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Biting midges (Diptera: Ceratopogonidae) as indicators of biostratigraphy, ecological reconstructions and identification of amber deposits

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ABSTRACT: Biting midges (Diptera: Ceratopogonidae) are a large family of flies that commononly appear in Lower Cretaceous to Miocene strata, with over 280 fossil species (4.3 % of the family), belonging to 49 genera (26 extant; 23 extinct). Morphological characters used in the identification of fossil genera and species are identical to those used in studies of extant Ceratopogonidae and, as a result, their potential indicative value is reliable. Two relictual extant genera, *Leptoconops* and Austroconops, reported from Lower Cretaceous Lebanese amber, are at least 125 million years old. Certain ceratopogonid genera are indicative for the Lower Cretaceous, Upper Cretaceous, Eocene or Miocene. A morphological character indicative for the Upper Cretaceous and Cenozoic is macrotrichia on the wing membrane of adults. Indicator species and genera are reviewed for all amber deposits. Eocene Baltic amber contains the best known fauna of biting midges, with 109 named species. Some genera are indicative of aquatic and semiaquatic habitats (predaceous genera, subfamily Ceratopogoninae), forests with rotting trees (*Forcipomyia*), sandy sea shore habitats (*Leptoconops*), a cold boreal climate (*Ceratopogon*) or warm climates (*Nannohelea*, *Austroconops*, *Leptoconops*, *Meunierohelea*, *Metahelea*). Females require a protein-rich meal and are well known for feeding on the blood of vertebrates, but many feed on other things, so this information can help with the interpretation of palaeoenvironments. *Washingtonhelea taimyrica* Szadziewski, 1996, described from Siberian amber, is transferred to the fossil genus *Palaeobrachypogon*: *P. taimyricus* (Szadziewski, 1996), comb. nov. For *Serromyia alphea,* mistakenly redescribed and illustrated from Eocene Bitterfeld amber (= Baltic amber) by Szadziewski (1993), a new name – *Serromyia errata* Szadziewski, nom. nov. – is proposed.

KEY WORDS: Cretaceous, fossil flies, Neogene, palaeohabitats, Paleogene, synonymy.

Biting midges (Diptera: Ceratopogonidae) are a relatively well studied, large family of nematocerous dipterans, inhabiting a wide range of aquatic, semiaquatic and terrestrial habitats, with almost 6,300 extant species in over 110 genera and four subfamilies. The phylogenetic history of the family probably goes back to the Jurassic, although the oldest records are dated as earliest Cretaceous (140–145 Ma) (Borkent *et al.* 2013). This family includes numerous fossils from the Lower Cretaceous to the Miocene, with over 280 species (4.3 % of the family) representing 49 genera (26 extant; 23 extinct) (Borkent 2016; present data). They are common amongst inclusions preserved in fossil resins (Fig. 1). Most fossil biting midges (253 species) have been described as amber inclusions, which preserved morphological details that allowed them to be studied with the same detail as extant species. The morphological criteria used in the identification of fossil genera and species are identical to those used in studies of the extant fauna and, as a result, the potential indicative value of fossils is reliable.

1. Biting midges as indicators of geological ages of amber and deposits

The family contains very old as well as younger genera (Fig. 2). Two relictual extant genera, *Leptoconops* Skuse and *Austroconops* Wirth & Lee, reported from Lower Cretaceous Lebanese amber are at least 125 million years old (Ma) (Azar *et al.* 2015; Granier *et al.* 2016; Maksoud *et al.* 2016). In Oligocene–Miocene deposits, no extinct genera have been reported. They contain younger genera such as *Baeodasymyia* Clastrier & Raccurt, *Phaenobezzia* Haeselbarth and *Heteromyia* Say from Dominican amber, which is about 16 Ma (Szadziewski 2008; Penney 2010) (Fig. 4B). Ceratopogonid genera indicative for the Lower Cretaceous are *Lebanoculicoides* Szadziewski, *Archiaustroconops* Szadziewski and *Archiculicoides* Szadziewski; genera indicative for the Upper Cretaceous include *Protoculicoides* Boesel, *Brachycretacea* Szadziewski and *Peronehelea* Borkent; and those for the Eocene include *Gedanohelea* Szadziewski, *Eohelea* Petrunkevitch, *Fossihelea* Szadziewski, *Mantohelea* Szadziewski, *Ceratopalpomyia* Szadziewski, and *Wirthohelea* Szadziewski (Fig. 3). The relictual extant genus *Austroconops* is indicative of the Cretaceous (Lower and Upper) period in the Northern Hemisphere (Szadziewski 2008) (Fig. 4A). Finally, it is worth mentioning than not only taxa of generic and specific level have indicative value in biostratigraphy. For example, Szadziewski *et al.* (2016) found that an easily recognizable indicative character: macrotrichia on the wing membrane of adults, which evolved during the mid-Cretaceous, and is diagnostic for the Upper Cretaceous and Cenozoic (Fig. 5).

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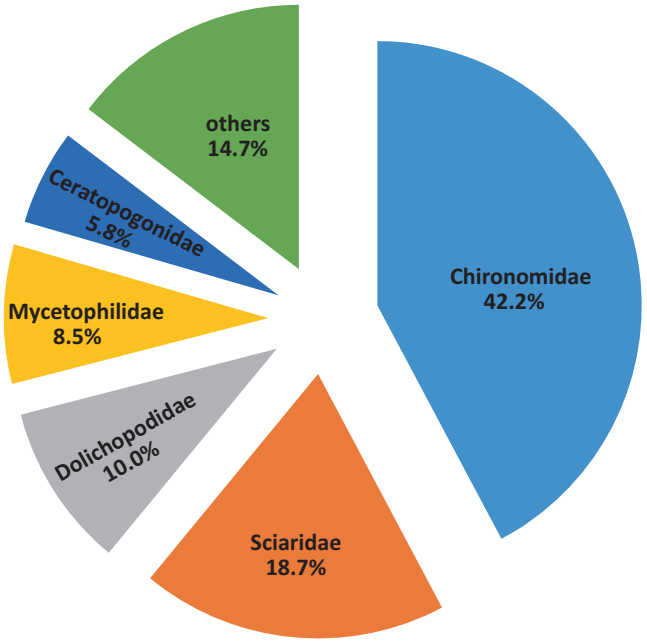

Figure 1 Percentage of biting midges in unselected sample of 2947 inclusions of Diptera in Baltic amber (E. Sontag, pers. comm. 2016).

Table 1 Species and genera of biting midges (Ceratopogonidae) reported from Cretaceous and Cenozoic ambers. Abbreviations: E = extant, F = fossil, LC = Lower Cretaceous, UC = Upper Cretaceous.

Amber	Age, Ma	Named species	Genera, Total (F, E)
Lebanese	LC, 125–129	31	8 (6, 2)
Austrian	LC, 129–133	1	1 (1, 0)
Spanish	LC, 101–113	8	5 (4, 1)
Burmese	UC, 99	12	5 (3, 2)
French	UC, 84–113	8	5 (1, 4)
New Jersey	UC, 90–94	14	7 (4, 3)
Siberian	UC, 84–86	16	7 (4, 3)
Hungarian	UC, 72–90	2	2 (1, 1)
Canadian	UC, 72–84	19	9 (6, 3)
Fushun	Eocene, 48–56	5	4 (3, 1)
Cambay	Eocene, 48–56	1	10 (3, 7)
Sakhalin	Eocene, 45	2	4 (1, 3)
Baltic	Eocene, 35–50	109	26 (6, 20)
Dominican	Miocene, 16	29	11 (0, 11)
Mexican	Miocene, 15–20	0	5 (0, 5)

2. Biting midges indicative for ambers

Inclusions of biting midges have been reported from nearly all amber deposits (Table 1). Their fauna is usually unique, as they include species known exclusively from their respective deposits/strata. Those species, which are unquestionably unique, can be regarded as "index fossils" of their respective amber deposits. For example, many species of Ceratopogonidae in Eocene amber from the Gulf of Gdańsk, Rovno and Bitterfeld are likely to be from the same source (Sontag & Szadziewski 2011). They evidently indicate that amber from Ukraine (Rovno), Germany (Bitterfeld) and Poland/Russia (Gulf of Gdańsk) is the same Baltic amber (Szwedo & Sontag 2013). Sedimentary impression fossils of biting midges have no diagnostic value for their deposits because they are often only determinable to generic level, and thus only have palaeoecological value. Similar value is accorded biting midges from groups and genera which include indistinct taxa that are difficult to determine to species.

2.1. Lebanese amber

(Lower Cretaceous, Barremian, 125–129 Ma) (Szadziewski 1996, 2000; Borkent 2000a, 2001; Choufani *et al.* 2014a, 2015; Azar *et al.* 2015; www.stratigraphy.org International Chronostratigraphic Chart v2016/10). A total of 31 species in eight genera (six fossil; two extant) have been reported from Lebanese amber:

†*Archiaustroconops* Szadziewski, 1996 (9 species)
A. annae Choufani *et al.*, 2014a; *A. bocoparvus* Borkent, 2000a; *A. ceratoformis* Szadziewski, 1996; *A. cretaceous* (Szadziewski, 1996); *A. dominiakae* Choufani *et al.*, 2014a; *A. hammanensis* Choufani *et al.*, 2014a; *A. hamus* Borkent, 2000a; *A. krzeminskii* (Choufani *et al.*, 2014a); *A. szadziewskii* Borkent, 2000a

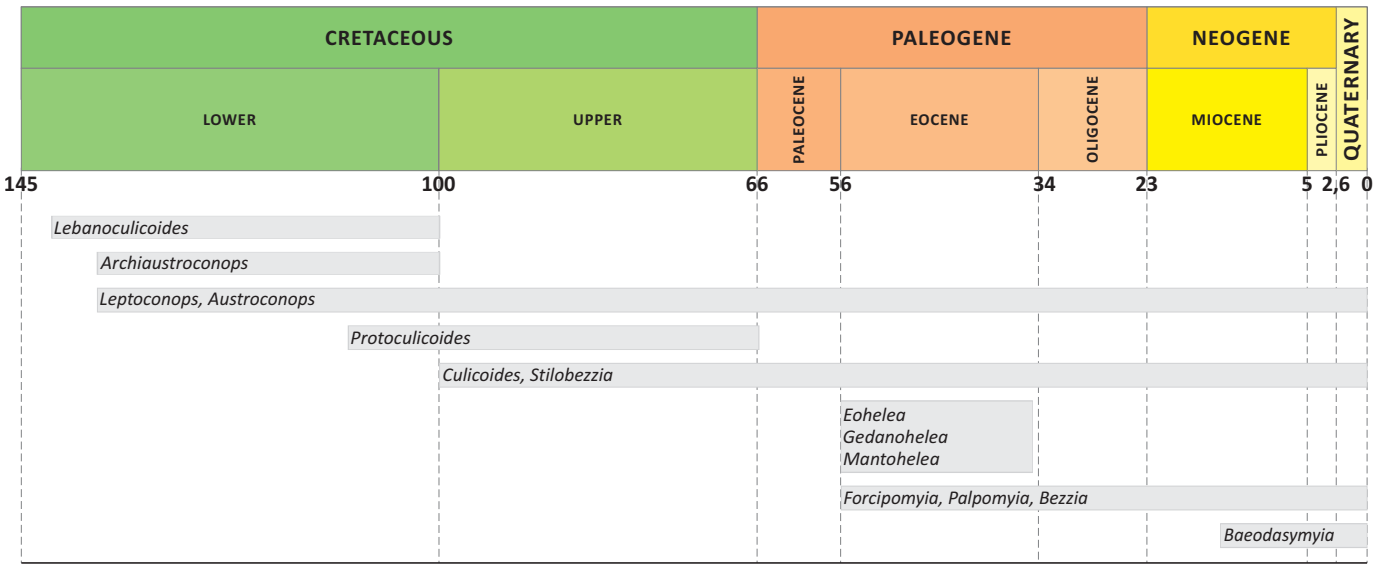

Figure 2 Examples of indicative genera of Ceratopogonidae in Lower Cretaceous, Upper Cretaceous, Eocene and Miocene amber deposits.

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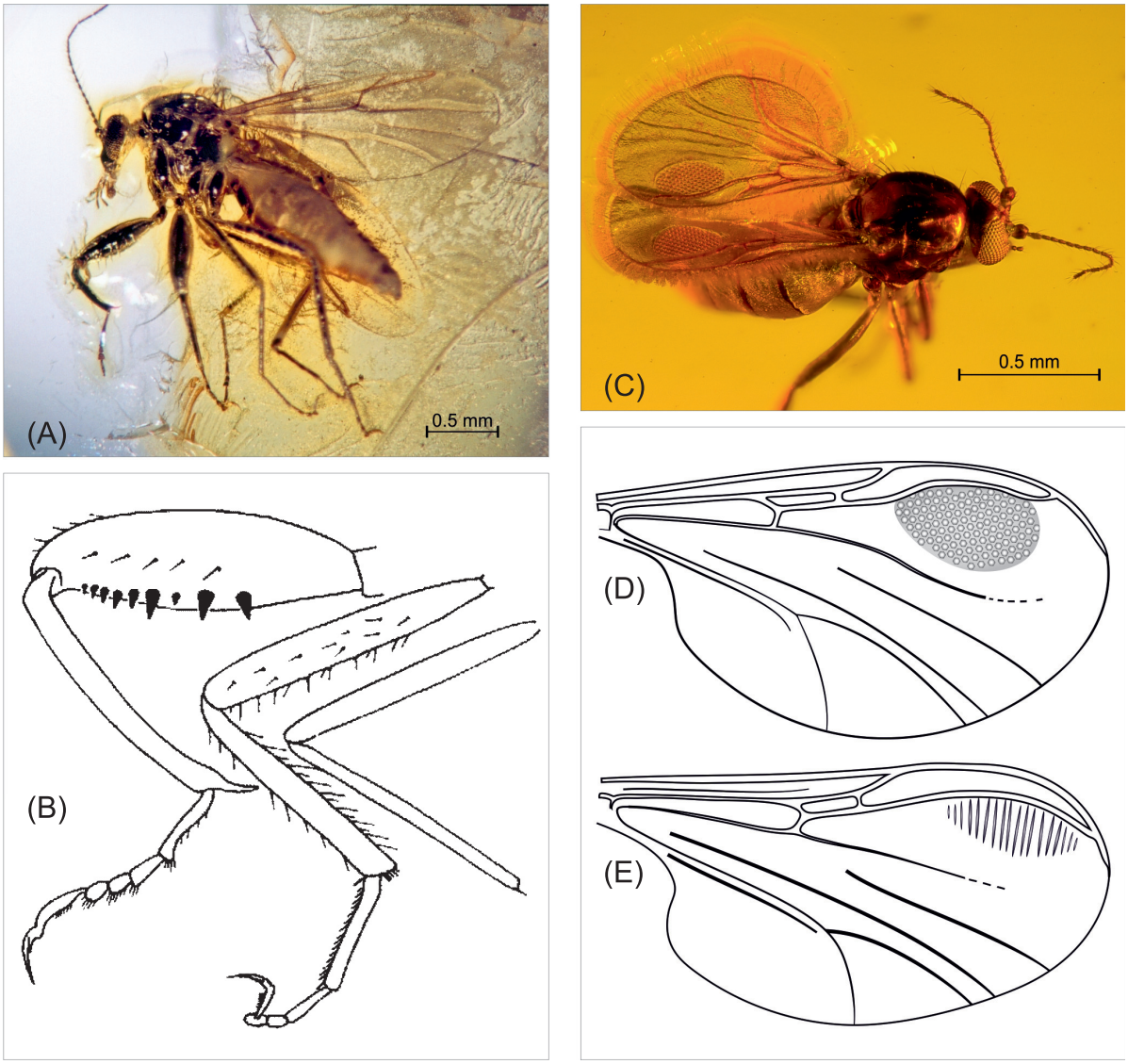

Figure 3 Extinct predaceous genera indicative for the Eocene. (A, B) *Mantohelea* with grasping forelegs: (A) female of *Mantohelea laca* (Meunier, 1904), indicative for Baltic amber (photo E. Sontag). (B) legs of *M. laca* (from Szadziewski 1988). (C–E) *Eohelea* with unique wing organ: (C) female of *Eohelea petrunkevitchi* Szadziewski, 1984 (photo E. Sontag); (D) female wing of *E. petrunkevitchi*, indicative for Baltic amber. (E) female wing of *E. sinuosa* (Meunier, 1904), indicative for Baltic amber.

†*Archiculicoides* Szadziewski, 1996 (5)
A. acraorum (Borkent, 2000a); *A. punctus* (Borkent, 2000a); *A. succineus* (Szadziewski, 1996); *A. schleei* Szadziewski, 1996; *A. unus* (Borkent, 2000a)
Austroconops Wirth & Lee, 1958 (4)
A. fossilis Szadziewski, 1996; *A. gladius* Borkent 2000a; *A. gondwanicus* Szadziewski, 1996; *A. megaspinus* Borkent, 2000a
†*Fossileptoconops* Szadziewski. 1996 (1)
F. lebanicus Szadziewski, 1996
†*Jordanonoconops* Szadziewski, 2000 (1)
J. weitschati Szadziewski, 2000
Leptoconops Skuse, 1889 (subg. †*Palaeoconops* Borkent, 2001) (2)
L. antiques Borkent, 2001; *L. amplificatus* Borkent, 2001
†*Lebanoculicoides* Szadziewski, 1996 (3)
L. bloudani Choufani *et al.*, 2015; *L. daheri* Choufani *et al.*, 2014a; *L. mesozoicus* Szadziewski, 1996
†*Minyohelea* Borkent, 1995 (6)
M. bacula Borkent, 2000a; *M. falcata* Borkent, 2000a; *M. lebanica* (Szadziewski, 1996); *M. minuta* (Szadziewski, 1996); *M. schleei* Szadziewski, 1996; *M. wirthi* (Szadziewski, 1996)

2.2. Austrian amber

(Lower Cretaceous, Hauterivian, 129–133 Ma) (Borkent 1997).

†*Minyohelea* Borkent (1)
M. casca Borkent, 1997

2.3. Spanish amber

(Lower Cretaceous, Albian, 101–113 Ma) (Szadziewski & Arillo, 1998, 2003; Pérez-de la Fuente *et al.* 2011; Szadziewski *et al.* 2016). Only eight species in five genera have been reported from this relatively recently discovered amber:

†*Lebanoculicoides* Szadziewski (1)
L. excantabris Pérez de la Fuente *et al.*, 2011
†*Archiaustroconops* Szadziewski (2)
A. alavensis Szadziewski & Arillo, 1998; *A. borkenti* Pérez-de la Fuente *et al.*, 2011
†*Archiculicoides* Szadziewski (1)
A. skalskii (Szadziewski & Arillo 1998)
†*Protoculicoides* Boesel, 1937 (3)
P. hispanicus Szadziewski & Arillo, 2016 (*in* Szadziewski *et al.* 2016); *P. sanjusti* Szadziewski & Arillo, 2016 (*in* Szadziewski *et al.* 2016); *P. szadziewskii* (Pérez-de la Fuente *et al.*, 2011)

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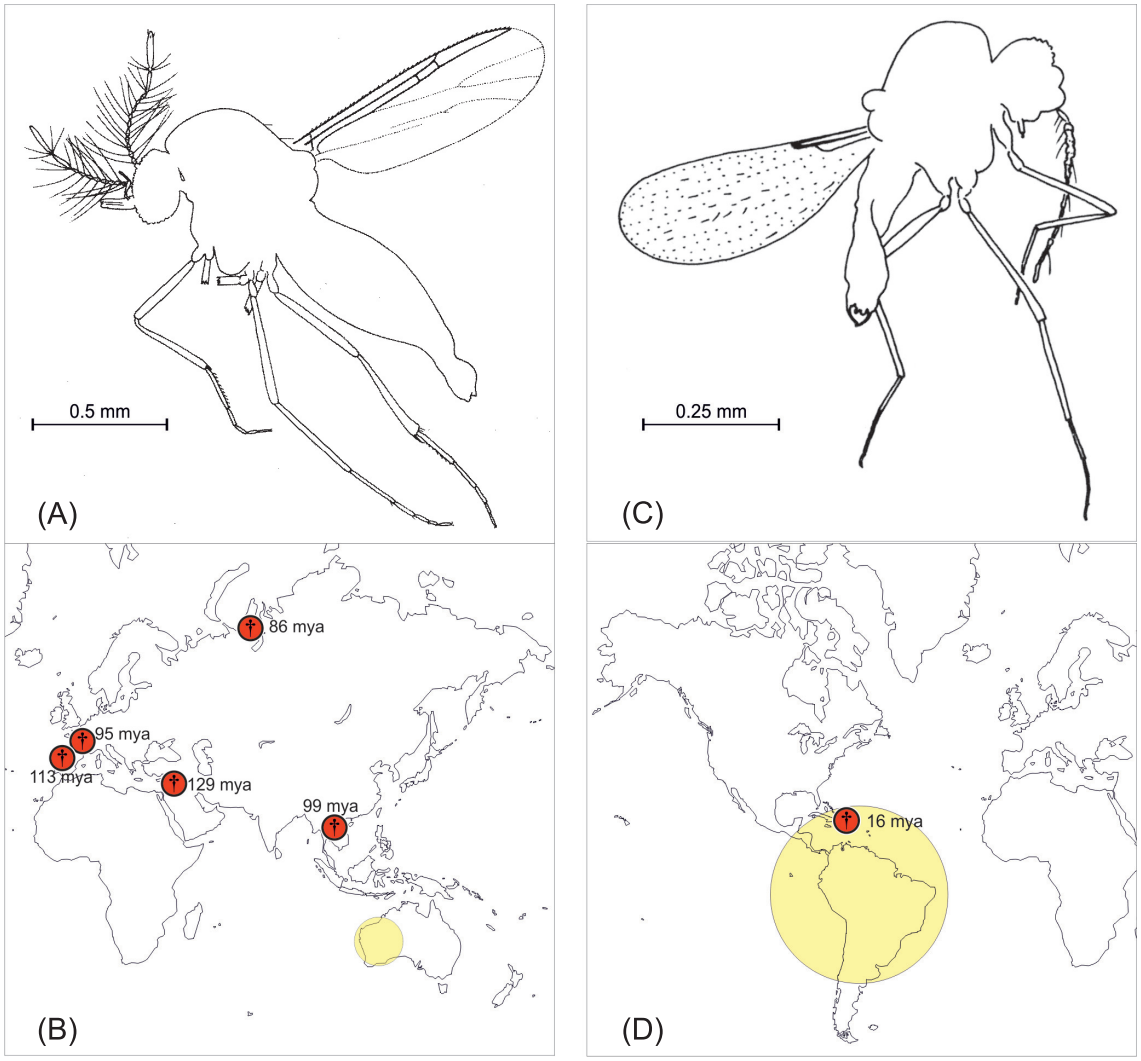

Figure 4 Habitus and distribution of indicative extant genera. (A, B) The living fossil genus *Austroconops*, indicative for the Cretaceous in the Northern Hemisphere: (A) male of *Austroconops sibiricus* Szadziewski, 1996 from Siberian amber (after Szadziewski 1996); (B) distribution of extinct and extant species (after Szadziewski 2008, modified). (C, D) The extant genus *Baeodasymyia*, indicative for the Miocene (after Szadziewski 2008): (C) male of *Baeodasymyia dominicana* Szadziewski & Grogan, 1994 from Dominican amber (after Szadziewski & Grogan 1994); (D) distribution of extinct and extant species (after Szadziewski 2008).

Leptoconops Skuse (s. str.) (1)
L. zherikhini Szadziewski & Arillo, 2003

2.4. Burmese amber

(Upper Cretaceous, Cenomanian, 99 Ma) (Szadziewski 2004; Szadziewski & Poinar 2005; Shi *et al*. 2012; Szadziewski *et al.* 2015a, b). Only 12 species in five genera are known from Burmese amber:

†*Archiaustroconops* Szadziewski (2)
A. gracilis Szadziewski & Poinar, 2005; *A. kotejai* Szadziewski & Poinar, 2005
†*Archiculicoides* Szadziewski (2)
A. andersoni Szadziewski *et al.*, 2015b; *A. burmiticus* (Szadziewski & Poinar, 2005)
Austroconops Wirth & Lee (1)
A. asiaticus Szadziewski, 2004
Leptoconops Skuse (6)
L. burmiticus Szadziewski, 2004; *L. ellenbergeri* Szadziewski, 2015 (*in* Szadziewski *et al*. 2015a); *L. myanmaricus* Szadziewski, 2004; *L. nosopheris* Poinar, 2008; *L. rossi* Szadziewski, 2004; *L. subrossicus* Szadziewski & Poinar, 2005
†*Protoculicoides* Boesel (1)
P. swinhoei (Cockerell, 1919)

2.5. French amber

2.5.1. French (NW) amber of Anjou (Upper Cretaceous, Cenomanian, 94–101 Ma) (Szadziewski & Schlüter 1992). Three species of biting midges have been reported from this amber:

†*Protoculicoides* Boesel (2)
P. cenomanensis (Szadziewski & Schlüter, 1992);
P. incompletus (Szadziewski & Schlüter, 1992)
Austroconops Wirth & Lee (1)
A. borkenti Szadziewski & Schlüter, 1992

2.5.2. French (NW) amber of Vendée (Upper Cretaceous, Cenomanian 94–101 Ma) (Perrichot *et al*., 2007; Choufani *et al.* 2014b). Only two haematophagous species have been reported from this amber:

Culicoides Latreille, 1809 (1)
C. doyeni Choufani *et al.*, 2014b
Leptoconops Skuse (1)
L. gravesi Choufani *et al.*, 2014b

2.5.3. French (SW) amber of Charentes (Upper Cretaceous, Albian-Cenomanian, 94-113 Ma) Choufani *et al.* 2011). So far, only one species has been recorded from this amber:

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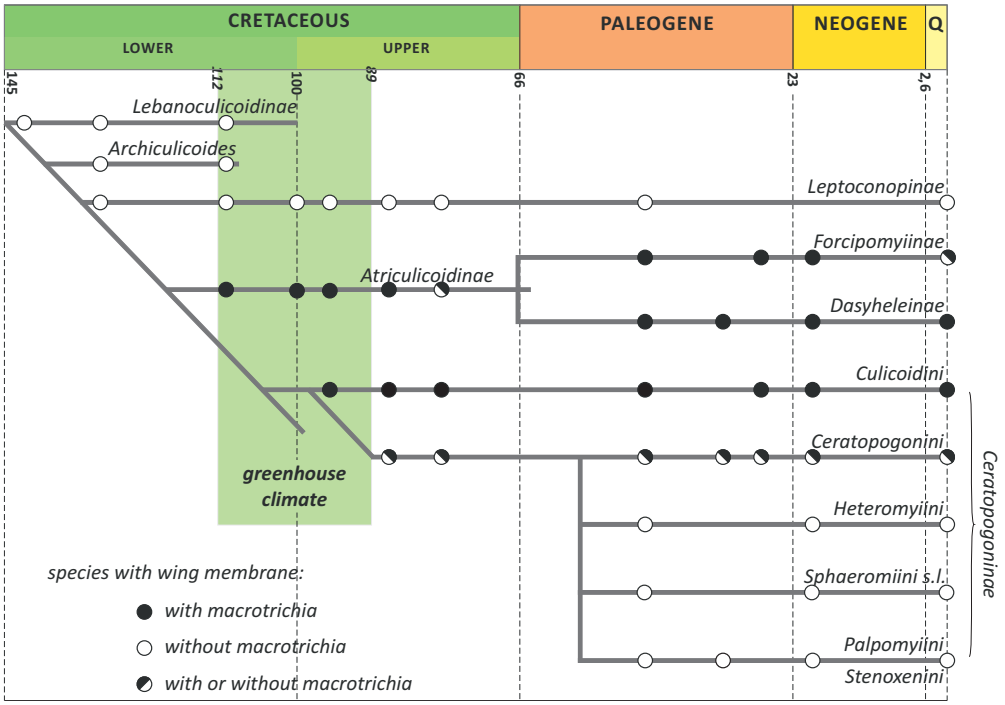

Figure 5 A readily recognisable indicative character – macrotrichia on wing membranes – which evolved during the mid-Cretaceous (after Szadziewski *et al.* 2016, modified).

Leptoconops Skuse (1)
L. daugeroni Choufani *et al.*, 2011

2.5.4. French (SE) amber of Provence (Upper Cretaceous, Santonian, 84–86 Ma) (Choufani *et al.* 2013; Szadziewski *et al.* 2016). Only two species in two extant genera have been described from this amber:

Culicoides Latreille, 1809 (1)
C. brisaci (Choufani & Nel, 2013 *in* Choufani *et al*. 2013)
Stilobezzia Kieffer, 1911a (1)
S. roggeroi (Choufani & Nel, 2013 *in* Choufani *et al*. 2013)

2.6. New Jersey amber

(Upper Cretaceous, Turonian, 90–94 Ma) (Borkent 1996, 2000b; Grogan & Szadziewski 1988). A total of 14 species in three extant and four fossil genera have been reported from this amber:

†*Alautunmyia* Borkent, 1996 (1)
A. elongata Borkent, 1996
Culicoides Latreille (5)
C. casei Grogan & Szadziewski, 1988;?*C. filipalpis* Remm, 1976; *C. grandibocus* Borkent, 1996; *C. truncatus* Borkent, 2000b; *C. yoosti* Borkent, 2000b
†*Heleageron* Borkent, 1995 (1)
H. grimaldii Borkent, 1996
Leptoconops Skuse (2)
L. copiosus Borkent, 1996; *L. curvachelus* Borkent, 1996
†*Palaeobrachypogon* Borkent, 1995 (2)
P. grandiforceps Borkent, 2000b; *P. remmi* Borkent, 1996
†*Protoculicoides* Boesel (2)
?*P. globosus* (Boesel, 1937); ?*P. incompletus* (Szadziewski & Schlüter, 1992)
Stilobezzia Kieffer, 1911a (1)
S. kurthi Borkent, 2000b

2.6.1. Remarks. Borkent (1996, 2000b) determined that three species of biting midges from New Jersey amber, were also present in older French amber (*Protoculicoides incompletus*), and in younger Siberian amber (*Culicoides filipalpis*) and Canadian amber (*Protoculicoides globosus*). I consider this doubtful, because these species have no unique diagnostic characters that indicate that they are only similar, not identical.

2.7. Siberian amber

(Upper Cretaceous, Santonian, 84–86 Ma) (Remm 1976; Szadziewski 1996). The following 16 named biting midges have been reported from Siberian amber:

Austroconops Wirth & Lee (1)
A. sibiricus Szadziewski, 1996
†*Brachycretacea* Szadziewski, 1996 (1)
B. taimyrica (Remm, 1976)
Culicoides Latreille (4)
C. filipalpis Remm, 1976; *C. kaluginae* Remm, 1976; *C. sphenostylus* Remm, 1976; *C. succineus* Remm, 1976
Leptoconops Skuse (2)
L. boreus Kalugina, 1991; *L. sibiricus* Szadziewski, 1996
†*Palaeobrachypogon* Borkent (2)
P. macronyx (Remm, 1976); *P. taimyricus* (Szadziewski, 1996), comb. nov.
†*Peronehelea* Borkent, 1995 (2)
P. frigida (Remm, 1976); *P. sibirica* Szadziewski, 1996
†*Protoculicoides* Boesel (= *Atriculicoides* Remm, 1976) (4)
P. dasyheleis (Szadziewski, 1996), *P. macrophtalmus* (Remm, 1976); *P. sibiricus* (Szadziewski, 1996); *P. taimyricus* (Szadziewski, 1996)

2.7.1. Remarks. *P. macronyx* (Remm) and *P. taimyricus* (Szadziewski, 1996), comb. nov. are included in *Palaeobrachypogon,* as proposed by Borkent (1995). The latter species was originally described in the extant genus *Washingtonhelea* Wirth & Grogan, 1988. My re-examination of the type species of this genus, *Washintonhelea frommeri* Wirth & Grogan, 1988, revealed that its legs lack palisade setae, but have small equal-sized simple claws and cylindrical fourth tarsomeres (as in species of *Culicoides*), sensilla coeloconica on the first flagellomere, pubescent eyes, wing membranes without macrotrichia, and female mandibles with eight coarse teeth and

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Figure 6 Diorama of the Baltic amber forest. Museum of Amber Inclusions, University of Gdańsk, Poland. Painting by K. Buczak.

greatly reduced laciniae. Despite the fact that females of *P. taimyricus* have small, equal-sized claws on all legs, it cannot be included in *Washingtonhelea* because it has two incomplete rows of palisade setae on the hind basitarsus and the wing membrane has some macrotrichia. Therefore, I assign *Washingtonhelea taimyrica* Szadziewski, 1996 to *Palaeobrachypogon*.

It is worth noting that within the tribe Ceratopogonini, one row of palisade setae is present in most genera. Two rows of palisade setae are present only in the extant genera *Stiloculicoides* Wirth & Grogan, 1988 and *Echinohelea* Macfie, 1940. Whereas an incomplete single row of palisade setae on the basal 2/3 of hind tarsomere 1 is present in *Ceratopogon* Meigen, 1803, *Nannohelea* Grogan & Wirth, 1980 and *Ceratoculicoides* Wirth & Ratanaworabhan, 1971 (Urbanek *et al.* 2015).

2.8. Hungarian amber

(Upper Cretaceous, Coniacian–Campanian, 72–90 Ma) (Borkent 1997). Only two species have been recorded from this amber:

†*Adelohelea* Borkent, 1995 (1)
  A. magyarica Borkent, 1997
Leptoconops Skuse (1)
  L. clava Borkent, 1997

2.9. Canadian amber

(Upper Cretaceous, Campanian, 72–84 Ma) (Borkent 1995, 2012). A total of 19 named species have been reported from this amber:

†*Adelohelea* Borkent (1)
  A. glabra Borkent, 1995
Culicoides Latreille (7)
  C. agamus Borkent, 1995; *C. annosus* Borkent, 1995;
  C. bullus Borkent, 1995; *C. canadensis* Borkent, 1995;
  C. filipalpis Remm, 1976; *C. obuncus* Borkent, 1995;
  C. tyrrelli (Boesel, 1937)
†*Heleageron* Borkent (1)
  H. arenatus Borkent, 1995
Leptoconops Skuse (1)
  L. primaevus Borkent, 1995
†*Minyohelea* Borkent (1)
  M. pumilis Borkent, 1995
†*Palaeobrachypogon* Borkent (3)
  P. aquilonius (Boesel, 1937); *P. remmi* Borkent, 1995;
  P. vetus Borkent, 1995
†*Peronehelea* Borkent (1)
  P. chrimikalydia Borkent, 1995
†*Protoculicoides* Boesel (3)
  P. ciliatus Borkent, 2012; *P. depressus* Boesel, 1937;
  P. globosus (Boesel, 1937)
Stilobezzia Kieffer (1)
  S. pikei Borkent, 2012

2.10. Fushun amber

(early Eocene, 48–56 Ma) (Stebner *et al.* 2016b). Five named species have been reported from this amber in the genera:

†*Eopalpomyitis* Hong *et al.*, 2000 (1 species)
  E. unca (Hong, 1981)
Forcipomyia Meigen (1)
  F. orientalus (Hong, 1981)
†*Gedanohelea* Szadziewski (2)
  G. fushunensis Stebner *et al.*, 2016a; *G. liaoningensis* Stebner *et al.*, 2016a
†*Mantohelea* Szadziewski (1)
  M. sinica Stebner *et al.*, 2016a

2.11. Cambay amber

(early Eocene, 48–56 Ma) (Stebner *et al.* 2016a, 2017). Ten genera, with one named species, have been reported from this amber:

Camptopterohelea Wirth & Hubert, 1960 (1)
  C. odora Stebner *et al.*, 2016a
Brachypogon Kieffer, 1899
Forcipomyia Meigen, 1818
†*Eohelea* Petrunkevitch, 1957
†*Gedanohelea* Szadziewski, 1988
Leptoconops Skuse, 1889
†*Mantohelea* Szadziewski, 1988
Meunierohelea Szadziewski, 1988
Serromyia Meigen, 1803
Stilobezzia Kieffer, 1911a

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2.12. Sakhalin amber

(middle Eocene, 45 Ma). (Szadziewski 1990; Szadziewski & Sontag 2013). Phytostratigraphic studies by Kodrul (1999) determined that the age of Sakhalin amber is middle Eocene. Only two named species and four genera have been recorded from this amber:

†*Eohelea* Petrunkevitch (1)
E. sakhalinica Szadziewski, 1990
Stilobezzia Kieffer
Forcipomyia Meigen (1)
F. nadicola Szadziewski & Sontag, 2013
Leptoconops Skuse

2.12.1. Remark. The indicative species for this amber is *Eohelea sakhalinica*.

2.13. Baltic amber

(Eocene, 35–50 Ma) (Szadziewski 1988; Szadziewski *et al.* 2007; Sontag & Szadziewski 2011). I prefer the traditional name, Baltic amber in its broadest sense, including ambers named Danish, Lithuanian, Scandinavian, Saxonian, Ukrainian and Sambian (or amber from Bitterfeld, Rovno, Bay of Gdańsk, Sambia, Poland, Russia, etc.), as it may have been collected from or purchased in different countries. In addition, Baltic amber was dispersed by Paleogene seas and, more recently, by glaciers during the Pleistocene, and is still continuing to be washed out from Eocene deposits in the Gulf of Gdańsk into the Baltic sea (Szwedo & Sontag 2013). The age of Baltic amber still is under discussion. In the literature, its age mostly ranges from 35 Ma to 50 Ma (Weitschat & Wichard 2010; Standke 2008; Ritzkowski 1997; Grimaldi & Ross 2017). I prefer a mid-Eocene age (45 Ma), because its fauna has links to well dated early to middle Eocene ambers of Sakhalin, Fushun and Cambay, as indicated by the common fossil genera of biting midges (*Eohelea*, *Mantohelea*, *Gedanohelea*).

This is the best studied amber, with 109 named species of biting midges in 26 genera (six fossil; 20 extant). Amongst many species described exclusively from this amber, there are very characteristic biting midges which are common and diagnostic for Baltic amber. I suggest treating as diagnostic the easily determinable females of *Eohelea sinuosa* (Meunier) (Fig. 3E), *E. petrunkevitchi* Szadziewski (Fig. 3C, D), or *Mantohelea laca* (Meunier) (Fig. 3A, B).

Serromyia alphea (Heyden, 1870) (= *S. colorata* Statz, 1944, = *S. austera* Statz, 1944, = *S. spinosifemorata* Statz, 1944), described from Miocene deposits of Rott in Germany as compression fossils, is excluded from the list of species reported from Baltic amber in Bitterfeld and its designated neotype, which I consider invalid. Szadziewski (1993) mistakenly redescribed the Miocene *S. alphea*, because at that time, the so called Saxonian amber from Bitterfeld and deposits from Rott were dated as Miocene. For *S. alphea*, mistakenly re-described and illustrated from Eocene Baltic amber from Bitterfeld by Szadziewski (1993: 633), I propose the new name *Serromyia errata* Szadziewski, nom. nov. The holotype male (MBI -8-91) and three female paratypes (MBI-8-77) designated herein are deposited in the Museum für Naturkunde, Paläontologische Museum, Berlin.

A complete alphabetic list of species reported from Baltic amber is as follows:

Alluaudomyia Kieffer, 1913 (1)
A. succinea Szadziewski, 1988
Atrichopogon Kieffer, 1906 (1)
A. eocenicus Szadziewski, 1988
Bezzia Kieffer, 1899 (1)
B. eocenica Szadziewski, 1988
Brachypogon Kieffer, 1899 (7)
B. balticus Szadziewski, 1988; *B. eocenicus* Szadziewski, 1988; *B. gedanicus* Szadziewski, 1988; *B. henningseni* Szadziewski, 1988; *B. miocaenicus* Szadziewski, 1993; *B. polonicus* Szadziewski, 1988; *B. prominulus* (Meunier, 1904)
Ceratoculicoides Wirth & Ratanaworabhan, 1971 (1)
C. danicus Szadziewski, 1988
†*Ceratopalpomyia* Szadziewski, 1988 (1)
C. eocenica Szadziewski, 1988
Ceratopogon Meigen, 1803 (20)
C. bitterfeldi Szadziewski, 1993; *C. ceranowiczi* Szadziewski, 1988; *C. crypticus* Szadziewski, 1988; *C. eminens* Meunier, 1904; *C. forcipiformis* Meunier, 1904; *C. gedanicus* Szadziewski, 1988; *C. grogani* Szadziewski, 1988; *C. hennigi* Szadziewski, 1988; *C. kotejai* Szadziewski, 1993; *C. margaritae* Szadziewski, 1988; *C. miocaenicus* Szadziewski, 1993; *C. nanalobus* Borkent & Grogan, 1995; *C. paraeminens* Borkent & Grogan, 1995; *C. piotrowskii* Szadziewski, 1988; *C. pisinnus* Borkent & Grogan, 1995; *C. remmicolus* Szadziewski, 1988; *C. ritzkowskii* Szadziewski, 1988; *C. subeminens* Szadziewski, 1993; *C. succinicolus* Szadziewski, 1993; *C. tertiaricus* Szadziewski, 1988
Culicoides Latreille, 1809 (9)
C. balticus Szadziewski, 1988; *C. ceranowiczi* Szadziewski, 1988; *C. dasyheleiformis* Szadziewski, 1988; *C. eoselficus* Szadziewski, 1988; *C. gedanensis* Szadziewski, 1988; *C. prussicus* Szadziewski, 1988; *C. speciosus* (Meunier, 1904); *C. subgedanensis* Szadziewski, 1993; *C. succivarius* Szadziewski, 1988
Dasyhelea Kieffer, 1911b (4)
D. eodicryptoscenica Szadziewski, 1988; *D. gedanica* Szadziewski, 1988; *D. miocaenica* Szadziewski, 1993; *D. stanislavi* Szadziewski, 1988
†*Eohelea* Petrunkevitch, 1957 (6)
E. fossicola Szadziewski, 1993; *E. gedanica* Szadziewski, 1988; *E. grogani* Szadziewski, 1988; *E. miocaenea* Szadziewski, 1993; *E. petrunkevitchi* Szadziewski, 1984; *E. sinuosa* (Meunier, 1904)
Forcipomyia Meigen, 1818 (21)
F. berendti Szadziewski, 1988; *F. bifidicola* Szadziewski, 1993; *F. eobreviflagellata* Szadziewski, 1988; *F. eocostata* Szadziewski, 1988; *F. eophytoheleana* Szadziewski, 1988; *F. eotrichoheleana* Szadziewski, 1988; *F. gedanicola* Szadziewski, 1988; *F. henningseni* Szadziewski, 1988; *F. krzeminskii* Szadziewski, 1988; *F. kulickae* Szadziewski, 1988; *F. lyneborgi* Szadziewski, 1988; *F. miocaenica* Szadziewski, 1993; *F. piriformis* (Meunier, 1904); *F. pseudomicrohelea* Szadziewski, 1988; *F. subgedanicola* Szadziewski, 1993; *F. succinea* Szadziewski, 1988; *F. succinicola* Szadziewski, 1993; *F. tuberculosa* Szadziewski, 1993; *F. turbinata* (Meunier, 1904); *F. uncula* (Meunier, 1904); *F. unculiformis* Szadziewski, 1993
†*Fossihelea* Szadziewski, 1988 (2)
F. gracilitarsis (Meunier, 1904); *F. miocaenica* Szadziewski, 1993
†*Gedanohelea* Szadziewski, 1988 (3)
G. loewi Szadziewski, 1988; *G. succinea* Szadziewski, 1988; *G. wirthi* Szadziewski, 1988
Leptoconops Skuse, 1889 (2)
L. rovnensis Sontag & Szadziewski, 2011; *L. succineus* Szadziewski, 1988
Mallochohelea Wirth, 1962 (1)
M. martae Szadziewski, 2005
†*Mantohelea* Szadziewski, 1988 (2)
M. gedanica Szadziewski, 1988; *M. laca* (Meunier, 1904)
Metahelea Edwards, 1929 (1)

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M. serafini Szadziewski, 1998
Meunierohelea Szadziewski, 1988 (4)
M. gedanicola Szadziewski, 1988; *M. miocaenica* (Szadziewski, 1993); *M. nielseni* Szadziewski, 1988; *M. wirthi* Szadziewski, 1988
Monohelea Kieffer, 1917 (2)
M. baltica Szadziewski, 1988; *M. clunipes* (Loew, 1850)
Nannohelea Grogan & Wirth, 1980 (2)
N. eocenica Szadziewski, 1988; *N. grogani* Szadziewski, 1988
Neurohelea Kieffer, 1925 (1)
N. cothurnata (Meunier, 1904)
Palpomyia Meigen, 1818 (4)
P. erikae Szadziewski, 1993; *P. jantari* Szadziewski, 1988; *P. riedeli* Szadziewski, 1988; *P. succinea* Szadziewski, 1988
Physohelea Grogan & Wirth, 1979 (1)
P. obtusa (Meunier, 1904)
Serromyia Meigen, 1818 (7)
S. anomalicornis (Loew, 1850); *S. errata* nom. nov.; *S. polonica* Szadziewski, 1988; *S. ryszardi* Borkent, 1990 in Borkent & Bissett 1990; *S. sinuosa* Borkent, 1990 in Borkent & Bissett 1990; *S. spinigera* (Loew, 1850); *S. succinea* Szadziewski, 1988
Stilobezzia Kieffer, 1911a (4)
S. falcata (Meunier, 1904); *S. kutscheri* Szadziewski, 1993; *S. saxonica* Szadziewski, 1993; *S. wirthicola* Szadziewski & Grogan, 1998a
†*Wirthohelea* Szadziewski, 1988 (1)
W. trifida Szadziewski, 1988

2.14. Dominican amber

(Miocene, 16 Ma) (Szadziewski & Grogan 1994, 1997, 1998a, b; Penney 2010). As diagnostic or indicative for this amber are several most distinct species, such as: *Dasyhelea hispaniolae*, *Forcipomyia domibicolor*, *Baeodasymyia dominicana* (Fig. 4), *Heteromyia dominicana*, and *Phaenobezzia wirthi*. The following list includes 29 named species in 11 extant genera from this amber:

Atrichopogon Kieffer, 1906 (1)
A. dominicanus Szadziewski & Grogan, 1998b
Baeodasymyia Clastrier & Raccurt, 1979 (1)
B. dominicana Szadziewski & Grogan, 1994
Brachypogon Kieffer (3)
B. americanus Szadziewski & Grogan, 1998a; *B. dominicanus* Szadziewski & Grogan, 1998a; *B. prominuloides* Szadziewski & Grogan, 1998a
Culicoides Latreille (5)
C. ambericus Szadziewski & Grogan, 1998a; *C. antilleanus* Szadziewski & Grogan, 1998a; *C. brodzinskyi* Szadziewski & Grogan, 1998a; *C. hispanicolus* Szadziewski & Grogan, 1998a; *C. mammalicolus* Szadziewski & Grogan, 1998a
Dasyhelea Kieffer (4)
D. antilleana Szadziewski & Grogan, 1998b; *D. dominicana* Szadziewski & Grogan, 1998b; *D. hispaniolae* Szadziewski & Grogan, 1998b; *D. minuticola* Szadziewski & Grogan, 1998b
Forcipomyia Meigen (10)
F. americana Szadziewski & Grogan, 1998b; *F. antilleana* Szadziewski & Grogan, 1998b; *F. chrysosuccinea* Szadziewski & Grogan, 1998b; *F. domibicolor* Szadziewski & Grogan, 1998b; *F. frutetosuccinea* Szadziewski & Grogan, 1998b; *F. fusiparamera* Szadziewski & Grogan, 1998b; *F. grimaldii* Szadziewski & Grogan, 1998b; *F. lepidosuccinea* Szadziewski & Grogan, 1998b; *F. tertiaricola* Szadziewski & Grogan, 1998b; *F. woodruffi* Szadziewski & Grogan, 1998b
Heteromyia Say, 1825 (1)
H. dominicana Szadziewski & Grogan, 1997
Palpomyia Meigen (1)
P. wirthorum Szadziewski & Grogan, 1997
Phaenobezzia Haeselbarth, 1965 (1)
P. wirthi Szadziewski & Grogan, 1997
Stilobezzia Kieffer (2)
S. antilleana Szadziewski & Grogan, 1998a; *S. dominicana* Szadziewski & Grogan, 1998a

2.15. Mexican amber

(Miocene, 15–20 Ma) (Szadziewski & Grogan 1996; Solórzano-Kraemer 2007, 2010). A small number of inclusions in Mexican amber have been examined and determined to the generic level. Szadziewski & Grogan (1996) and Solórzano-Kraemer (2007) reported the following five genera:

Brachypogon Kieffer (subg. *Isohelea* Kieffer, 1917)
Culicoides Latreille
Dasyhelea Kieffer
Forcipomyia Meigen
Nannohelea Grogan & Wirth

2.15.1. Remark. *Nannohelea* is pantropical; the others have a worldwide distribution today.

3. Biting midges as indicators of palaeoenvironments

Ceratopogonidae are useful for ecological reconstructions, as their biology and ecological requirements are greatly diversified and usually the same for all species within their genera. The immature stages of the genera included in the subfamily Ceratopogoninae are generally aquatic or semiaquatic and inhabit a wide variety of inland bodies of water including lakes, rivers, ponds, springs, pools and their margins (Szadziewski 1988; Szadziewski *et al.* 1997). The fossil record of adults in this subfamily indicate that aquatic or semiaquatic habitats were present in or near the ancient amber forest.

Biting midges of the subgenus *Forcipomyia* s. str. (Fig. 8A) are indicative for forests because their larvae and pupae are terrestrial and usually live under bark of rotting trees (Urbanek *et al.* 2011). They are moderately common in Eocene Baltic amber (nearly 16 % of all biting midges; Szadziewski 1988), and very common in Miocene Dominican amber (nearly 42 % of all ceratopogonids; Szadziewski & Grogan 1998b).

Species of the genus *Leptoconops* are good indicators of sea shore or estuarine environments near amber forests, as their larvae usually live in sand of coastal and inland beaches. Fossil records of *Leptoconops*, a relictual pantropical genus that was distributed worldwide during the Cretaceous (Fig. 7), indicate that coastal or estuarine ecosystems close to amber forests were present (Szadziewski *et al.* 2015a).

Some Recent genera of biting midges that presently inhabit warm climate ecosystems are indicators of subtropical or tropical climatic conditions in the past. For example, extant species of *Leptoconops* are of pantropical distribution (Fig. 7) and *Austroconops* now includes just two extant species, which are only found in western Australia (Fig. 4A). These two genera, together with termites, indicate that during the Upper Cretaceous, the climate of the Taimyr amber forests of Siberia were much warmer than today (Szadziewski 1996). In addition, the pantropical recent distribution of the genus *Nannohelea* extended to more northern latitudes during the Paleogene and Neogene (Szadziewski 2008). The Oriental and Australian regions are currently limited to the distribution of the tropical genera *Meunierohelea* and *Metahelea,* which occurred in Europe in the Eocene (Szadziewski 1988, 2008).

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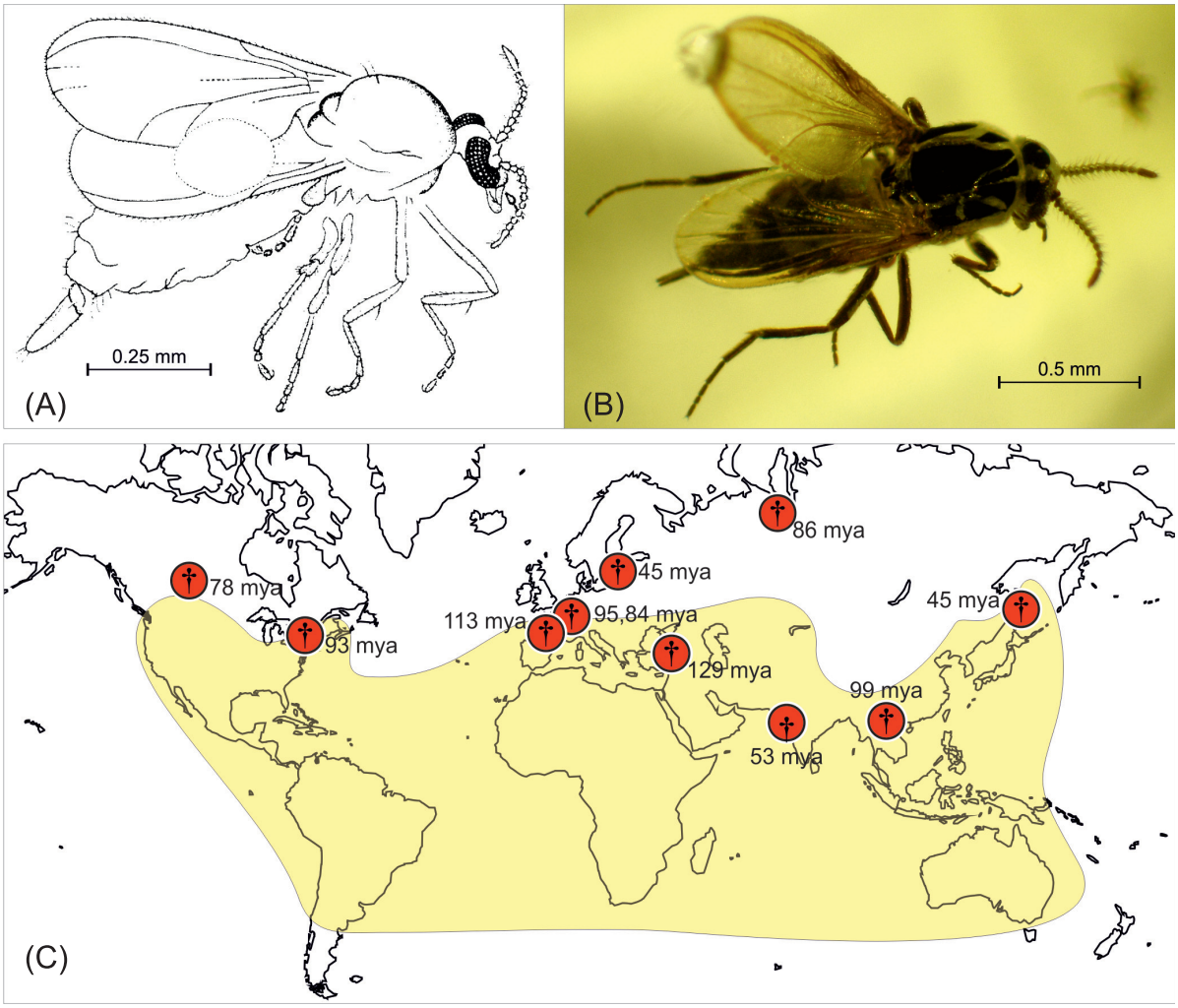

Figure 7 Biting midges of the genus *Leptoconops* as indicators of seashore or estuarine sandy habitats and warm climates, with vertebrates as sources of blood meals: (A) *Leptoconops zherikhini* Szadziewski & Arillo, 2003 from Spanish amber; (B) *Leptoconops rovnensis* Sontag & Szadziewski, 2011 from Baltic amber; (C) Distribution of extinct and extant species (after Szadziewski 2008, modified).

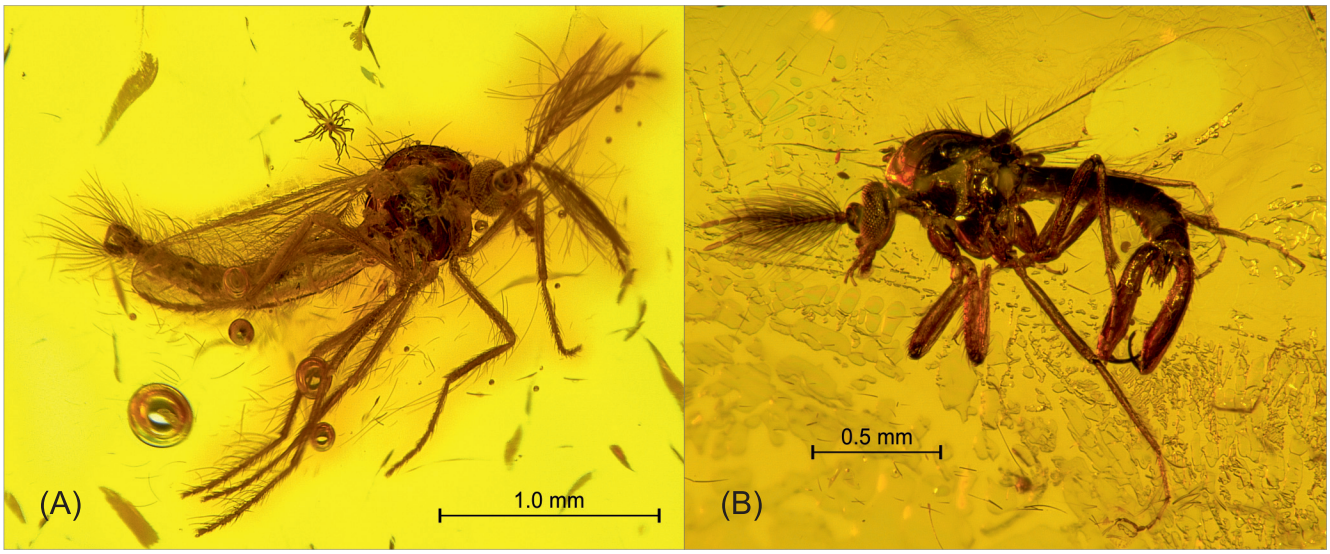

Figure 8 (A) Biting midges of the genus *Forcipomyia* are good indicators of moist forests with rotting trees. Male of unidentified *Forcipomyia* from Baltic amber (Photo E. Sontag). (B) Species in the genus *Ceratopogon* are indicators of boreal temperate or cold climatic conditions. Male of *Ceratopogon forcipiformis* Meunier, 1904 from Baltic amber (Photo E. Sontag).

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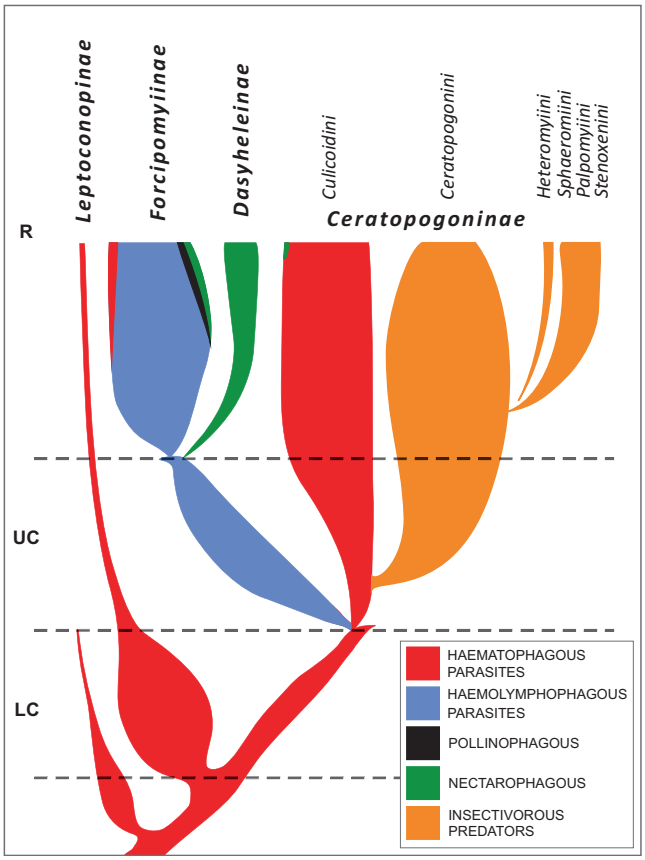

Figure 9 Chart illustrating the lineages of Ceratopogonidae during the Cretaceous and Cenozoic and the evolution of adult female feeding habits.

The type genus of Ceratopogonidae, *Ceratopogon* (Fig. 7B), which includes 43 extant and 20 fossil species, is presently a boreal genus of Holarctic distribution. This relictual genus was moderately common in Eocene Baltic amber, but is now a relatively rare inhabitant of cold boreal regions of the Northern Hemisphere, and is restricted to isolated mountains in the southern-most regions of its present range (Szadziewski 1988, 2008; Borkent & Grogan 1995; Hagan *et al.* 2000). This pattern of occurrence may be explained by the presence of cold habitats in the Baltic amber forests, probably in mountains. However, the suggestion that this genus would serve as an indicator of cold climates or mountainous habitats requires further investigation.

Information on food sources in palaeoenvironments is important for females in most genera of biting midges, as they require a protein-rich meal in order to produce a clutch of eggs. Feeding habits of biting midges are highly diverse (Fig. 9); however, both sexes of all biting midges visit flowers of angiosperms with easily accessible nectar. The females of the extant subfamilies Leptoconopinae, Forcipomyiinae and Ceratopogoninae, and of the extinct subfamilies Atriculicoidinae and Lebanoculicoidinae, require a protein–rich meal. Only females of *Dasyhelea* (Dasyheleinae) have greatly reduced, vestigial mandibles and laciniae and exclusively feed on nectar. Females of basal lineages, including *Archiaustronops*, *Lebanoculicoides* (Lebanoculicoidinae), all Leptoconopinae in the extant genera *Leptoconops* and *Austroconops, Culicoides* (subfamily Ceratopogoninae) and *Forcipomyia* in the subgenus *Lasiohelea* (Forcipomyiinae), feed on the blood of vertebrates, primarily mammals and birds (Urbanek *et al.* 2014). Most species of Forcipomyiinae are ectoparasites and have mandibles with small teeth that allow them to pierce cuticles of other insects and feed on their haemolymph. Parasites of the extinct subfamily Atriculicoidinae (*Protoculicoides*) most probably fed on the haemolymph of other insects. Females in the tribes Ceratopogonini, Sphaeromiini, Heteromyiini, Palpomyiini and Stenoxenini have mandibles with large teeth and are predators of other, usually small insects (Szadziewski 1988; Urbanek *et al.* 2015).

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