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Upper and Lower Cretaceous Biting Midges (Ceratopogonidae: Diptera) from Hungarian and Austrian Amber and the Koonwarra Fossil Bed of Australia

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With 2 figures

Abstract

Three new Cretaceous biting midge fossils are described and named, one from Lower Cretaceous Austrian amber (Hauterivian; 127–130 my), *Minyohelea casca* n.sp., and two from Upper Cretaceous Hungarian amber (80–90 my), *Leptoconops clava* n.sp. and *Adelophelea magyarica* n.sp. A fourth species, represented by a wing compression fossil from the Lower Cretaceous (115 ± 6 my – 118 ± 5 my) Koonwarra Fossil Bed in Australia, is redescribed and identified as a male member of *Leptoconops*. The phylogenetic position of these taxa confirms earlier reports that successively older fossils represent successively older cladistic lineages.

Zusammenfassung

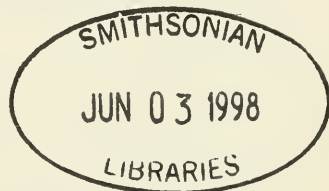
Drei neue Arten fossiler Kriebelmücken aus der Kreidezeit werden beschrieben und benannt, eine aus österreichischem Bernstein der Unterkreide (Hauterive; 127–130 my), *Minyohelea casca* n.sp., und zwei aus ungarischem Bernstein (80–90 my), *Leptoconops clava* n.sp. und *Adelophelea magyarica* n.sp.

Eine vierte Art, vertreten durch einen Flügel aus dem unterketazischen (115 ± 6 – 118 ± 5 my) Koonwarra Fossil Bed in Australien, wird beschrieben und bestimmt als männliches Individuum aus der Gattung *Leptoconops*.

Die phylogenetische Position dieser Taxa, wie sie sich aus cladistischer Analyse ergibt, steht im Einklang mit ihrer stratigraphischen Altersrelation.

Introduction

The Ceratopogonidae have an outstanding fossil record in both the Tertiary and Cretaceous periods (BORKENT, 1995, 1996; SZADZIEWSKI, 1996). Combined with an increasingly resolved cladogram of the extant lineages, the group provides wonderful insights into the diversification of a major group of insects. This paper reports on four further fossils; one is from Lower Cretaceous Austrian amber, two are from



Upper Cretaceous Hungarian amber and one is a wing compression fossil from the Lower Cretaceous of Australia. All belong to early lineages within the Ceratopogonidae.

Materials and Methods

The three amber specimens were treated, examined, measured and analyzed in the manner described by BORKENT (1995). The Austrian specimen was mounted on a microscope slide while the two Hungarian specimens are in plastic mountant between two coverslips. These amber specimens are housed in the Staatliches Museum für Naturkunde in Stuttgart, Germany. The compression fossil from the Koonwarra Fossil Bed in Australia, housed in the Victoria Museum in Melbourne, Victoria, Australia, was studied under a Wild M3 dissecting microscope at up to $90\times$ magnification. Wetting the specimen briefly with alcohol increased the contrast and allowed for some further details to be seen.

Terms for structures follows those in BORKENT (1995). However, the changes of wing vein names proposed by SZADZIEWSKI (1996) are accepted.

Results

Minyohalea casca n. sp.

Figs. 1A–E

Holotype: male adult in amber on microscope slide, SMNS No. OB-38-X.

Type locality: Golling, Austria.

Type horizon: Lower Cretaceous.

Derivation of name: *casca* (lat.) = very ancient. Refers to the age of the species, amongst the oldest of all known Ceratopogonidae.

Diagnosis. – Male: only member of the genus with flagellomere 13 longer than preceding flagellomeres and parameres (apparently) somewhat stout, not extending far beyond tergite 9 and curved apically. – Female: unknown.

Description. – Male adult. Most details not visible.

Antenna with moderately developed plume, 13 separate flagellomeres, flagellomere 13 more elongate than preceding flagellomeres (Fig. 1B).

Wing (Fig. 1A): Length = 0.43 mm, costal ratio = 0.38. Macrotrichia absent, microtrichia present. Alula not visible. Both radial cells apparently fused. Details of M, Cu not visible.

Legs: Femora, tibiae slender. Legs lacking armature (Figs 1D–E). Pair of thick setae on fore and midleg trochanter not visible. TR of midleg = 2.7, hindleg = 1.9, midleg/hindleg = 1.4. Midleg tibia apparently without apical spur (if present, very small). Hindleg first tarsomere without thick basal spine, with scattered setae (Fig. 1E). Claws simple, inner tooth not visible, equal. Without empodium.

Genitalia (Fig. 1C): Two posterolateral prongs (likely to be parameres), gradually narrowing near apex. Further details not visible.

Female adult. – Unknown.

Distribution and bionomics. – *Minyohalea casca* is known only from the type locality at Golling, Austria. The amber is considered to have originated from an

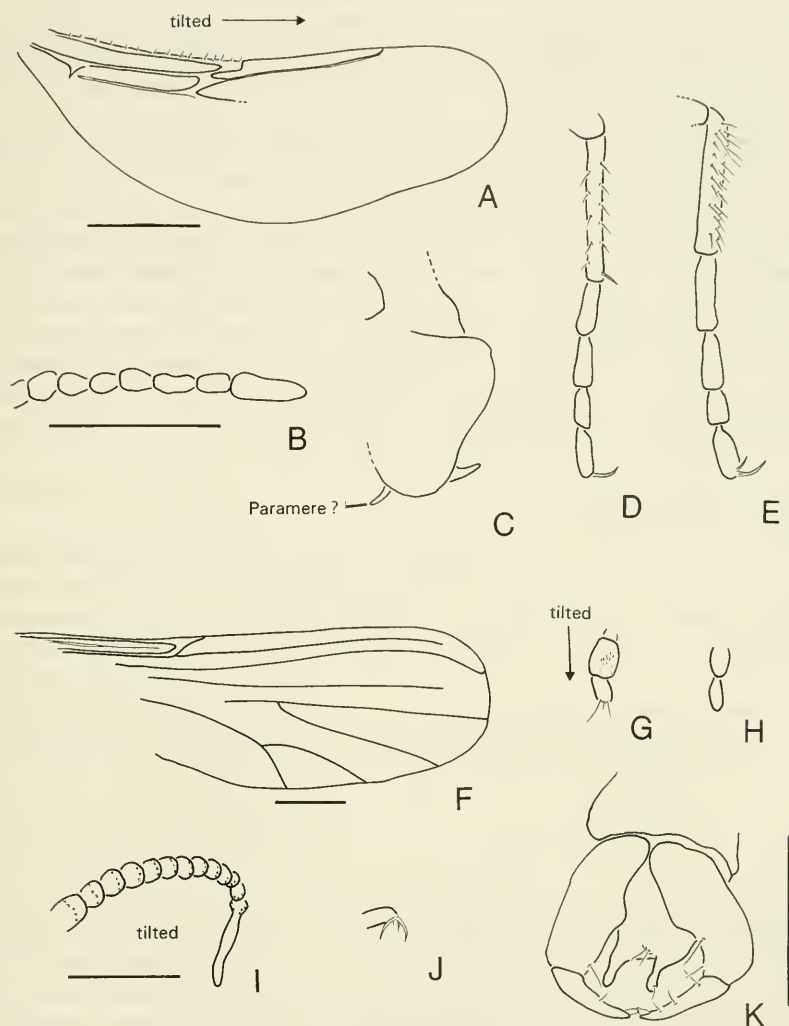


Fig. 1. A–E: Structures of male *Minyohelea casca*. A: wing. B: terminal flagellomeres. C: genitalia (same scale as B). D: midleg (same scale as B). E: hindleg (same scale as B). F–K: Structures of male *Leptoconops clava*. F: wing. G: right palp (same scale as K). H: left palp (same scale as K). I: antenna. J: tarsal claws of hindleg (same scale as I). K: genitalia. Scale = 0.1 mm.

Araucariaceae, to be of Lower Cretaceous (Hauterivian) age, contemporaneous with Lebanese amber (SCHLEE, 1984; VAVRA, 1984; WELLER & WERT, 1984) and therefore 127–130 million years old (OBRADOVICH, 1993). BANDEL & VAVRA (1981) described the infrared and mass spectroscopy and thin layer chromatography of Austrian amber.

The amber containing *M. casca* was different from any other with which I have worked (Mexican, Dominican Republic, Baltic, Canadian, New Jersey, Lebanese).

Unlike other Cretaceous ambers, this Austrian amber was not very fragile and therefore relatively easy to cut, was of a milky brown colour and had a somewhat “plastic” feel to it. When broken this amber produced small conchoidal fracture patterns as in other ambers. The matrix was filled with very small contaminants, partially obscuring the inclusions.

A Porricondylinae (moderate condition), a male Chironomidae (poor condition) and two unidentified leg fragments were also in the amber.

Taxonomic discussion. – The holotype of *M. casca* is in somewhat poor condition, being partially distorted in the amber and with much of the body opaque. Furthermore, fine particles in the amber made some details impossible to see clearly.

The details of the wing venation at the apex of the radial cells differs in *M. casca* and *M. schleei* SZADZIEWSKI, in that there was no evidence of a costal extension beyond the apex of the radial cells in *M. casca*. I have not used these as diagnostic features because of some uncertainty in the interpretation of this area in both species; the costa extension can be difficult to see in some fossils. Further resolution must await further material in better condition and position.

The species described here was the one referred to by SCHLEE (1984) as an unidentified member of the family.

Phylogenetic analysis. – SZADZIEWSKI (1996) placed a new species, *Minyobealea schleei*, from Lower Cretaceous Lebanese amber in the previously monotypic Upper Cretaceous Canadian amber genus *Minyobealea* BORKENT (type species *M. pumilis* BORKENT). His new species and *M. pumilis* shared the presence of only the terminal flagellomere elongate, a reduced wing venation and elongate male parameres (or what are apparently parameres). SZADZIEWSKI (1996) stated that the phylogenetic placement of *Minyobealea* by BORKENT (1995) as a member of the Ceratopogoninae was likely mistaken. Reexamination of the type material of *M. pumilis* indicates that he was correct in considering the genus misinterpreted. The relative tarsal ratios of the foreleg/hindleg is 1.5–1.7 (males, n=2) and the original report of the presence of a thick pair of setae on the midleg trochanter, a character state restricted to another group of Ceratopogonidae, could not be confirmed. The tarsal ratio character is likely a synapomorphy of the Austroconopinae and is further discussed in detail by BORKENT (in prep.). The report of the presence of palisade setae on the first tarsomere of the hindleg presents problems; the character state is more difficult to determine than was initially apparent. In some fossils stout setae may be present on the hind first tarsomere and especially in outline, appear to present a distinct row of palisade setae. The problem is discussed in more detail in BORKENT (in prep.).

SZADZIEWSKI (1996) placed *Minyobealea*, with *Lebanoconops* SZADZIEWSKI, as the sister group of *Austroconops* WIRTH & LEE. These conclusions are discussed further by BORKENT (in prep.) on the basis of a reanalysis of Lebanese amber ceratopogonids.

Leptoconops (Leptoconops) clava n. sp.

Figs. 1F–K

Holotype: male adult in amber, embedded in plastic, mounted between two microscope coverslips, SMNS No. UB-1-WK-1.

Type locality: Ajka, Hungary.

Type horizon: Upper Cretaceous.

Derivation of name: clava (lat.) = club. Refers to the distinctive shape of the gonostylus.

Diagnosis. – Male: only Cretaceous species of *Leptoconops* SKUSE with apicolateral processes thick and slightly enlarged apically and gonostylus tapering gradually from base to apex (lacking subapical projections). – Female: unknown.

Description. – Male adult.

Head: Eyes bare. Ommatidia broadly separated dorsomedially, vertex without single dorsomedial seta. Antenna with well developed plume, 13 separate flagellomeres, antennal ratio not measurable, flagellomere 10/11 not measurable, flagellomere 13 more elongate than preceding flagellomeres (Fig. 1I). Mouthparts very short, mouthpart length/length of fifth tarsomere of fore leg not measurable. Palp (Figs. 1G–H) with four segments, third segment somewhat ovoid, with capitate sensilla arranged on surface (Fig. 1G), palp segment $3/4 = 1.17$.

Thorax: Anterior pronotal apodemes not visible. Scutum pruinose, with a few scattered elongate setae, humeral pit present. Anapleural suture not visible. Katepisternum setae not visible.

Wing (Fig. 1F): Length = 0.65 mm, costal ratio = 0.35. Without macrotrichia, with fine microtrichia on all membrane. Alula not visible. Radial cells compacted anteriorly, not distinguishable. Base of M poorly defined.

Legs: Femora, tibiae slender. Legs lacking armature. Setae on fore and midleg trochanter not visible. Midleg tibia with apical spur. Hindleg first tarsomere without thick basal spine, without palisade setae. Claws with slender basal tooth (Fig. 1J). Empodium not visible.

Genitalia (Fig. 1K): Apicolateral processes broadly separated, each elongate, thick, expanded apically, with apical seta. Gonocoxite moderately elongate. Gonostylus thick basally, tapering to toothed apical spine, lacking thick seta on outer face. Paramere, aedeagus not visible.

Female adult. – Unknown.

Distribution and bionomics. – *Leptoconops clava* is known from Upper Cretaceous amber collected at Ajka, Hungary. The amber is found in a coal seam deposited in a mesohaline environment (HASS, 1995) and is considered to be 80–90 million years old (SCHLEE, 1990:27). BANDEL & RIEDEL (1994) reported a mixture of brackish and freshwater gastropods from the same deposit. Immatures of extant species of *Leptoconops* are commonly associated with haline or alkaline substrates and the presence of *L. clava* in an apparently similar habitat is consistent for the group.

Females of extant species of the genus *Leptoconops* suck blood from a variety of vertebrates (BORKENT, 1995) and it is likely that the female of this fossil species did the same.

Taxonomic discussion. – The holotype was in excellent condition in a clear piece of amber. Only a fracture plane obscured parts of the legs and a gas bubble was present at the base of the abdomen.

The male genitalia, lack of heavy spines on the legs and shape of the claws is consistent with a placement of this species in the subgenus *Leptoconops*, as are all other fossil *Leptoconops*.

Adelophelea magyarica n. sp.

Figs. 2A-F

Holotype: male adult in amber, embedded in plastic, mounted between two microscope coverslips, SMNS No. UB-1-WK-2.

Type locality: Ajka, Hungary.

Type horizon: Upper Cretaceous.

Derivation of name: *magyarica* derived from Magyar, the predominant ethnic group in Hungary. Refers to the type locality in Hungary.

Diagnosis. – Male: only Cretaceous species of *Adelophelea* BORKENT with a gonostylus tapering from an enlarged base to a slender apex; also only species with 13 separate flagellomeres. Female: unknown.

Description. – Male adult.

Head: Eyes bare. Ommatidia narrowly separated dorsomedially, with single dorsomedial seta not visible. Antenna with 13 separate flagellomeres, antennal ratio = 0.82, flagellomere 10/11 = 0.42, flagellomeres 11-13 more elongate than preceding flagellomeres (Figs 2C,D), first flagellomere sensilla coeloconica not visible. Mouthparts moderately long, mouthpart length/length of fifth tarsomere of fore leg not measurable. Palp not clearly visible.

Thorax: Anterior pronotal apodemes not visible. Scutum pruinose, with scattered elongate setae, humeral pit not visible. Anapleural suture not visible. Katepisternum setae not visible.

Wing (Fig. 2A): Length = 0.45 mm, costal ratio = 0.48. Macrotrichia absent, with fine microtrichia present on all membrane. Alula macrotrichia not clearly visible but apparently absent. Radial cells separate but cell r_1 difficult to discern. M_2 apparently originating from near base of wing.

Legs: Femora, tibiae slender. Legs lacking armature (Fig. 2E,F). TR foreleg = 1.5, hindleg = 1.9, foreleg/hindleg = 0.8. Pair of thick setae on fore and midleg trochanter not visible. Midleg tibia apical spur not visible. Hindleg first tarsomere without thick basal spine, without palisade setae (Fig. 2F). Claws simple. Empodium not visible.

Genitalia (Fig. 2B): Apicolateral process elongate, slender, apical seta not visible. Gonocoxite of moderate length. Gonostylus thick basally, elongate apically. Paramere, aedeagus not visible.

Female adult. – Unknown.

Distribution. – *Adelophelea magyarica* is known only from the holotype in 80-90 million year old Upper Cretaceous amber collected at Ajka, Hungary. Further discussion about the amber is given under *Leptoconops clava* above.

Taxonomic discussion. – This species is tentatively placed in *Adelophelea*, primary on the basis of the similarity in size, wing venation, and the relative lengths of antennal flagellomeres. However, *A. magyarica* lacks the partially fused flagellomeres present in the only other known species, *A. glabra*. This inclusion in the genus necessitates a modification to the generic diagnosis for the male adult as follows: the only genus of Cretaceous Ceratopogonidae with ommatidia narrowly separated dorsomedially, with a wing costal ratio equal to or less than 0.6, without macrotrichiae on the wing membrane, with two well developed radial cells, and the first tarsomere of the hindleg without palisade setae. This diagnosis does not separate *Adelophelea* from some extant *Culicoides* (although most have macrotrichia on the wing). The generic key in BORKENT (1995) will successfully identify *A. magyarica* to genus.

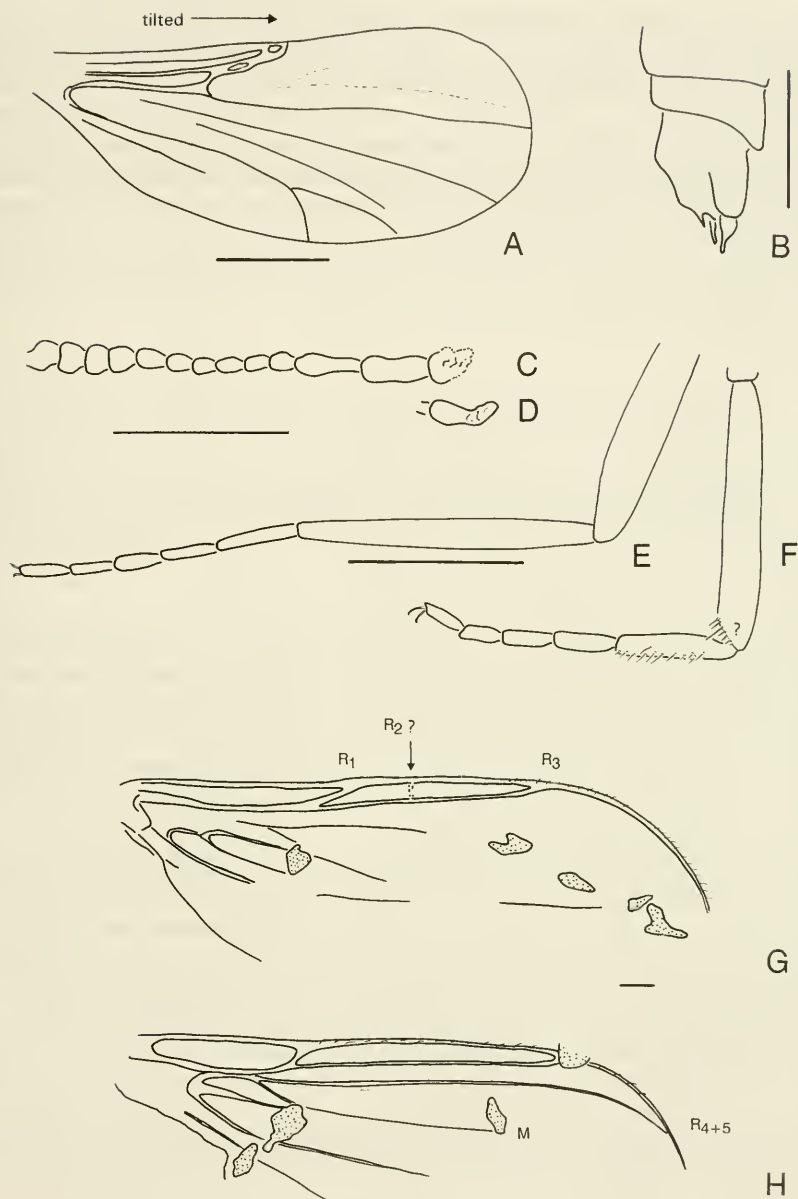


Fig. 2. A–F: Structures of male *Adelophelea magyarica*. A: wing. B: genitalia. C: left antenna. D: flagellomere 13 of right antenna. E: foreleg. F: hindleg. G–H: wing of *Leptoconops* from Koonwarra Fossil Bed. G: first face. H: second face (image reversed to allow better comparison with Fig. 2G). Scale = 0.1 mm.

Wing vein M_2 appears to originate near the base of the wing in *A. magyarica*, which differs from the type species *A. glabra*. Considering that only one wing was visible, I prefer to await for further material before interpreting this difference as significant.

The phylogenetic position of *Adelobelea* was discussed by BORKENT (1995). The new species described here sheds no further cladistic light on the closest relatives of the genus. Nor can any synapomorphies be proposed to indicate that the two included species form a monophyletic group.

The holotype was partially obscured by fine gas bubbles in the otherwise clear amber; in addition there was a small fracture plane just ventral of the head capsule, making the mouthparts difficult to see.

Fossil from the Koonwarra Fossil Bed in Australia Figs. 2G–H

The compression fossil is known only as a single wing from the Lower Cretaceous Koonwarra Fossil Bed, South Gippsland, Victoria, Australia, and is late Aptian in age (115 ± 6 my – 118 ± 5 my) (DRINNAN & CHAMBERS, 1986). It was briefly described with an accompanying photograph by JELL & DUNCAN (1986:179) and recognized as “Simuliid? indet. 2”. Subsequently, SZADZIEWSKI (1990) considered the specimen to be a member of *Austroconops* but without any supporting evidence.

Reexamination of the specimen indicated that the wing, although in rather poor condition, had at least some veins clearly present (Figs. 2G–H). Veins R_1 and R_3 were definitely visible, R_2 was questionably present on one face of the fossil (Fig. 2G) and R_{4+5} was present but faint on one face (Fig. 2H). The base of M and Cu were also present, originating from near the base of the wing but their apices were not evident. Total length of the wing was 1.62 mm.

The visible wing venation is very similar to that of male *Leptoconops* (as seen with phase contrast) with the exception that the apex of R_3 does not clearly reach the wing margin and the costa does not appear as clearly defined in extant and other fossil members of the genus (compare with Fig. 1F). Extant male *Leptoconops* have a poorly defined costa beyond R_1 but the presence of some pigmentation and of thick setae to nearly the wing tip in some species indicates its presence. The origin of R_{4+5} and M from near the base of the wing is typical of the genus and is otherwise unknown within the family (probably synapomorphic). The presence of these features in the fossil wing suggest that it is likely a male *Leptoconops* but I refrain from naming the specimen, considering its poor condition. The better developed R_3 in the fossil may provide evidence that this species represents the sister group of *Leptoconops*. Further material will be required to test that possibility.

With a wing length of 1.62 mm, this compression fossil has the largest wing of known Lower Cretaceous Ceratopogonidae. Otherwise the largest wing is amongst Lebanese amber material in which maximum length for males is 0.91 mm and for females, 1.01 mm (BORKENT, in prep.).

Material examined. – Single wing, compression fossil, labelled “Diptera wing, Jell, 1985, MEM.AAP.3”, “Museum of Victoria – Natural History, Reg. No. P103203, ? Simuliid indet. 2, Formation Korumburra Gp., Age Early Cretaceous, Locality PL425 nr Koonwarra on 5th. Gippsland H’way Vic., Jell & Duncan 1986 Mem AAP3, fig. 49F, Origin P. Duncan Colln.”.

Conclusions

BORKENT (1995, 1996) pointed out that successively older fossil Ceratopogonidae represent successively older phylogenetic lineages. This report of Upper Cretaceous *Leptoconops* and *Adelohelva* from Hungarian amber, of *Minyohelva* from Lower Cretaceous Austrian amber and of *Leptoconops* from Lower Cretaceous beds in Australia confirms this pattern: there is an excellent correlation between the age of fossil species and their phylogenetic position as interpreted through cladistic analysis.

Acknowledgments

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