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# Age and recent distribution of extant genera of Ceratopogonidae (Diptera) present in the fossil record

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**ABSTRACT**

Extant genera of biting midges (Ceratopogonidae) present in the fossil record are reviewed and their age and distribution analysed. The biting midges found in the Lower Cretaceous-Miocene deposits are assigned to 25 extant and 19 extinct genera. The oldest extant genera are at least 125 million years old. The percentage of extant genera in the fossil record was found to gradually increase from 20% in the Lower Cretaceous to 43% in the Upper Cretaceous to 77% in the Palaeocene-Eocene and to 100% in the Oligocene-Miocene. Most of the extant genera have or had broad (mostly global) distributions. The relict genera *Austroconops, Metahelea, Meunierohelea,* and *Physohelea,* found in fossil records in the Northern Hemisphere, show limited modern distributions in the Southern Hemisphere. The wide distributions, present or past, of most biting midge genera analysed indicate that neither complete land bridges nor continental drift affected migrations into new territories in any significant way. The distributions of biting midges lend support to the opinion that ecological conditions controlled primarily by climate and competition are the most important factors affecting animal distribution.

**KEY WORDS**: Diptera. Ceratopogonidae. Extant genera. Fossil record. Historical biogeography.

## INTRODUCTION

The Ceratopogonidae (biting midges) is one of the best studied families in the order Diptera. The family is well-known worldwide and has produced rich fossil records, mostly from amber (Szadziewski 1988, 1996). The phylogenetic history of the family probably goes back to the Jurassic, although the oldest records are dated at the Lower Cretaceous.

Fossil biting midges have been mostly described from amber inclusions. They show well-preserved morphological detail, which allows them to be studied as if they were extant (Fig. 1). As a result, the morphological criteria used in the identification of fossil genera are identical to those used in studies of the extant fauna.

The family Ceratopogonidae groups about 6300 species assigned to 129 genera (Borkent & Wirth 1997, updated by Borkent in 2007). Fossil ceratopogonids reported from the Lower Cretaceous to Miocene comprise 253 well-diagnosed species (4.0% of this total) representing 44 genera (25 extant and 19 extinct) listed below.

## RESULTS AND DISCUSSION

The following genera of biting midges have been found in the fossil record (†, extinct; LC, Lower Cretaceous; UC, Upper Cretaceous; P, Palaeocene; E, Eocene; O, Oligocene; M, Miocene).

**Lower Cretaceous**

†*Fossileptoconops* Szadziewski

†*Lebanoculicoides* Szadziewski

†*Archiaustroconops* Szadziewski

†*Jordanoconops* Szadziewski

†*Archiculicoides* Szadziewski

†*Protoculicoides* Boesel

Figure 1. Female *Eohelea petrunkevitchi* Szadziewski with the characteristic stridulatory organ on the wing membrane. The fossil genus *Eohelea* Petrunkevitch, comprising seven species, inhabited the Tertiary of Laurasia (Europe, Sakhalin) (Szadziewski 1988, 1990, 1993). Photo: Volker Arnold of Heide near Hamburg (Germany).

†*Atriculicoides* Remm

†*Minyohelea* Borkent

*Austroconops* Wirth & Lee, Australia, relict

*Leptoconops* Skuse, pantropical, relict

**Upper Cretaceous**

†*Protoculicoides* Boesel

† *Atriculicoides* Remm

† *Minyohelea* Borkent

† *Alautanmyia* Borkent

† *Adelohelea* Borkent

† *Heleageron* Borkent

† *Peronehelea* Borkent

† *Palaeobrachypogon* Borkent

*Austroconops* Wirth and Lee, Australia, relict

*Leptoconops* Skuse, LC, UP, P, E, pantropical, relict

*Culicoides* Latreille, UC, E, M, worldwide

*Ceratopogon* Meigen, UC, E, Holarctic, relict

*Stilobezzia* Kieffer, UC, P, E, O, M, worldwide

*Washingtonhelea* Wirth & Grogan, UC, Nearctic, relict

**Tertiary**

† *Eohelea* Petrunkevitch, P, E

† *Ceratopalpomyia* Szadziewski, E

† *Fossihelea* Szadziewski, E

† *Gedanohelea* Szadziewski, E

† *Mantohelea* Szadziewski, E

† *Wirthohelea* Szadziewski, E

*Alluaudomyia* Kieffer, E, worldwide

*Atrichopogon* Kieffer, E, M, worldwide

*Baeodasymyia* Clastrier & Raccurt, M, Neotropics (Central and South America)

*Bezzia* Kieffer, E, M, worldwide

*Brachypogon* Kieffer, E, M, worldwide

*Ceratoculicoides* Wirth & Ratanaworabhan, E, Holarctic

*Ceratopogon* Meigen, UC, E, Holarctic, relict

*Culicoides* Latreille, UC, E, M, worldwide

*Dasyhelea* Kieffer, E, M, worldwide

*Forcipomyia* Meigen, P, E, M, worldwide

*Heteromyia* Say, M, Neotropics

*Leptoconops* Skuse, LC, UC, P, E, pantropical, relict

*Mallochohelea* Wirth, E, worldwide

*Metahelea* Edwards, E, Philippines and Australia, relict

*Meunierohelea* Szadziewski, E, Australia, relict

*Monohelea* Kieffer, E, worldwide

*Nannohelea* Grogan & Wirth, E, M, pantropical

*Neurohelea* Kieffer, E, Western Europe, relict

*Palpomyia* Kieffer, E,O, M, worldwide

*Phaenobezzia* Haeselbarth, M, worldwide

*Physohelea* Wirth & Grogan, E, Patagonia, relict

*Serromyia* Meigen, E, M, worldwide (except the Neotropics)

*Stilobezzia* Kieffer, UC, P, E, O, M, worldwide

The oldest extant genera of biting midges are *Austroconops* and *Leptoconops*, reported from the Lower Cretaceous Lebanese amber with an absolute age of at least 125 million years. Their age is probably older than documented, but no older fossil biting midges are known. The Lower Cretaceous record has yielded ten genera: two extant (20%) and eight fossil (80%). The number of extant genera found in the Upper Cretaceous ambers increases to six, with the number of fossil genera remaining unchanged (eight). From the Palaeocene–Miocene, 6 fossil and 23 extant genera have been reported, while the Oligocene and Miocene deposits produced as few as 12 extant genera. The contribution of extant genera increases gradually from 20% in the Lower Cretaceous to 43% in the Upper Cretaceous to 77% in the Paleocene-Eocene to 100% in the Oligocene-Miocene (Fig. 2).

The oldest records of extant biting midge genera are as follows:

**125-130 mya.** Lower Cretaceous Lebanese amber: *Austroconops* Wirth & Lee and *Leptoconops* Skuse (Szadziewski 1996, Borkent 2000a, 2001). Both genera belong to the subfamily Leptoconopinae. The females are haematophagous parasites of vertebrates.

**94 mya.** Upper Cretaceous New Jersey amber: *Culicoides* Latreille (tribe Culicoidini) (Grogan & Szadziewski, 1988) and *Stilobezzia* Kieffer (tribe Ceratopogonini) (Borkent 2000a,b). Both genera represent the subfamily Ceratopogoninae. Females of the extant *Culicoides* are parasites feeding on vertebrate blood, while the females of

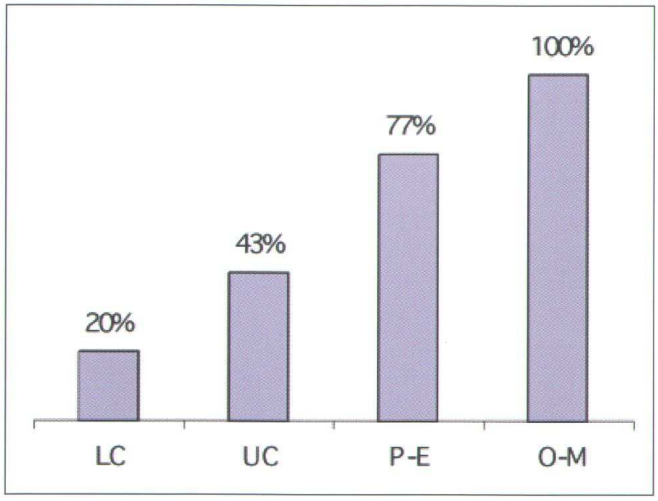


Figure 2. Increase in the contribution of extant genera of biting midges in the fossil record.

LC, Lower Cretaceous; UP, Upper Cretaceous; P-E, Palaeocene-Eocene; O-M, Oligocene-Miocene.

*Stilobezzia* are predators which feed on the haemolymph of small insects.

**85 mya.** Upper Cretaceous Taimyr amber: *Ceratopogon* Meigen and *Washingtonhelea* Wirth & Grogan (Ceratopogoninae: Ceratopogonini) (Szadziewski 1996). The females are predators on other insects.

**60-65 mya.** Palaeocene Sakhalin amber: *Forcipomyia* Meigen (Szadziewski 1990). Feeding habits of adults are diverse. The larvae are mostly terrestrial and usually live under bark of rotten trees (Szadziewski *et al.* 1997).

**40 mya.** Eocene Baltic amber: *Alluaudomyia* Kieffer, *Atrichopogon* Kieffer, *Bezzia* Kieffer, *Brachypogon* Kie-

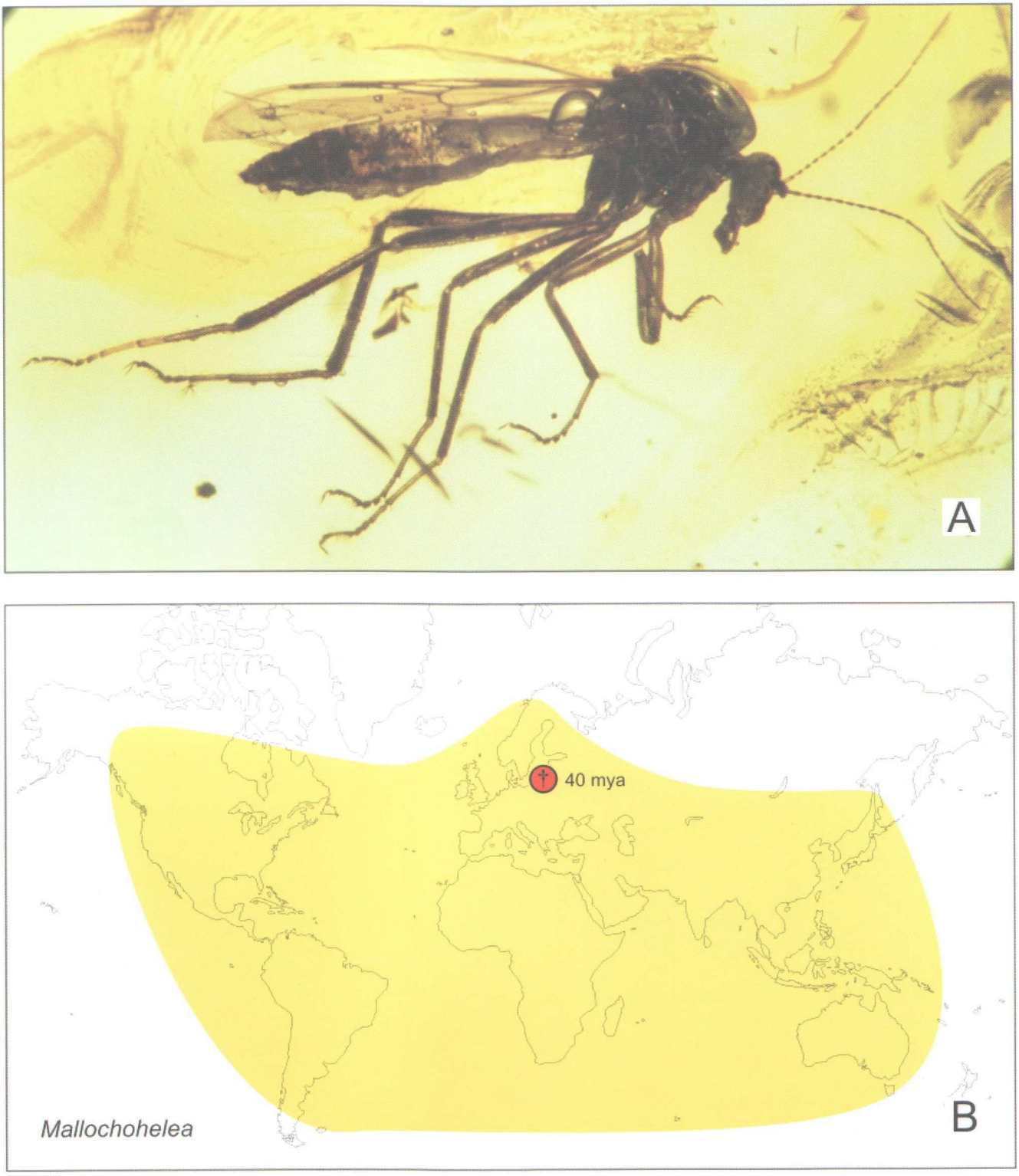


Figure 3. Worldwide distribution of the genus *Mallochohelea* Wirth; A, female *Mallochohelea martae* Szadziewski from Baltic amber; B, ancient (red) and recent (yellow) distributions. Abbreviation: mya, million years ago.

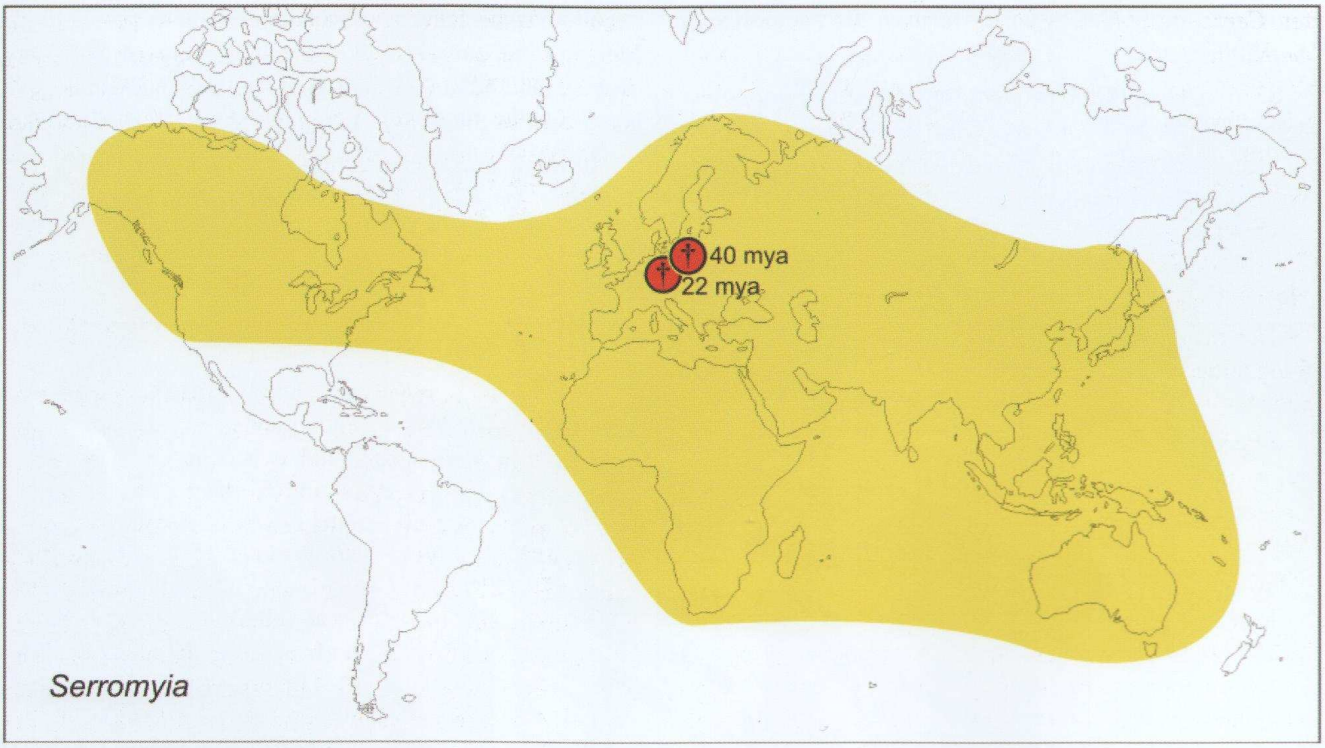


Figure 4. Distribution of the genus *Serromyia* Kieffer. Fossil localities marked red; extant distribution marked yellow. Abbreviation: mya, million years ago.

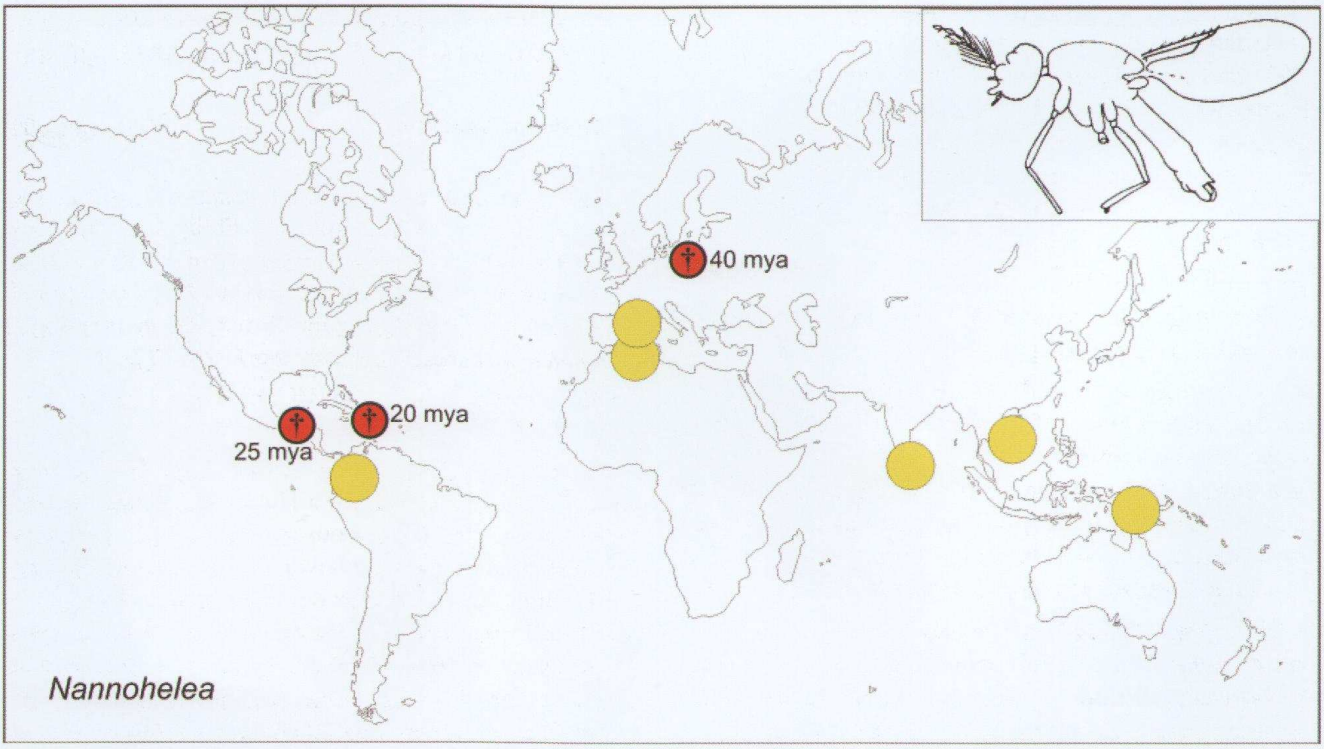


Figure 5. Pantropical distribution of the genus *Nannohelea* Wirth & Grogan. Fossil localities marked red; extant distribution marked yellow. Abbreviation: mya, million years ago.

ffer, *Ceratoculicoides* Wirth & Ratanaworabhan, *Dasyhelea* Kieffer, *Mallochohelea* Wirth, *Metahelea* Edwards, *Meunierohelea* Szadziewski, *Monohelea* Kieffer, *Nannohelea* Grogan & Wirth, *Neurohelea* Kieffer, *Palpomyia* Kieffer, *Physohelea* Wirth & Grogan, *Serromyia* Meigen (Szadziewski 1988, 2005).

**15-20 mya.** Miocene Dominican amber: *Baeodasymyia* Clastrier & Raccurt, *Heteromyia* Say, *Phaenobezzia* Haeselbarth (Szadziewski & Grogan 1994, 1997).

The recent geographic distributions of the 25 extant biting midge genera found in the fossil record are as follows (see above for explanation of abbreviations):

**Worldwide:** *Culicoides* (UC, E, M), *Alluaudomyia* (E), *Atrichopogon*, (E, M), *Bezzia* (E, M), *Brachypogon* (E, M), *Dasyhelea* (E, M), *Forcipomyia* (P, E, M), *Mallochohelea* (E) (Fig. 3), *Monohelea* (E), *Palpomyia* (E, O, M), *Phaenobezzia* (M), *Stilobezzia* (UC, P, E, O, M).

Almost half (48%) of the extant genera reported from the Upper Cretaceous (2) and Tertiary (the remaining 10) have worldwide or nearly worldwide distributions in temperate and tropical climates, e.g., *Mallochohelea* (Fig. 3). They are mostly successful lineages including numerous extant species (Borkent & Wirth 1997): 1210 in *Culicoides*, 877 in *Forcipomyia*, 466 in *Dasyhelea*, 391 in *Atrichopogon*, 310 in *Stilobezzia*, 270 in *Bezzia*, 234 in *Palpomyia*, 180 in *Alluaudomyia*, 120 in *Brachypogon*, 83 in *Monohelea*, 52 in *Mallochohelea*, and 29 in *Phaenobezzia*.

**Worldwide, except the Neotropics:** *Serromyia* (E, M).

This widely distributed genus (Fig. 4) consisting of 33 extant and 7 extinct species absent from the Neotropics is interesting from a biogeographic perspective. The genus was common in the Tertiary of Europe (Szadziewski 1988, 1993) and absent from the Miocene Dominican amber (Szadziewski & Grogan 1998b). The apparent absence of the genus from the Western Hemisphere during the Tertiary is difficult to explain. It is possible that the genus is a fairly recent immigrant to North America, the migration – as already suggested (Szadziewski 1993)– having occurred later than the Miocene.

**Pantropical:** *Nannohelea* (E, O, M) (Fig. 5) and *Leptoconops* (LC, UP, P, E) (Fig. 6).

A pantropical recent distribution is attributed to *Nannohelea*, a small genus of minute predatory biting midges comprising 4 extant and 2 fossil species found in the Tertiary amber in Europe and Central America (Szadziewski 1988, Szadziewski & Grogan 1996, 1998a) (Fig. 5). The distribution of the genus during the Tertiary was somewhat broader and extended to more northern latitudes.

The genus *Leptoconops* which contains about 140 extant species has a relictual, pantropical distribution (Fig. 6). Most species occur in tropical and subtropical regions. However, some species have been reported from as far north as the Moscow region in Russia and Yukon Territory in Canada. This old genus has left rich fossil records and 14 named extinct species. During the Cretaceous, the distribution of the genus was broad, virtually worldwide. The extant larvae of the genus live in moist and usually saline desert sand and in coastal or inland beaches. Inclusions of the genus are more commonly found in Cretaceous than in the Tertiary ambers (Szadziewski 1988, Szadziewski & Schlüter 1992, Borkent 2001, Szadziewski & Arillo 2003, Szadziewski 2004, Szadziewski & Poinar 2005), which may indicate that during the Cretaceous *Leptoconops* larvae occurred in a wider range of habitats than at present.

**Australia:** *Austroconops* (LC, UC) (Fig. 7) and *Meunierohelea* (E) (Fig. 9).

*Austroconops*, regarded as a living fossil (Szadziewski 1996), is known from seven extinct species reported from the Northern Hemisphere and two extant species occurring now in Western Australia (Borkent & Craig 2004). The genus was common in the Lower Cretaceous amber of Lebanon (Szadziewski 1996, Borkent 2000a), Spain (Szadziewski & Arillo 2003) and Myanmar (Szadziewski 2004). In addition, *Austroconops* was found in the Upper Cretaceous ambers of France (Szadziewski & Schüter 1992) and Siberia (Szadziewski 1996). The distribution of the genus in the Lower Cretaceous was probably worldwide, similar to that of *Araucaria* (Grimaldi & Engel 2005). *Araucaria* is a relictual coniferous genus comprising 19 extant species living in restricted populations in the Southern Hemisphere (S. America, Eastern Australia, New Guinea, New Caledonia, and Norfolk Island). The genus occurred formerly, from the Jurassic until the end of the Cretaceous, in the Northern Hemisphere. Groups of such history are regarded as Gondwanan elements (Eskov 2002), austral elements or remnants of Gondwana (Grimaldi & Engel 2005).

A similar relict distribution is found in the Tertiary genus *Meunierohelea* known from four named species reported from the European Baltic amber (Szadziewski 1988, 1993) and one extant species occurring in NE Australia (Fig. 9).

**Oriental and Australian Regions:** *Metahelea* (E) (Fig. 8).

*Metahelea* is a small relict genus comprising two extant species described from the Philippines and Australia. The third species in the genus was described from the Eocene Baltic amber (Szadziewski 1998). Therefore, it can be assumed that, during the Tertiary the distribution of *Metahelea* was broad, probably worldwide (Fig. 8).

**Holarctic:** *Ceratopogon* (UC, E) (Fig. 11) and *Ceratoculicoides* (E).

*Ceratopogon*, comprising 42 extant and 21 fossil species, is a boreal genus with a Holarctic distribution (Fig. 11). In the Upper Cretaceous Siberian amber, the genus is represented by *Ceratopogon macronyx* Remm. Borkent (1995) transferred the species to *Palaeobrachypogon*, a new fossil genus, but the transfer has not been accepted (Szadziewski 1996). While the genus was predominant (25.3% of biting midge specimens) in the Eocene Baltic amber, it is now a very rare inhabitant of cold boreal parts of the Northern Hemisphere, often restricted to isolated mountain areas. Szadziewski (1988) explained this pattern by contending that the genus has been on the decline since

the Eocene. The explanation offered by Borkent & Grogan (1995), whereby the dominance and high diversity of *Ceratopogon* in the Baltic amber depended mostly on the midges occurring in early spring is less plausible because as few as 2.0% of the Ceratopogonidae found in the recent material collected in boreal forests during spring and summer were contributed by *Ceratopogon*, represented by a single species (Hagan *et al.* 2000).

*Ceratoculicoides* is a small genus comprising six extant species known from Europe, North America and Mexico, and one fossil species reported from the Eocene Baltic amber (Szadziewski 1988).

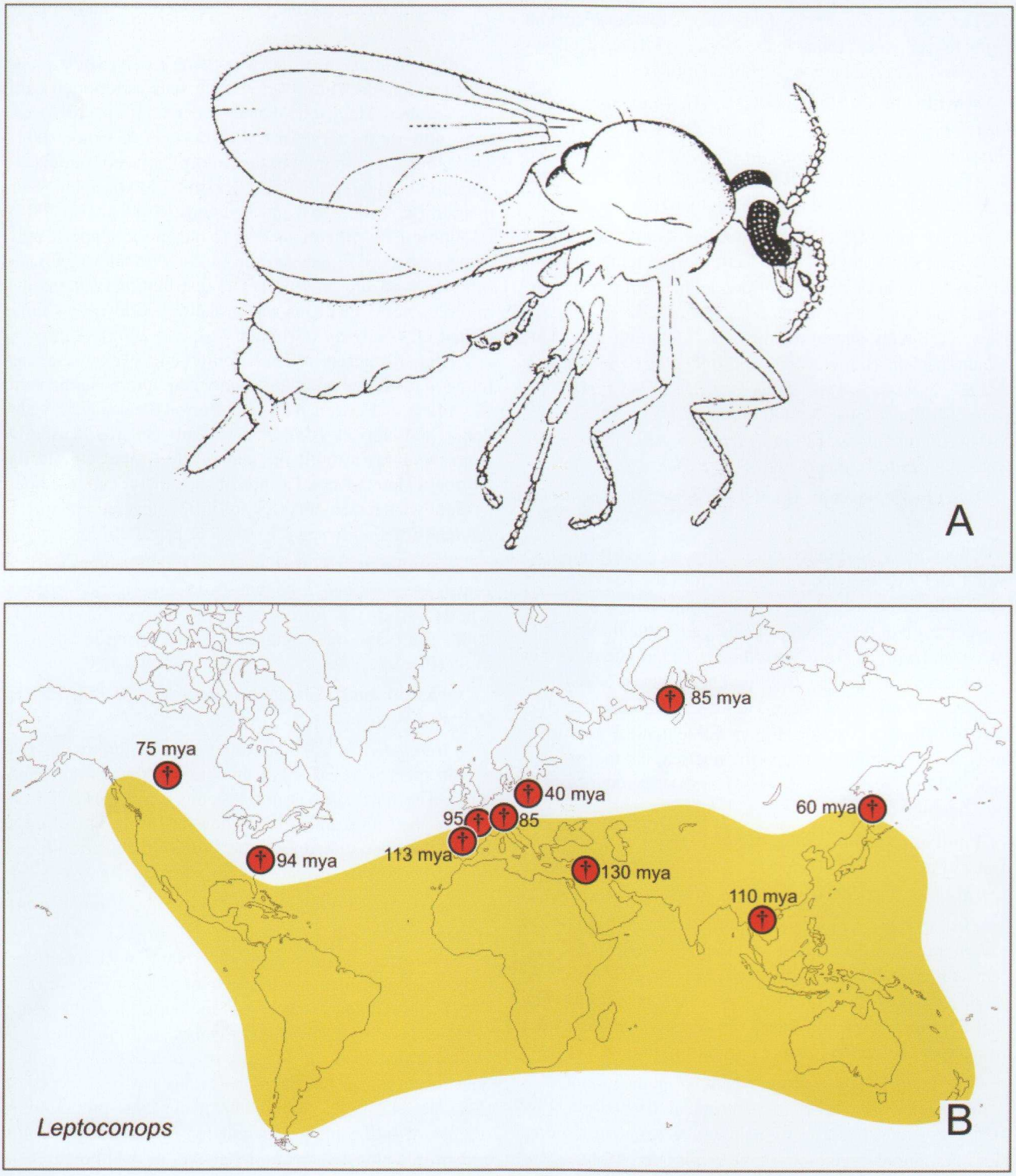


Figure 6. Pantropical genus *Leptoconops* Skuse. A, female *Leptoconops* (*L.*) *zherikhini* Szadziewski & Arillo from Lower Cretaceous amber of Alava, 113 mya; B, ancient (red) and recent (yellow) distributions. Abbreviation: mya, million years ago.

**Nearctic:** *Washingtonhelea* (UC).

The genus consists of a single extant species known from California and two fossil species reported from the Upper Cretaceous Siberian and Canadian amber (Szadziewski 1996). However, the generic position of *W. aquilonia* (Boesel) from the Canadian amber was questioned by Borkent (2000b). The genus was originally placed in the predatory tribe Ceratopogonini (Wirth & Grogan 1988). The taxonomic position of the genus within the subfamily Ceratopogoninae, and the species it comprises, requires further studies.

**Western Europe:** *Neurohelea* (E) (Fig. 12).


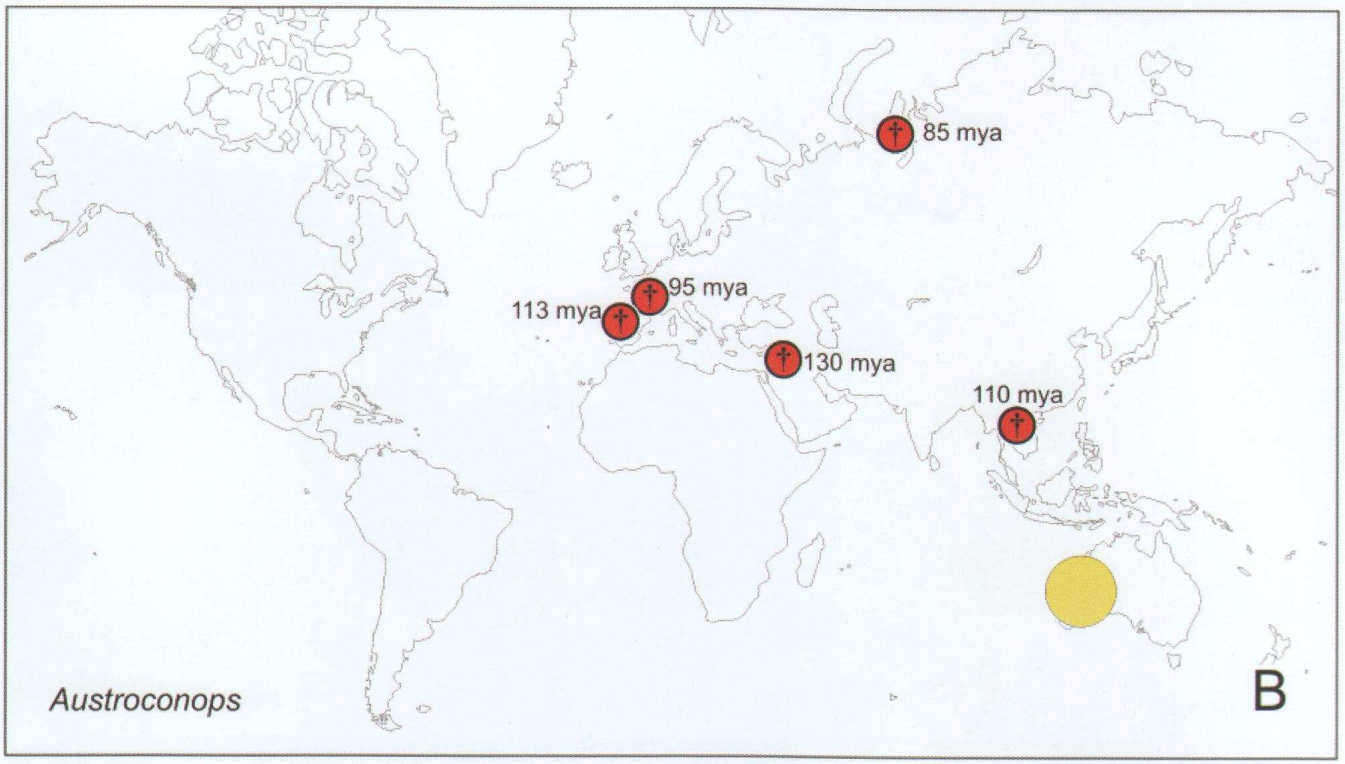


Figure 7. Relict genus *Austroconops* Wirth & Lee; A, male *Austroconops sibiricus* Szadziewski from Upper Cretaceous amber of Taimyr, drawing and photograph; B, ancient (red) and recent (yellow) distributions. Abbreviation: mya, million years ago.

*Neurohelea* contains a single extant species, *N. luteitarsis* (Waltl) which has a limited distribution in Western Europe (Germany, Belgium and Great Britain) (Borkent 1998). It probably represents an Atlantic biogeographic element in Europe, similar to *Fagus sylvatica*, a more widely distributed and common tree. This genus of predatory biting midges was represented in the Eocene fauna of Europe by *N. cothurnata* (Meunier) from the Baltic amber (Szadziewski 1988, 1998). The extant species are extremely rarely collected in Western Europe, which may suggest that the genus is a relict undergoing extinction.

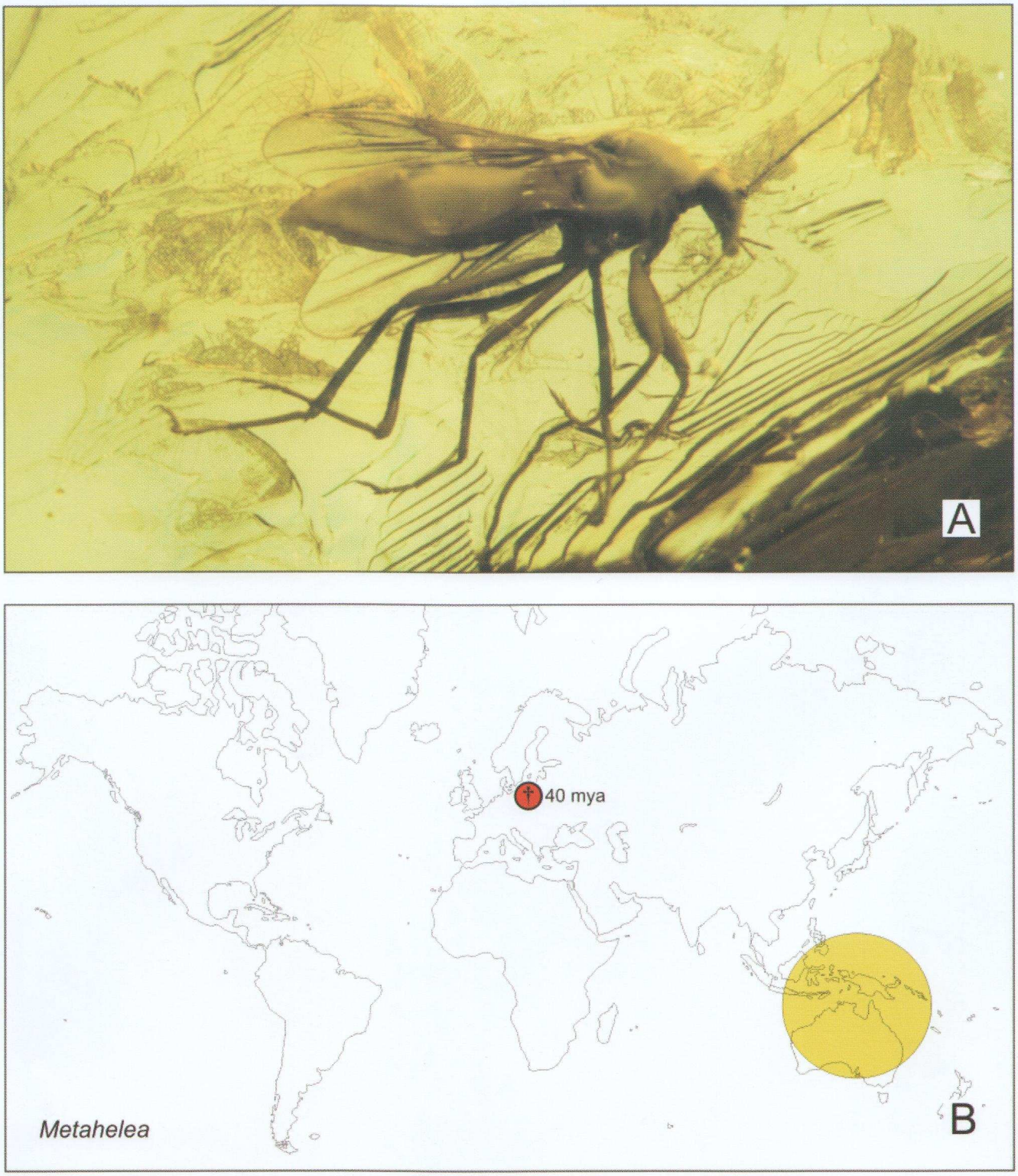


Figure 8. Relict genus *Metahelea* Edwards; A, female *M. serafini* Szadziewski from Eocene Baltic amber; B, ancient (red) and recent (yellow) distributions. Abbreviation: mya, million years ago.

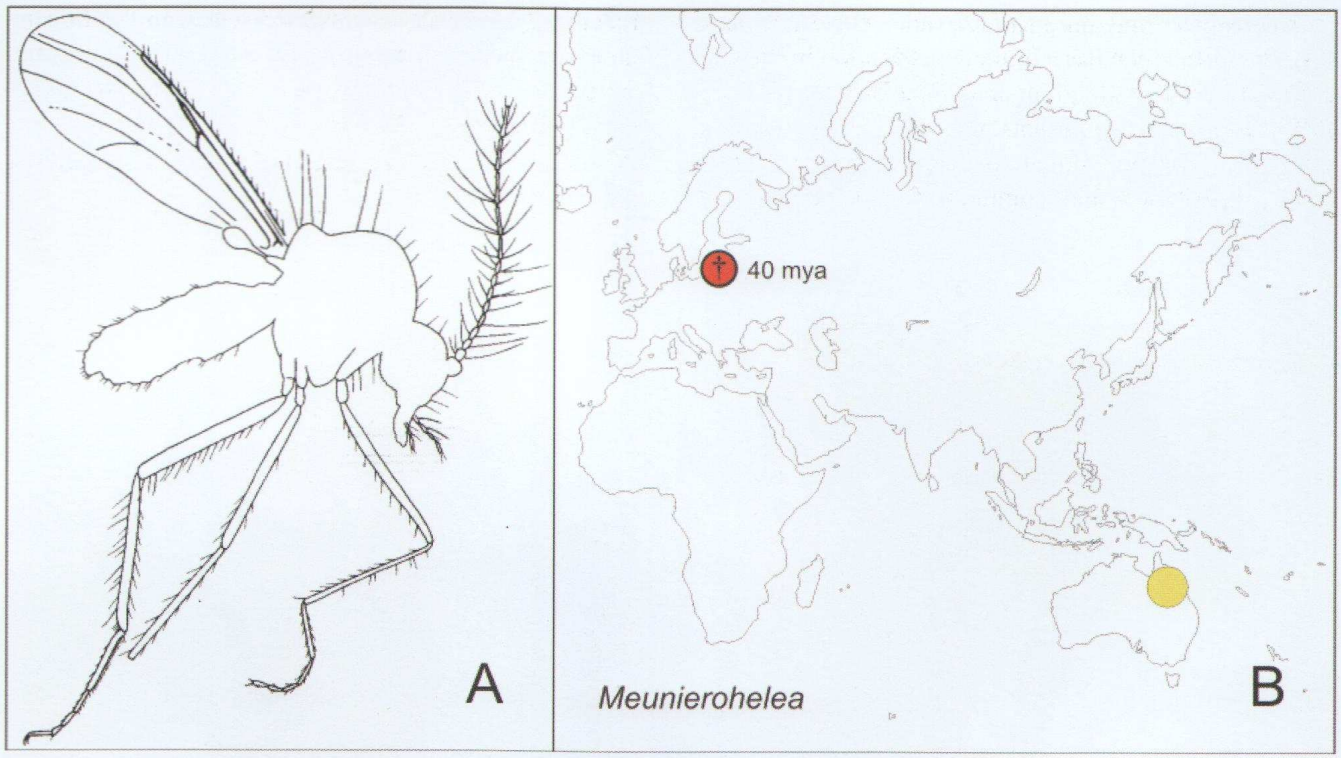


Figure 9. Relict genus *Meunierohelea* Szadziewski; A, female *M. nielseni* Szadziewski from Eocene Baltic amber; B, ancient (red) and recent (yellow) distributions. Abbreviation: mya, million years ago.

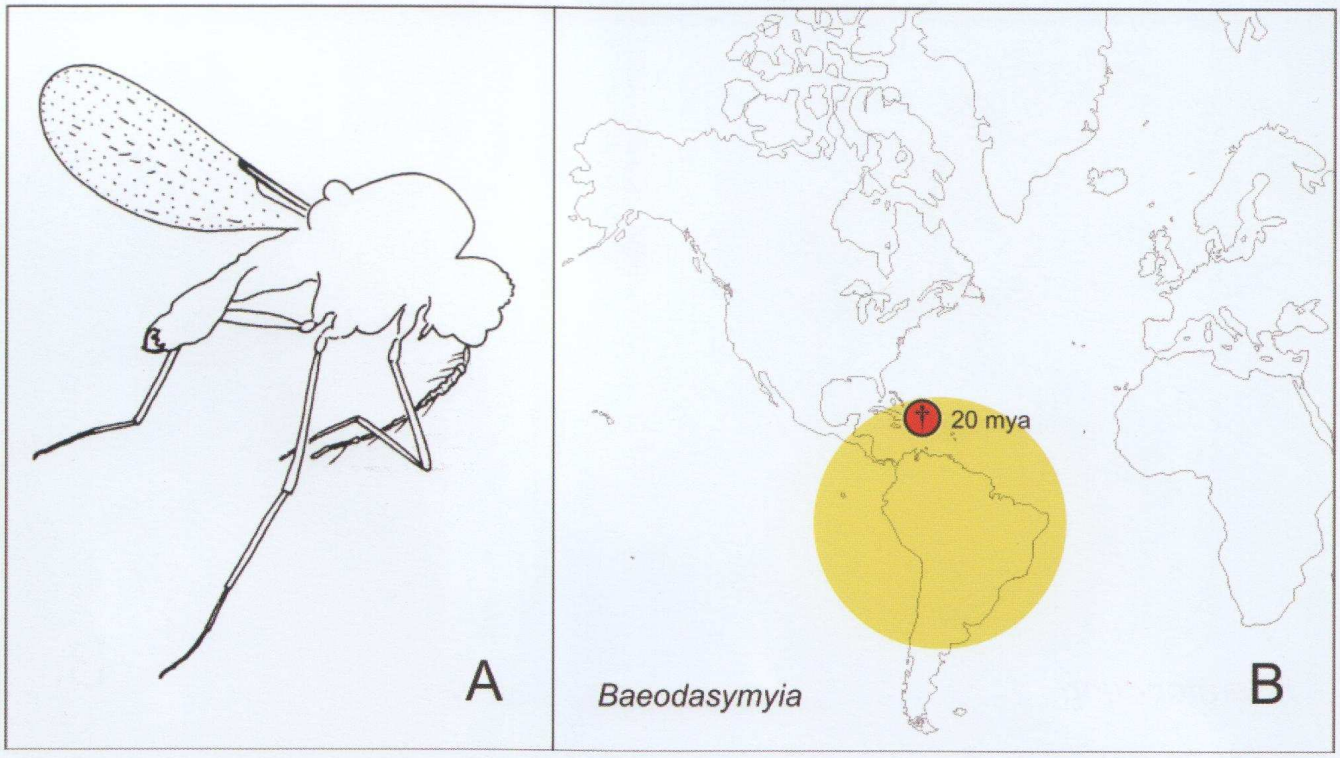


Figure 10. Neotropical genus *Baeodasymyia* Clastrier & Raccurt; A, male *B. dominicana* Szadziewski & Grogan from Miocene Dominican amber; B, ancient (red) and recent (yellow) distributions. Abbreviation: mya, million years ago.

**Neotropics:** *Baeodasymyia* ( M) (Fig. 10), *Heteromyia* (M), *Physohelea* (E) (Fig. 12).

*Baeodasymyia* is a small Neotropical genus comprising five extant species distributed in Central and South Ame-


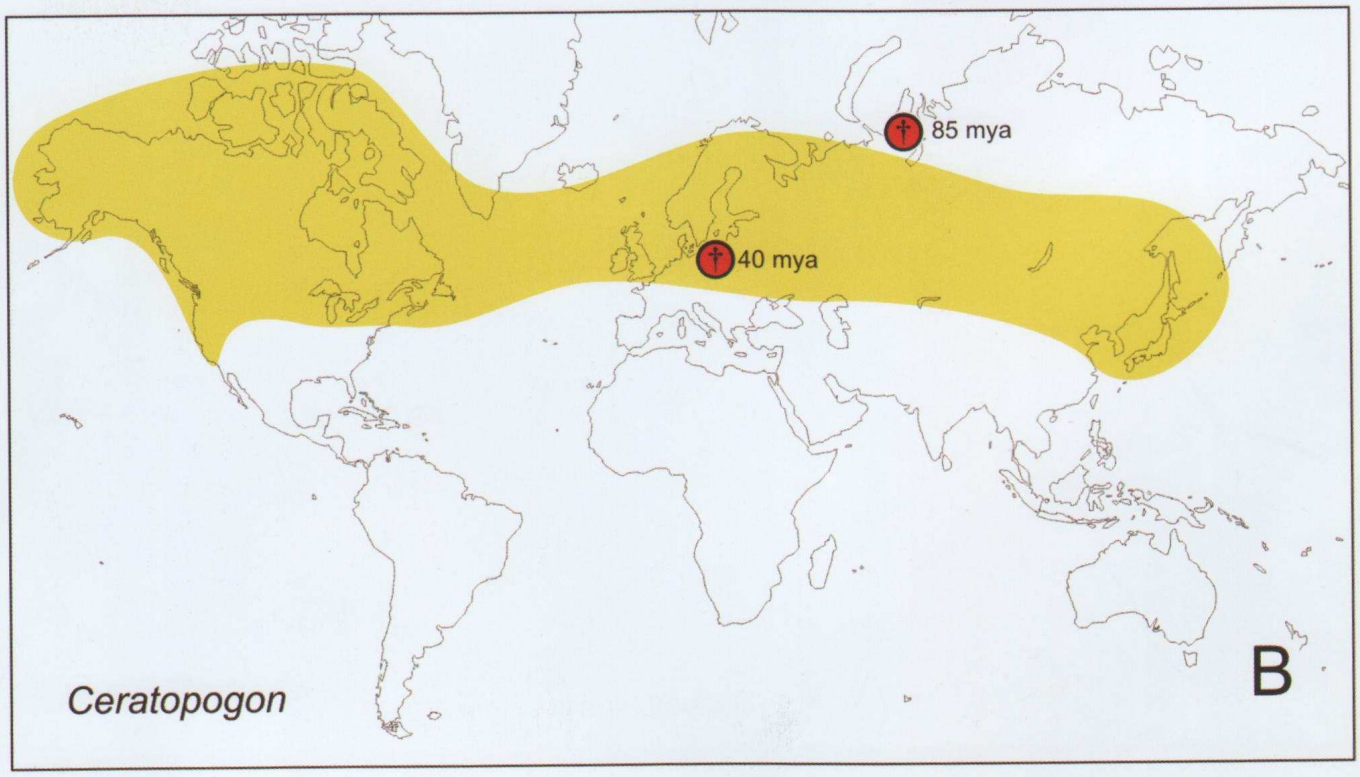


Figure 11. Holarctic genus *Ceratopogon* Meigen; A, male *C. forcipiformis* Meunier from Eocene Baltic amber; B, ancient (red) and recent (yellow) distributions. Abbreviation: mya, million years ago.

rica (Borkent & Craig 1999) and one fossil species recorded from the Miocene Dominican amber (Szadziewski & Grogan 1994) (Fig. 10). A similar Neotropical distribution has been attributed to *Heteromyia* with its 11 extant species occurring in South and Central America and two other species inhabiting the eastern states of the USA; there is also one fossil species described from the Miocene Dominican amber (Szadziewski & Grogan 1997). Both genera have probably been distributed in a more or less stable manner in the New World since the Miocene.

*Physohelea* is a genus comprising two extant species inhabiting the temperate *Nothofagus* forest of southern

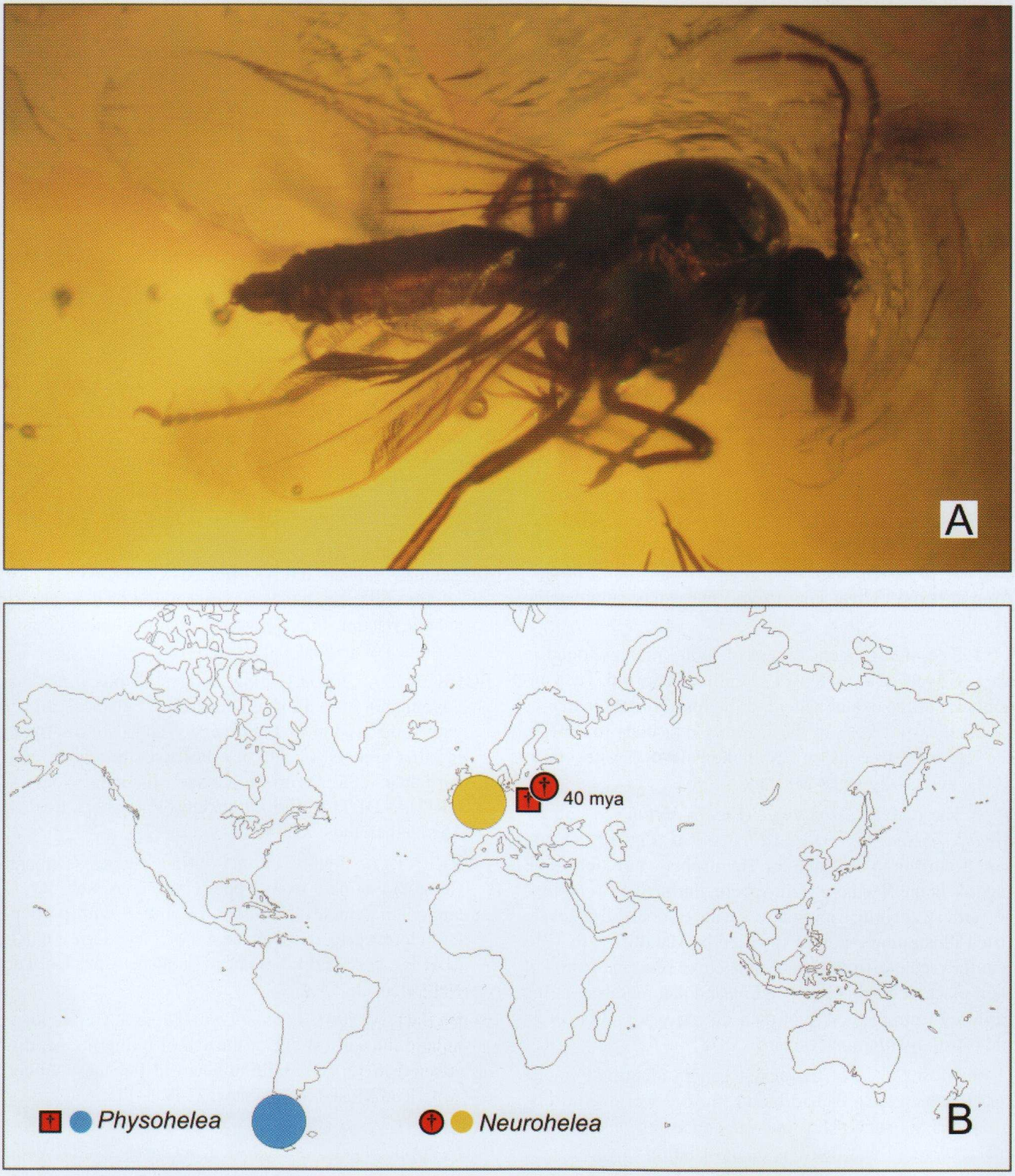


Figure 12. Relict distributions of sister genera *Neurohelea* Kieffer and *Physohelea* Grogan & Wirth; A, male *Physohelea obtusa* (Meunier) from Eocene Baltic amber; B, ancient (red) and recent (yellow) distributions. Abbreviation: mya, million years ago.

Argentina and Chile (Patagonia) (Spinelli 1994) and one fossil species, *Physohelea obtusa* (Meunier) reported from the Eocene Baltic amber (Szadziewski 1988). *Neurohelea* and *Physohelea,* regarded as sister genera within the tribe Heteromyiini (Szadziewski 1988), show a pattern of extant distribution similar to that of the tree genera *Fagus* and *Nothofagus* dating back to the Tertiary. At present, *Fagus* (Fagaceae) is distributed in the Northern Hemisphere, while *Nothofagus* (Nothofagaceae) occurs in the Southern Hemisphere; their ancestral forms have been observed in Tertiary deposits in North America, Eastern Asia, and South America, both genera having rich fossil records indicative of a distribution wider than that at present (Kostrowicki 1999). Evidently, the distribution of *Physohelea* in Patagonia is relictual.

## CONCLUDING REMARKS

Evolution of any group proceeds in time and space; each taxon, like a specimen, has its own life, with a beginning and an end. Consequently, phylogenetic relationships between taxa and scenarios explaining their geographic distributions require studies using fossils, such studies being helpful in, or even necessary for, testing phylogenetic and biogeographic hypotheses. In many cases, neontological studies on distribution and phylogeny result in hypotheses which are not testable. This happens mostly with respect to insects whose fossil materials are poor or ignored.

The relatively well-studied family Ceratopogonidae provides good examples illustrating the problems and previously formulated rules of historical biogeography. The analysis of genera identified among fossil biting midges from the Lower Cretaceous to Miocene can be summarized as follows:

1. The oldest extant genera of biting midges found in the fossil record are at least 125 million years old. The contribution of the extant genera to the fossil record increases gradually from 20% in the Lower Cretaceous to 43% in the Upper Cretaceous to 77% in the Palaeocene-Eocene to 100% in the Oligocene-Miocene.

2. The genera *Austroconops* (Fig. 7), *Metahelea* (Fig. 8), *Meunierohelea* (Fig. 9), and *Physohelea* (Fig. 12), at present occurring in the Southern Hemisphere, have left fossil records in the Northern Hemisphere; during the Cretaceous or Tertiary, their distribution was wide (global). The genera listed illustrate the point expressed by Handlirsch in 1913 that the recent distribution of many taxa is no indication of their place of origin or dispersion, and that members living far away from the centre of their diversity are relicts of an old broad distribution (Udvardy 1978).

3. Most (76%) of the extant genera identified among fossils which have or had broad (mostly worldwide) distributions are successful lineages consisting of numerous species. Broad distributions of most biting midge genera analyzed, present or past, indicate that neither complete land bridges nor continental drift affected their immigration to new territories, which supports the opinion put forth by Darlington (Grimaldi & Engel 2005) that ecological conditions, controlled mostly by climate and competition, are the most important factors affecting animal distributions.

4. The view of Truessart (Udvardy 1978) that a taxon has its centre of origin where most species are present should be treated with utmost caution. This view can be supported by the distributions of only a few genera: *Ceratopogon* (Fig. 11), *Ceratoculicoides*, and *Neurohelea* (Fig. 12), which originated in Laurasia during the Upper Cretaceous or Tertiary and still live here, and *Baeodasymyia* (Fig. 10) and *Heteromyia*, reported from the Miocene Dominican amber and still present in the Neotropics.

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