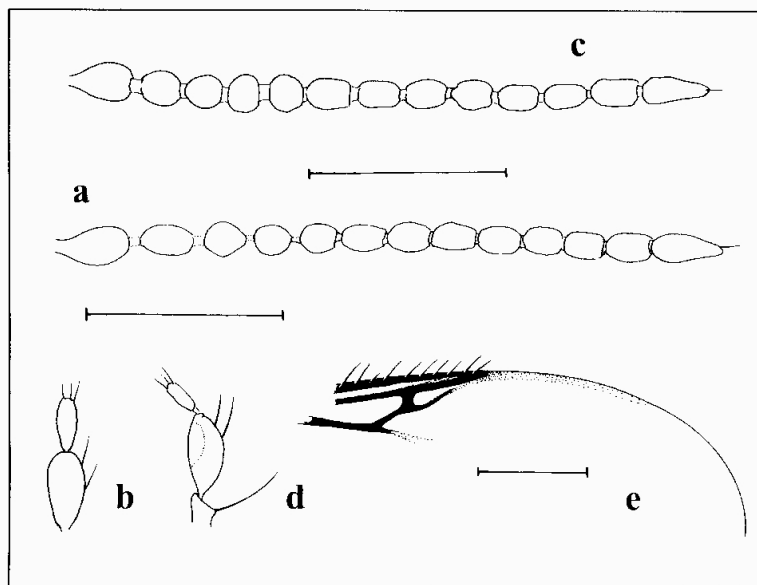
Type-species *Lebanoconops lebanicus* spec. nov., present designation.

**Diagnosis:** very small, with wing length 0.4-0.5 mm. Male antenna with flagellomeres 12 and 13 elongated, both without subbasal constriction, and bearing some sensilla basiconica. First flagellomere with single whorl of plume setae. Female antenna with flagellomeres 2-13 gradually increasing in length (Fig. 13 a, c). Palpus 4 segmented. Proboscis rather



short, straight or slightly bent forward. Radial cell single. Vein *r-m* oblique. Wing membrane without macrotrichia. Scutellum with rounded apex bearing 4 setae on margin. Male claws short, equal, simple. Tibial spurs indistinct. Tarsal ratio of hind leg 1.5-2.7 times lower than of fore and mid legs. TR(I) 2.8-3.3, TR(II) 2.7-3.2, TR(III) 1.2-1.8. Parameres or ventral expansions of gonocoxites very long. Gonostylus simple or double, with or without apical spine.

**Figs. 12 (a-f):** *Austroconops sibiricus* spec. nov., male; holotype PIN 3130/136 (a, c-f), paratype PIN 3311/427 (b). - a: flagellum; - b: palpus; - c: tibial spur of fore (left) and hind leg (right); - d: fifth tarsomeres of hind, mid and fore legs (from left to right); - e: radial cells; - f: laterodorsal aspect of genitalia. Scale bar = 0.1 mm.



**Fig. 13 (a-e):** *Lebanconops* indet., females. - a-b: B4/9; - c-e: C17/10; - a, c: flagellum; - b, d: palpus; - e: radial sector of wing. Scale bar = 0.1 mm.

**Discussion**

It is possible that the structures in the male genitalia which I interpret as parameres actually are ventral projections of the gonocoxites (volsellae) as are present in *Archaeochlus* BRUNDIN (Chironomidae) (CRANSTON et al. 1987). This genus is included in the subfamily Austroconopinae along with *Austroconops* and

*Archiaustroconops* because it has 2 elongate terminal flagellomeres, a 4 segmented palpus in which the 4th and 5th segments are fused, at least in *L. minutus* spec. nov. with a subapical spine on the gonostylus, bare wing membrane, and the tarsal ratio of the hind leg distinctly lower than that of fore and mid legs. Of the characters mentioned above the latter one is unique within the family, where as a rule the tarsal ratio of the hind leg is similar to that of the fore leg, while the tarsal ratio of the middle leg is somewhat higher.

Key to species of *Lebanconops*

## Males

- 1 Paramere-like structures with forked apices. Gonostylus double (Fig. 16) ..... *L. wirthi* spec. nov. (Lebanese amber)  
 - Paramere-like structures with simple apices. Gonostylus single ..... 2  
 2 Gonostylus slender, greatly curved, with basal lobe (Fig. 14 g) ..... *L. lebanicus* spec. nov. (Lebanese amber)  
 - Gonostylus stout, straight, simple (Fig. 15 f) ..... *L. minutus* spec. nov. (Lebanese amber)

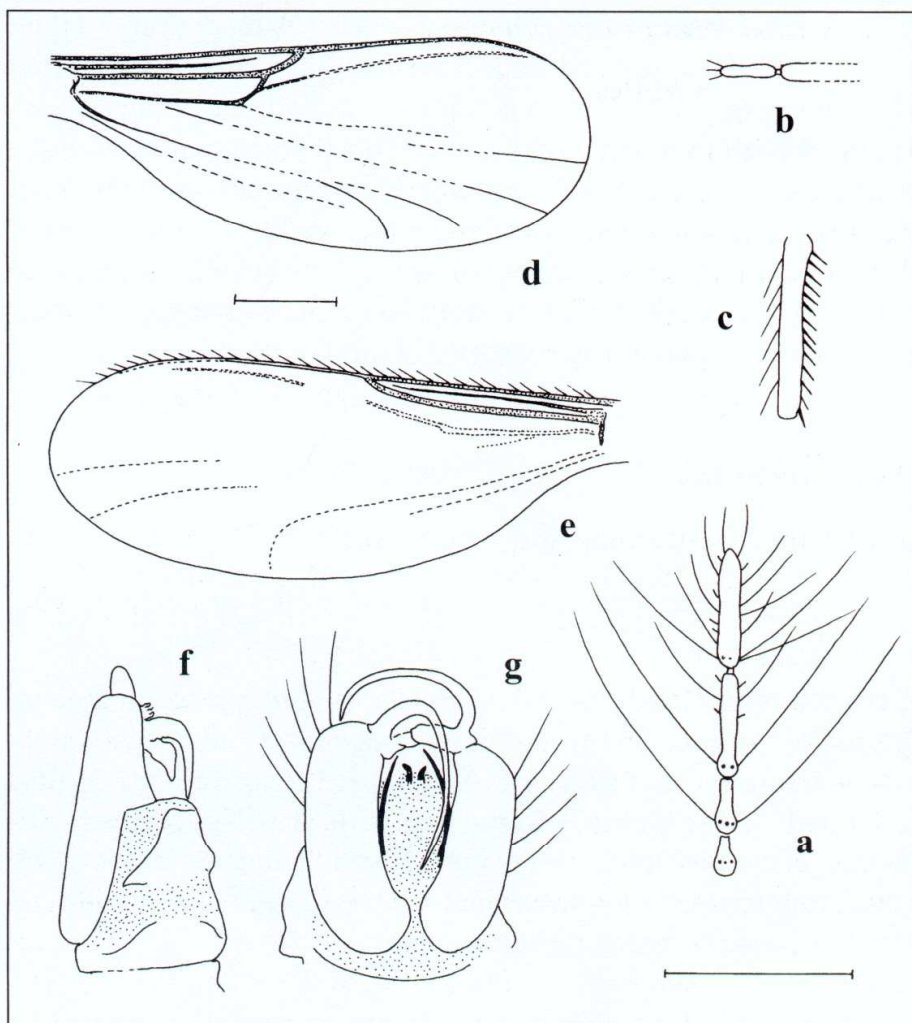
*Lebanconops* indet. (1 wing, 1 ♂, 3 ♀♀)

Lebanese amber, Lower Cretaceous, Neocomian, near Jezzine, SMNS: C 31/73, leg. D. SCHLEE, 1969, 1 ♂ [wing length 0.68 mm; TR(II) 2.7, TR(III) 1.7, + Mycetophilidae]; B 4/9, leg. D. & H.-B, 1968, 1 ♀ [body length 0.6 mm; eyes fused above antennae, flagellum as in Fig. 13 a, proboscis moderately long, 3rd palpal segment stout (Fig. 13 b), legs slender, TR(I) 2.8, TR(II) 2.8, TR(III) 1.7, claws small, simple; costa short, venation as in male of the genus; cerci short, slightly pointed]. C 17/10, leg. D. SCHLEE, 1969, 1 ♀ [eyes touching above antennae, flagellomeres increasing in length from 2 to 13, Fig. 13 c; 3rd palpal segment stout (Fig. 13 d), TR(I) 2.4, TR(II) 2.5, TR(III) 1.7; wing length 0.48 mm, *r-m* transverse,  $R_{2+3}$  greatly reduced, costa probably prolonged beyond  $R_1$  (Fig. 13 e), C 17/15, 1 wing at *Austroconops gondwanicus* spec. nov. described above [wing length 0.54 mm, ground by mistake]. C 22/24/34, leg. D. SCHLEE, 1969, 1 ♀ [body length 0.8 mm, eyes narrowly separate or touching, flagellomeres increasing in length from 2nd to 13th, clypeus greatly convex, proboscis relatively long, palpus 4-segmented, scutellum with at least 4 marginal setae, TR(I) 2.5, TR(III) 1.8, vein  $R_{2+3}$  almost totally reduced, cerci short].

*Lebanconops lebanicus* spec. nov. (Fig. 14 a-g)

**Diagnosis:** characteristic in having long, slender, curved gonostyli with broad basal inner lobe.

**Description:** ♂: total length 0.8 mm. Proboscis moderately long and probably straight. Flagellum composed of 13 units, terminal two elongate (Fig. 14 a). First and second flagellomeres with at least 4 sensilla trichodea. Flagellomeres 2-11 short, gradually increasing in length from 2 to 11. Length of flagellomere 13, 64  $\mu\text{m}$ , of 12, 52  $\mu\text{m}$ . Both elongated flagellomeres with some sensilla basiconica and without subbasal constriction; 13 cylindrical, 12 with somewhat enlarged base. Plume sparse, perpendicular to long axis of flagellum, first flagellomere with single whorl of plume setae. Palpus slender, 4-segmented (Fig. 14 b). **Thorax:** scutellum with rounded margin bearing 2 submedian and 2 lateral setae. **Legs** slender. Tibial spurs not discernable. Tibial comb composed of at least 4 spines of similar length. Hind basitarsus with palisade-like setae (Fig. 14 c). Fourth tarsomeres cylindrical. Claws equal, simple. TR(I) about 3.3, TR(II) about 3.2, TR(III) 1.8. **Wing** length 0.54 mm. CR 0.88. Distal portion of costa and vein  $R_{2+3}$  barely visible (Fig. 14 d, e). Radial cell probably single and long, closed or open. Transverse vein *r-m* oblique. Media petiolate, barely visible. Wing membrane without macrotrichia. **Genitalia** (Fig. 14 f, g) rotated 90°. Sternite IX barely visible. Tergite IX short with blunt apex. Cerci not discernable. Gonocoxites long and slender, with bases close each other.



Gonostylus long, slender, distinctly curved, with broad basal lobe. Two widely separated, pointing rods, probably parameres, extending almost to apex of gonocoxite. Aedeagus not visible.

♀: unknown.

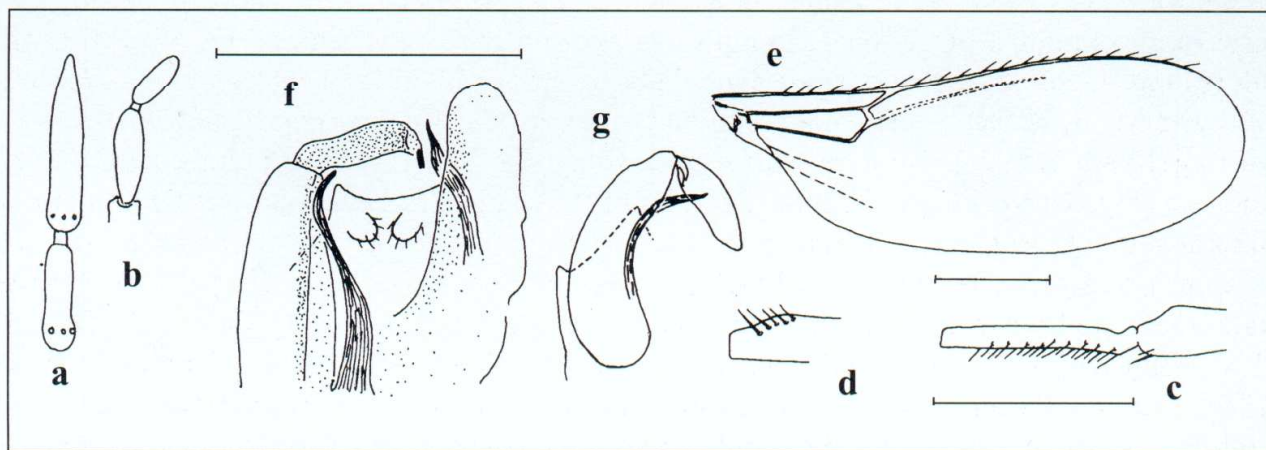
**Material examined** (1♂): Holotype ♂, Lebanese amber, Lower Cretaceous, SMNS C31/2. In the amber with the holotype are 2 large, barely visible nematocerous Diptera which look like Mycetophiloidea.

**Fig. 14 (a-g):** *Lebanconops lebanicus* spec. nov., holotype male SMNS C31/2. - a: distal flagellomeres; - b: palpus; - c: hind basitarsus; - d-e: wing venation; - f: lateral aspect of genitalia; - g: ventral aspect of genitalia. Scale bar = 0.1 mm.

*Lebanconops minutus* spec. nov. (Fig. 15 a-g)

**Diagnosis:** with single, straight, stout gonostylus and large stout paramere-like structures in male genitalia.

**Description:** ♂: total length 0.8 mm. **Head:** proboscis well elongated, bent forward. Flagellomere 13, 56 µm long, cylindrical, without subbasal constriction; flagellomere 12 about 32 µm long (Fig. 15 a). Palpus 4-segmented. Third palpal segment about 32 µm



**Fig. 15 (a-f):** *Lebanconops minutus* spec. nov., holotype male SMNS C32/67. - a: distal flagellomeres; - b: palpus; - c: hind basitarsus; - d: tibial comb; - e: wing; - f-g: genitalia. Scale bar = 0.1 mm.



long, sensilla not visible (Fig. 15 b). **Thorax** barely visible. **Legs** with slender tarsi. Tibial spurs probably indistinct. Tibial comb composed of 4-5 short spines (Fig. 15 d). Hind basitarsus with palisade-like setae (Fig. 15 c). Fourth tarsomeres cylindrical. Claws equal, simple. TR(II) 2.7, TR(III) 1.4. **Wing** length about 0.47 mm. Transverse vein *r-m* oblique (Fig. 15 e). Other veins barely visible. CR probably about 0.80. Wing membrane without macrotrichia. **Genitalia** (Fig. 15 f, g) rotated 90°. Sternite IX not visible. Tergite IX short and broad, with blunt, short apicolateral processes. Gonocoxite long and slender. Gonostylus stout with blunt tip, armed with apical tooth. Aedeagus not visible. Rod-like "parameres" with evenly pointed, converging apices extending to apex of gonocoxite.

♀: unknown.

**Material examined** (1 ♂): Holotype ♂, Lebanese amber, Lower Cretaceous, SMNS C32/67.

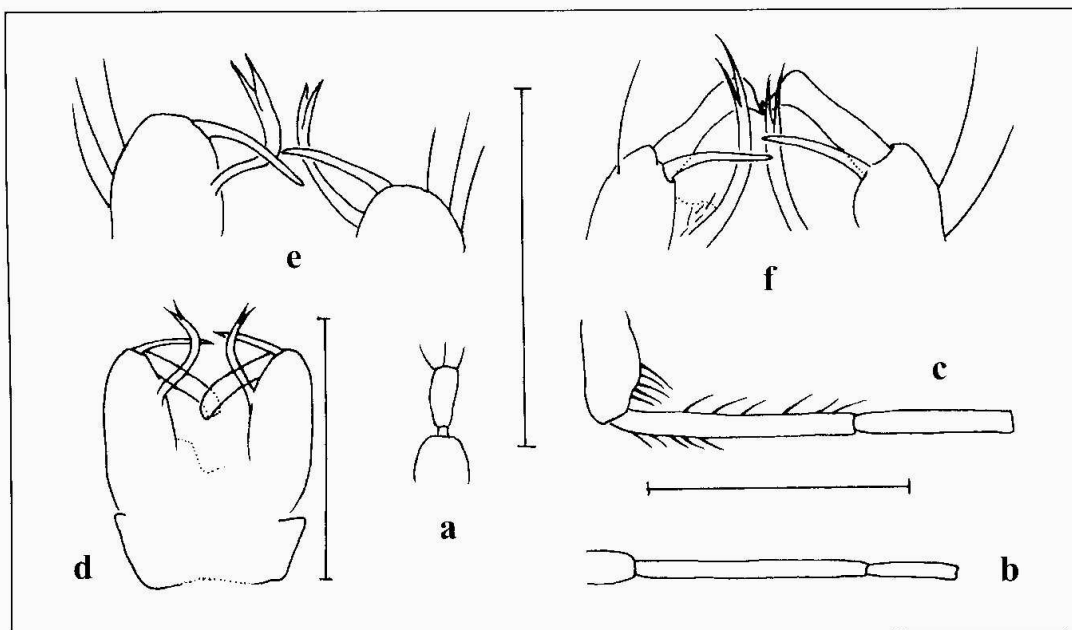
*Lebanoconops wirthi* spec. nov. (Fig. 16 a-f)

**Diagnosis:** very small biting midges with males having paramere-like projections with forked apices; gonostylus double with ventral branch slender and dorsal stout.

**Description :** ♂: body length 0.8 mm. **Head:** flagellum barely visible, probably 2 distal flagellomeres elongate. Palpus 4 segmented, with 3rd palpal segment stout and 4th slender and short (Fig. 16 a). **Legs** incomplete. TR(II) 2.8, TR(III) 1.7 (Fig. 16 b, c). **Wings** barely visible, distorted, typical of the genus. **Genitalia** (Fig. 16 d-f) rotated 90°. Gonocoxite moderately slender. Gonostylus double; ventral branch slender, smooth, tapering to pointed apex; dorsal branch stout, with somewhat beak-like apex. Two paramere-like projections long, sinuous, each with distinctly forked apex.

♀: unknown.

**Material examined** (1 ♂): Holotype ♂, SMNS C25/13, Nähe Jezzine, leg. D. SCHLEE, 1969. Lebanese amber. Lower Cretaceous.



**Fig. 16 (a-f):** *Lebanoconops wirthi* spec. nov., holotype male SMNS C25/13. - a: palpus; - b: proximal tarsomeres of middle leg; - c: proximal tarsomeres of hind leg; - d: ventral aspect of genitalia; - e-f: oblique aspects of genitalia. Scale bar = 0.1 mm.

### Genus *Minyohelea* BORKENT, 1995

*Minyohelea* BORKENT, 1995: 68, type-species *Minyohelea pumilis* BORKENT, 1995, original designation. Campanian amber of Canada.

**Diagnosis:** only 13th male flagellomere elongate, female cerci short, wing membrane bare and venation greatly reduced. Lower to Upper Cretaceous.

#### Discussion

BORKENT (1995) did not measure tarsal ratios for biting midges in his monograph. As a result the TR of the type-species of the genus is unknown. According to the original illustration it has distinctly longer second hind leg tarsomere than that of the mid leg which may suggest that the TR of the hind leg is lower than of other legs as in other genera included in Austroconopinae. BORKENT (l.c.) stated that the gonostylus of *Minyohelea pumilis* was slender, slightly curved, while in his fig. 13 b the gonostyli are stout and straight. This genus is very similar or closely related to *Lebanconops*. Both sexes of *Minyohelea* may be distinguished from Leptoconopinae and *Lebanconops* by the presence of a greatly reduced last (4th) palpal segment, low tarsal ratio of hind leg, and males by their single elongated 13th flagellomere and long paramere-like structures.

BORKENT (l.c.) placed *Minyohelea* in the tribe Ceratopogonini because he found that *M. pumilis* had a pair of thick setae on trochanter of middle leg which in Austroconopinae and Leptoconopinae are thin (BORKENT et al. 1987). In my studies on fossil biting midges I treat some characters which are barely visible or may be changed due to preservation (artefacts) in amber with a great caution. I doubt that it is possible to observe in a very small midge embedded in amber the difference between thin and thicker minute setae on trochanter. Moreover, males of Ceratopogonini have 3 distal flagellomeres elongated while *Minyohelea* has only one.

#### Key to species of *Minyohelea*

##### Males

- 1 Paramere-like structures curved, longer than gonocoxites. Costa prolonged beyond  $R_1$  (Fig. 17 d, e) ..... *M. schleei* spec. nov. (Lebanese amber)  
 - Paramere-like structures straight, shorter than gonocoxites. Costa ending at  $R_1$ .  
 ..... *M. pumilis* BORKENT (Canadian amber)

#### *Minyohelea schleei* spec. nov. (Figs. 17 a-e, 48 c)

**Diagnosis:** male characteristic in having only terminal flagellomere elongate and long gonocoxal (or parameres) projections with simple apices. Lower Cretaceous.

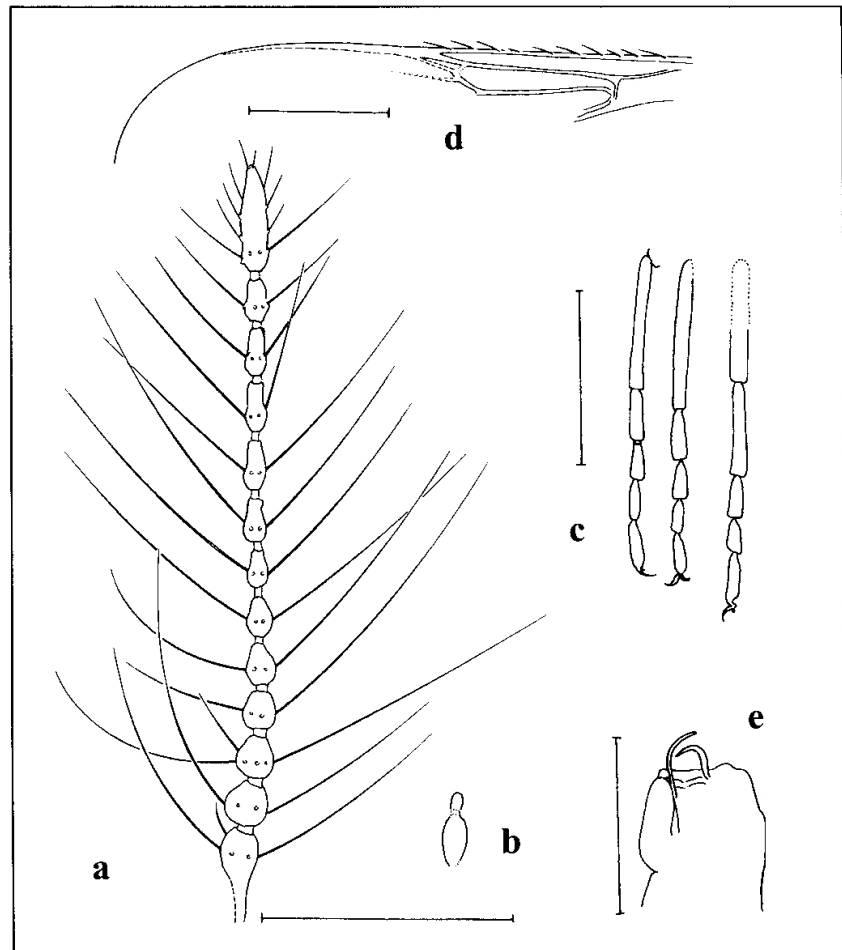
**Description:** ♂: total habitus as in Fig. 48 c. Body length 0.7 mm. **Head:** antenna with 13 flagellomeres; terminal flagellomere elongate, cylindrical with evenly pointed apex; plume sparse (Fig. 17 a). Eyes separated. Palpus 4-segmented, with very short apical segment (Fig. 17 b). **Legs** slender. Fore tibia with spine-like spur. Fourth tarsomeres cylindrical, claws simple (Fig. 17 c). TR(I) 2.8, TR(II) 3.2, TR(III) 1.2. **Wing** length 0.38 mm. Veins barely visible (Fig. 17 d). Costa likely prolonged beyond vein  $R_{2+3}$ . **Genitalia** (Fig. 17 e) rotated 90°, barely visible. Sternite IX probably horse-shoe like. Gonocoxite cylindrical and relatively long. Gonostylus not clearly visible, simple or double. Rod-like structures (parameres or gonocoxal projections) long, curved, with simple, evenly pointed apices.



Anteriorly directed V-shaped sclerotization located between bases of gonocoxites barely visible (parameres or gonocoxal apodemes?).

♀: unknown.

**Material examined** (1 ♂): Holotype ♂, SMNS C32/74, Nähe Jezzine, leg. D. SCHLEE, 1969. Lebanese amber. Lower Cretaceous.



**Fig. 17 (a-e):** *Minyohelea schleei* spec. nov., holotype male SMNS C32/74. - a: flagellum; - b: palpus; - c: tarsi of fore, mid and hind legs; - d: - wing venation; - e: genitalia. Scale bar = 0.1 mm.

### Subfamily Leptoconopinae NoÉ, 1907

The subfamily includes only the single extant genus *Leptoconops* divided into several subgenera (SZADZIEWSKI 1988). A few fossil *Leptoconops* are recorded from Upper Eocene Baltic amber (SZADZIEWSKI 1988), Palaeocene amber of Sakhalin (SZADZIEWSKI 1990b), Campanian amber of Canada (BORKENT 1995), Coniacian-Santonian amber of Taimyr (KALUGINA 1977), as well as from Cenomanian amber of Taimyr (KALUGINA 1991) and of France (SZADZIEWSKI & SCHLÜTER 1992). All previously described and named fossil species seem to belong to the subgenus *Leptoconops* s.str. GROGAN et SZADZIEWSKI (1988) suggested that *Simulidium priscum* WESTWOOD, 1854 from the Purbeck Formation of the Lower Cretaceous of England appeared to be a species of *Leptoconops*. Actually that fossil fly named by WESTWOOD (1854) is a member of the family Rhagionidae (ROSS et. al. in press).

*Fossileptoconops lebanicus* spec. nov. described below from Lower Cretaceous Lebanese amber is the oldest record of the subfamily and seems to represent the basal lineage of the subfamily.

### Genus *Fossileptoconops* gen. nov.

Type-species *Fossileptoconops lebanicus* spec. nov., present designation.

**Diagnosis:** costa much prolonged beyond end of radial vein  $R_3$ ,  $R_2$  not clearly visible, absent or present,  $R_3$  well developed and ending in costa distinctly away of  $R_1$ . Female antenna composed of 13 flagellomeres, cerci relatively short. Lower Cretaceous biting midge.

## Discussion

This is the first record of the oldest member of the subfamily. It represents the oldest known lineage and may be recognized as a prototype for the subfamily as the female has antennae with 13 flagellomeres (plesiotypic for the family), costa prolonged beyond tip of vein  $R_3$ , and veins  $R_1$  and  $R_3$  are well separated. These plesiomorphies are unique within known extant and fossil Leptoconopinae. The short cerci (even shorter than now described) are known only in the subgenera *Brachyconops* and *Styloconops* of *Leptoconops*. However, the latter character state evolved in these subgenera secondarily, as other characters are typical of the genus *Leptoconops*. The shape of tergite X with U-shape caudomedian excavation of *Fossileptoconops*, unique for the Leptoconopinae, leave doubts that this genus actually is a member of that subfamily (Fig. 19 c).

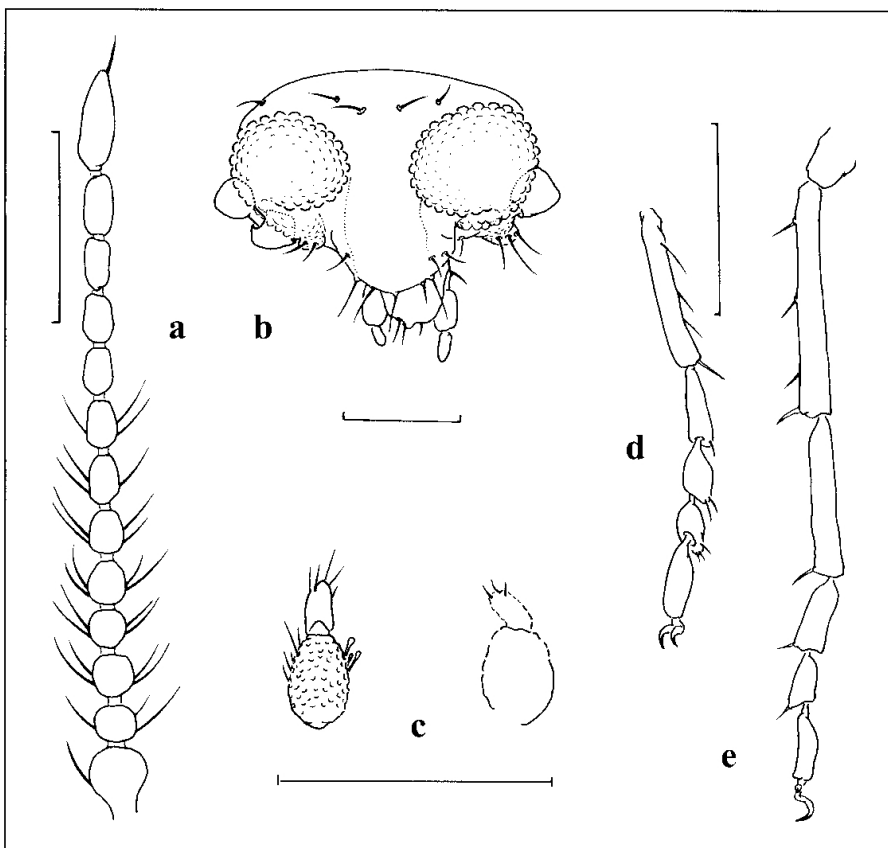
### *Fossileptoconops lebanicus* spec. nov. (Figs. 18 a-e, 19 a-c)

**Diagnosis:** as for the genus.

**Description:** ♂: unknown.

♀: body length 1.1 mm. **Head:** eyes widely separate; clypeus highly convex (Fig. 18 b). Flagellum composed of 13 flagellomeres (Fig. 18 a); length 376  $\mu\text{m}$ ; flagellomeres gradually increasing in length from 2nd to 13th. Proboscis short; 3rd palpal segment stout and short, probably completely covered with sensilla (Fig. 18 c); 4th palpal segment short, slender. **Thorax:** scutellum with broadly rounded caudal margin. Fourth tarsomeres subcylindrical to cylindrical (Fig. 18 d, e). Claws simple. TR(I) 2.2, TR(II) 1.4, TR(III) 1.8. Wing length 0.63 mm; basal portion almost invisible. Transverse vein  $r-m$  probably absent.  $R_1$  clearly visible, ending in costa at about half of wing length. Vein  $R_3$  ending in costa distal to  $R_1$ ; vein  $R_2$  probably absent (?). Costal vein prolonged beyond  $R_3$  almost to half way of

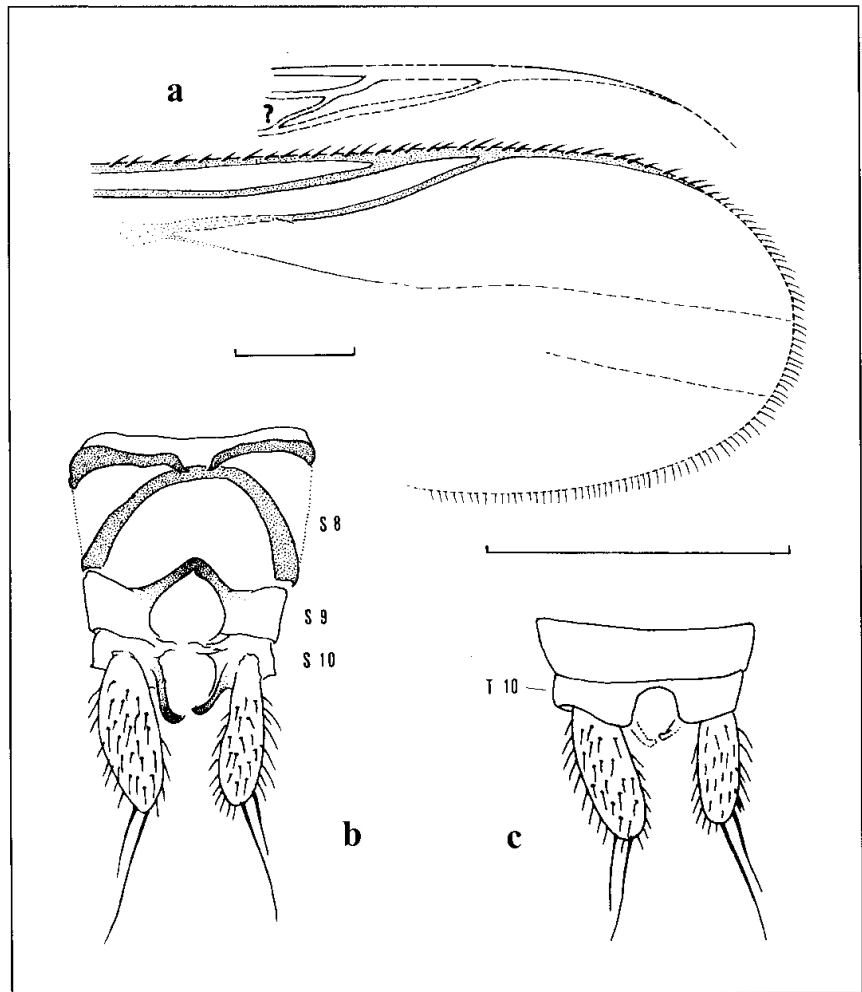
distance between wing tip and  $R_3$  (Fig. 19 a). Genitalia typical of subfamily (Fig. 19 b, c). Sternite VIII with anterolateral sclerites (gonocoxsternapodemes VIII) and broad arch-shaped, heavily sclerotized caudal notch.



**Fig. 18 (a-e):** *Fossileptoconops lebanicus* spec. nov., holotype female SMNS C32/5, - a: flagellum; - b: frontal aspect of head; - c: palpi; - d: tarsus of fore leg; - e: tarsus of mid leg. Scale bar = 0.1 mm.

Sternite IX with strong rami. Sternite X separated into 2 lateral projections directed caudally. Tergite X with U-shaped dorsal caudomedian notch. Cerci relatively short, only slightly elongated.

**Material examined** (1 ♀): Holotype ♀, Lower Cretaceous Lebanese amber, SMNS C32/5, Libanon-Bernstein, Unterkreide (Neocom), Nähe Jezzine, leg. D. SCHLEE 1969. In the same amber piece one incomplete male of Chironomidae is present.



**Fig. 19 (a-c):** *Fossileptoconops lebanicus* spec. nov., holotype female SMNS C32/5, - **a**: wing venation; - **b**: ventral aspect of genitalia; - **c**: dorsal aspect of terminalia. Scale bar = 0.1 mm. Abbr. S - sternite, T - tergite.

**Genus *Leptoconops* SKUSE, 1899**

**Diagnosis:** see SZADZIEWSKI (1988) and BORKENT (1995).

**Key to fossil named species of *Leptoconops***

**Females**

- 1 Claws with long basal tooth (Fig. 22 d, e) ..... *L. sibiricus* spec. nov. (Siberian amber)
- Claws simple ..... **3**
- 3 Flagellomere 11 cylindrical ..... *L. succineus* SZADZIEWSKI (Baltic amber)
- Flagellomere 11 spherical ..... *L. boreus* KALUGINA (Siberian amber, Cenomanian)
- ..... *L. primaevus* BORKENT (Canadian amber, Campanian)

***Leptoconops* indetermined (1 ♂)**

1 ♂, PIN 3130/129 (+ ?*Atriculicoides* 1 ♀), Yandardakh, Taimyr, Coniacian-Santonian, Upper Cretaceous. Barely preserved. Body length 1.3 mm. Wing length 0.95 mm, 13th flagellomere 204 µm long. Tibial comb composed of 4 spines. Genitalia not rotated; tergite IX with distinct apicolateral processes; gonostylus with strong ventral spines. This male may be included in the subgenus *Leptoconops* s. str. or *Proleptoconops* CLASTRIER.

***Leptoconops boreus* KALUGINA, 1991** (Fig. 20 a, b)

*Leptoconops boreus* KALUGINA, 1991: 71 (♀, Siberian amber, Nizhnyaya Agapa, Upper Cenomanian).

**Diagnosis:** female claws simple. Flagellum composed of 12 flagellomeres. Terminal flagellomere short (72 µm), 3.6 times longer than spherical preceding one (Fig. 20 a). Proboscis short. 3rd palpal segment stout and long (Fig. 20 b). Wing length 0.82 mm.

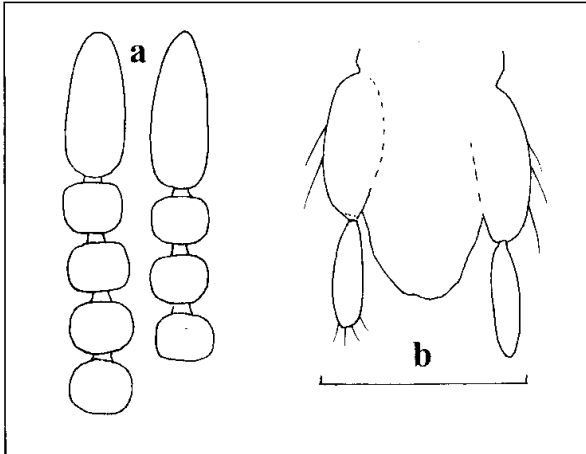
Cerci elongate. Body length 1.6 mm. Male unknown.

**Material examined** (1♀): Holotype ♀, PIN 3426/119 (in the same amber piece is a poorly preserved tip of the abdomen and legs of an undetermined male which probably is a member of the genus *Leptoconops*).

**Discussion**

KALUGINA (1991) placed this species within the subgenus *Leptoconops* s. str.

**Fig. 20 (a-b):** *Leptoconops boreus* KALUGINA, holotype female PIN 3426/119, - a: distal flagellomeres; - b: proboscis. Scale bar = 0.1 mm.

***Leptoconops sibiricus* spec. nov.** (Figs. 21 a-h, 22 a-e)

**Diagnosis:** Upper Cretaceous fossil species with female claws armed with basal tooth.

**Description:** ♂: total length 1.4 mm. **Head:** eyes widely separated. Flagellum composed of 13 flagellomeres (Fig. 21 a); plume well developed. Terminal flagellomere 152 µm long, 5.2 times longer than preceding one. Proboscis short (Fig. 21 b); 3rd palpal segment slender, 40 µm long, sensorium superficial; 4th palpal segment as long as 3rd (Fig. 21 c). **Thorax:** scutum dotted, covered with short setae. **Legs** slender. Tibial comb with at least 3 spines (Fig. 21 d). Claws similar on all legs, equal, simple, one claw with long basal seta (Fig. 21 e). TR(I) 1.7, TR(II) 1.8, TR(III) 1.6. **Wing** length 0.74 mm. Costal vein very short, ending at radial veins (Fig. 21 f). Microtrichia distinct, macrotrichia absent. **Genitalia** (Fig. 21 g, h) not rotated or inverted, barely visible. Gonostylus enlarged on basal half, with inner process on midlength and with subapical tooth. Tergite IX probably shorter than gonocoxite; apicolateral processes not visible.

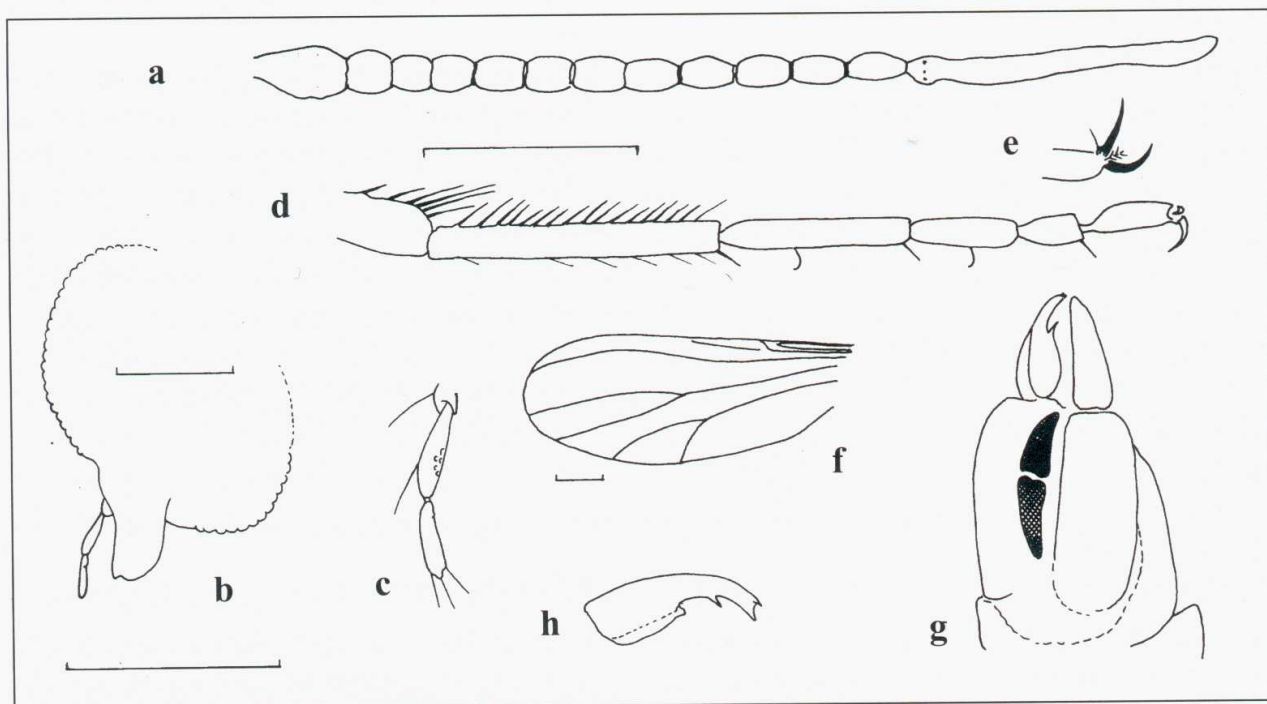
♀: apex of **abdomen** not preserved. **Head:** eyes widely separate. Antenna with 12 flagellomeres, length about 400 µm. Flagellomeres 2-11 slightly increasing in length from spherical to slightly cylindrical (Fig. 22 a). Terminal, 12th flagellomere cylindrical, 108 µm long, 4 times longer than preceding one. Proboscis short (Fig. 22 b), mandible armed with small teeth. 3rd palpal segment short, 42 µm; 4th palpal segment slender and long (Fig. 22 c). **Thorax:** katepisternum with 2 setae visible. Tibial spur of fore leg distinct, serrated. All claws with long basal tooth (Fig. 22 d, e). TR(I) 2.2, TR(II) 2.0, TR(III) 2.1. **Wing** length 0.765 mm, CR 0.43.

**Material examined** (1♂, 1♀): Holotype ♀, PIN 3311/416, Siberian amber, Upper Cretaceous, Coniacian-Santonian, Yantardakh. 1♂ not included in type series, same data, PIN 3311/374.

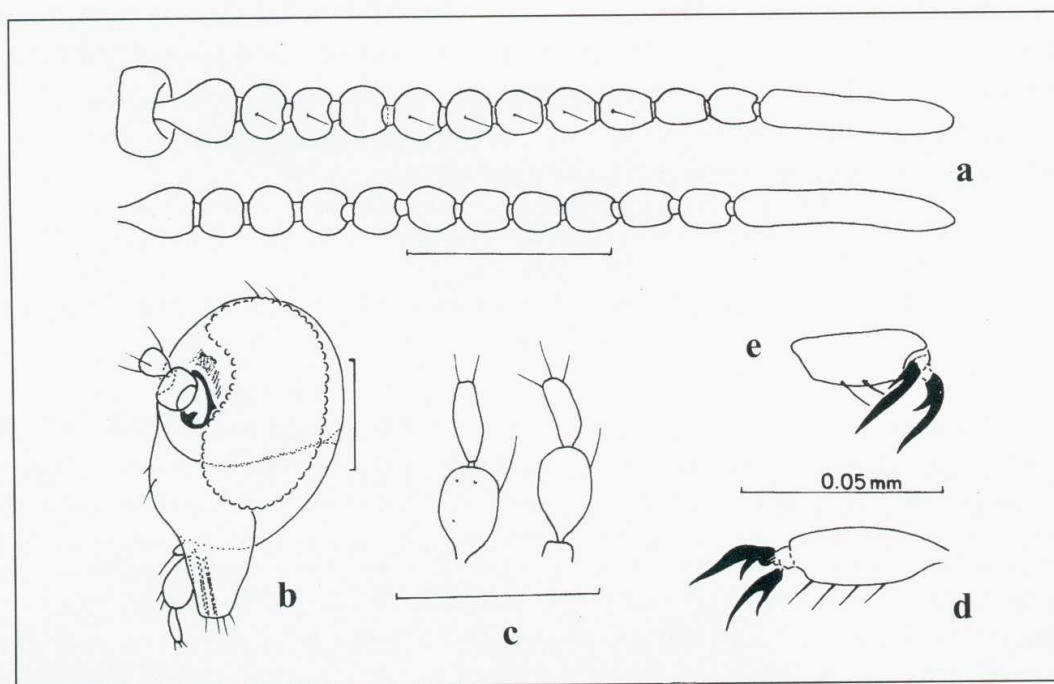
**Discussion**

The new species may be included in the sub-genus *Leptoconops* s. str. or *Proleptoconops* CLASTRIER. The female is very similar to that of extant *Leptoconops* (*Proleptoconops*) *avi-arum* GUTSEVICH known from Algeria and Tad-zhikistan in the shape of antennae, pro-

boscis, palpi and claws (GUTSEVICH 1973, CLASTRIER & BOORMAN 1987, personal observations). This does not mean that they are conspecific since within *Leptoconops* there are known other species with similar claws and details of their external and internal morphology, invisible in amber, are used in their determination. It is possible that the male associated with the holotype female does not belong to the same species, it was therefore not recognized as a paratype.



**Fig. 21 (a-h):** *Leptoconops sibiricus* spec. nov., male PIN 3311/374, - a: flagellum; - b: head; - c: palpus; - d: tarsus of hind leg; - e: claws; - f: wing (drawn by KALUGINA); - g: lateroventral aspect of genitalia; - h: gonostylus. Scale bar = 0.1 mm.



**Fig. 22 (a-e):** *Leptoconops sibiricus* spec. nov., holotype female PIN 3311/416, - a: flagellum; - b: head; - c: palpi; - d: claws of fore leg; - e: claws of mid leg. Scale bar = 0.1 mm.

## Subfamily Forcipomyiinae LENZ, 1934

### Tribe Atriculicoidini, tribus nov.

**Diagnosis:** first flagellomere of male with 2 verticils of plume setae and distal 4 flagellomeres elongate, female mandible armed with small teeth, eyes in both sexes broadly fused above antennae, female claws with distinctly bifid apices, wing membrane covered with numerous macrotrichia. Parameres fused into single structure. Larvae unknown.

#### Discussion

I adopt here REMM's (1975) proposition to treat Forcipomyiini and Dasyheleini as tribes within the subfamily Forcipomyiinae. *Atriculicoides* may form the ancestral stock for both extant tribes (SZADZIEWSKI 1990 a) and may be treated as a sister group of Forcipomyiini (*Forcipomyia* and *Atrichopogon*) plus Dasyheleini (including the single genus *Dasyhelea*) (Fig. 47) as proposed by BORKENT (1995), or all three tribes may form unresolved trichotomy. Cladistically this genus is paraphyletic as tribes Forcipomyiini and Dasyheleini certainly evolved from different species of *Atriculicoides* at the end of Upper Cretaceous or during Tertiary. Moreover, no synapomorphy can be presently proposed for Atriculicoidini. In order to fulfil the criteria of monophyly Forcipomyiini + Dasyheleini, a reduction of second whorl of plume setae on first male flagellomere could be used. However, this is a weak synapomorphy because it would happen independently within Dasyheleini and Forcipomyiini as a simple reversion to the plesiomorphic condition present in basal lineage of the Ceratopogonidae.

SZADZIEWSKI & SCHLÜTER (1992) and BORKENT (1995) suggested that females of *Atriculicoides* were parasites on vertebrates and fed on their blood. At present I suggest they were parasites on insects like extant *Atrichopogon* and some *Forcipomyia*. That type of feeding may be evidenced by female claws which resemble claws of *Atrichopogon*, the genus including mostly insect parasites. They are distinctly forked apically and the inner tooth is shorter than the outer. However, slightly forked apices of female claws are broadly distributed within the family Ceratopogonidae (*Culicoides nubeculosus* (MEIGEN), *Ceratopogon* spec., *Palpomyia* spec., etc.). Generally all males have forked tips, sometimes difficult to observe. In some *Forcipomyia* for example of the subgenus *Lasiohelea* KIEFFER feeding on vertebrates female claws have single apices.

### Genus *Atriculicoides* REMM, 1976

*Atriculicoides* REMM, 1976: 108, type-species *Atriculicoides macrophthalmus* REMM, 1976 (Coniacian-Santonian, Siberian amber, Yantardakh, Upper Cretaceous);  
SZADZIEWSKI 1990a: 131 (Upper Cretaceous amber of France and Siberia);  
SZADZIEWSKI & SCHLÜTER 1992: 74 (Cenomanian amber of France);  
BORKENT 1995: 36 (Campanian amber of Canada).

**Diagnosis:** wing membrane covered with dense macrotrichia, female mandible with small teeth, female claws with distinctly bifid apices, male flagellum with 4 distal flagellomeres elongate and first flagellomere with 2 rings of plume setae, sensilla coeloconica with ring setae absent, paramere single, dissymmetrically located between bases of gonocoxites.

#### Discussion

This fossil genus is known only from the Upper Cretaceous. It could serve as an indicator fossil for this time period.

It seems that parameres in male genitalia of the genus are asymmetrically located between bases of gonocoxites as in most extant *Dasyhelea* KIEFFER.



Key to named species of *Atriculicoides*

- 1 Palpus 4-segmented .....  
 ..... *A. incompletus* SZADZIEWSKI et SCHLÜTER (Cenomanian amber of France)  
 - Palpus 5-segmented ..... 2  
 2 Gonostylus with enlarged apex .....  
 ..... *A. cenomanensis* SZADZIEWSKI et SCHLÜTER (Cenomanian amber of France)  
 - Gonostylus gradually tapering to slender apex, or almost cylindrical ..... 3  
 3 Male frons with large tubercle (Fig. 25 a, b) .....  
 ..... *A. dasyheleis* spec. nov. (Siberian amber)  
 - Male frons flat, without tubercle ..... 4  
 4 3rd and 4th palpal segments with capitate sensilla (Fig. 27 a) .....  
 ..... *A. taimyricus* spec. nov. (Siberian amber)  
 - Only 3rd palpal segment with capitate sensilla ..... 5  
 5 Paramere with expanded T-shape apex (Fig. 26 e) .....  
 ..... *A. sibiricus* spec. nov. (Siberian amber)  
 - Paramere with pointed apex ..... 6  
 6 Gonostylus cylindrical, slightly sinuous. Aedeagus short. Paramere with straight apical portion directed ventrally (Fig. 23 g-i) .....  
 ..... *A. macrophthalmus* REMM (Siberian amber)  
 - Gonostylus tapering to apex, slightly curved or straight. Aedeagus long. Paramere with recurved or greatly curved apical portion .....  
 ..... *A. globosus* (BOESEL) (Canadian amber)

*Atriculicoides* indet.

(4♀♀ Upper Cenomanian; 3♂♂ and 16♀♀ from Yantardakh, Coniacian-Santonian). Siberian amber: Upper Cretaceous: Upper Cenomanian, Nizhnyaya Agapa in Taimyr: (4♀♀) PIN: 3426/241 1♀, (3rd palpal segment with distinct sensory field, wing as in fig. 49 b); 3426/242, 1♀ (wings incomplete); 3426/243, 1♀ (+1♂ Chironomidae); 3426/244, 1♀, fig. 49 a. All females with claws bifid apically, and 5-segmented palp. Coniacian-Santonian, Yantardakh in Taimyr: 3♂♂, 16♀♀: PIN: 3130/129, 1♀ at *Leptoconops* indet. 3311/412, 2♀♀, (claws bifid); 3311/413, 1♀ (claws bifid apically, eyes touching above antennae, sternite VIII with broad and shallow caudomedian excavation, body incomplete, wings absent); 3311/414, 1♀ (mandible with small teeth); 3311/418, 1♂ (+ Chironomidae 1♀, barely visible); 3311/420, 1♂ (barely visible, genitalia incomplete); 3311/421, 1♂ (incomplete); 3311/422, 1♀ (barely visible); 3311/425, 1♀ (barely preserved, 3rd palpal segment with sensory depression; anterior anepisternum with rounded posterior margin); 3311/430, 1♀ (sensilla grouped on inner surface of 3rd palpal segment); 3311/431, 1♀ (barely preserved); 3311/433, 1♀ (3rd palpal segment with deep sensory depression); 3311/434, 1♀ (barely preserved); 3311/436, 1♀ (barely preserved); 3311/438, 1♀ (claws with deeply bifid apices, complex setae on tarsomeres clearly visible); 3311/no number among specimens numbered 412-441, 1♀ (+ small Hymenoptera); no number, 2 amber pieces, 2♀♀.

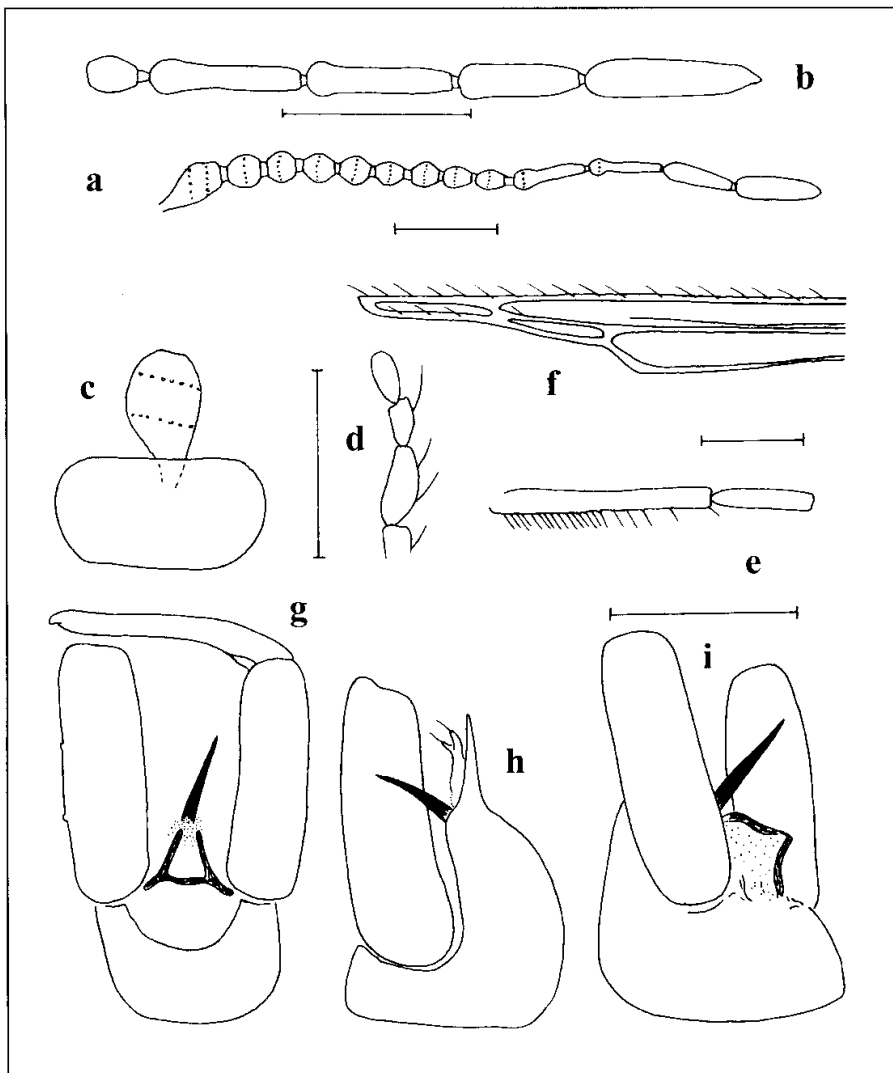
***Atriculicoides macrophthalmus* REMM, 1976** (Figs. 23 a-i, 24 a-h, 48 f, 50 e)

*Atriculicoides macrophthalmus* REMM, 1976: 108 (♂, ♀, Siberian amber, Yantardakh, Coniacian-Santonian, Upper Cretaceous).

*Atriculicoides squamiciliatus* REMM, 1976: 110 (♂, ♀, Siberian amber, Yantardakh, Coniacian-Santonian, Upper Cretaceous), **syn. nov.**

**Diagnosis:** palpus 5-segmented, sensilla scattered on whole surface of 3rd palpal segment. Male with short tergite IX bearing long and stout apicolateral processes lacking apical seta; paramere single, sword-like, with straight weakly pointed and ventrally directed apex.

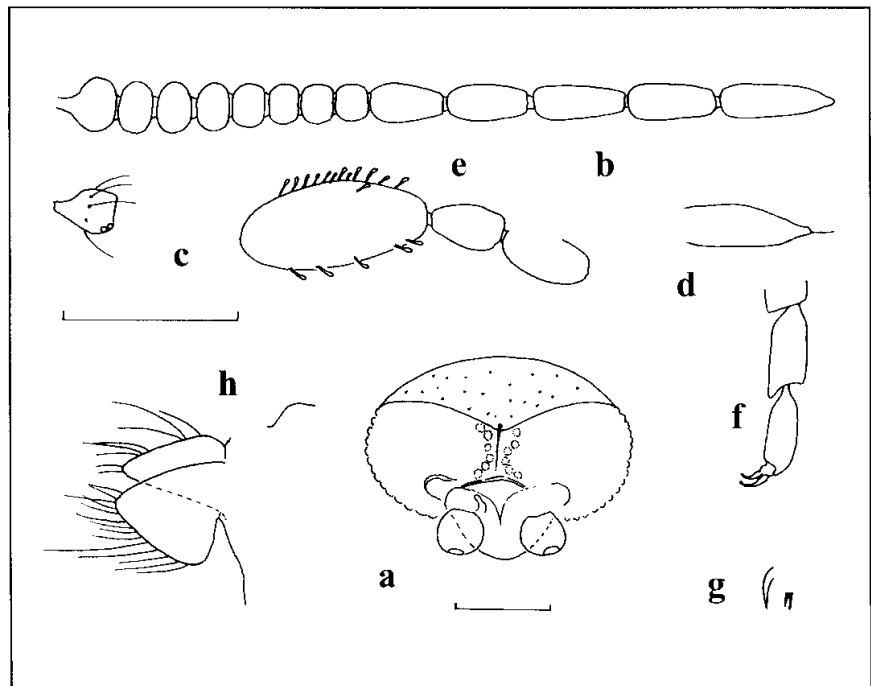
**Description:** ♂: total habitus as in fig. 48 f. Body length 1.4-1.5 mm. **Head:** Frons without distinct tubercle. Flagellum length 612-698 µm; distal 4 flagellomeres elongate (Fig. 23 a); pedicel short and broad, 1st flagellomere with 2 verticils of plume setae (Fig. 23 c); apex of terminal flagellomere pointed (Fig. 23 b). Palpus 5-segmented (Fig. 23 d); 3rd palpal segment with sensilla scattered over surface. **Legs** typical of genus. Tibial spur of fore leg long. Hind basitarsus with dense row of setae on proximal half (Fig. 23 e). TR(I) 2.4, TR(II) 2.3, TR(III) 2.3. **Wing** length 0.81-0.87 mm, CR 0.71-0.74. Both first radial cells of almost same length (Fig. 23 f). Wing membrane covered with rows of long macrotrichia; basal radial cell with or without some macrotrichia. **Genitalia** (Fig. 23 g-i) slightly rotated. Sternite IX with relatively small caudomedian excavation. Tergite IX short with long and stout apicolateral processes lacking apical seta. Cerci distinct, placed medially, not shifted laterally. Gonocoxite rather stout. Gonostylus long, cylindrical, slightly sinuous. Aedeagus H-shaped, with low basal arch and short basal arms; caudolateral arms long, blunt. Paramere single, stout, long, with evenly pointed almost straight distal portion directed caudoventrally.



**Fig. 23 (a-i):** *Atriculicoides macrophthalmus* REMM, paratype males PIN 3311/398 (b-i), 3311/399 (a); - a: flagellum; - b: distal flagellomeres; - c: first flagellomere; - d: palpus; - e: proximal tarsomeres of hind leg; - f: radial cells; - g-i: ventral and lateral aspects of genitalia. Scale bar = 0.1 mm.

♀: total habitus as in Fig. 50 e. Body length 1.0-1.4 mm. **Head:** eyes fused above antennae (Fig. 24 a). Flagellum with proximal flagellomeres transverse to spherical, distal 5 elongate (Fig. 24 b). Some pits present on proximal flagellomere (Fig. 24 c), probably bases of sensilla trichodea. Palpus 5-segmented; 3rd palpal segment stout and covered with numerous sensilla capitata (Fig. 24 e). Proboscis moderately long with convex clypeus. **Thorax:** scutellum with numerous bristles. Katepisternum bare. **Legs:** tibial comb composed of 7 spines. Claws with distinctly bifid apices (Fig. 24 g). TR(I) 2.3, TR(II) 2.1-2.3, TR(III) 2.1. Hind leg as in Fig. 49 c. **Wing** length 0.73-1.04 mm, CR 0.69-0.72. Wing membrane including basal radial cell densely covered with macrotrichia. **Abdomen:** cerci short and broad, in lateral view triangular (Fig. 24 h).

**Fig. 24 (a-g):** *Atriculicoides macrophthalmus* REMM, female, paratype 3311/376 (b), paratype 3311/378 (f), paratype 3311/379 (d, e), paratypes 3311/388-389 (g), paratype 3311/381 (a, c) paratype 3311/390-391 (h); - **a:** dorsal aspect of head; - **b:** flagellum; - **c:** first flagellomere; - **d:** terminal flagellomere; - **e:** palpus; - **f:** distal tarsomeres of hind leg; - **g:** claws; - **h:** lateral aspect of cerci. Scale bar = 0.1 mm. Fig. g out of scale.



**Material examined** (4♂♂, 19♀♀): Types of *Atriculicoides macrophthalmus*: Holotype ♀ not examined. Paratypes: 3311/398, 1♂; 3311/399, 1♂, 1♀; 3311/376, 1♀; 3311/378, 1♀; 3311/379, 1♀; 3311/380, 2♀♀ (only 1 female designated as paratype); 3311/381, 1♀; 3311/382, 1♀; 3311/383, 1♀; 3311/384-386, 3♀♀ in single amber piece; 3311/388-389, 2♀♀; 3311/390-391, 2♀♀ (+1♂ not indicated as paratype, barely visible); 3311/392, 1♀; 3311/393, 1♀.

Paratypes of *A. macrophthalmus* which belong to other species of *Atriculicoides*: 3311/377, 1♂ (3rd palpal segment with distinct sensory pit, as *Atriculicoides* spec. indet. described below); 3311/387, 1♀, claws with enlarged base and long tooth at midlength, Fig. 28 f.

Types of *Atriculicoides squamiciliatus*: PIN: Holotype female and paratypes females not available for present study. Paratypes: 3311/400, 1♂ (actually is *Culicoides sphenostylus* REMM, see below); 3311/402, 1♂ is *Atriculicoides* with well defined sensory pit and is associated with a female with a similar character state as the species indetermined, see below).

Other materials: PIN 3311/423, 1♂; 3311/390-391, 1♂ not indicated as a paratype among female paratypes (see above).

## Discussion

REMM (1976) designated females as holotypes for *A. macrophthalmus* and *A. squamiciliatus*. He stated that the latter species was characteristic in having lanceolate scales along the wing margin. Actually that character is an artefact due to a sheath of air which very often is present in amber and which makes normal setae look stouter or scale-like. Among numerous paratypes designated by REMM are specimens which belong to *Culicoides sphenostylus* and other species of *Atriculicoides*. However, females with sensilla scattered on 3rd palpal segment and forked apices of claws are very similar and cannot yet be sepa-

rated into different species. The male described here as *A. macrophthalmus* allows for the determination of the species. It is possible that *A. macrophthalmus* as recognized here is a species complex.

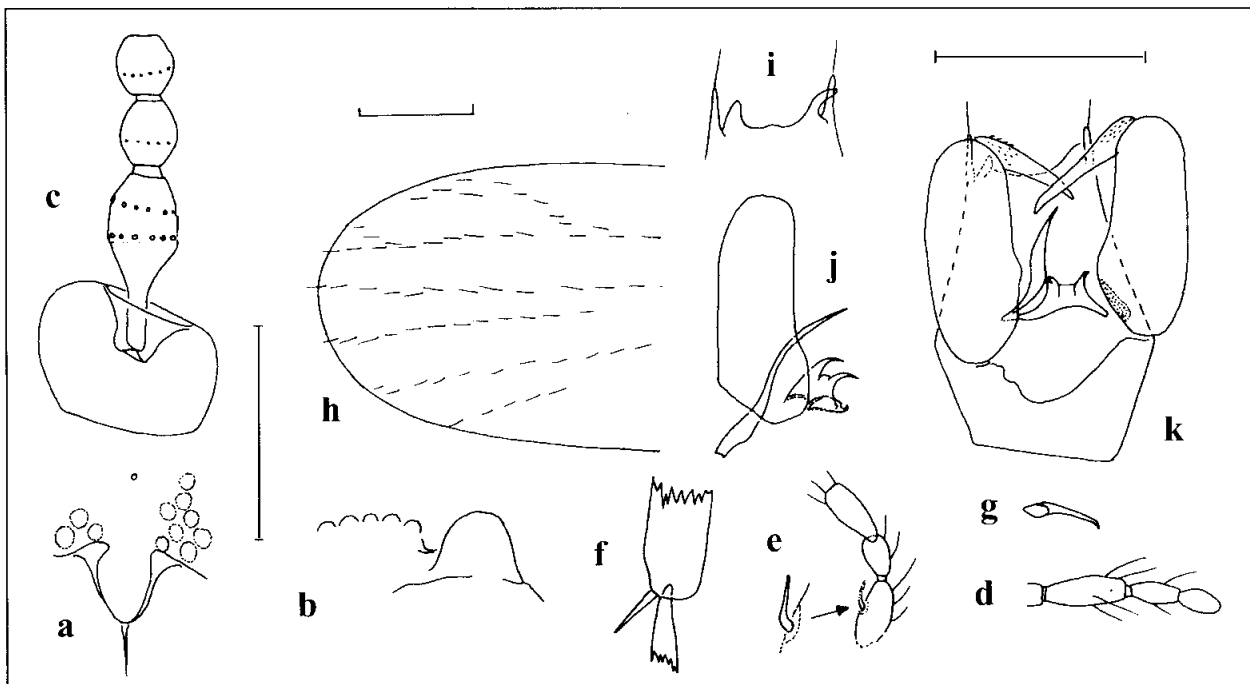
*Atriculicoides dasyheleis* spec. nov. (Fig. 25 a-k)

**Diagnosis:** male with 3rd palpal segment with single long hyaline seta on inner surface, frons swollen into large tubercle, paramere slender with evenly pointed apex, aedeagus short, with 2 apicolateral arms. Siberian amber.

**Description:** ♂: body length 1.3 mm. **Head:** ommatidia separate above antennae; frons swollen into large median tubercle (Fig. 25 a, b). First flagellomere with 2 verticils of plume setae (Fig. 25 c). Proboscis relatively short. Palpus 5-segmented (Fig. 25 d, e); 3rd palpal segment 44 µm long, bearing on inner surface single long hyaline sensory seta, visible only on one palp. **Legs:** trochanter with simple seta. Tibial spur of fore leg distinct, straight (Fig. 25 f); hind tibial spur very small. Claws almost straight (Fig. 25 g). TR(I) 2.1, TR(II) 1.9, TR(III) 1.9. **Wing** length 0.81 mm. Radial cells barely visible. Wing membrane covered with long, sparse macrotrichia (Fig. 25 h). **Genitalia** (Fig. 25 i-k). Sternite IX with distinct caudomedian excavation. Tergite IX long, as long as gonocoxite; apicolateral processes long, cylindrical. Cerci widely separated, large, located at bases of apicolateral processes (Fig. 25 i). Gonocoxite moderately slender. Gonostylus straight, evenly tapering to tip, basal portion covered with distinct setae. Aedeagus short with low basal arch and pointed lateral processes directed ventrally. Paramere single, asymmetrical, with gradually pointed apex directed ventrally (Fig. 25 j, k).

♀: unknown.

**Material examined** (1 ♂): Holotype ♂, Siberian amber, Coniacian-Santonian, PIN, Yantardakh, 1970, 25.



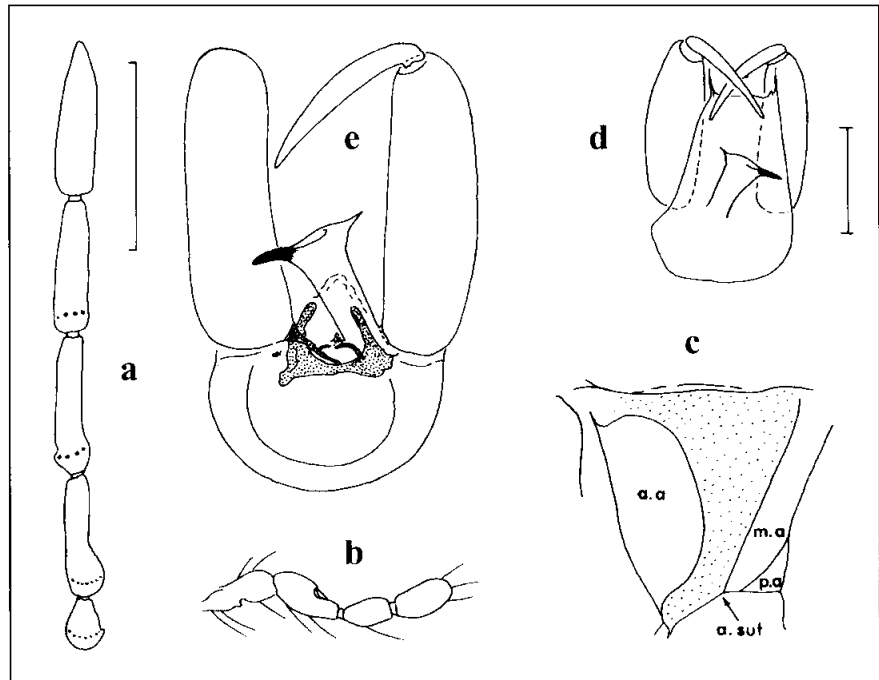
**Fig. 25 (a-k):** *Atriculicoides dasyheleis* spec. nov., holotype male PIN 1970, 25; - a: eyes separation; - b: lateral aspect of frontal tubercle; - c: proximal flagellomeres; - d-e: palpi; - f: tibial spur of fore leg; - g: claw; - h: distribution of macrotrichia on wing membrane; - i: apex of tergite IX; - j: lateral aspect of genitalia; - k: ventral aspect of genitalia. Scale bar = 0.1 mm.

*Atriculicoides sibiricus* spec. nov. (Fig. 26 a-c)

**Diagnosis:** male with large T-shaped paramere.

**Description:** ♂: body length 1.5 mm. **Head:** eyes broadly fused. Frons without distinct tubercle. Antenna with distal 4 flagellomeres elongate and of same length (Fig. 26 a). First flagellomere with 2 distinct verticils of plume setae. Proboscis moderately long. Palpus 5-segmented (Fig. 26 b); 3rd palpal segment with 1 or 2 small sensory pits. **Thorax:** anepisternum bare (Fig. 26 c). Anepisternal suture on anterior half oblique. Claws with bifid apices. TR(III) 2.3.

**Fig. 26 (a-e):** *Atriculicoides sibiricus* spec. nov., holotype male PIN3311/417; - **a**: distal flagellomeres; - **b**: palpus; - **c**: anepisternal sclerites and suture; - **d**: dorsal aspect of genitalia; - **e**: ventral aspect of genitalia. Scale bar = 0.1 mm. Abbreviations: a.a - anterior anepisternum, m.a - median anepisternum, p.a - posterior anepisternum, a.sut - anepisternal suture.



**Wing** length about 0.8 mm; membrane densely covered with macrotrichia. **Genitalia** (Fig. 26 d, e). Sternite IX with broad, deep caudomedian excavation. Tergite IX shorter than gonocoxite; apicolateral processes long, cylindrical; cerci small, located at bases of apicolateral processes. Gonocoxite slender. Gonostylus slender, slightly bent. Aedeagus U-shaped with low basal arch and short basal arms; lateral processes blunt. Paramere single, stout, T-shaped; ventral expansion strong and blunt, dorsal expansion short and sharp.

♀: unknown.

**Material examined** (1 ♂): Holotype ♂, PIN 3311/417, Siberian amber, Yantardakh, Upper Cretaceous, Coniacian-Santonian.

### Discussion

The obliquely situated proximal portion of anepisternal suture is present in many recent *Dasyhelea*, *Forcipomyia*, *Atrichopogon* and *Palpomyiini*. In other biting midges the anepisternal suture is straight.

*Atriculicoides taimyricus* spec. nov. (Fig. 27 a-b)

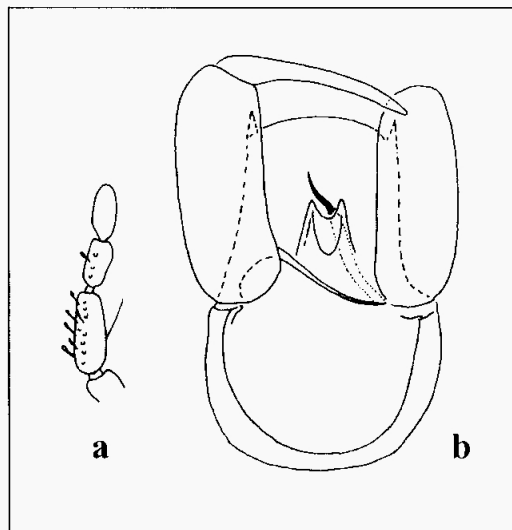
**Diagnosis:** male with 3rd and 4th palpal segments with capitate sensilla scattered on surface, tergite IX long with fine triangular apicolateral processes, aedeagus long, paramere asymmetrical with pointed recurved apex.

**Description:** ♂: body length 1.1 mm. **Head:** frons without tubercle. Antenna typical of the genus with distal 4 flagellomeres elongated, length 328 µm. Palpus 5-segmented (Fig. 27 a); 3rd and 4th palpal segments with capitata sensilla on inner surface; 3rd palpal segment 36 µm long. **Legs** incomplete. **Wing** barely visible, length 0.76 mm. **Genitalia** (Fig. 27 b). Sternite IX with broad, deep caudomedian excavation, Tergite IX shorter than gonocoxite; apicolateral processes triangular. Gonocoxite slender. Gonostylus slender, almost straight. Aedeagus long with shallow apical excavation. Paramere single, asymmetrically situated; apex pointed, recurved; one gonocoxal apodeme very long reaching base of next gonocoxite.

♀: unknown.

**Material examined** (1 ♂). Holotype ♂, Siberian amber, Upper Cretaceous, Coniacian-Santonian, Yandardakh, PIN 3311/440.

**Note:** sensilla capitata on the 3rd and 4th palpal segments are known also in some recent *Dasyhelea* (subg. *Dasyhelea*) (SZADZIEWSKI 1986).

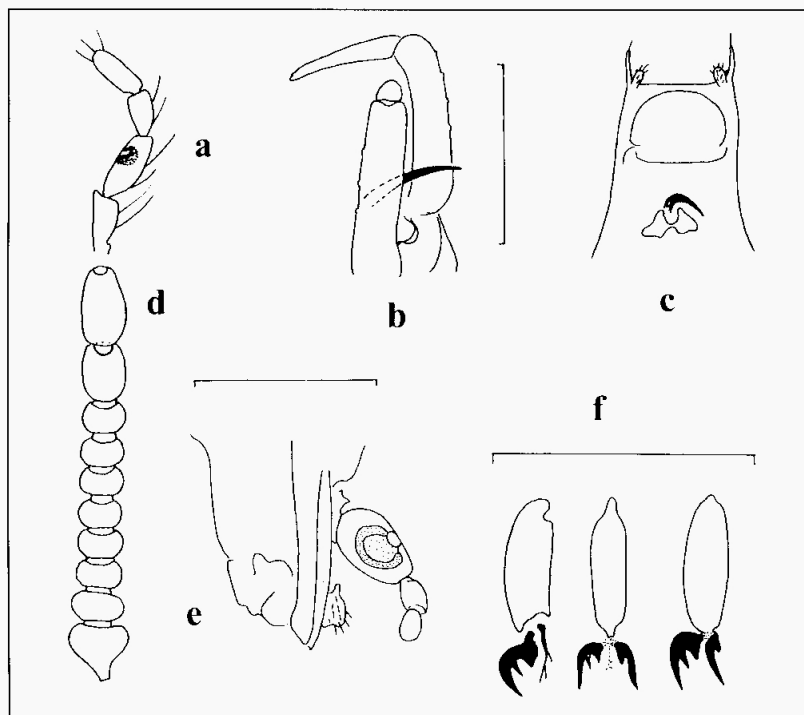


**Fig. 27 (a-b):** *Atriculicoides taimyricus* spec. nov., holotype male PIN 3311/440; - a: palpus; - b: ventral aspect of genitalia. Scale bar = 0.1 mm.

#### *Atriculicoides* spec. (Fig. 28 a-c)

**Diagnosis:** third palpal segment with distinct sensory pit (Fig. 28 a, e). Female proximal flagellomeres short, squat (Fig. 28 d). Tergite IX in male genitalia long, with short, slender apicolateral processes; paramere slender, pointed and directed ventrally (Fig. 28 b, c).

**Material examined** (1 ♂, 1 ♀): PIN 3311/377, 1 ♀, paratype of *Atriculicoides macrophthalmus*; 3311/402, 1 ♂, paratype of *Atriculicoides squamiciliatus*.



#### Discussion

Although the species seems to be distinctive I do not name it here in order to avoid confusion in the recognition of types, as both specimens are already paratypes of two different species.

**Fig. 28 (a-f):** *Atriculicoides* indet. PIN 3311/402 (a-c) paratype male of *A. squamiciliatus* REMM; 3311/377 (d-c) paratype female of *A. macrophthalmus* REMM; paratype female of *A. macrophthalmus* REMM, 3311/387 (f); - a: male palpus; - b: lateral aspect of male genitalia; - c: male tergite IX; - d: female proximal flagellomeres; - e: female palpus; - f: female claws. Scale bar = 0.1 mm.



## Subfamily Ceratopogoninae NEWMAN, 1834

### Tribe Culicoidini KIEFFER, 1911

### Genus *Culicoides* LATREILLE, 1802

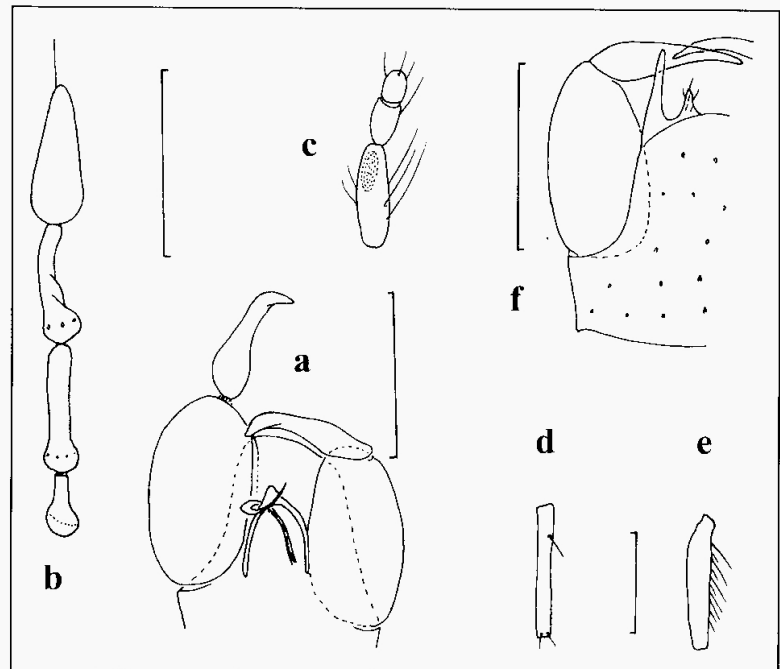
**Diagnosis:** SZADZIEWSKI (1988), BORKENT (1995).

#### Discussion

BORKENT (1995) questioned whether Cretaceous *Culicoides* actually are members of that genus. I see no important differences. At least in females of *C. kaluginae* numerous sensilla coeloconica are clearly visible (generally in amber these are difficult to see) and widely separated eyes present in some fossils are found in many extant species. Moreover females of the Siberian fossil *Culicoides* have transverse suture on vertex like most extant members of the genus.

#### *Culicoides* indet. (5 ♂♂, 4 ♀♀)

PIN 3311/397, 1 ♀, paratype of *Culicoides succineus* REMM (proximal flagellomeres transverse while the holotype has spherical ones). 3311/407, 1 ♂, paratype of *Culicoides sphenostylus* REMM (Fig. 29 a). Barely visible. Wing length 0.78 mm, CR 0.58. Genitalia as in Fig. 29 a; tergite IX barely visible, aedeagus arch-shaped with short apical cone, parameres pointed with recurved portion. Gonostylus with weakly enlarged base and evenly bent and blunt apex. In the same amber piece 1 ♂ of Chironomidae. 3311/415, 1 ♂ (barely preserved, gonostyli as in *C. sphenostylus*).



**Fig. 29 (a-h):** *Culicoides* indet., male.  
- a: male genitalia PIN 3311/407; - b-f: male PIN 3311/419; - b: distal flagellomeres; - c: palpus; - d: first tarsomere of mid leg; - e: first tarsomere of hind leg; - f: dorsal aspect of genitalia. Scale bar = 0.1 mm.

3311/419, 1 ♂ (+ 1 ♂ Ceratopogonini indet.) (Figs. 29 b-f). Incomplete. Distal 3 flagellomeres elongate (Fig. 29 b). Third palpal segment about 52 µm long (Fig. 29 c). First tarsomere of middle leg with distinct subbasal spine-like seta (Fig. 29 d); first tarsomere of hind leg with distinct row of setae (Fig. 29 e). Wing length 0.81 mm, CR 0.58, membrane including basal radial cell covered with macrotrichia. Apicolateral processes of tergite IX large (Fig. 29 f). 3311/424, 1 ♀, possibly *C. kaluginae*. 3311/426 a, c, 1 ♂, see *C. filipalpis* and *C. kaluginae* (Fig. 30 a-f). Body length about 1.0 mm. Proboscis relatively short (Fig. 30 a, b). Flagellum with distal 3 flagellomeres elongate, Fig. 30 c. 3rd palpal segment about 22 µm long, sensorium composed of 3 pits, Fig. 30 d. Genitalia with moderately long apicolateral processes, gonostylus simple, straight (Fig. 30 e); parameres separate, with apices weakly curved as in Fig. 30 f. That male cannot be recog-

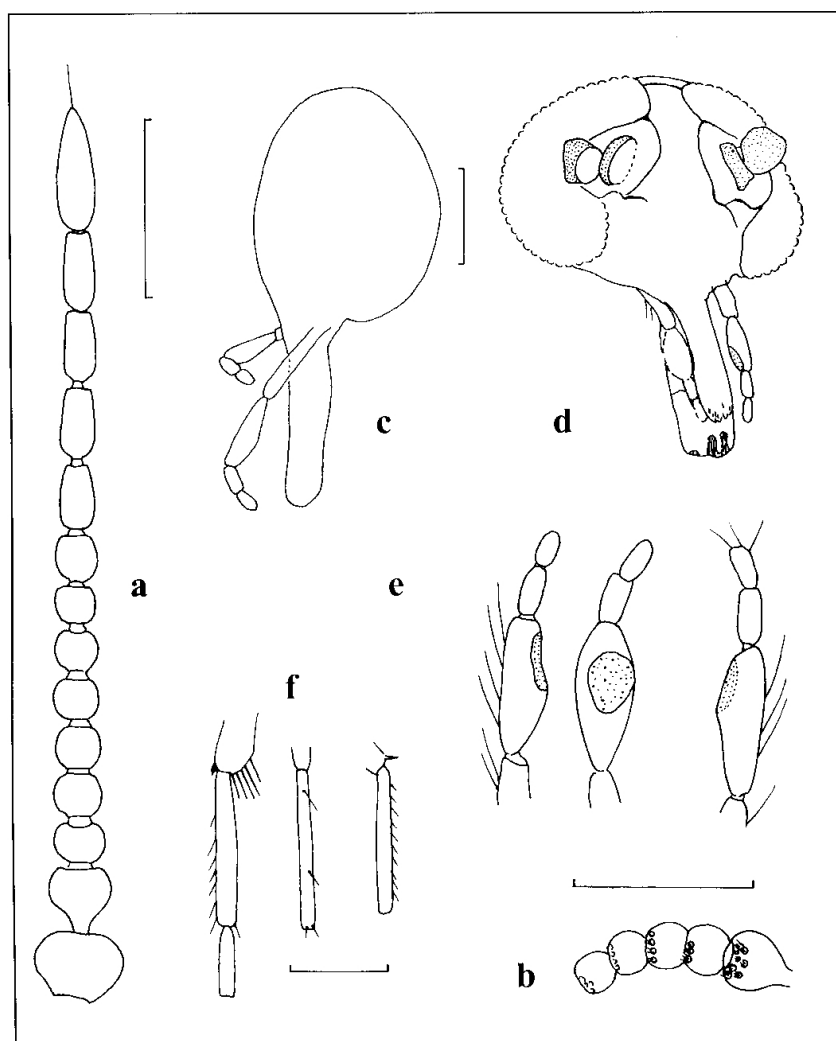
***Culicoides kaluginae* REMM, 1976 (Figs. 32 a-f, 49 e)**

*Culicoides kaluginae* REMM, 1976: 110 (♀, Yantardakh, Coniacian - Santonian, Siberian amber).

**Diagnosis:** female proboscis as long as head, eyes widely separate, with transverse suture on vertex, 3rd palpal segment stout with broad, shallow sensory pit, no macrotrichia in basal radial cell.

**Description:** ♂: unknown.

♀: body length 1.1-1.3 mm. **Head:** eyes broadly separate (Fig. 32 d), transverse suture on vertex visible, trace of lower vertical seta not visible below suture. Flagellum 458 µm long, AR 0.91-1.03; proximal flagellomeres spherical, distal 5 slightly elongate (Fig. 32 a); proximal flagellomeres with numerous sensilla coeloconica clearly visible (Fig. 32 b). Proboscis as long as head height (Figs. 32 c, d, 49 e), length of head incl. proboscis 465 µm. Apex of proboscis probably slightly bent caudally. 3rd palpal segment 80 µm long, slightly enlarged, with shallow, broad sensory pit on distal half (Fig. 32 e). **Legs:** basitarsus of middle leg with subbasal, submedian and 2 apical spines; tibial comb composed of 5 spines (Fig. 32 f). TR(I) 2.4, TR(II) 2.6-2.7, TR(III) 2.2. **Wing** length 0.77 mm, CR 0.67. Macrotrichia sparse in all marginal cells, basal radial cell without macrotrichia.



**Fig. 32 (a-f):** *Culicoides kaluginae* REMM, female, PIN 3311/426 a,b,c; - a: antenna; - b: proximal flagellomeres; - c: lateral aspect of head; - d: frontolateral aspect of head; - e: palps; - f: first tarsomeres of hind, middle and fore leg. Scale bar = 0.1 mm.

**Material examined** (10 ♀ ♀): Types were not available for the present study. PIN 3311/426, a,b,c, 9 ♀ ♀ (+ *Culicoides filipalpis*, *Culicoides* indet. 1 ♂, Chironomidae 1 ♂ 1 ♀). Other material: PIN, Yantardakh, 1 ♀ (not numbered; clearly visible proboscis, much longer than head, 3rd palpal segment enlarged; single median seta on vertex present).

### Discussion

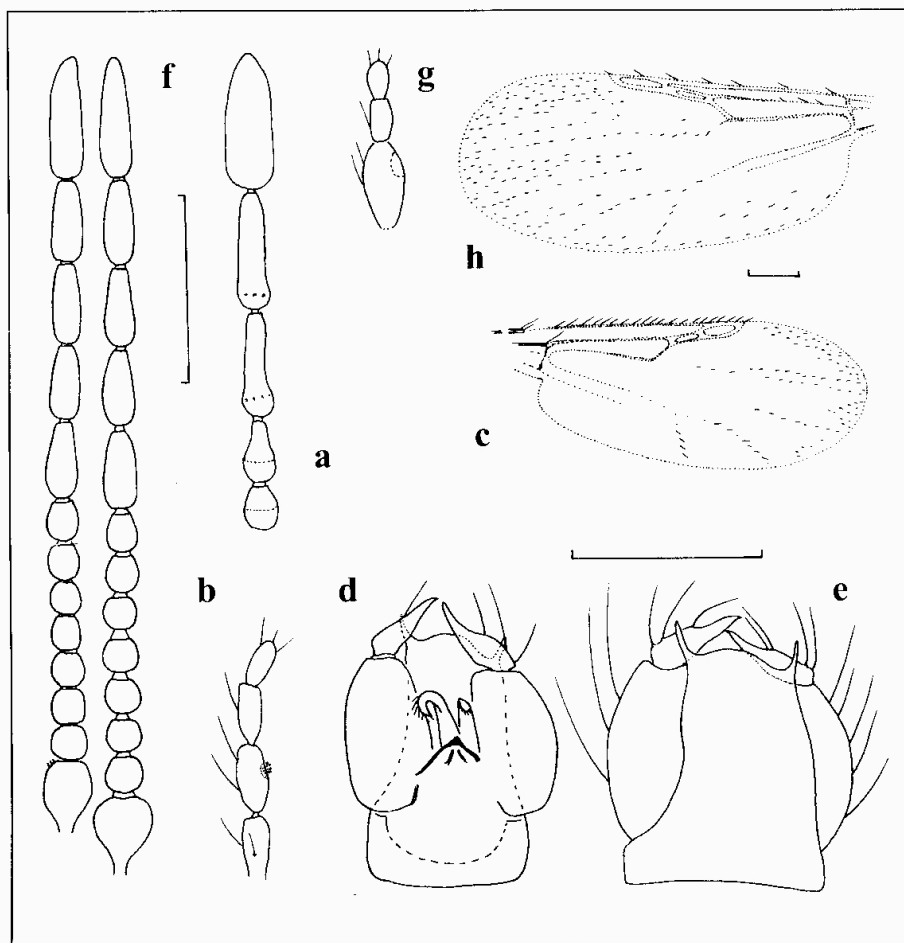
Shape of frons and vertex, numerous sensilla coeloconica are typical of the genus.

***Culicoides sphenostylus* REMM, 1976 (Fig. 33 a-h)**

*Culicoides sphenostylus* REMM, 1976: 112 (♂, ♀, Yandardakh, Coniacian - Santonian, Siberian amber).

**Diagnosis:** basal radial cell without macrotrichia. Gonostyli short, simple, triangular, enlarged on basal half.

**Description:** ♂: body length 1.04 mm. **Head:** Flagellum with distal 3 flagellomeres elongate (Fig. 33 a), length 495-510 µm, AR 1.24, sensilla coeloconica not visible, first flagellomere with 2 verticils of plume setae. Palpus slender (Fig. 33 b); 3rd palpal segment 38 µm long; sensory pit small located at midlength. **Thorax:** scutellum with 6 marginal long setae. **Legs:** tibial comb composed probably of 3 or 4 spines. TR(I) 2.1, TR(III) 2.1. **Wing** length 0.64-0.70 mm, CR 0.54-0.59; macrotrichia at wing tip present (Fig. 33c). **Genitalia** (Fig. 33 d, e). Sternite IX with deep caudomedian excavation. Tergite IX longer than gonocoxite, with long cylindrical apicolateral processes. Gonocoxite normal. Gonostylus simple, enlarged on basal half and bearing long and strong setae, distal half abruptly tapering to pointed apex and somewhat recurved. Aedeagus arch-shaped, with short apical process. Parameres on apical portion strongly curved and bearing fringe of setae.



**Fig. 33 (a-h):** *Culicoides sphenostylus* REMM, holotype male PIN 3311/405 (a-c, e), paratype male 3311/406 (d), paratype female 3311/394. - a: distal male flagellomeres; - b: palpus; - c: wing; - d: ventral aspect of genitalia; - e: dorsal aspect of genitalia; - f: female flagella; - g: female palpus; - h: female wing. Scale bar = 0.1 mm.

♀: body length 1.2 mm. **Head:** eyes moderately separate, with distinct inverted Y-shaped transverse vertical suture and median seta below. Proximal flagellomeres spherical; sensilla coeloconica on first flagellomere visible (Fig. 33 f). 3rd palpal segment stout with rounded sensory pit (Fig. 33 g). Wing length 0.80 mm, CR 0.63; macrotrichia in basal radial cell absent (Fig. 33 h).

**Material examined** (4♂♂ 1♀): Siberian amber, Upper Cretaceous, Coniacian-Santonian, Yantardakh, PIN: Holotype ♂, 3311/405; paratypes: 3311/406, 1♂ (+ Diptera indet.1); 3311/408, 1♂; 3311/394 1♀. The paratype male of *Atriculicoides squamiciliatus* REMM, PIN 3311/400, actually is *Culicoides sphenostylus* with genitalia characteristic of the species. The paratype male 3311/404 belongs to *Peronehelea frigida* REMM (Ceratopogonini). The paratype male 3311/407 does not belong to the same species and is treated as *Culicoides* indet. (see above).

**Note:** the characteristic transverse vertical suture in shape of inverted Y with lower vertical seta located below the fork [for example as in females of *C. nubeculosus* (MEIGEN)] is not found outside of *Culicoides*.

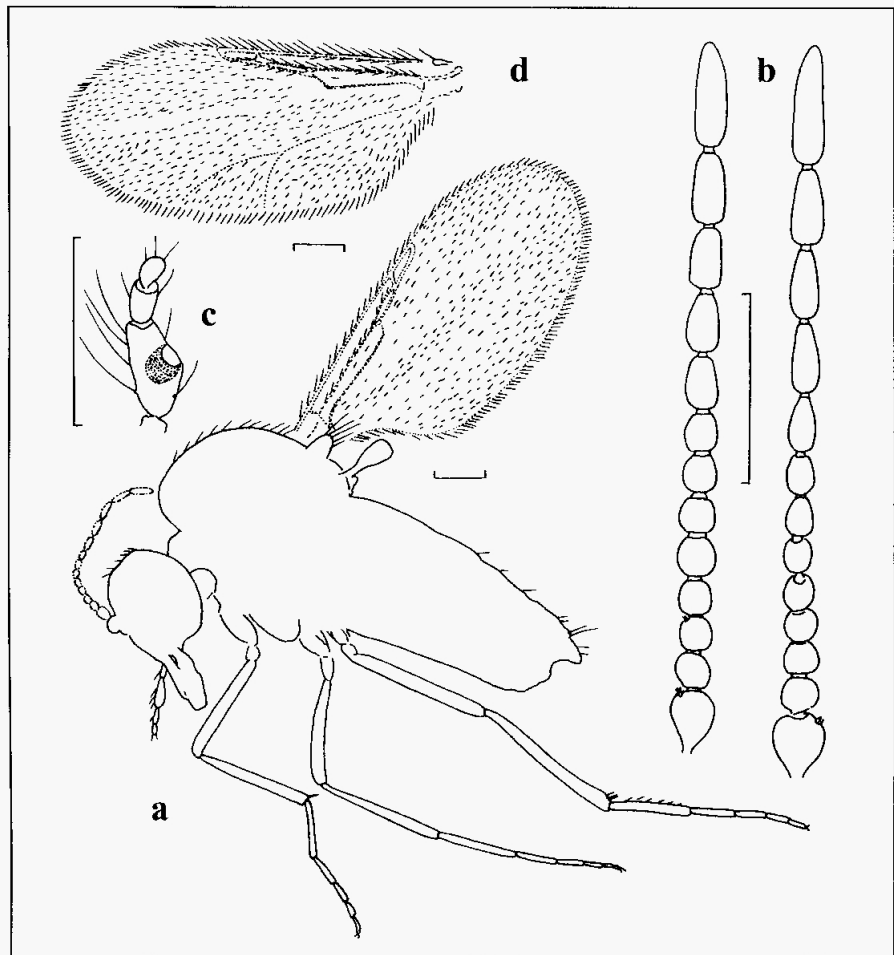
***Culicoides succineus* REMM, 1976** (Figs. 34 a-d, 49 f)

*Culicoides succineus* REMM, 1976: 113 (♂, ♀, Yantardakh, Coniacian - Santonian, Siberian amber).

**Diagnosis:** female wing including basal radial cell covered with macrotrichia.

**Description:** ♂: Unknown.

♀: body length 1.0 mm. Habitus as in Figs. 34a, 49 f. **Head:** eyes narrowly separate. Flagellum with transverse to slightly ovoid proximal flagellomeres. Sensilla coeloconica on 1st and 3rd flagellomeres visible (Fig. 34 b). Proboscis moderately long. 3rd palpal segment short and stout, with deep sensory pit (Fig. 34 c); length 34-38 µm. **Thorax:** humeral pits large. **Legs:** tarsi without stronger spines. **Wing** length 0.69-0.71 mm, CR 0.57-0.60. Whole wing membrane densely covered with macrotrichia (Fig. 34 a, d). Basal radial cell with 1-2 macrotrichia.



**Fig. 34 (a-d):** *Culicoides succineus* REMM, 1976, female. Holotype 3311/396 (b, left flagellum; c, d), paratype 3311/395 (a, b right flagellum). - a: total habitus; - b: flagella; - c: palpus; - d: wing. Scale bar = 0.1 mm.

**Material examined** (2♀♀): Siberian amber, Taimyr, Yantardakh, Upper Cretaceous, Coniacian-Santonian, PIN: Holotype ♀, 3311/396 (+ Acarina 1), paratype ♀ 3311/395. The paratype ♀ 3311/397 represents another *Culicoides* as it has transverse proximal flagellomeres and is placed here among indetermined species. The paratype ♂ PIN 3311/403 actually is Ceratopogonini and treated here as a doubtful member of *Peronehelea sibirica* spec. nov.

## Tribe Ceratopogonini NEWMAN, 1834

Genus *Brachycretacea* gen. nov.Type-species *Baeohelea taimyrica* REMM, 1976, present designation.

**Diagnosis:** the only genus within the tribe Ceratopogonini with males having 9 flagellomeres, well developed but single radial cell ( $r_1+r_2$ ), wing membrane bare, distinct traces of veins  $R_{4+5}$ , one palpal segment distal to primitive 3rd, tergite IX with long apicolateral processes armed with strong apical seta.

**Discussion**

*Brachycretacea* is a highly apomorphic (by reduction) genus for which it is presently impossible to find a clear phylogenetic position as it could originate from many different lineages of Upper Cretaceous Ceratopogonini. Formally *B. taimyrica* could be placed within *Nannohelea* GROGAN et WIRTH (one first radial cell, male antenna with 7-8 flagellomeres, tergite IX in male genitalia with or without apicolateral processes, palp with 3-5 segments). However, the important difference is in the configuration of the single radial cell which in the new genus is formed by the reduction of vein  $R_2$  and in fact is a cell  $r_1+r_2$  while in *Nannohelea* the preserved cell is only  $r_2$  because the proximal portions of veins  $R_1$ ,  $R_2$  and  $R_3$  are fused. The new genus cannot be placed in the basal lineage of the Ceratopogonidae, which may be suggested by bare wings, as other characters show that it lost macrotrichia secondarily.

***Brachycretacea taimyrica* (REMM, 1976), comb. nov.** (Figs. 35 a-f, 50 a)*Baeohelea taimyrica* REMM, 1976: 115 (♂, Taimyr amber, Yandardakh);

WIRTH &amp; GROGAN 1988: 24 (discussion on taxonomic position);

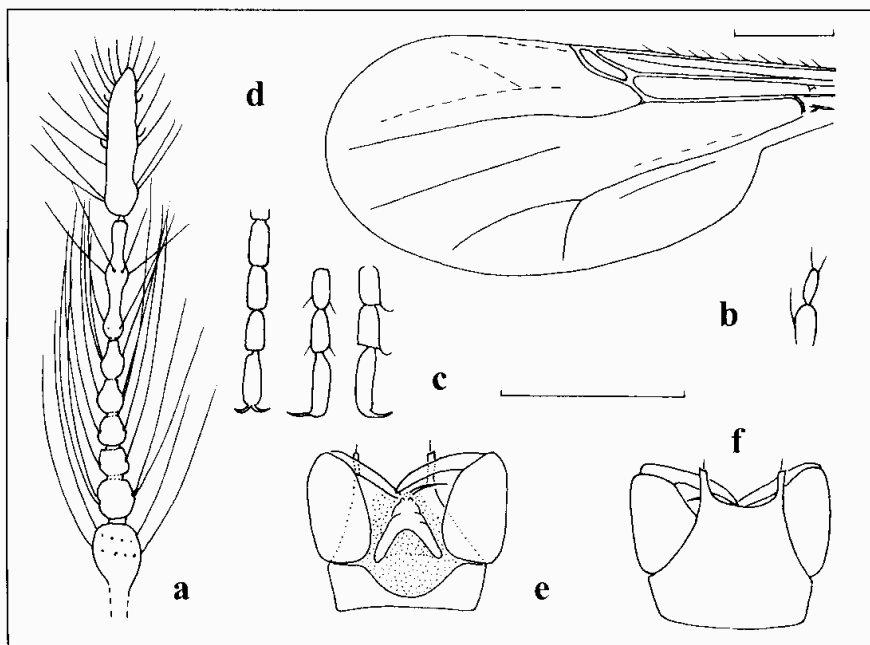
*Leptohelea taimyrica*: SZADZIEWSKI, 1988: 238 (combination);

BORKENT 1995: 114 (discussion of taxonomic position).

**Diagnosis:** as for genus.

**Description:** ♂: total habitus as in Fig. 50 a. Body length 0.8 mm. **Head:** flagellum with 9 flagellomeres (Fig. 35 a); 1st flagellomere with 2 verticils of plume setae; flagellomeres 1-6 separated, each with well developed verticil; flagellomeres 7-8 fused as indicated by 2

verticils of plume setae; terminal (or 9th) flagellomere elongated, stout; sensilla coeloconica not visible; flagellum length 293 µm. Proboscis relatively short. Primitive palpal segments 4th and



**Fig. 35 (a-f):** *Brachycretacea taimyrica* (REMM), holotype male PIN 3311/401; - a: flagellum; - b: palpus; - c: distal tarsomeres of fore and hind legs; - d: wing; - e: ventral aspect of genitalia; - f: dorsal aspect of genitalia. Scale bar = 0.1 mm.

5th fused, slender, 20  $\mu\text{m}$  long (Fig. 35 b). **Thorax**: scutellum with 4 lateral and 2 submedian long setae. **Legs**: fore tibia with long spur. Row of palisade setae present on hind first tarsomere. Fourth tarsomeres cylindrical, claws normal (Fig. 35 c). **Wing** length 0.49 mm, CR 0.48. First radial cell single, short (Fig. 35 d). Traces of vein  $R_{4+5}$  well visible. Wing membrane without macrotrichia, microtrichia visible. **Genitalia** relatively small (Fig. 35 e, f). Sternite IX with shallow caudomedian excavation. Tergite IX with long cylindrical apicolateral processes reaching tip of gonocoxite; each with strong apical seta. Aedeagus barely visible, rather triangular. Parameres barely visible, only apex of one paramere; distal portion slender, tapering to apex directed ventrally.

♀: unknown.

**Material examined** (1♂): Holotype ♂, PIN 3311/401, Siberian amber, Yantardakh in Taimyr, Coniacian-Santonian, Upper Cretaceous.

**Note**: it is possible that the parameres are actually fused into a single structure.

### *Ceratopogon* MEIGEN, 1803

**Diagnosis**: SZADZIEWSKI (1988); BORKENT & GROGAN (1995).

#### Discussion

This genus is common in European Tertiary ambers and may include *Ceratopogon macronyx* REMM, 1976 from Upper Cretaceous Siberian amber. BORKENT (1995) placed this species within the new fossil genus *Palaeobrachypogon* with wide limits. *C. macronyx* has a broad aedeagus with a bilobed apex, large and almost equal female claws armed with a basal tooth, and short 4th tarsomeres and therefore seems to be typical member of *Ceratopogon* as diagnosed by BORKENT & GROGAN (1995: 14). The species has a distinct hind tibial spur and palisade setae are not restricted to the basal half of the hind basitarsus as in the most extant species. BORKENT (1995) disagreed in his analysis that some Tertiary species have a relatively well developed hind tibial spur (SZADZIEWSKI 1988). The partly developed row of palisade setae on the proximal half of the basal tarsomere of the hind leg found in most extant and fossil *Ceratopogon* is a homoplastic character found in *Washingtonhelea* too (see below). All extant *Ceratopogon* have aedeagus with 4 projections (prongs) which sometimes are difficult to see (BORKENT & GROGAN 1995). In *C. macronyx* presence of a lateroventral pair of prongs cannot be excluded.

*Palaeobrachypogon remmi* (BORKENT, 1995) from Campanian Canadian amber is superficially similar to *Ceratopogon macronyx* with similar claws in the female. However the male genitalia are quite different which enables to include it in *Ceratopogon*.

#### *Ceratopogon macronyx* REMM, 1976 (Figs. 36 a-f, 37 a-e, 38 a-f, 50 b)

*Ceratopogon macronyx* REMM, 1976: 113 (♂, ♀, Yantardakh, Coniacian-Santonian, Siberian amber);

*Palaeobrachypogon macronyx*: BORKENT 1995: 72 (combination).

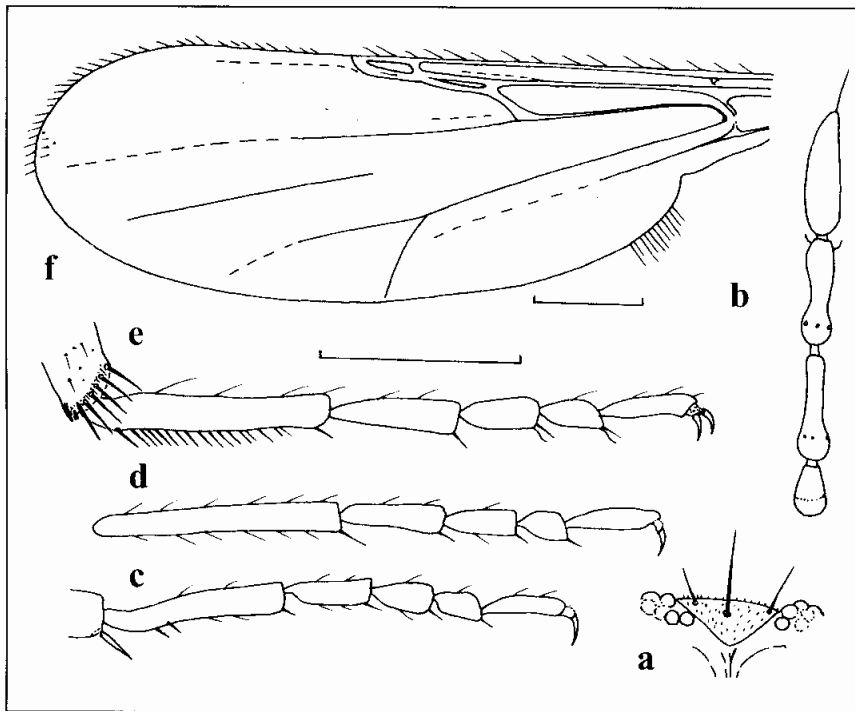
**Diagnosis**: female claws large, similar on all legs, almost equal, each with basal inner tooth, 4th tarsomeres almost cordiform, aedeagus large, shield-shaped and with 2 distinct submedian projections.

**Description**: ♂: body length about 1.0-1.1 mm. **Head**: eyes broadly separate (Fig. 36 a). Flagellum 452-500  $\mu\text{m}$  long, AR 0.82-0.95. All flagellomeres separate, distal 3 elongate (Figs. 36 b); sensilla coeloconica not visible. Proboscis moderately short. Palpus 5-seg-



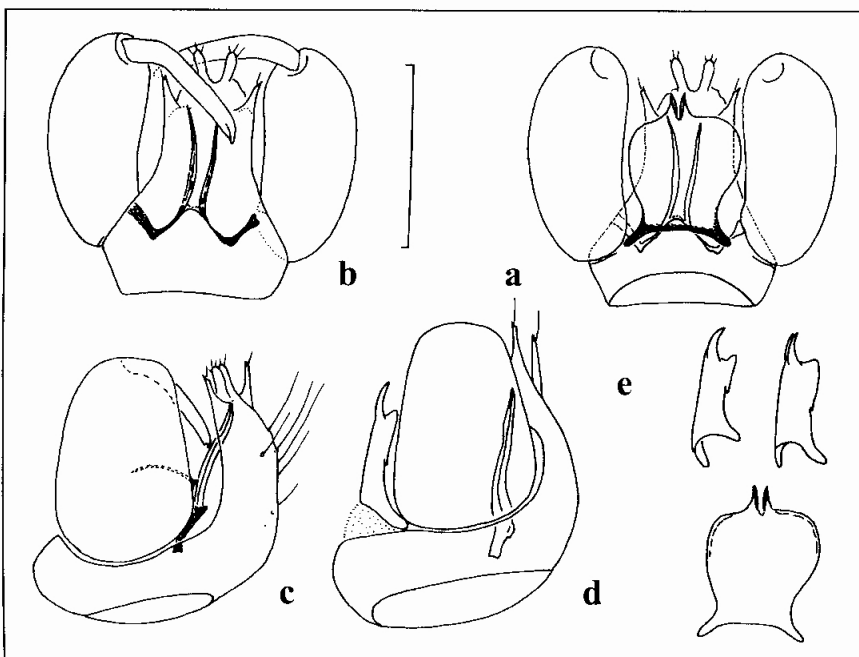
mented, barely visible; 3rd palpal segment 24-32  $\mu\text{m}$  long; sensory pit small, placed subapically. **Thorax**: katepisternum lacking setae. Scutellum with 2 lateral, 2 submedian long setae plus short apicomedian one. **Legs** moderately slender, hind leg somewhat stouter than others. Tibial spur of fore leg long and straight

(Fig. 36 c), of hind legs short (Fig. 36 e). Hind basitarsus with distinct subbasal spine and palisade-like setae clearly visible on proximal portion. Tibial comb composed of 6 stout spines of



**Fig. 36 (a-f):** *Ceratopogon macronyx* REMM, paratype male PIN 3311/409. - **a**: eyes separation; - **b**: distal 4 flagellomeres; - **c**: tarsus of fore leg; - **d**: tarsus of middle leg; - **e**: tarsus of hind leg; - **f**: wing. Scale bar = 0.1 mm.

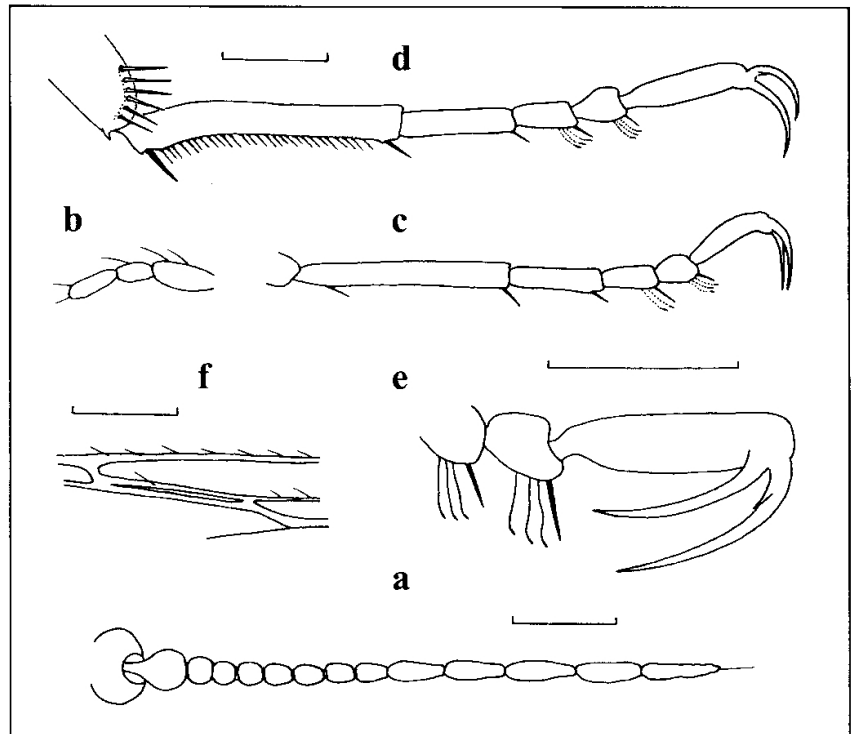
equal size. Fourth tarsomeres rather cylindrical (Figs. 36 c-e). **Wing** length 0.64-0.75 mm, CR 0.54. First and second radial cells of almost same size (Fig. 36 f). Wing membrane with only a few macrotrichia at wing apex. **Genitalia** broader than abdomen, rotated 90° (Fig. 37 a-e). Sternite IX barely visible. Tergite IX with prominent apicolateral processes armed with apical seta. Proctiger greatly developed, with cerci extending much beyond apex of tergite IX. Gonocoxite stout. Gonostylus long, slender, cylindrical, slightly bent on proximal third, with evenly pointed claw-like apex. Aedeagus shield-shaped with low basal arch and expanded laterally distal portion, with 2 submedian triangular expansions.



♀: total habitus as in Fig. 50 b. Body length 1.6 mm. **Head**: eyes narrowly separate. Flagellum 555  $\mu\text{m}$  long, AR 1.26 (Fig. 38 a); distal 5 flagellomeres elongate, sensilla coeloconica not visible. Proboscis moder-

**Fig. 37 (a-e):** *Ceratopogon macronyx* REMM, paratype male, PIN 3311/409, genitalia. - **a**: ventral aspect; - **b**: dorsal aspect; - **c-d**: lateral aspects; - **e**: lateral and ventral aspects of aedeagus. Scale bar = 0.1 mm.

ately long. Palpus 5-segmented (Fig. 38 b), 3rd palpal segment 64  $\mu\text{m}$  long; sensory pit not visible. **Thorax:** katapisternum without distinct setae. Anapleural suture straight. Scutellum with about 10 marginal setae. **Hind legs** slightly stouter than fore and mid legs. First tarsomere of middle and hind legs with subbasal spine (Fig. 38 c, d). Hind tibial spur greatly reduced. Tibial comb composed of 6 spines (Fig. 38 d). Palisade setae visible on whole length of hind basitarsus. Fourth tarsomeres almost cordiform. 4th and 3rd tarsomeres with fine capitate



**Fig. 38 (a-f):** *Ceratopogon macronyx* REMM, holotype female, PIN 3311/372; - **a:** flagellum; - **b:** palpus; - **c:** tarsus of middle leg; - **d:** tarsus of hind leg; - **e:** distal tarsomeres of hind leg; - **f:** preserved radial cells. Scale bar = 0.1 mm.

hair-like sensilla. Claws long, equal, each with distinct inner basal tooth (Fig. 38 e). TR(III) 2.5. Only proximal half of **wing** preserved measuring about 0.7 mm. First radial cell slit-like, second broader (Fig. 38 f). Microtrichia distinct, macrotrichia absent from at least proximal portion.

**Material examined** (2♂♂ 1♀): Holotype ♀, PIN 3311/372. Paratypes: 3311/409 1♂; 3311/410 1♂.

### Genus *Peronehelea* BORKENT, 1995

*Peronehelea* BORKENT, 1995: 80. Type-species *Peronehelea chrimikalydia* BORKENT, 1995, by original designation.

**Diagnosis:** female hind femur and tibia enlarged and hind claw single, greatly elongated and armed with 1-2 teeth.

### Discussion

BORKENT (1995) selected males as holotypes for the species in the similar or related genera *Peronehelea* and *Palaeobrachypogon*. However, within the tribe Ceratopogonini males are of little diagnostic value at the generic level and in both fossil genera associations of males and females are not certain. As a result, the genera in question which would otherwise be easily determined on the basis of females, in fact may be incorrectly interpreted. *Peronehelea* is similar or related to *Monohalea* KIEFFER of traditional limits (presently divided into many small extant genera by WIRTH & GROGAN 1988). *Monohalea clunipes* (LOEW) from Baltic amber does not fit any genus of the *Monohalea* complex and needs a new genus. Further phylogenetic studies are necessary.

**Species included:** - *Peronehelea chrimikalydia* BORKENT, 1995 (Canadian amber)  
- *P. frigida* (REMM, 1976) (Siberian amber)  
- *P. sibirica* spec. nov. (Siberian amber).

Key to species of *Peronehelea*

Females

- 1 Hind claw with single, long, basal tooth ..... *P. chrimikalydia* BORKENT
- Hind claw with 2 basal teeth, 1 long, 2nd short ..... 2
- 2 Long tooth c-shaped (Fig. 41 h)..... *P. frigida* (REMM)
- Long tooth sinuous (Fig. 43 h)..... *P. sibirica* spec. nov.

***Peronehelea frigida* (REMM, 1976), comb. nov.** (Figs. 39 a-l, 40, 41 a-i, 50 c)

*Ceratopogon frigidus* REMM, 1976: 115 (♂, ♀, Yandardakh, Coniacian-Santonian, Siberian amber);

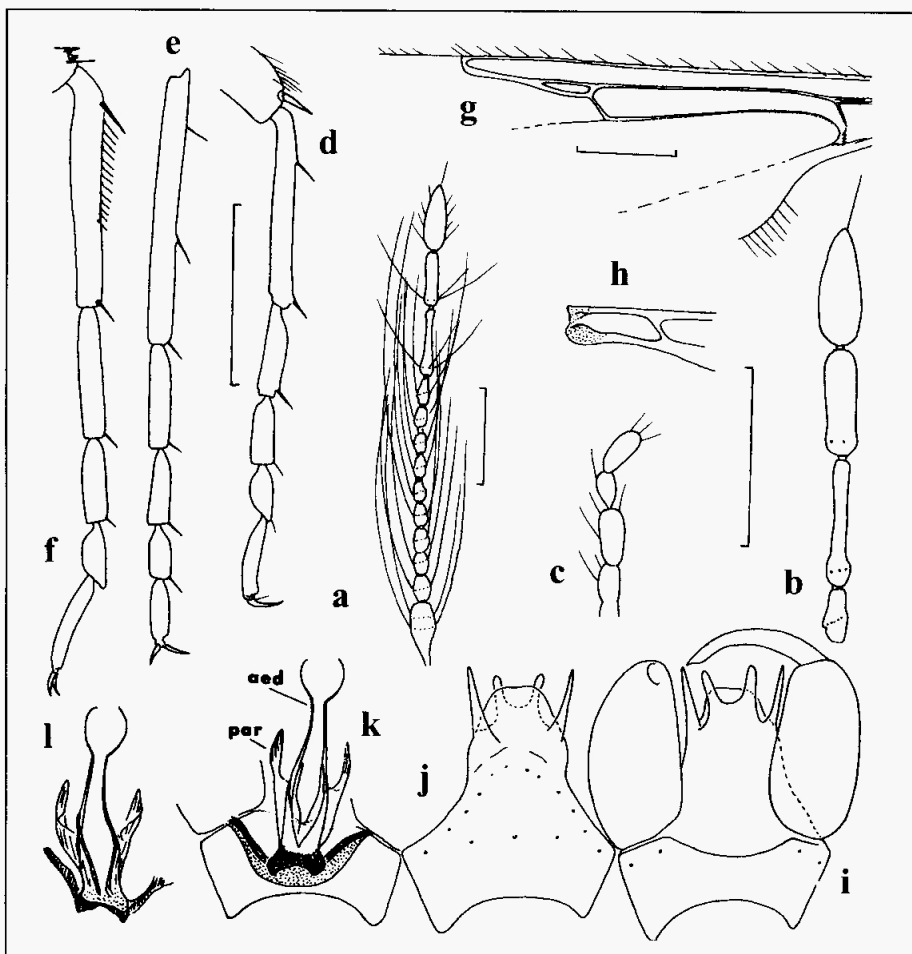
*Brachypogon frigidus*: SZADZIEWSKI 1988: 237 (combination);

*Palaeobrachypogon frigidus*: BORKENT 1995: 72 (combination).

**Diagnosis:** female with hind claw armed with one short and second C-shaped, long talon-like tooth; wing membrane with numerous strong macrotrichia along anterior margin.

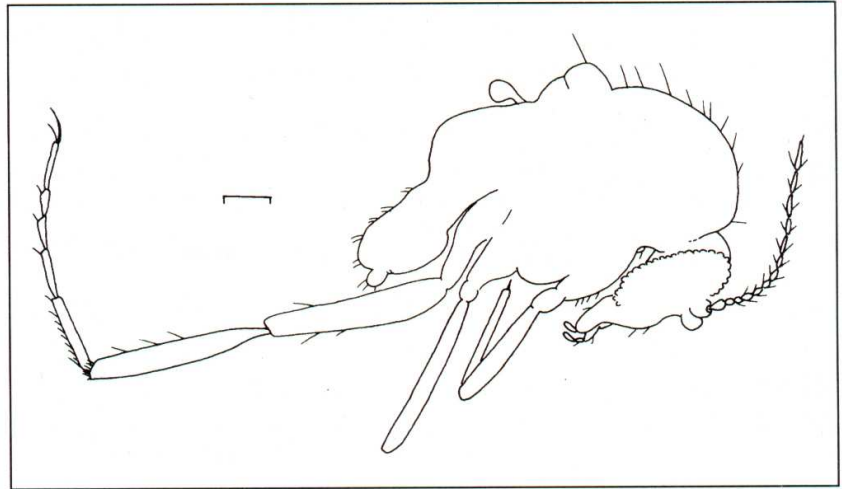
**Description:** ♂: body length 1.2 mm. **Head:** flagellum length 450-495 µm, AR 0.83. All flagellomeres separate, distal 3 elongate, sensilla coeloconica not visible (Fig. 39 a, b). Proboscis short. Palpus 5-segmented (Fig. 39 c), 3rd palpal segment 32 µm long, sensory pit not visible. **Thorax:** katepisternum without setae. Scutellum with 4 marginal setae. **Legs** slender with stouter hind legs. Tibial spur of fore leg distinct, of hind leg small (Fig. 39 d, f). Basitarsus of hind and fore leg with subbasal and apical spines, of middle leg with subbasal, median, apical spines (Fig. 39 d-f). Palisade setae of hind basitarsus well developed on proximal half (Fig. 39 f). Fourth tarsomeres rather cylindrical. Claws short, equal.

TR(I) 2.3, TR (II) 2.7, TR(III) 1.9. **Wing** length 0.64-0.68 mm, CR 0.56. Macrotrichia and microtrichia on wing membrane not visible.



**Fig. 39 (a-l):** *Peronehelea frigida* (REMM), paratype male PIN 3311/411 (a-g,i-l) and paratype of *Culioides sphenostylus* REMM, PIN 3311/404 (h): - a: flagellum; - b: distal 4 flagellomeres; - c: palpus; - d: fore tarsus; - e: tarsus of middle leg; - f: tarsus of hind leg; - g: wing venation; - h: second radial cell; - i: ventral aspect of genitalia; - j: tergite IX and proctiger; - k-l: aedeagus and parameres. Scale bar = 0.1 mm. Abbr.: aed - aedeagus, par - paramere.

Distal portion of vein  $R_1$  visible or not (Fig. 39 g, h). Distal end of  $R_3$  seems to be swollen and cell  $r_2$  seems to be open on distal end (see discussion). **Genitalia** moderately large, rotated  $90^\circ$  (Fig. 39 i-l). Sternite IX barely visible, probably with shallow caudomedian excavation. Tergite IX with long, tapering, apico-lateral processes devoid of distinguishable apical seta. Proctiger large, with long cerci reaching nearly to apex of apicolateral processus.

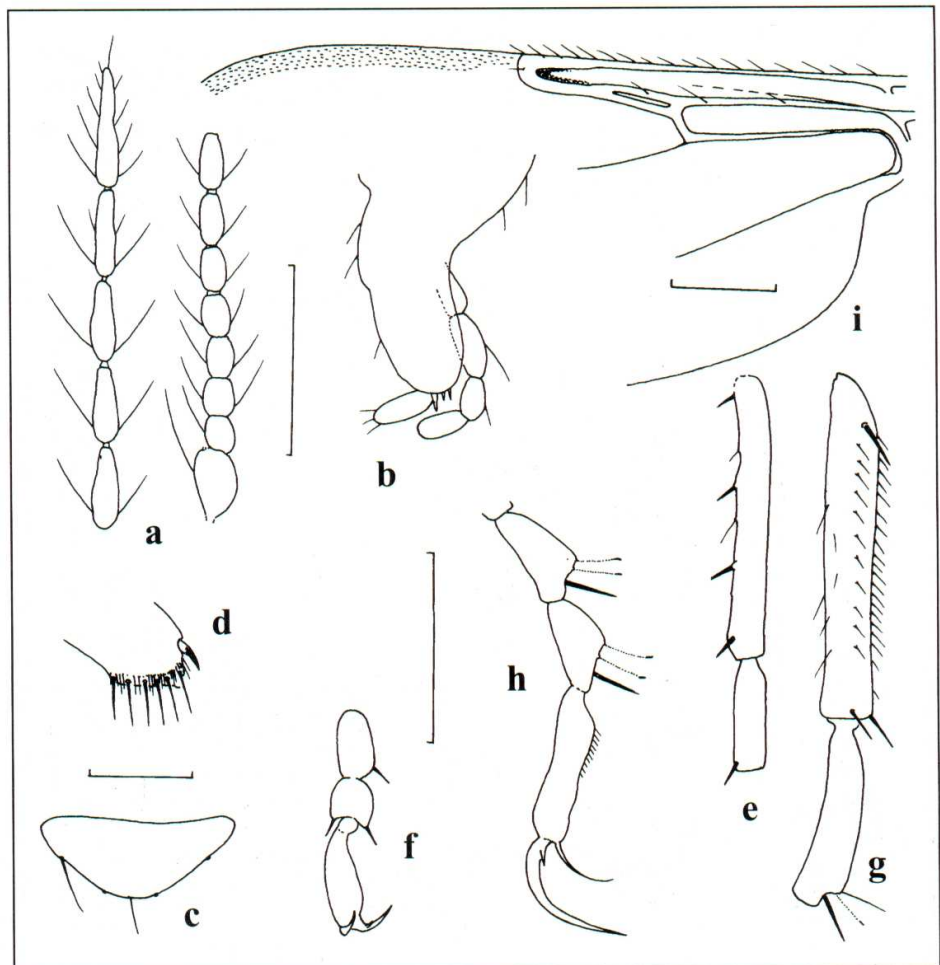


**Fig. 40:** *Peronehelea frigida* (REMM), holotype female 3311/371 (wings not shown). Scale bar = 0.1 mm.

Gonocoxite stout. Gonostylus slender, cylindrical, C-shaped with short, pointed apex. Aedeagus narrow and long, deeply divided into 2 long submedian rods bent subapically, forming characteristic ()-like structure. Parameres short, symmetrical, forming broadly U-shaped structure articulating with long gonocoxal apodemes.

♀: body as in Figs. 40, 50 c. **Head:** eyes probably narrowly separate. Flagellum length  $440\ \mu\text{m}$ , AR 1.2. Flagellomeres gradually elongate from 2nd to 13th, sensilla coeloconica not visible (Fig. 41 a).

Proboscis moderately short, palpus 5-segmented, 3rd palpal segment  $34\ \mu\text{m}$  long, sensory pit not visible (Fig. 41 b). **Thorax** strongly convex, covered with sparse setae. Scutellum with 5 long setae on margin (Fig. 41 c). **Legs:** hind femur



**Fig. 41 (a-i):** *Peronehelea frigida* (REMM), holotype female, PIN 3311/371: - a: flagellum; - b: proboscis; - c: scutellum; - d: tibial comb; - e: proximal tarsomeres of middle leg; - f: distal tarsomeres of middle leg; - g: proximal tarsomeres of hind leg; - h: distal tarsomeres of hind leg; - i: wing. Scale bar = 0.1 mm.

and tibia enlarged, unarmed. Hind tibial comb with 6 spines, spur distinct (Fig. 41 d). Basitarsus of middle leg with subbasal, 2 median and apical spines (Fig. 41 e). Hind basitarsus with distinct subbasal spine and 2 rows of weak palisade setae (Fig. 41 g). Fourth tarsomeres almost cordiform (Fig. 41 f, h). Claws of fore and middle legs short, equal, each with basal inner tooth (Fig. 41 f). Claw of hind leg greatly enlarged, C-shaped, armed with short basal tooth and slender, shorter C-shaped second claw. TR(II) 2.5, TR(III) 1.8.

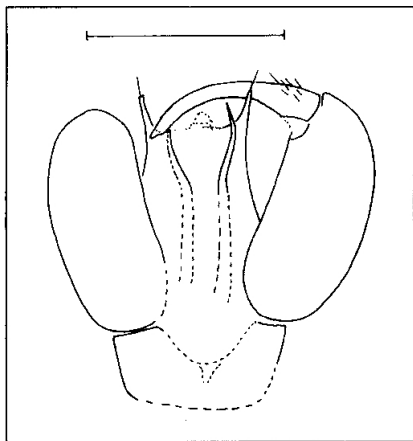
**Material examined** (2♂♂ 1♀): Holotype ♀ of *Ceratopogon (Fanthamia) frigidus*, PIN 3311/371. Paratype ♂ of *Ceratopogon (Fanthamia) frigidus* PIN 3311/411. Paratype ♂ of *Culicoides sphenostylus*, PIN 3311/404.

***Peronehelea sibirica* spec. nov.** (Figs. 42, 43 a-h)

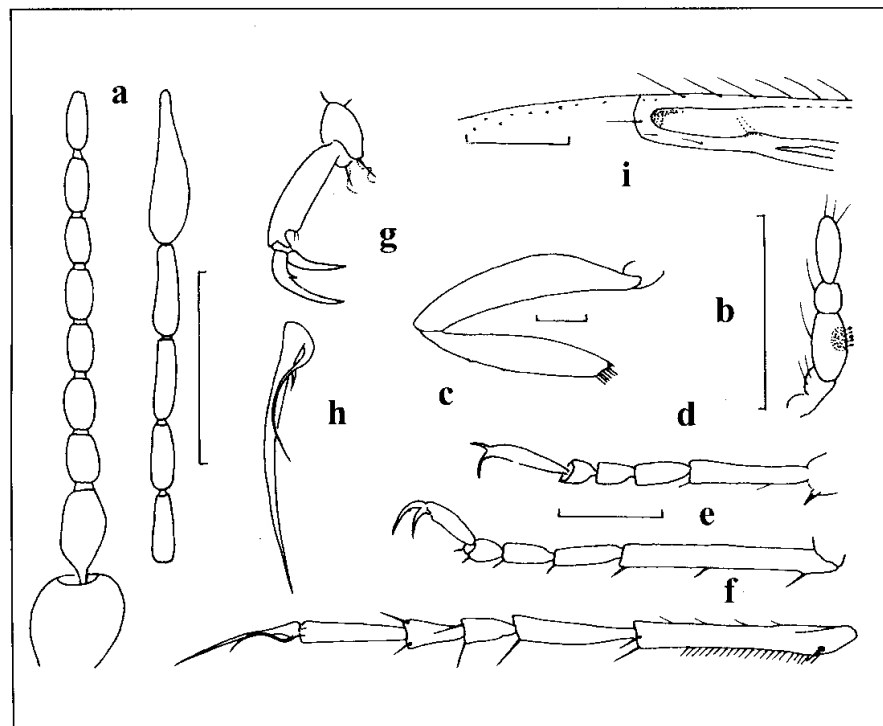
**Diagnosis:** shorter branch of female hind claw sinuous, wing membrane covered with normal microtrichia on anterior margin; hind 4th tarsomere cylindrical.

**Description:** ♂: doubtful. Similar to paratype male of *Peronehelea frigida*. **Thorax:** scutellum with 4 long setae. **Legs:** hind tibial spur small. TR(III) 2.2. **Wing** length 0.78 mm, CR 0.59, length of costa 0.46 mm. Both first radial cells present; microtrichia and macrotrichia not visible. **Genitalia** inverted. Sternite IX probably with distinct caudomedian excavation. Apicolateral processes of tergite IX short, armed with apical seta (Fig. 42). Gonocoxite moderately stout. Gonostylus slender, evenly bent. Aedeagus barely visible, on distal portion stout and moderately curved.

♀: body length 1.6 mm. **Head:** eye separation not visible. Flagellum (Fig. 43 a) with flagellomeres 2-13 gradually increasing in length; total length 496 µm, AR about 1.0; sensilla coeloconica not visible. Palpus 5-segmented; 3rd palpal segment about 40 µm long, with well defined sensory pit (Fig. 43 b). **Thorax:** scutum barely visible. **Legs:** fore and middle legs slender, femur, tibia of hind leg greatly enlarged (Fig. 43 c). Basitarsus of middle leg with subbasal, median



**Fig. 42:** *Peronehelea sibirica* spec. nov., doubtful male PIN 3311/403, ventral aspect of genitalia. Scale bar = 0.1 mm



**Fig. 43 (a-i):** *Peronehelea sibirica* spec. nov., female holotype PIN 3311/432; - a: flagellum; - b: palpus; - c: femur and tibia of hind leg; - d: tarsus of fore leg; - e: tarsus of middle leg; - f: tarsus of hind leg; - g: 5th and 4th tarsomeres of middle leg; - h: claw of hind leg; - i: radial cells. Scale bar = 0.1 mm.

and apical spine. Basitarsus of hind leg with distinct subbasal spine and row of palisade setae reaching 2/3 length of segment. Fourth tarsomeres of fore and middle legs short, almost cordiform, while of hind leg cylindrical (Fig. 43 d-g). Claws of fore and mid legs short, equal, each with basal inner tooth (Fig. 43 g). Claw of hind leg complex, composed of elongated C-shaped talon, shorter sinuous branch and basal inner tooth (Fig. 43 h). TR(I) 2.2, TR(II) 3.1, TR(III) 1.8. **Wing** length about 0.90 mm. First radial cell clearly visible, second barely visible but detectable. Macrotrichia at wing tip present, microtrichia of equal density (Fig. 43 i). **Abdomen** with short cerci.

**Material examined** (1 ♂ 1 ♀): Holotype ♀, Siberian amber, Coniacian-Santonian, Yantardakh, PIN 3311/432. Not included in the type series 1 ♂, PIN 3311/403.

### Genus *Washingtonhelea* WIRTH et GROGAN, 1988

*Washingtonhelea* WIRTH & GROGAN, 1988: 97;

Type-species *Washingtonhelea frommeri* WIRTH et GROGAN, 1988, by original designation.

**Diagnosis:** females characteristic in having short, equal, simple claws on all legs; both radial cells well developed; legs moderately slender, unarmed. Upper Cretaceous - Recent.

#### Discussion

Within the predatory biting midges only a few extant genera include females with small, simple, equal claws (e.g. *Nannohelea* WIRTH et GROGAN). However, these genera are usually highly modified with greatly reduced wing venation, lower number of palpal segments or flagellomeres, etc. and clearly are not related to *Washingtonhelea* which is the only genus of the tribe Ceratopogonini with females having short, simple equal claws and is fully adapted to feed on insects. I also consider *Ceratopogon aquilonius* BOESEL, 1937 from Canadian amber to be a member of *Washingtonhelea*. This species was placed by BORKENT (1995) in *Palaeobrachypogon* BORKENT. At present it cannot be resolved whether the character state "simple claws" is plesiotypic or apotypic to the genus. Bifid apices of the female claws of the type-species *W. frommeri* mentioned by WIRTH & GROGAN (l.c.) are not unique within the tribe or family. *W. taimyrica* spec. nov. has first tarsomere of hind leg with distinct subbasal spine and incomplete row of palisade setae, *W. aquilonia* similarly but with a complete row of palisade setae (BORKENT 1995) while extant *W. frommeri* is lacking the subbasal spine and palisade setae. These differences are rather of specific level (as in *Ceratopogon* MEIGEN or *Stilobezzia* KIEFFER). The fossil species of the genus are more plesiomorphic than extant *W. frommeri* also in having macrotrichia on wing membrane as *Ceratopogon* or *Brachypogon* from Baltic amber in relation to extant species.

#### Key to species of *Washingtonhelea*

##### Females

- |   |  |   |
|---|--|---|
| 1 | Wing membrane bare. 3 terminal flagellomeres elongate .....                |   |
|   | ..... <i>W. frommeri</i> WIRTH et GROGAN (extant, California)              |   |
| - | Wing membrane with macrotrichia. 2-3 terminal flagellomeres elongate ..... | 2 |
| 2 | 3 terminal flagellomeres elongate. Wing length 0.65-0.74 mm .....          |   |
|   | ..... <i>W. aquilonia</i> (BOESEL, 1937) comb. nov. (Canadian amber),      |   |
| - | 2 terminal flagellomeres elongate. Wing length 0.56 mm .....               |   |
|   | ..... <i>W. taimyrica</i> spec. nov. (Taimyr amber)                        |   |



*Washingtonhelea taimyrica* spec. nov. (Figs. 44 a-f, 50 d)

**Diagnosis:** the only species of the tribe Ceratopogonini with females having 2 well developed radial cells, macrotrichia at wing tip, slender legs and simple, short, equal claws. Moreover 2 terminal flagellomeres elongate. Male unknown. Upper Cretaceous.

**Description:** ♂: unknown.

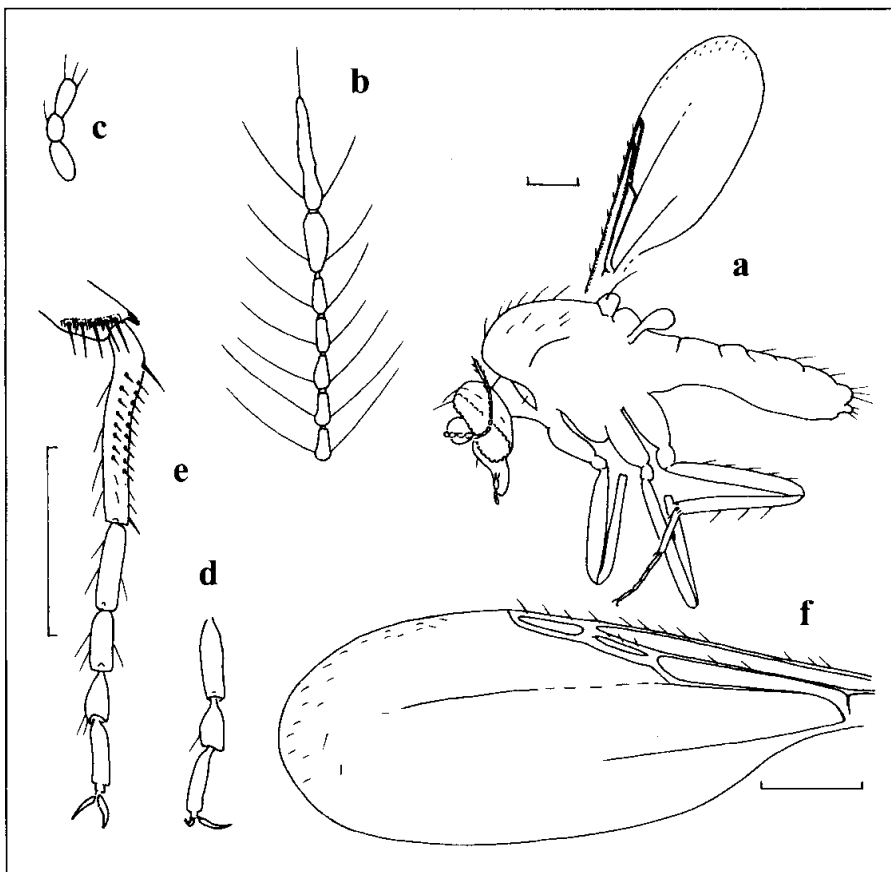
♀: body length 0.8 mm. Total habitus as in Figs. 44 a, 50 d. **Head:** eyes separation not visible. Flagellum obliquely situated in amber. Only 2 terminal flagellomeres distinctly longer than preceding ones (Fig. 44 b). Proboscis short. Palpus 5-segmented, 3rd palpal segment short (Fig. 44 c). **Thorax:** scutum with sparse long setae. Scutellum possibly with 2 strong submedian setae. Lateral sclerites barely visible. **Legs** slender, unarmed. Tibial spur of fore leg distinct, spine-like. Hind tibial spur short; tibial comb composed of 5 spines; hind basitarsus slightly bent, with distinct subbasal spine and 2 rows of palisade setae ending at 2/3 of tarsomere (Fig. 44 e). Fourth tarsomeres cylindrical, claws short, equal, simple (Fig. 44 d). **Wing** length 0.56 mm, CR 0.59. Both radial cells well developed, almost same length (Fig. 44 f). Some macrotrichia present along wing apex. Median veins barely visible. **Abdomen:** cerci short. Structures of genitalia not visible.

**Material examined** (1♀): Holotype ♀, PIN 3311/375, Siberian amber, Yandardakh in Taimyr, Coniacian-Santonian, Upper Cretaceous. Present with the holotype 1 male of Chironomidae.

**Discussion**

The position of a chironomid male and the female of the new species in amber (Fig. 50 d) may suggest that they were trapped in resin together when the predatory biting midge caught a prey. The suggested prey is distinctly larger than the predator as it has a wing length 1.5 times and thorax 1.6 times larger. This may be an evidence against BORKENT'S

(1995) suggestion that slightly enlarged claws of *Washingtonhelea aquilonia* indicated that they fed on preys which were of similar or smaller size. Moreover, it is not easy to find in the field chironomids which are smaller than small predators of the tribe Ceratopogonini, including those with enlarged claws.



**Fig. 44 (a-f):** *Washingtonhelea taimyrica* spec. nov., holotype female, PIN 3311/375; - a: habitus; - b: distal flagellomeres; - c: palpus; - d: distal tarsomeres of mid leg; - e: hind tarsus; - f: wing. Scale bar = 0.1 mm.



## Discussion

### Cretaceous faunas

The taxonomic and quantitative composition of the Lower Cretaceous biting midges fauna is very different from the Upper Cretaceous, as well as the latter from Tertiary faunas (Table, Fig. 45). Among Lower Cretaceous biting midges the subfamily Austroconopinae predominates, while among Upper Cretaceous faunas Atriculicoidini and Ceratopogoninae are the most common.

ZHERIKHIN (1978) concluded that the Neocomian (Lower Cretaceous) should be recognized as a final stage of the evolution of the Mesozoic insects and generally its entomofauna is similar to that of the Jurassic. By the analogy the Jurassic biting midges fauna should be composed mostly of Austroconopinae.

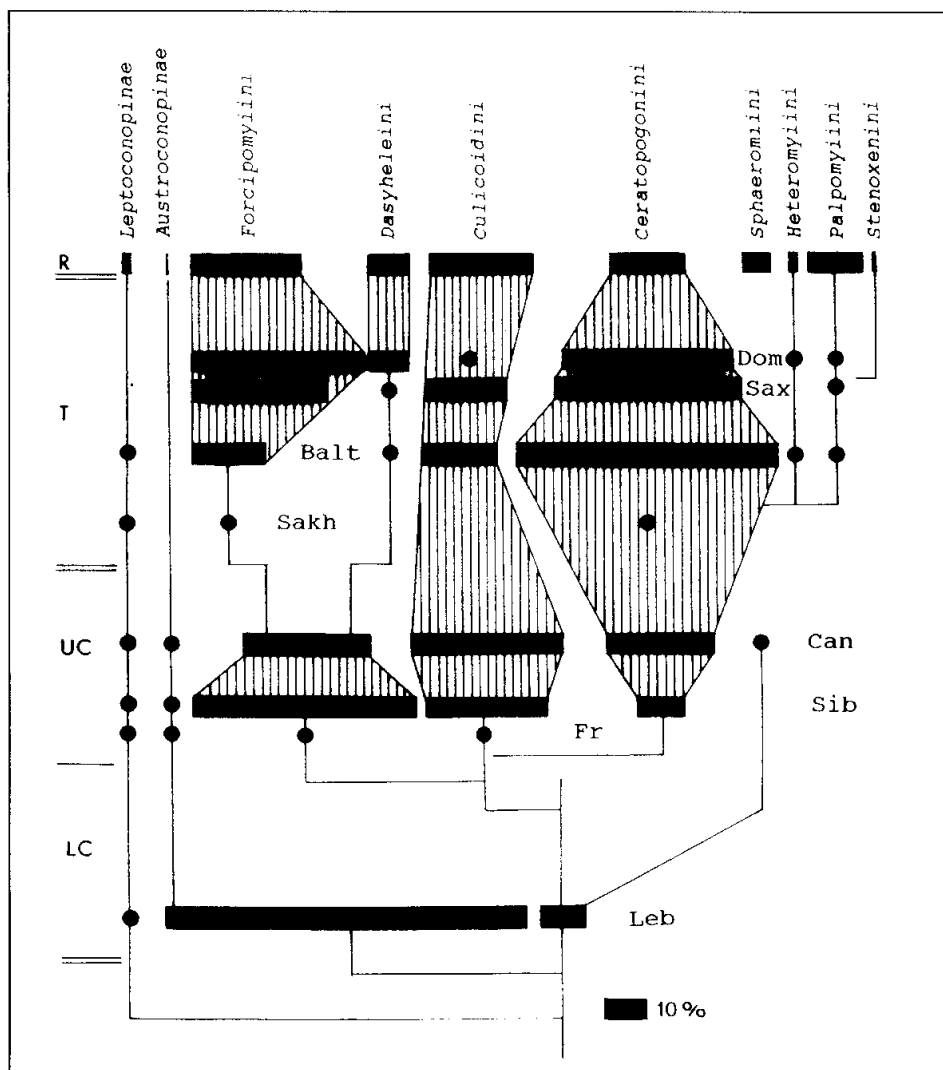
The important faunal turnover among insects took place between the Lower and Upper Cretaceous (ZHERIKHIN l.c.). This is observed among biting midges too. During the Upper Cretaceous evolved extant subfamilies which form Tertiary and extant faunas.

**Table:** Numbers of specimens examined. Abbr. **Leb** - Lower Cretaceous Lebanese amber, **Aga** - Upper Cenomanian amber of Taimyr from Agapa, **Yan** - Coniacian - Santonian amber of Taimyr from Yantardakh, † - extinct

<b>Taxon</b>	<b>Leb</b>	<b>Aga</b>	<b>Yan</b>	<b>Total</b>
<b>Stem groups</b>	<b>3</b>	-	-	<b>3 (3♀♀)</b>
† <i>Archiculicoides</i> gen. nov.	1	-	-	1 (1♀)
† <i>Lebanoculicoides</i> gen. nov.	1	-	-	1 (1♀)
† <i>Protoculicoides</i> BOESEL	1	-	-	1 (1♀)
<b>Austroconopinae</b>	<b>26</b>	-	<b>2</b>	<b>28 (17♂♂ 10♀♀ 1?)</b>
† <i>Archiaustroconops</i>	3	-	-	3 (1♂ 2♀♀)
<i>Austroconops</i> WIRTH et LEE	14	-	2	16 (11♂♂ 5♀♀)
† <i>Lebanconops</i> gen. nov.	8	-	-	8 (4♂♂ 3♀♀ 1?)
† <i>Minyohelea</i> BORKENT	1	-	-	1 (1♂)
<b>Leptoconopinae</b>	<b>1</b>	-	<b>3</b>	<b>6 (4♂♂ 2♀♀)</b>
† <i>Fossileptoconops</i> gen. nov.	1	-	-	1 (1♀)
<i>Leptoconops</i> SKUSE	-	2	3	5 (4♂♂ 1♀)
<b>Forcipomyiinae</b>	-	<b>4</b>	<b>47</b>	<b>51 (11♂♂ 40♀♀)</b>
<b>Atriculicoidini tribus nov.</b>				
† <i>Atriculicoides</i> REMM	-	4	47	51 (11♂♂ 40♀♀)
<b>Ceratopogoninae</b>	-	-	<b>42</b>	<b>42 (18♂♂ 24♀♀)</b>
<b>Culicoidini</b>	-	-	<b>27</b>	<b>27 (9♂♂ 18♀♀)</b>
<i>Culicoides</i> LATREILLE	-	-	27	27 (9♂♂ 18♀♀)
<b>Ceratopogonini</b>	-	-	<b>15</b>	<b>15 (9♂♂ 6♀♀)</b>
† <i>Brachycretacea</i> gen. nov.	-	-	1	1 (1♂)
<i>Ceratopogon</i> MEIGEN	-	-	3	3 (2♂♂ 1♀)
† <i>Peronehelea</i> BORKENT	-	-	5	5 (3♂♂ 2♀♀)
<i>Washingtonhelea</i> WIRTH et GROGAN	-	-	1	1 (1♀)
<b>Indetermined</b>	-	-	<b>3</b>	<b>3 (sex?)</b>
<b>Total</b>	<b>30</b>			<b>133 (50♂♂ 79♀♀ 4?)</b>

The genus *Atriculicoides* can be considered as an indicator group characteristic of the Upper Cretaceous period. Its evolution, as well as that of the Forcipomyiini during Tertiary, was probably associated with the growing importance of pine and deciduous forests in land ecosystems since the Upper Cretaceous.

In the Lower Cretaceous only 1 extant genus is known (12.5%), while in Upper Cretaceous Siberian amber 5 (41.7%) extant genera have been recorded. In European Lower Eocene Baltic amber the rate of extant genera is 75%, in Miocene Saxonian amber it is

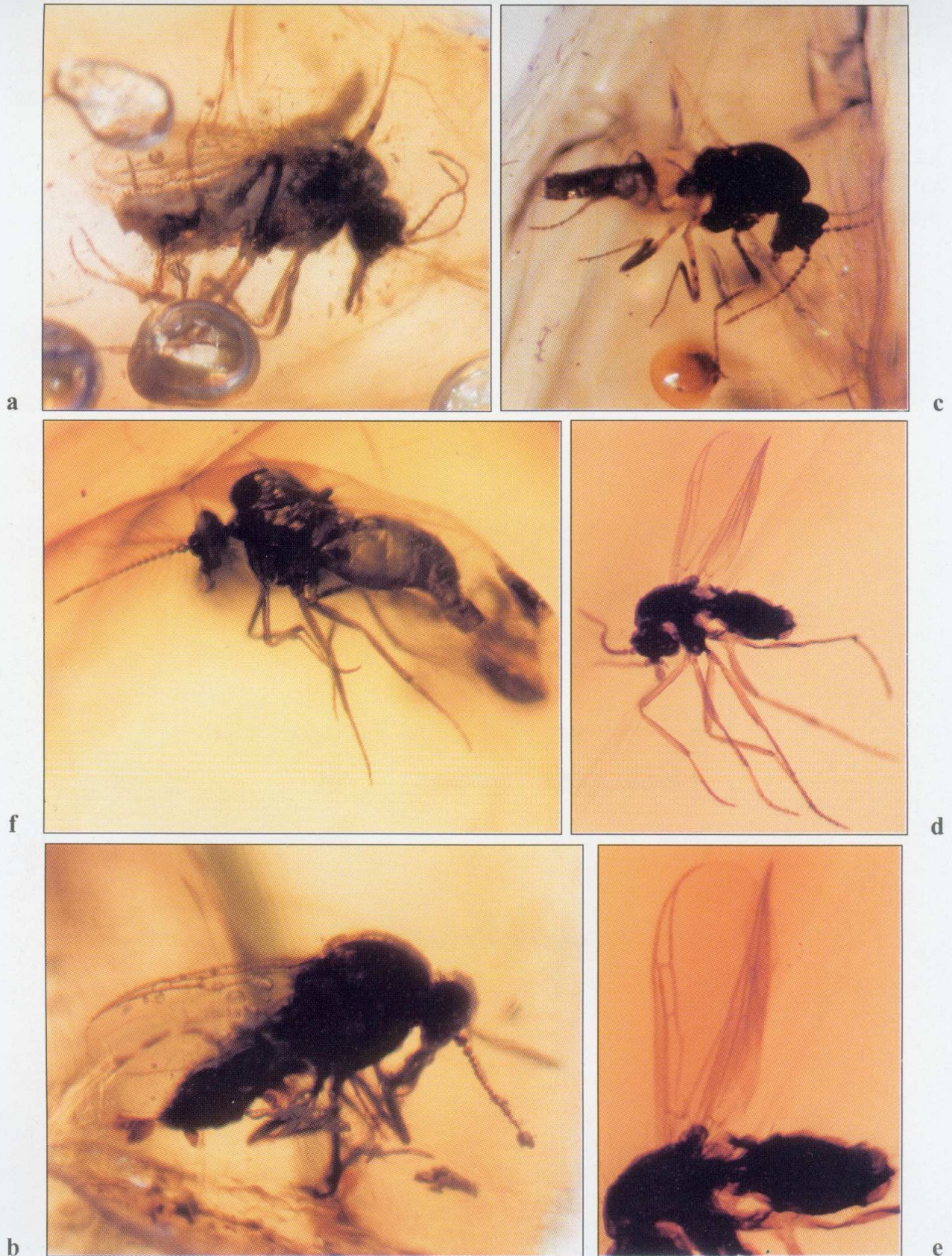


**Fig. 45:** Quantitative composition of the Ceratopogonidae of the Cretaceous and Tertiary and extant faunas expressed in percentages using number of specimens for fossil and number of species for extant biting midges. Abbr. R - Recent, T - Tertiary, UC - Upper Cretaceous, LC - Lower Cretaceous. Dom - Dominican amber (SZADZIEWSKI & GROGAN 1994); Sax - Saxonian amber (SZADZIEWSKI 1993); Balt - Baltic amber (SZADZIEWSKI 1988); Sakh - Sakhalin amber (SZADZIEWSKI 1990b); Can - Canadian amber (BORRANT 1995); Fr - French and New Jersey amber (GROGAN & SZADZIEWSKI 1988; SZADZIEWSKI & SCHLÜTER 1992); Sib - Siberian or Taimyr amber (present materials); Leb - Lebanese amber (present materials).

79% (SZADZIEWSKI 1993), while all genera recorded from Miocene-Oligocene Dominican amber are extant (SZADZIEWSKI & GROGAN 1994).

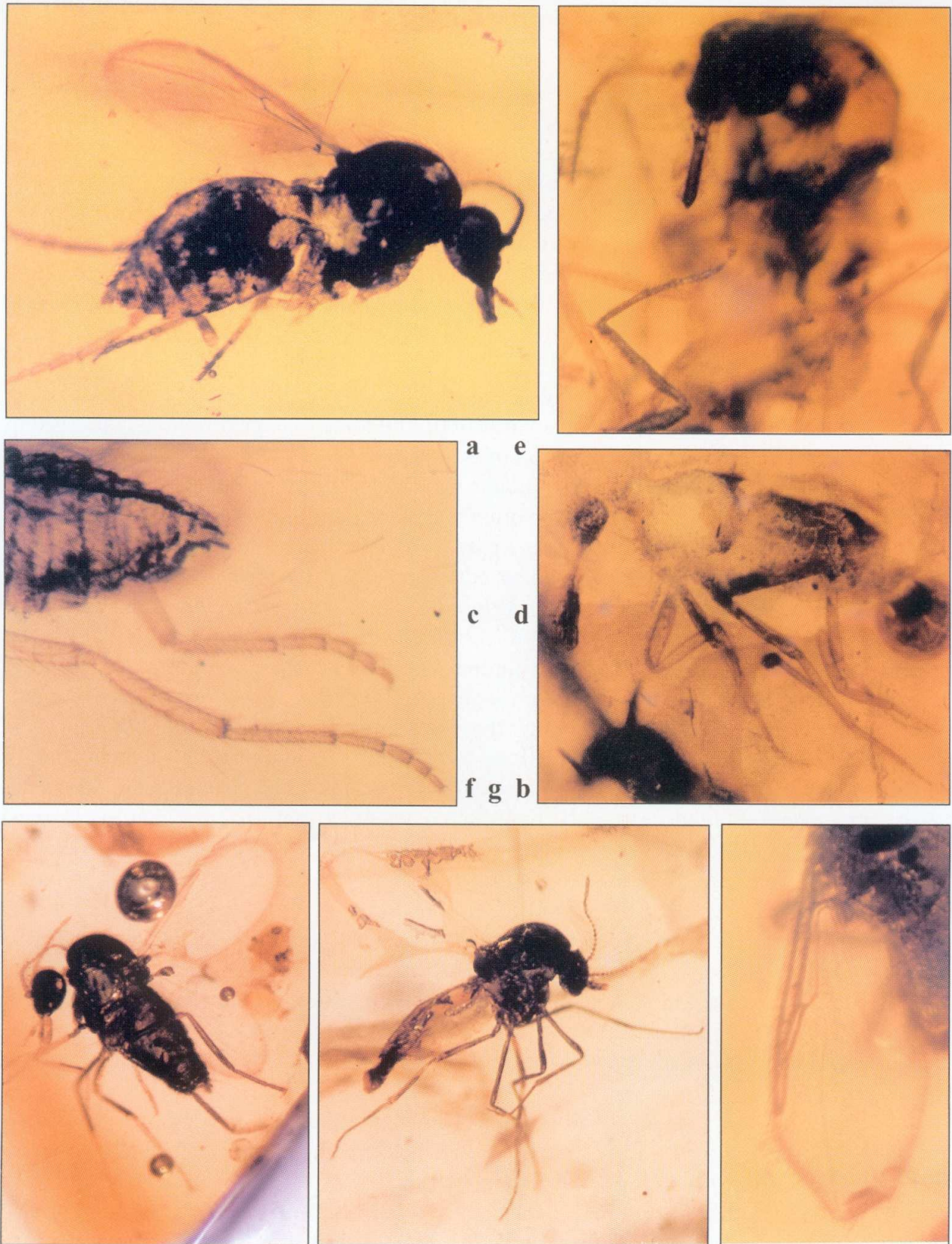
The biting midges are small and well preserved only as inclusions in fossil resins and the Lower Cretaceous fossils probably will be the oldest available materials of taxonomic value.





**Fig. 48 (a-f):** Biting midges from Cretaceous amber (a-e: Biting midges from Lebanese amber, f: Biting midge from Siberian amber): - **a:** *Lebanoculicoides mesozoicus* spec. nov., female, SMNS C32/23; - **b:** *Protoculicoides succineus* spec. nov., female, SMNS C3114; - **c:** *Minyohelea schleei* spec. nov., male SMNS 32/74; - **d:** *Austroconops* indet. female, SMNS C2; - **e:** wing venation of female of *Austroconops* indet., SMNS C2; - **f:** *Atriculicoides macrophthalmus* REMM, paratype male PIN 3311/398 (for female of this species is see fig 50 e).





**Fig. 49 (a-g):** Biting midges from Siberian amber (a-c: *Atriculicoides* females, d-g: biting midges of other genera): - **a:** *Atriculicoides*, lateral aspect female indet., PIN 3426/244; - **b:** wing of female indet., PIN 3426/241; - **c:** hind leg of *A. macrophthalmus* REMM, paratype PIN 3311/378; - **d:** *Culicoides filipalpis* REMM, female PIN 3311/426.b; - **e:** *Culicoides kaluginae* REMM, female head with elongate proboscis, PIN 3311/426; - **f:** *Culicoides succineus* REMM, female PIN 3311/395; - **g:** *Austroconops sibiricus* spec. nov., male PIN 3311/417.

### Evolution of feeding habits

The present study of Lower Cretaceous biting midges supports the hypothesis (DOWNES 1978, GROGAN & SZADZIEWSKI 1988, SZADZIEWSKI 1988, BORKENT 1995) that feeding by females on the blood of vertebrates is a plesiotypic feature of the family.

Females of a basal lineage and of the earliest successful lineages (Austroconopinae and Leptoconopinae) were certainly haematophagous parasites of vertebrates (Figs. 45, 46). The plesiotypic type of feeding is preserved in extant Leptoconopinae, Austroconopinae, as well as within *Culicoides* within the Ceratopogoninae. The latter likely evolved from the stock of such haematophages in the Upper Cretaceous. Presumably during the Tertiary within the lineage of insect parasites in the Forcipomyiinae secondarily evolved midges feeding on blood of mammals and amphibians (subgenus *Lasiohelea* KIEFFER of *Forcipomyia*).

During the Upper Cretaceous parasites evolved which fed on the haemolymph of larger insects, represented by *Atriculicoides* in the Forcipomyiinae lineage. Previously this group was recognized to feed on vertebrate blood by SZADZIEWSKI & SCHLÜTER (1992) and BORKENT (1995). Present examination of more females shows that they have relatively deeply bifid apices of claws, with an inner tooth or branch shorter than the outer one. These closely resemble those found in females of many extant *Atrichopogon* and some *Forcipomyia* of unknown feeding habit or parasitic on insects (present obs.). Females of the subgenus *Lasiohelea* which secondarily feed on vertebrate blood within *Forcipomyia* again have single apices. However, feeding habit of *Atriculicoides* cannot be determined conclusively, and a blood-sucking habit cannot be excluded, as slightly bifid claws are present also in females of some haematophagous biting midges, such as *Culicoides nubeculosus* (MEIGEN). Males usually have bifid claws, although these are sometimes difficult to observe.

The general correlation between the possession of finely serrated mandibles, laciniae with retrorse teeth and the feeding habit on blood of vertebrates within Nematocera (BORKENT 1995) can be applied to indicate only that the females of extinct *Atriculicoides* were parasites on insects or vertebrates. Actually teeth of female laciniae within extant Forcipomyiini feeding on blood of amphibians [*Forcipomyia (Lasiohelea) velox* (WINNERTZ)], on blood of mammals (*F. sibirica* BUJANOVA) and feeding on haemolymph of insects [*Forcipomyia fuliginosa* (MEIGEN), *Atrichopogon winnertzi* GOETGHEBUER] (present examination; see also GLUKHOVA 1981) are very similar and more or less retrorse. Moreover, teeth of laciniae are difficult to discern even in extant females mounted on slides, so their shape observed in Canadian amber by BORKENT (1995) should be treated with a great caution and should not be an evidence in the discussion what females of *Atriculicoides* ate during the Upper Cretaceous.

Within the Forcipomyiini some pollinophages and saprophages evolved during the Tertiary within *Atrichopogon*. At the end of Cretaceous or during the Tertiary *Dasyheleini* evolved which stopped feeding on a protein-rich meal.

During the Upper Cretaceous period insectivour predators of the tribe Ceratopogonini probably evolved from a stock of haematophages. Other tribes of predatory Ceratopogoninae which inject proteolytic enzymes into a prey in order to dissolve its solid tissues are known only from the Tertiary. However, so late an origin of those predators based on paleontological records cannot be supported by biogeographical patterns because the most apomorphic tribe Stenoxenini of that group now lives only in Africa and South America (some species migrated to Central America and southern states of the USA), and both continents lost land connections on the beginning of the Cretaceous period. Obviously, the recent distri-

bution of the Stenoxenini may also be explained by migrations during the Tertiary via Europe or across the Atlantic Ocean, or that they were present in the Northern Hemisphere during Tertiary, etc.

It is possible that within the infraorder Culicomorpha the blood sucking habit is the plesiotypic feature of females as suggested by Wood & BORKENT (1989) and BORKENT (1995). That habit would totally be lost in Dixidae, Chironomidae, all Thaumaleidae, Chaoboridae, some Ceratopogonidae and some Simuliidae. It is likely that the haematophagy of Culicidae evolved secondarily by reversion to the plesiotypic condition of the infraorder during the Upper Cretaceous when they branched from the Chaoboridae which do not take a protein meal. The Chaoboridae are known as a diverse group since the Lower Jurassic (KALUGINA 1977) while Culicidae since the Upper Cretaceous (EVENHUIS 1994). The ancestral or plesiotypic feeding habit of lower Diptera adults and the origin of blood sucking has been a subject of many speculations supported by various investigations and observations. All possible hypotheses on the primitive feeding mode have been put forward: 1/ saprophagy (GLUKHOVA 1989), 2/insectophagy (BEKLEMISHEV 1957, ROHDENDORF 1964, REMM 1975, NARTSHUK 1977), 3/haematophagy (MARTINI 1932, DOWNES 1978), and 4/phytophagy (MONCHADSKII 1936, RUBTSOV 1974).

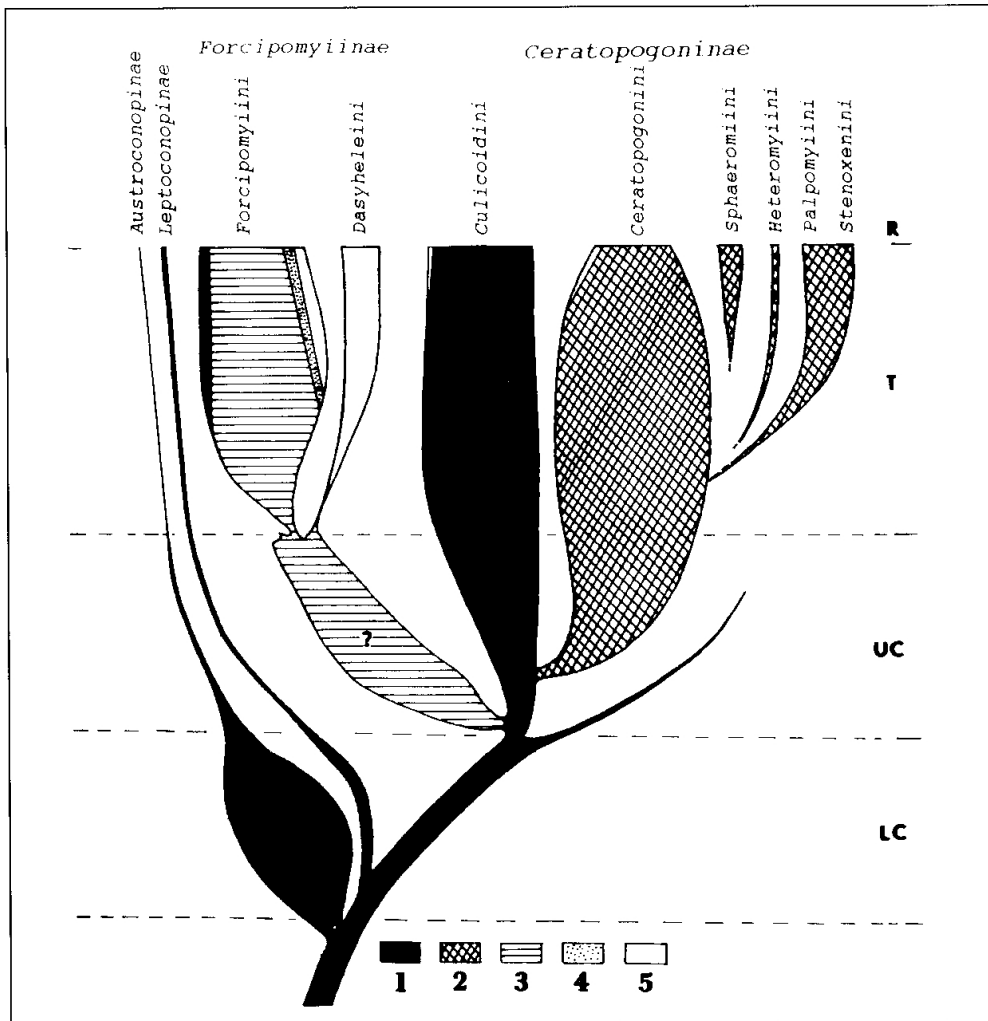
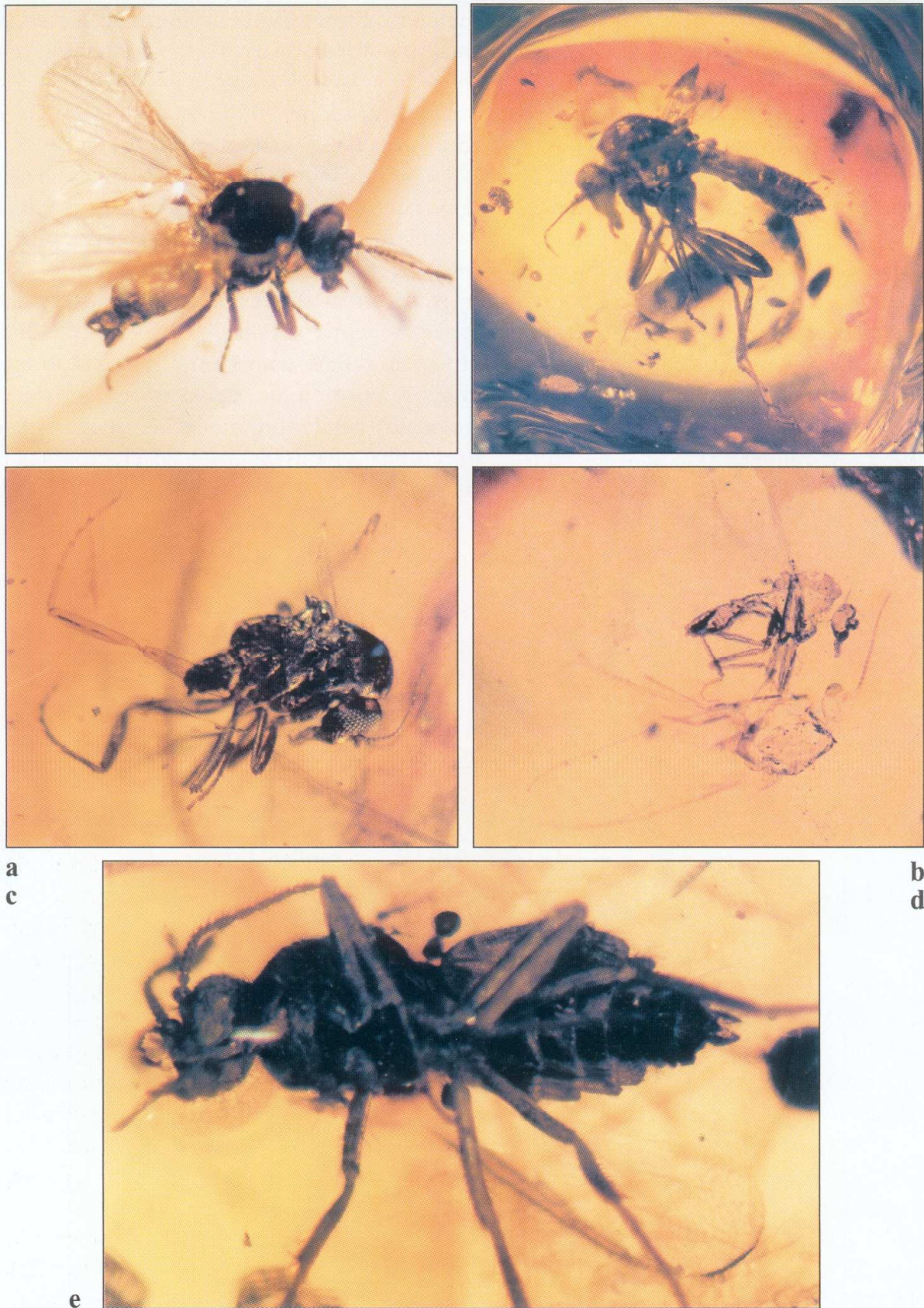


Fig. 46: Evolution of female feeding habits of Ceratopogonidae. Abbr. R - Recent, T - Tertiary, UC - Upper Cretaceous, LC - Lower Cretaceous, 1 - haematophagous parasites on vertebrates, 2 - insectivour predators, 3 - haemolymphophagous parasites, 4 - polliniphagous or necrophagous (dead insects), 5 - nectarophagous.





**Fig. 50 (a-e):** Biting midges from Siberian amber. (a-d: predatory biting midges, e: female of *Atriculicoides macrophthalmus* REMM); - **a:** *Brachycretacea taimyrica* (REMM), male PIN 3311/401; - **b:** *Ceratopogon macronyx* REMM, female, PIN 3311/372; - **c:** *Peronehelea frigida* (REMM), female, PIN 3311/371; - **d:** *Washingtonhelea taimyrica* spec. nov., female with a chironomid prey, PIN 3311/375; - **e:** *Atriculicoides macrophthalmus* REMM, paratype female 3311/382 (for male of this species see fig. 49 f).



All hypotheses agreeing with the DOLLO rule are based on the fact that functional, piercing, mouthparts should be continuously present in all old dipteran lineages which used the proboscis to feed on liquid rotting debris (saprophagy), to pierce insects (insectophagy) or vertebrates (haematophagy) or to feed on plants (phytophagy). Subsequently, mouthparts were reduced in most lineages and became unsuitable for piercing. Two explanations, haematophagy or insectophagy, are the most widely accepted by dipterists, are logical and may be supported by fossils. The Tanyderidae forming the oldest lineage within Diptera (KRZEMIŃSKI 1992), which evolved during the Triassic probably had well developed mouthparts and probably were able to take blood or haemolymph (KALUGINA 1991, BORKENT 1995).

The most extensively developed scenario of origin and evolution of feeding habits within Diptera and Ceratopogonidae was presented by GLUKHOVA (1989). According to her saprophagous theory, haematophagy evolved by a series of transformations from plesiotypic feeding on debris with the help of proteolytic enzymes, to feeding on dead large vertebrates, then on external secretions of vertebrates and finally on their blood. That scenario may be applied to the explanation of the evolution of blood-sucking Muscidae but is unlikely for lower Diptera and is not confirmed by paleontological data.

Based on the fact that during the evolution of each group reversions are common to the plesiotypic conditions I suggest that the evolution of the feeding habit of Diptera may be explained more simply, i.e. that plesiotypic for the Diptera is feeding, both males and females, on carbohydrates of plant origin derived from honey-dew, nectar, sap seeping from wounds, juice from fruits, etc.). Feeding of lower Diptera such as Ceratopogonidae and Chironomidae on honey-dew was observed by DOWNES (1978, p. 31). The most plesiotypic Diptera had more or less reduced mouthparts unsuitable for piercing and they used relatively short and broad proboscis to drink water and carbohydrates of plant origin. All oldest fossil Diptera had short proboscis (KRZEMIŃSKI, personal comm.). That type of adult feeding is preserved almost in all groups of extant Diptera. Cutting and piercing functional female mouthparts evolved secondarily few times within nematocerous Diptera simply by reversion to the more plesiotypic condition of the Diptera ancestor (Mecoptera like?). Reversions or returning to plesiotypic condition or habit are common events during the evolution of each group. For example, if the hypothesis presented by WOOD & BORKENT (1989) that Culicidae and Chaoboridae are sister groups is correct, then the Culicidae evolved during the Upper Cretaceous from very old Chaoboridae which evolved at least in the Lower Jurassic. Extant and, at least, Tertiary chaoborids lost their functional mouthparts and fed/or feed exclusively on nectar or similar food. From that lineage evolved culicids with long piercing proboscis armed with all orthopteroid elements. In summary I support the phytophagous hypothesis, that feeding on carbohydrates of plant origin is a plesiotypic habit for the Diptera while the supplementary feeding on protein-rich meal by females evolved secondarily (in many groups of lower and higher Diptera, incl. parasites and predators of insects, vertebrate haematophags).

The phytophagous hypothesis supports the fact that the plesiotypic feeding habit should be similar for both sexes as in other insects. This argument suggests that feeding of females on proteins evolved secondarily. In those groups of lower Diptera which secondarily acquired a piercing proboscis only females use it to take protein-rich meal (blood of vertebrates, haemolymph and liquefied solid tissues of living and dead insects, juice from pollens). In addition females have retained the plesiotypic habit of feeding on carbohydrates as males. Honey-dew could have been produced by some Homoptera since the Upper Palaeozoic, while nectar was a likely food source since the Lower Cretaceous (GRINFELD 1978).

## Phylogeny

Phylogenetic analyses of biting midges have been developed mostly by BORKENT. Studies of fossils are helpful in the determination of character polarity. It seems that outgroup comparisons without paleontological data cannot show the correct direction of character changes during phylogeny, as reversions or secondary developments of the same character states are very common.

The history of the Ceratopogonidae probably goes back at least to the Mid Jurassic. During the Triassic many secondarily aquatic insects evolved, while during the Jurassic inland waters became oligotrophic. During that time among aquatic insects evolved groups with predatory larvae (KALUGINA 1977). The oldest known Culicomorpha are Chaoboridae and Chironomidae (Podonominae) with predatory larvae recorded from Lower Jurassic deposits (KALUGINA 1977, 1991).

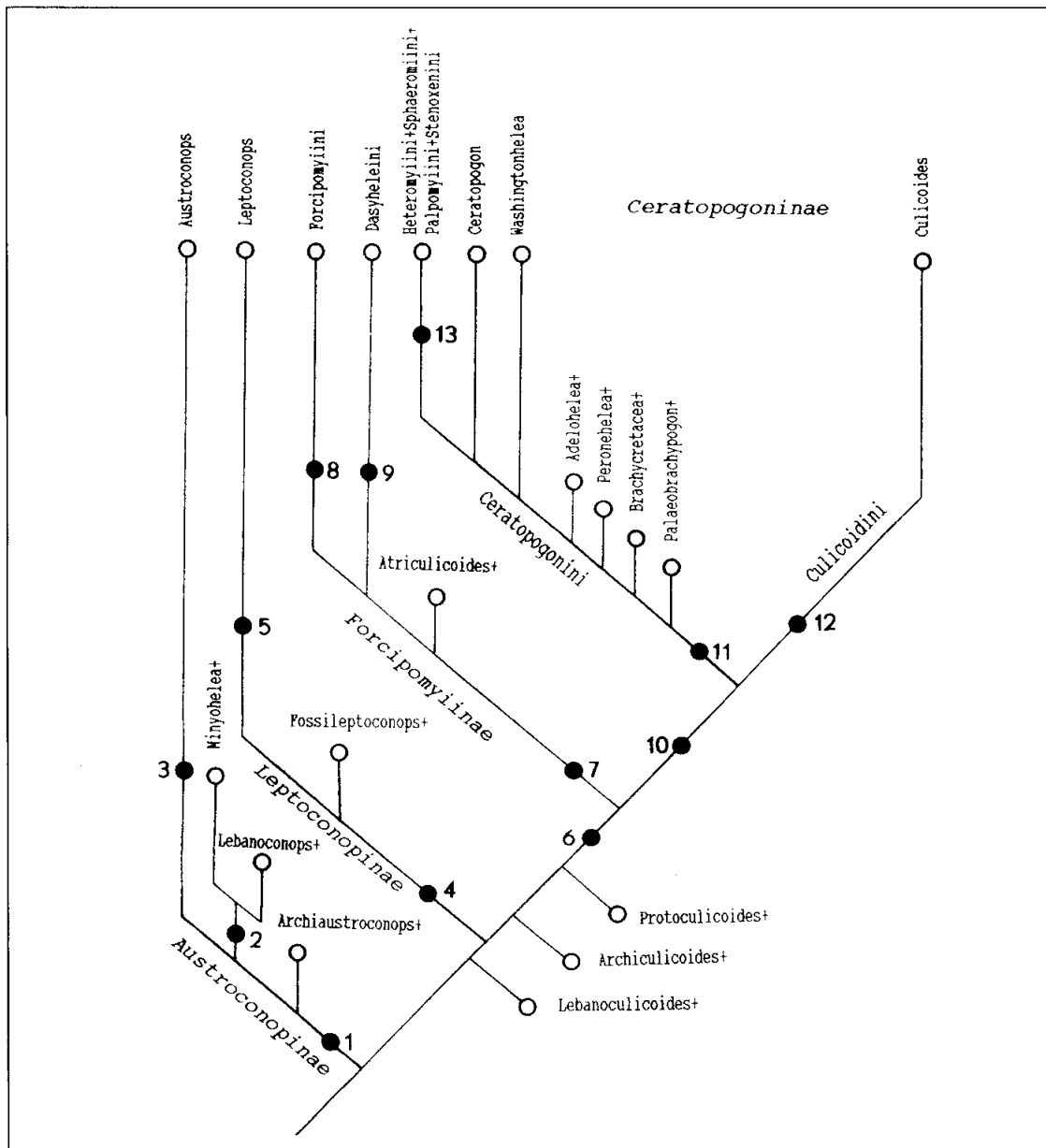
All other families of the infraorder have been recorded from the Lower Cretaceous, except for the Culicidae reported from the Upper Cretaceous (EVENHUIS 1994).

The cladogram proposed below (Fig. 47) includes new data and interpretations of character polarity differing in some points from those proposed by BORKENT et al. (1987), SZADZIEWSKI (1988), and BORKENT (1995). Some character states proposed by BORKENT which are barely visible in amber or need further investigations are not included. I propose here many paraphyletic groups (without synapomorphies).

Only few synapomorphies could be proposed for the whole of the Ceratopogonidae: 1/ unique larval pharyngeal apparatus acting as pumping, and crushing and sifting structure used to suck destroyed tissues from inside a prey (BORKENT et al. 1987; SZADZIEWSKI 1988; BORKENT 1995) 2/ prolegs absent in larvae of II-IV instars; this is an adaptation to a special predatory mode of feeding in which older larvae make a hole in a prey and feed inside its body; prolegs in Forcipomyiinae developed secondarily (SZADZIEWSKI 1988, trend 4.2), 3/ vertex without longitudinal or sagittal suture. Within Culicomorpha all or almost all adults bearing plumose male antennae (Chironomidae, Chaoboridae, Culicidae) plus the Corethrellidae (no plume) have the vertex reinforced with a sagittal suture or suture-like plate (Chaoboridae). The sagittal suture is absent in Simuliidae, Thaumaleidae and Dixidae which traditionally are not treated as possible sister groups of Ceratopogonidae. However the opposite polarity of that character state is more likely. 4/ Female subgenital plate without notum (BORKENT et al. 1987). In some Forcipomyiinae a notum is present but probably developed secondarily.

The following synapomorphies are used to explain the phylogeny within the Ceratopogonidae (Fig. 47). (a - apomorphic, p - plesiomorphic character state).

- 1.1. Tarsal ratio of all legs similar (p); tarsal ratio of hind leg distinctly lower than that of fore and mid legs (a). The apomorphic character state is unique within the Culicomorpha.
- 1.2. Palpus 5-segmented (p); 4 segmented (a). The apomorphic state highly homoplastic, evolving many times within different lineages. Only one species within Austroconopiniae has reverted to the plesiotypic condition.
- 2.1. Radial cells long (p); very short (a).
- 3.1. Veins *r-m* transverse (p); more or less parallel to veins  $R_1$  and  $R_3$  (a).
- 4.1. Tergite X in female not modified (p); with caudomedian u-shaped dorsal excavation (a). The apomorphic condition probably is unique within the Culicomorpha.
- 4.2. Sternite X in female genitalia plate-shaped (p); fork-like (a) (SZADZIEWSKI 1986, 1988).
- 4.3. Larva with 12 segments (p); with more segments secondarily divided (a) (BORKENT et al. 1987).



**Fig. 47:** Cladogram of Ceratopogonidae showing phylogenetic positions of fossil and extant genera recorded in Cretaceous ambers. [*Heleageron* BORKENT from Canadian amber of unprecised (Forcipomyiinae or Ceratopogoninae) phylogenetic position not included]. Numbered solid black circles are synapomorphies explained in the text.

- 4.4. Head of larva strongly sclerotized (p); desclerotized with internal rods (a) (SZADZIEWSKI 1988).
- 4.5. Female cerci short (p); elongate (a) (SZADZIEWSKI 1988; BORKENT 1995). Within some extant *Leptoconops* short cerci evolved secondarily.
- 4.6. Vertex and frons separated (p); fused (a). BORKENT (1995) proposed the opposite polarity. Fusion of vertex and frons has evolved several times within the Culicomorpha (Simuliidae, Thaumaleidae, Leptoconopinae). In Chaoboridae, Culicidae, Corethrellidae, Chironomidae and Dixidae vertex and frons are separated by a more or less developed suture. Within Culicomorpha there are 3 main types of construction of the head surface between eyes, 1/ vertex and frons separate which seems to be plesiomorphic condition (Dixidae, plesiotypic Ceratopogonidae), 2/ vertex and frons separate and vertex with sagittal suture (apomorphic condition a') (Chaoboridae,

- Chironomidae, Culicidae and Corethrellidae), 3/ vertex and frons fused, no sagittal suture (apomorphic condition a") (Simuliidae, Thaumaleidae, and independently in Leptoconopinae). This is weak synapomorphy and further studies are necessary.
- 4.7. Palpus 5 segmented (p); 4 segmented (a). No reversions to the plesiotypic condition within Leptoconopinae.
  - 5.1. Number of female flagellomeres 13 (p); 10-12 (a) (SZADZIEWSKI 1988).
  - 5.2. Costal vein long, prolonged beyond vein  $R_3$  (p); costa short, fused with other radial veins into stigma (a).
  - 6.1. Wing membrane bare (p); or with macrotrichia (a). Within Culicomorpha macrotrichia on the wing membrane are present only in Chironomidae and Ceratopogonidae and certainly their presence is not homologous. Within the Ceratopogonidae that character state evolved independently of Chironomidae during the Upper Cretaceous in the Forcipomyiinae + Ceratopogoninae lineage, and was secondarily reduced in many younger lineages. Therefore the bare wing membrane of many Ceratopogoninae and some Forcipomyiinae is not homologous with the primarily bare wing of biting midges within the Austroconopinae, Leptoconopinae and other Cretaceous midges belonging to basal lineages (*Lebanoculicoides*, *Archiculicoides*, *Protoculicoides*).
  - 6.2. First male flagellomere with 1 whorl of plume setae (p); with 2 whorls of plume setae (a). All examined male adult Culicomorpha with an antennal plume have a single whorl of setae on the first flagellomere. The basal lineage of the Forcipomyiinae, formed by fossil *Atriculicoides*, also has 2 whorls. Secondarily within the Forcipomyiini and Dasyheleini males again exhibit the plesiotypic condition. It is possible to treat that secondary reduction as a weak synapomorphy for Forcipomyiini + Dasyheleini. Within the Ceratopogoninae some groups with a weakly developed or totally reduced plume have setae on the first flagellomere which do not form a distinct ring.
  - 6.3. Male antenna with 1 or 2 flagellomeres elongate (p); 3 or 4 terminal flagellomeres elongate (a). At present it cannot be resolved whether 1 or 2 terminal flagellomeres represent the plesiotypic condition within the family, and similarly whether 3 or 4 condition is derived. Chaoboridae and Culicidae have 2, while Chironomidae usually 1 terminal flagellomere elongated.
  - 7.1. Larva prognathous, without prolegs in instars 2-4, mostly predatory (p); larva hypognathous with distinct prolegs, saprophagous or phytophagous (a) (SZADZIEWSKI 1988). Larvae of fossil *Atriculicoides* are unknown.
  - 7.2. Parameres in male genitalia double, symmetrical (p); single, mostly asymmetrical (a). That apomorphic condition is known in some extant Dasyheleini, while in Forcipomyiini parameres again are symmetrical.
  - 7.3. Eyes with ommatidia more or less separated (p); broadly fused (a) (BORKENT 1995).
  - 8.1. Terminal flagellomere of adult with blunt or pointed apex (p); with distinct apical nipple (a) (SZADZIEWSKI 1988, BORKENT 1995). Apical prolongation is present in Corethrellidae, Culicidae, some Dasyheleini, and in *Archiculicoides* gen. nov. but these lack a distinct basal constriction.
  - 8.2. Empodium indistinct (p); empodium greatly developed, branching (a) (SZADZIEWSKI 1988).
  - 8.3. Body segments of larva almost bare (p); with distinct setae and tubercles (a) (BORKENT et al. 1987; SZADZIEWSKI 1988). Polarity of that character state (and 7.1) is not certain because larvae of *Atriculicoides* are unknown. It is more likely that a terrestrial type of larva evolved earlier and the synapomorphy would belong at node no. 7.

- 9.1. Flagellomeres not sculptured (p); sculptured (a)(BORKENT et al. 1987, SZADZIEWSKI 1988, BORKENT 1995).
- 10.1. Female and male eyes of similar size, vertex and frons separated in both sexes (p); female eyes larger than in male, vertex with additional transverse suture above lower vertical seta and frons separated (a'), lower portion of vertex and frons fused (a''). The transverse vertical suture is unique within the Diptera. However, the phylogenetic interpretation of this character is not certain. The character state a' is present in some *Culicoides*, while a'' in almost all *Culicoides* and some genera of Ceratopogonini. Distribution of character state a'' within the Ceratopogoninae exhibits the similar pattern to that of sensilla coeloconica or macrotrichia on the wing membrane. At present it can be explained that all of them are reversals within Ceratopogonini.
- 10.2. Rami of female subgenital plate fused (p); separated (a) (BORKENT et al. 1987; SZADZIEWSKI 1988). This synapomorphy is susceptible to homoplasy as all species of the subgenus *Wirthomyia* VARGAS of *Culicoides* have the plesiotypic condition.
- 11.1. Mandible with small and numerous teeth (p); with a small number of coarse teeth (a)(SZADZIEWSKI 1988).
- 11.2. Female claws without basal inner tooth (p); with basal inner tooth (a). Only within some genera have inner teeth been secondarily reduced.
- 12.1. Head of larva with simple and multiple setae (p); head with only simple setae (a). Multiple setae on the head capsule are present in all known larvae of Ceratopogoninae except for *Culicoides*, *Paradasyhelea* (KETTLE et ELSON 1975), and *Serromyia* MEIGEN (GLUKHOVA 1979). If the proposed polarity is correct then for the tribe Culicoidini (*Culicoides* + *Paradasyhelea*) would be the first reliable synapomorphy. In *Serromyia* the absence of multiple head setae can be explained by an independent reduction. The outgroup comparisons show that the present interpretation is possible because variously shaped multiple setae are common in larvae of the infraorder. In semiaquatic or aquatic larvae of Dasyheleini or terrestrial Forcipomyiini and *Leptoconops* however, all setae are simple.
- 13.1. Veins  $M_1$  and  $M_2$  petiolate (p); sessile, forking at/or proximally of level of crossvein  $r-m$  (a) (SZADZIEWSKI 1988).
- 13.2. Wing membrane with macrotrichia (p); without macrotrichia (a). Weak synapomorphy susceptible to homoplasy.

All modern classifications of biting midges proposed by dipterists (REMM 1975, BORKENT et al. 1987, SZADZIEWSKI 1988, GLUKHOVA 1989) treat the Leptoconopinae as a sister group of all other biting midges. REMM, GLUKHOVA and all other Russian authors even treat it as a separate family.

The Leptoconopinae can be treated as one of the earliest known lineages which evolved by cladogenesis from a basal lineage of the Ceratopogonidae like Austroconopinae, *Lebanoculicoides*, *Archiculicoides*, and *Protoculicoides*. Looking for synapomorphies within the basal lineage for the rest groups after the cladogenesis of any group has no practical and theoretical purpose, because after the origin of each of those groups, basal lineages continue their anagenetic evolution. The Leptoconopinae actually is the most apomorphic taxon within the family with many morphological adaptations in larvae and adults to live in sandy habitats of dry desert areas. Larvae are able to make deep burrows and adults are diurnal in activity. Within the Culicomorpha only Leptoconopinae, most Forcipomyiini and a few Orthocladiinae (Chironomidae) have secondarily become terrestrial in the larval stage.

BORKENT et al. (1987) erected the new subfamily Austroconopinae and BORKENT (1995) proposed 6 synapomorphies for Austroconopinae + Dasyheleinae + Forcipomyiinae + Ceratopogoninae, these forming a sister group of Leptoconopinae: 1/ gonostylus without apical spine, 2/ median vertical seta single, 3/ tentorium at a horizontal plane, 4/ male with bifid claws, 5/ mid tibia lacking spur, 6/ eyes moderately to narrowly separated. They all are weak synapomorphies which do not support the proposition to include Austroconopinae to the same clade together with Forcipomyiinae + Ceratopogoninae (Fig. 47). Present studies showed that plesiotypic conditions of two proposed states (1 and 5) are present in some Austroconopinae, "synapomorphy" 6 is difficult to evaluate as widely separated eyes are found not only within many Ceratopogonini, some *Culicoides* and very often within Palpomyiini and related tribes of predatory biting midges. Synapomorphies 3 and 4 proposed by BORKENT are most probably symplesiomorphies. Male claws with bifid apices are present at least in Orthoclaudiinae (Chironomidae) and a tentorium at a horizontal plane is found in Chaoboridae, Dixidae, Culicidae and Simuliidae. Synapomorphy no. 2 is difficult to confirm in oldest fossil biting midges of a basal lineage, and is absent in many "higher" Ceratopogoninae (for example *Palpomyia*, *Bezzia*). It is true that it may be explained by secondary changes.

It is impossible to find synapomorphies for Ceratopogonini because numerous reversions obscure phylogenetic relationships. It is probably a paraphyletic group as proposed by BORKENT (1995). It may be even a polyphyletic group composed of genera which evolved several times within *Culicoides*. The latter genus or Culicoidini (*Culicoides* + *Paradasyhelea*) seem to be paraphyletic groups also. BORKENT (1995) proposed a synapomorphy for *Culicoides* - at least 3 flagellomeres with sensilla coeloconica and questioned whether the Upper Cretaceous *Culicoides*, with sensilla coeloconica recorded on first flagellomere only, actually are members of that genus. However, among extant *Culicoides* a similar condition (i.e. sensilla coeloconica only on the first flagellomere) is present in *Culicoides cameroni* CAMPBELL et PELHAM-CLINTON and possibly in some others. Sensilla coeloconica are difficult to observe in fossil midges, and are clearly visible only in some specimens. Their "absence" cannot be treated seriously, for example in one specimen of *Culicoides kaluginae* (Fig. 32 b) sensilla were present on at least 5 flagellomeres. Similarly the subgenus *Leptoconops* s. str. which evolved during the Upper Cretaceous is likely paraphyletic and was the group from which several Tertiary groups of species now classified into subgenera arose. BORKENT (1995) recognized short cerci of some extant species, which certainly evolved secondarily within that genus, as plesiomorphic. As a result the oldest subgenus which developed anagenetically became in the proposed cladogram one of the youngest.

Present studies support REMM's (1975) proposition to treat the traditional subfamilies Forcipomyiinae and Dasyheleinae as tribes.

REMM explained his decision by noting only weak differences between the two groups. His proposal is supported here to allow for the inclusion of the fossil genus *Atriculicoides*. A new tribe Atriculicoidini is proposed as a stem group for both extant tribes. BORKENT (1995) recognized *Atriculicoides* as a sister group of both extant taxa.

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