The Phylogenetic Relationships of Cretaceous Biting Midges, with a Key to All Known Genera (Diptera: Ceratopogonidae)

Author: Borkent, Art

Source: American Museum Novitates, 2019(3921) : 1-48

Published By: American Museum of Natural History

URL: https://doi.org/10.1206/3921.1

AMERICAN MUSEUM NOVITATES

Number 3921, 48 pp. February 25, 2019

The phylogenetic relationships of Cretaceous biting midges, with a key to all known genera (Diptera: Ceratopogonidae)

ART BORKENT[1]

ABSTRACT

The phylogenetic positions of Cretaceous species of Ceratopogonidae previously placed in the genera *Archiculicoides* Szadziewski, *Protoculicoides* Boesel, and *Atriculicoides* Remm are reappraised in light of synapomorphies. Character states are discussed in detail, supported by new photographs of *Protoculicoides depressus* Boesel, the description of *Protoculicoides revelatus*, n. sp., from Burmese amber, and a compilation of previously published illustrations. The recent article by Szadziewski et al. (2016) proposing that *Protoculicoides* and *Atriculicoides* are congeneric is shown to be inaccurate. At least three separate lineages are represented by species in these two genera, requiring a new genus, *Gerontodacus* (type species, *G. succineus* (Szadziewski)), to include some of them. *Archiculicoides*, *Protoculicoides*, *Gerontodacus*, *Adelohelea* Borkent and *Alautunmyia* Borkent remain undetermined to subfamily. As a result of phylogenetic and other taxonomic considerations, the following are new combinations: *Gerontodacus krzeminskii* (Choufani, Azar, and Nel), *Gerontodacus punctus* (Borkent), *Gerontodacus skalskii* (Szadziewski and Arillo), *Archiaustroconops andersoni* (Szadziewski, Ross, and Giłka), *Atriculicoides ciliatus* (Borkent), *Atriculicoides hispanicus* (Szadziewski and Arillo), *Atriculicoides sanjusti* (Szadziewski and Arillo) and *Adelohelea burmitica* (Szadziewski and Poinar). The following species are returned to the genera they were assigned to before Szadziewski et al. (2016): *Atriculicoides cenomanensis* Szadziewski and Schlüter, *Atriculicoides dasyheleis* Szadziewski, *Atriculicoides globosus* (Boesel), *Atriculicoides incompletus* Szadziewski and Schlüter, *Atriculicoides macrophthalmus* Remm, *Atriculicoides sibiricus* Szadziewski, *Atriculicoides swinhoei* (Cockerell), *Atriculicoides szadziewskii* Pérez-de la Fuente, Delclòs, Peñalver, and Arillo and *Atriculicoides taimyricus* Szadziewski. A key is provided to all Cretaceous Ceratopogonidae genera.

---

[1] Royal British Columbia Museum, Victoria, and the American Museum of Natural History, New York.

ISSN 0003-0082

INTRODUCTION

The Ceratopogonidae have one of the most diverse and abundant fossil records of any family of insects, with 283 species known from throughout the Tertiary Era and Cretaceous Period (Borkent, 2016). Because the phylogenetic relationships among many genera, and especially those of extant basal lineages, are well established, many of these fossils are particularly informative regarding the diversification of the family in time and space (Borkent, 2000a; Szadziewski, 2017). In this paper, some problematic Cretaceous genera are discussed, a number of species reassigned generically, and a phylogenetic interpretation of those with identifiable synapomorphies is provided. A new key to all Cretaceous genera is also provided, allowing future students of this group to better identify newly discovered material.

With the addition of a new genus described here, there are currently 19 genera of Ceratopogonidae recognized in Cretaceous ambers, four of which are extant and 15 extinct (Borkent, 2016). These genera were first recognized in a variety of early articles based on relatively few species (Boesel, 1937; Remm, 1976; Szadziewski, 1996, 2000; Borkent, 1995, 1996, 2000a). Over the past few years, as more species have been described, there has been increasing confusion over the identity of some of these taxa, making some species nearly impossible to classify to genus. In particular, Szadziewski et al. (2016) redefined *Archiculicoides* Szadziewski, *Protoculicoides* Boesel, and *Atriculicoides* Remm with new features that do not actually include all described species and they also synonymized *Protoculicoides* and *Atriculicoides* based on features that are nebulous and that conflict with the distribution of synapomorphies.

A primary challenge in the classification of fossils is the identification of individual species by means of characters that ideally can be easily seen and interpreted, but in practice are often not diagnostic phylogenetically. A further goal of systematists is to provide a classification based on synapomorphies that reflects genealogical relationships of included species. Meeting both these goals is sometimes impossible for those species known from incomplete or poorly preserved specimens, from a single sex, or from questionably associated sexes. Species of Cretaceous Ceratopogonidae that pose such challenges of identification are individually discussed here in some detail.

Identifying the phylogenetic position of various fossil genera of Ceratopogonidae is fundamental to proper interpretation of their historical zoogeography and palaeoecology, including features such as the likely hosts of adult females, adult activity times, and larval habitats, features that have already been at least partially interpreted (Borkent, 1995, 1996; Borkent and Craig, 2004; Szadziewski, 1996). As their fossil record continues to be described, these genera will also become increasingly valuable as indicators of stratigraphy and the dating of fossil deposits (Borkent, 1995, 2000a; Pérez-de la Fuente et al., 2011; Szadziewski, 1996, 2008, 2017). As such, evidence for the hypothesized phylogenetic position of various genera needs to be explicitly understood. As shown below, some species are placed to genus based on shared similarity, with only select species providing diagnostic indicators of recognized synapomorphies.

Herewith is a reinterpretation of the Cretaceous Ceratopogonidae genera *Archiculicoides*, *Protoculicoides*, and *Atriculicoides*, a description of the new genus *Gerontodacus*, and a framework for the identification of included species. The phylogenetic relationships of these three genera are discussed within a context of other early lineages of Ceratopogonidae.

A new key to Cretaceous genera is also provided, with illustrations to better identify additional fossils from further investigations of rich amber deposits.

MATERIALS AND METHODS

Specimens were examined and photographed using a Wild M3 dissecting microscope and a Zeiss Jenaval compound microscope. Photomicrographs were taken with a Canon Rebel T34i mounted on these microscopes and compiled using Zerene Stacker version 1.04.

Terms for structures follow those used in the *Manual of Central American Diptera* (Brown et al., 2009) and *Manual of Afrotropical Diptera* (Borkent, 2017). The costal ratio (CR) is the length of the costa from the arculus divided by the wing length.

Only limited material was studied for this publication. The holotype of *Protoculicoides depressus* Boesel is housed at the Royal Ontario Museum, Toronto, Ontario, Canada (ROM). Some Ceratopogonidae in Burmese amber were studied firsthand, as follows: two pieces, one containing the holotype of *Protoculicoides revelatus* and another that held 26 females including specimens of *Protoculicoides* and other genera, are housed at the Natural History Museum at the University of Kansas (KU). A further 32 pieces included 46 Ceratopogonidae, with four of the pieces with specimens of either *Atriculicoides* or *Gerontodacus*, are now at the American Museum of Natural History (AMNH). Finally, seven pieces of Burmese amber containing 21 Ceratopogonidae, with two of these pieces including specimens of *Gerontodacus* or *Protoculicoides* are in my personal collection and will be donated to the Canadian National Collection, Ottawa (CNCI), at a later date. Otherwise character states were taken from previously published papers and the author's previous experience and notes from earlier studies of fossil Ceratopogonidae cited herein.

RESULTS

Protoculicoides revelatus, n. sp.

Figure 1A–E

Diagnosis (male unknown): The only species of Cretaceous Ceratopogonidae with an elongate pedicel (fig. 1B, C) and flagellomeres 9–13 elongate (fig. 1C).

Description (male unknown): *Female adult*. **Head** (fig. 1A–C): Ommatidia narrowly abutting dorsomedially, with dorsomedial seta (fig. 1B). Antenna with 13 separate flagellomeres, flagellomeres 9–13 more elongate than 1–8 (fig. 1C), AR = 1.1, sensilla coeloconica not visible on flagellomere 1. Mouthparts elongate, length of mouthparts/length of tarsomere 5 of foreleg = 2.8, with details not visible (fig. 1B). Palpus with five segments, segment 3 elongate, sensilla not visible, segments 3/4 = 2.2. **Thorax** (fig. 1A–C): Scutal setae elongate, in well-defined rows (fig. 1C). Scutal suture well developed. Anapleural suture elongate (fig. 1A). **Wing** (fig. 1A, E): Length = 0.59 mm, costal ratio = 0.85, without costal extension. Membrane with dense coarse microtrichia, without macrotrichia. Long macrotrichia on veins R_1, R_3, margin, and alula. Both radial cells present. M bifurcating distal to r-m. **Legs:** Femora, tibiae slender, hind femur thicker than fore-, midfemora. Legs lacking armature, except apical pair of thick spines on apex of all tarsomeres 1–4. TR foreleg = 2.2, hind leg = 1.8, foreleg/hind leg = 1.2. Pair of thick setae on each of fore- and midleg trochanter (fig. 1D). Midleg tibia spur not visible; if present, short. Hind-leg tarsomere 1 with scattered setae. Claws short, simple. Empodium shorter than claws, somewhat bifurcating. **Genitalia:** Most details not visible. Cercus short (fig. 1A).

Remarks: The holotype was exceptionally preserved, with most thoracic sclerites visible. Wing veins R_1, R_2, and R_3 were lightly pigmented and, although not strongly evident in figure 1A, E, were more clearly visible when studying the specimen. The pair of thick setae on the midleg trochanter was represented by one seta and a barely discernable setal socket. Antennal flagellomeres 9–13 were longer than preceding flagellomeres but some appear short in figure 1A–C due to the antennae being at an angle.

Type: Holotype, female adult in amber, placed in plastic box, labeled "HOLOTYPE Protoculicoides revelatus Borkent," "AMBER: MYANMAR (BURMA) Middle Cretaceous (Cenomanian) Kachin: Tanai Village (on Ledo Rd. 105 km NW Myitkya) coll. Leeward Capital Corp. KU-NHM-ENT, Bu-055," "DIPTERA Ceratopogonidae (Culicoides)." Housed in the Natural History Museum at the University of Kansas, Lawrence (KU).

Etymology: The name *revelatus* ("revealed, unveiled"), from Latin, refers to the holotype's combination of two otherwise difficult-to-see features: a plesiomorphic anapleural suture and the apomorphic presence of fore- and midtrochanter thick setae.

Historical Taxonomic Treatment of Protoculicoides, *Archiculicoides*, and *Atriculicoides*

The first of these three genera, *Protoculicoides*, with its single species, *P. depressus* (fig. 2A–F), based on a single female at the time of its discovery, was originally briefly described by Boesel (1937) within a broader context of Diptera from Canadian amber. The Ceratopogonidae from Canadian amber were comprehensively described by Borkent (1995), who agreed that *Protoculicoides* was a distinctive genus, diagnosed it as: "Male: only Cretaceous Ceratopogonidae with a CR = 0.80 (all others with CR ≤ 0.62). Female: only Cretaceous Ceratopogonidae with CR = 0.89 and a wing without macrotrichia on the membrane (all other taxa with or without macrotrichia and CR ≤ 0.74)."

Remm (1976) described the genus *Atriculicoides*, from Yantardakh Siberian amber, including males and females of two species, *A. macrophthalmus* Remm and *A. squamiciliatus* Remm (later synonymized by Szadziewski, 1996). Remm's (1976) diagnosis of the genus was (translated from the original Russian): "Female. Proboscis short, thick. Palps with scattered sensilla. Entire body and legs densely covered with long setae. Setae on scutellum numerous. Macrotrichia on entire surface of wing. Two long radial cells. Length of costa equal to 0.70–0.75 of wing length. Alula fringed. Male resembles female, except that the third segment of the palp is better proportioned, the radial cells are shorter, the macrotrichia on the wings are fewer in number distally." Szadziewski and Schlüter (1992) described two further species from Cenomanian French amber. Borkent (1995) recognized a species earlier identified by Boesel (1937) as a *Lasiohelea* Kieffer (now a subgenus of *Forcipomyia* Meigen) as a member of *Atriculicoides* in Canadian amber and diagnosed the genus as "Male and female: only Ceratopogonidae with eyes broadly contiguous, a terminal flagellomere tapering gradually to its apex (no basally constricted nipple present) and a hind tibial spur." This diagnosis could have included "with a foretibial spur," to further distinguish it from *Dasyhelea* Kieffer, which lack both fore- and hind-tibial spurs.

In a major work on Lebanese and Siberian amber Ceratopogonidae, Szadziewski (1996) diagnosed a new monotypic genus *Archiculicoides*, based on a single female from Lebanese amber, as "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." He noted that the male of *P. depressus* was likely incorrectly associated by Borkent (1995; modified by Borkent, 2012a) and in adding a further species from Lebanese amber (female), further modified a diagnosis of *Protoculicoides* as follows: "Female wing membrane without macrotrichia, palpus 5 segmented, costa reaching almost to wing tip, both first radial cells large [referring to the two radial cells], 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." Szadziewski (1996) also described additional species of *Atriculicoides* and modified the diagnosis of the genus with "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." His key to Cretaceous genera used some of these features to key these three genera as follows (reduced here to pertinent taxa):

"2. Terminal flagellomere with apical styletlike prolongation .... *Archiculicoides*
– Terminal flagellomere with rounded apex.. 9
9. Palpus 4 segmented .... *Atriculicoides* (part)
– Palpus 5 segmented... 12
12. Costa prolonged almost to wing apex. Radial cells large. Wing membrane without macrotrichia. Female claws equal, simple................................ *Protoculicoides*
– Costa not elongated to wing apex. Radial cells small to moderately large. Female claws deeply bifid. Male flagellomeres 10–13 elongate. Parameres fused into a single structure . ... *Atriculicoides* (part)"

Borkent (2000a) provided a new comprehensive study of Lebanese amber Ceratopogonidae, based on both earlier and fresh specimens, described several new species, revised the concept of *Protoculicoides*, and regarded *Archiculicoides* as a new synonym of this genus. *Atricu-*

licoides are not present in this early, 127 Ma amber. The combined genera were diagnosed as: "Male. The only Cretaceous Ceratopogonidae with well-developed radial cells, no R_{4+5}, a costal ratio >0.8, a foreleg/hindleg tarsal ratio <1.3 and scattered setae on the first tarsomere of the hindleg. Female. The only Cretaceous Ceratopogonidae with wings bare of macrotrichia, with well-developed radial cells, no R4+5, a costal ratio >0.7, a foreleg/hindleg tarsal ratio ≤1.3 and scattered setae on the first tarsomere of the hindleg." Borkent (2000a) stated that the only distinguishing feature of *Archiculicoides* separating it from *Protoculicoides* as given by Szadziewski (1996) was the "elongate, pointed shape of flagellomere 13" of the female and that this feature was present in *P. succineus* Szadziewski and *P. punctus* Borkent, making the two genera indistinguishable.

Szadziewski and Poinar (2005) disagreed with the synonymy of *Protoculicoides* and *Archiculicoides* and accented two characters: the presence or absence of sensilla coeloconica and presence of 1 or 2 radial cells. Their revised diagnoses of the two genera are as follows:

Protoculicoides: "Wing membrane without macrotrichia, two radial cells, sensilla coeloconica absent, legs unmodified, 4th tarsomeres cylindrical, claws simple, tarsal ratios of all legs similar. Male antenna with 3 elongate terminal flagellomeres, tergite IX of male with distinct apicolateral processes, parameres double, gonostylus with apical tooth."

Archiculicoides: (females only): "Wing membrane without macrotrichia, single radial cell, costa almost reach wing apex, palpus 4–5 segmented, legs unmodified, claws simple, first flagellomere with sensilla coeloconica or group of sensilla trichodea." They therefore assigned *P. acraorum* Borkent and *P. unus* Borkent to *Archiculicoides* as new combinations.

Choufani et al. (2015) provided a key to the genera in Lebanese amber and distinguished *Archiculicoides* and *Protoculicoides* as part of their key:

"8. Wing with single radial cell, female antennal flagellomere 13 with apical elongate projection . . . . *Archiculicoides*
– Wing with two radial cells, female antennal flagellomere 13 without apical elongate projection . . . . *Protoculicoides*"

These authors also discussed the similarity of *Heleageron* Borkent to *Archiculicoides* and *Protoculicoides*. However, *Heleageron* has a markedly shorter costa, with a CR for males of 0.57–0.68 and for females of 0.71–0.73 and no costal extension. *Archiculicoides* females (males unknown) have a CR of 0.89–0.90 and a costal extension and *Protoculicoides* males have a CR of 0.82–0.85 with no costal extension and females have a CR of 0.84–0.96 with or without a costal extension.

Szadziewski et al. (2015b) considered *Archiculicoides*, *Protoculicoides*, and *Culicoides* Latreille as "morphologically very similar" and indicated that *Archiculicoides* and *Culicoides* have sensilla coeloconica on at least flagellomere 1, whereas these sensilla are not present in *Protoculicoides*. In providing a key to the species in Burmese amber, they used solely the presence or absence of sensilla coeloconica to recognize *Archiculicoides* (with one species, *A. andersoni* Szadziewski, Ross, and Giłka) and *Protoculicoides* (with one species, *P. burmiticus*

Szadziewski and Poinar), respectively. However, I consider that *Archiculicoides andersoni* belongs to *Archiaustroconops* Szadziewski. His single Burmese amber *Protoculicoides*, *P. burmiticus*, was put into *Archiculicoides* by Szadziewski et al. (2016) but is here considered to belong to *Adelohelea* Borkent (discussed below). The phylogenetic interpretation of sensilla coeloconica on the flagellum is also discussed further below.

Szadziewski et al. (2016) revised the genus *Protoculicoides*, described two more species, and proposed that *Atriculicoides* be considered a new synonym of *Protoculicoides* (table 1). They proposed that this more inclusive concept of the latter genus be recognized as the sole genus of the new subfamily Atriculicoidinae and noted that it may form an unresolved trichotomy with Forcipomyiinae and Dasyheleinae. *Atriculicoides* was previously considered the sole genus in the tribe Atriculicoidini (Szadziewski, 1996: 51). The diagnosis of *Protoculicoides* (and Atriculicoidinae) was presented by Szadziewski et al. (2016) as follows:

> Eyes broadly fused. Apex of flagellomere 13 usually rounded, without nipple-like prolongation; flagellomere 1 without sensilla coeloconica ringed with microtrichia, in male with 2 verticils of plume setae and distal 4 flagellomeres 10–13 usually elongate, female flagellomeres 9/10–13 elongate. Palpus 4 or 5 segmented, segment 3 with or without sensory pit. Female mandible with small teeth. Wing membrane usually with macrotrichia; both first radial cells well developed [referring to the two radial cells], costa not prolonged beyond vein R_3. Legs slender, unarmed; hind tarsomere 1 without palisade setae; tarsomeres 4 cylindrical; female claws small, equal sized with distinctly bifid apices; empodium greatly reduced, vestigial; tarsal ratios of fore and hind legs similar, usually 1.9–2.1. Female cerci short. Parameres of male genitalia usually fused.

In providing this new arrangement of 13 species in *Protoculicoides*, transferring some species previously in *Protoculicoides* to *Archiculicoides* (table 1) and discussing their broader classification, Szadziewski et al. (2016) did not mention cladistic relationships based on synapomorphies, numbers of which have been proposed earlier by Borkent (1995, 2000a) and Borkent and Craig, 2004) and also discussed by Pérez-de la Fuente et al. (2011).

Szadziewski et al. (2016) considered *Protoculicoides* to be “superficially similar” to *Archiculicoides*, noting that they

> both have well developed wing venation, usually with two distinct radial cells and costa ending at vein R_3, a similar tarsal ratio on the fore and hind legs, and tarsomeres 4 cylindrical. However, *Archiculicoides* has sensilla coeloconica ringed by microtrichia on proximal flagellomeres (often difficult to observe), the wing membrane without macrotrichia, eyes separated in females, and distal 3 flagellomeres elongated in males. In *Protoculicoides* of the Atriculicoidinae + Forcipomyiinae + Dasyheleinae lineage (Szadziewski, 1996) the wing membrane is covered with macrotrichia (sometimes secondarily reduced, especially in males), the eyes are broadly fused, the distal 4 flagellomeres are elongated in males and sensilla coeloconica ringed by microtrichia are absent.

TABLE 1. Features of species of *Archiculicoides*, *Gerontodacus*, *Protoculicoides*, and *Atriculicoides*. Species names in bold are the type species of their respective genera. Horizontal lines separate the four genera recognized as valid here.

Species and current generic placement	Generic placement by Szadziewski et al., 2016	Genus prior to Szadziewski et al,. 2016	Sex known	Deposition	Age (mya)	Female ommatidia medially
Archiculicoides acraorum	*Archiculicoides*	*Protoculicoides*	female	Lebanon	125–129	separated
Archiculicoides schleei	*Archiculicoides*	*Archiculicoides*	female	Lebanon	125–129	narrowly separated
Archiculicoides unus	*Archiculicoides*	*Protoculicoides*	female	Lebanon	125–129	unknown
Gerontodacus krzeminskii	*Archiaustroconops*	*Protoculicoides*	female	Lebanon	125–129	unknown
Gerontodacus punctus	*Archiculicoides*	*Protoculicoides*	male, female	Lebanon	125–129	narrowly separated
Gerontodacus skalskii	*Archiculicoides*	*Protoculicoides*	female	Spain	110–116	separated
Gerontodacus succineus	*Archiculicoides*	*Protoculicoides*	male, female	Lebanon	125–129	touching or narrowly separated
Protoculicoides depressus	*Protoculicoides*	*Protoculicoides*	male, female	Canada	78–79	narrowly separated
Protoculicoides revelatus			female	Burma	99	barely touching
Atriculicoides cenomanensis	*Protoculicoides*	*Atriculicoides*	male	France	83–97	"probably" contiguous
Atriculicoides ciliatus	*Protoculicoides*	*Protoculicoides*	male	Canada	78–79	unknown
Atriculicoides dasyheleis	*Protoculicoides*	*Atriculicoides*	male	Siberia (Yantardakh)	83–87	separate?
Atriculicoides globosus	*Protoculicoides*	*Atriculicoides*	male, female	Canada, New Jersey	78–79, 90–94	broadly contiguous
Atriculicoides hispanicus	*Protoculicoides*	*Protoculicoides*	male, female	Spain	110–116	contiguous
Atriculicoides incompletus	*Protoculicoides*	*Atriculicoides*	female	France, New Jersey	83–97	broadly contiguous
Atriculicoides macrophthalmus	*Protoculicoides*	*Atriculicoides*	male, female	Siberia (Yantardakh)	83–87	broadly contiguous
Atriculicoides sanjusti	*Protoculicoides*	*Protoculicoides*	male	Spain	110–116	contiguous
Atriculicoides sibiricus	*Protoculicoides*	*Atriculicoides*	male	Siberia (Yantardakh)	83–87	broadly continguous
Atriculicoides swinhoei	*Protoculicoides*	*Atriculicoides*	male	Burma	99	unknown
Atriculicoides szadziewskii	*Protoculicoides*	*Atriculicoides*	female	Spain	110–116	contiguous
Atriculicoides taimyricus	*Protoculicoides*	*Atriculicoides*	male	Siberia (Yantardakh)	83–87	unknown
Atriculicoides sp.	*Protoculicoides*	*Atriculicoides*	male, female	Siberia (Agapa)	94–97	unknown
Atriculicoides sp.	*Protoculicoides*	*Atriculicoides*	female	Burma	99	unknown
Atriculicoides sp.	*Protoculicoides*	*Atriculicoides*	female	Canada	78–79	broadly contiguous

TABLE 1 *Continued*

Species and current generic placement	Female mandible	Female laciniae	Female palpal segment 3	Male pedicel basal width	Male elongate flagellomeres	Female pedicel
Archiculicoides acraorum	unknown	unknown	moderate long, no pit	unknown	unknown	simple
Archiculicoides schleei	unknown	unknown	medium, no pit	unknown	unknown	unknown
Archiculicoides unus	unknown	10 teeth	elongate, no pit?	unknown	unknown	unknown
Gerontodacus krzeminskii	unknown	unknown	elongate, pit?	unknown	unknown	simple
Gerontodacus punctus	>7 fine teeth	26 teeth	elongate, no pit	unknown	10–13	simple?
Gerontodacus skalskii	unknown	unknown	elongate, no pit	unknown	unknown	simple
Gerontodacus succineus	fine teeth	unknown	elongate, no pit	large	(10), 11–13	simple
Protoculicoides depressus	unknown	unknown	elongate, no pit	unknown	unknown	elongate
Protoculicoides revelatus	unknown	unknown	elongate, no pit	unknown	unknown	elongate
Atriculicoides cenomanensis	unknown	unknown	unknown	unknown	10–13	unknown
Atriculicoides ciliatus	unknown	unknown	unknown	unknown	11–13	unknown
Atriculicoides dasyheleis	unknown	unknown	unknown	uncertain	unknown	unknown
Atriculicoides globosus	fine teeth	>6 large teeth	short, shallow broad pit	intermediate	10–13	simple
Atriculicoides hispanicus	unknown	unknown	short, pit?	unknown	10–13	unknown
Atriculicoides incompletus	unknown	unknown	short, no pit	unknown	unknown	simple
Atriculicoides macrophthalmus	unknown	unknown	short, no pit	unknown	10–13	simple
Atriculicoides sanjusti	unknown	unknown	unknown	unknown	10–13	unknown
Atriculicoides sibiricus	unknown	unknown	unknown	unknown	10–13	unknown
Atriculicoides swinhoei	unknown	unknown	unknown	unknown	(10), 11–13	unknown
Atriculicoides szadziewskii	unknown	unknown	medium length, pit?	unknown	unknown	simple
Atriculicoides taimyricus	unknown	unknown	unknown	unknown	10–13	unknown
Atriculicoides sp.	unknown	unknown	short, with pit	unknown	unknown	unknown
Atriculicoides sp.	unknown	unknown	moderate, with pit	unknown	unknown	unknown
Atriculicoides sp.	unknown	5 large teeth	moderate, deep pit	unknown	unknown	simple

TABLE 1 *Continued*

Species and current generic placement	Female elongate flagellomeres	Flagellomere 1 with sensilla coeloconica	Anapleural suture length	Male wing macro-trichia	Female wing macro-trichia	Radial cells (no.)	Male wing length
Archiculicoides acraorum	graduated	not clearly visible	unknown	unknown	bare	1	unknown
Archiculicoides schleei	9–13	present	unknown	unknown	bare	1	unknown
Archiculicoides unus	graduated	not visible	unknown	unknown	bare	1	unknown
Gerontodacus krzeminskii	graduated	unknown	unknown	unknown	bare	2	unknown
Gerontodacus punctus	9–13	present	unknown	bare	bare	2	0.69
Gerontodacus skalskii	9–13	unknown	unknown	unknown	bare	2	unknown
Gerontodacus succineus	9–13	unknown	long	bare	bare	2	unknown
Protoculicoides depressus	10–13	absent	unknown	bare	bare	2	0.97
Protoculicoides revelatus	9–13	unknown	long	unknown	bare	2	unknown
Atriculicoides cenomanensis	unknown	unknown	unknown	present	unknown	2	0.77
Atriculicoides ciliatus	unknown	unknown	unknown	present	unknown	2	1.16–1.19
Atriculicoides dasyheleis	unknown	unknown	unknown	present	unknown	2?	0.81
Atriculicoides globosus	9–13	absent	short	present	present	2	0.57–1.05
Atriculicoides hispanicus	(10), 11–13	unknown	unknown	bare	a few	2	0.88–0.89
Atriculicoides incompletus	9–13	absent	unknown	unknown	present	2	unknown
Atriculicoides macrophthalmus	9–13	absent	unknown	present	present	2	0.81–0.87
Atriculicoides sanjusti	unknown	unknown	unknown	bare	unknown	2	1.25–1.32
Atriculicoides sibiricus	unknown	unknown	short	present	unknown	2?	0.8
Atriculicoides swinhoei	unknown	unknown	unknown	bare	unknown	2	0.53–0.73
Atriculicoides szadziewskii	9–13	unknown	unknown	unknown	present	2	unknown
Atriculicoides taimyricus	unknown	unknown	unknown	unknown	unknown	unknown	0.76
Atriculicoides sp.	unknown	unknown	unknown	unknown	unknown	2	unknown
Atriculicoides sp.	9–13	unknown	unknown	unknown	present	2	unknown
Atriculicoides sp.	9–13	absent	unknown	unknown	present	2	unknown

TABLE 1 *Continued*

Species and current generic placement	Female wing length	Male CR	Female CR	Costal extension	Fore-, midtrochanter with pair of thick setae	Male or female fore-/hind leg tarsal ratios
Archiculicoides acraorum	0.52	unknown	0.94	yes	unknown	1.3
Archiculicoides schleei	0.65	unknown	0.94	yes	unknown	1.05
Archiculicoides unus	0.55	unknown	0.89	yes	unknown	unknown
Gerontodacus krzeminskii	0.54	unknown	0.96	yes	unknown	0.90
Gerontodacus punctus	0.64	0.82	0.94	no male, slight in female	unknown	1.1, 1.0
Gerontodacus skalskii	1.15	unknown	0.84	no	unknown	0.85
Gerontodacus succineus	0.75	uncertain	0.92	no male, yes in female	unknown	1.0–1.2
Protoculicoides depressus	1.63	0.85	0.89	no	unknown	0.90
Protoculicoides revelatus	0.59	unknown	0.85	no	present	1.19
Atriculicoides cenomanensis	unknown	0.58	unknown	no	unknown	0.91
Atriculicoides ciliatus	unknown	0.80	unknown	no	present	unknown
Atriculicoides dasyheleis	unknown	unknown	unknown	no	uncertain	1.1
Atriculicoides globosus	0.92–1.26	0.54–0.76	0.73–0.84	no	present	0.93
Atriculicoides hispanicus	1.14	0.73–0.75	0.70	no	unknown	1.0
Atriculicoides incompletus	0.65–1.14	unknown	0.71–0.82	no	present	unknown
Atriculicoides macrophthalmus	0.73–1.04	0.71–0.74	0.69–0.72	no	unknown	1.04
Atriculicoides sanjusti	unknown	0.68	unknown	no	unknown	unknown
Atriculicoides sibiricus	unknown	unknown	unknown	unknown	unknown	likely low
Atriculicoides swinhoei	unknown	0.70–0.75	unknown	no	unknown	1.3–1.5
Atriculicoides szadziewskii	unknown	unknown	unknown	no	unknown	0.94
Atriculicoides taimyricus	unknown	unknown	unknown	unknown	unknown	unknown
Atriculicoides sp.	unknown	unknown	unknown	no	unknown	unknown
Atriculicoides sp.	0.75	unknown	0.67	no	unknown	unknown
Atriculicoides sp.	0.88–1.11	unknown	0.65–0.72	no	present	unknown

TABLE 1 *Continued*

Species and current generic placement	Midtibial spur	Female claws	Parameres
Archiculicoides acraorum	with	simple	unknown
Archiculicoides schleei	unknown	simple	unknown
Archiculicoides unus	unknown	simple	unknown
Gerontodacus krzeminskii	unknown	simple	unknown
Gerontodacus punctus	unknown	simple	unknown
Gerontodacus skalskii	unknown	simple	unknown
Gerontodacus succineus	with	simple	2 separate
Protoculicoides depressus	with?	simple	2 separate
Protoculicoides revelatus	absent	simple	unknown
Atriculicoides cenomanensis	unknown	unknown	unknown
Atriculicoides ciliatus	absent	unknown	1 fused?
Atriculicoides dasyheleis	unknown	unknown	1 asymmetrical?
Atriculicoides globosus	absent	inner sliver	fused
Atriculicoides hispanicus	unknown	simple	unknown
Atriculicoides incompletus	absent	simple	unknown
Atriculicoides macrophthalmus	unknown	bifid apex	1 present
Atriculicoides sanjusti	unknown	unknown	1 shown
Atriculicoides sibiricus	unknown	unknown	1 asymmetrical
Atriculicoides swinhoei	unknown	unknown	1 present
Atriculicoides szadziewskii	unknown	simple	unknown
Atriculicoides taimyricus	unknown	unknown	1 asymmetrical?
Atriculicoides sp.	unknown	bifid apex	1 asymmetrical
Atriculicoides sp.	unknown	bifid apex	unknown
Atriculicoides sp.	absent	inner sliver	unknown

Numbers of the features presented by the publications discussed above are variable (indicated by the term “usually”), are used to distinguish the taxa from members of other subfamilies of Ceratopogonidae, are incorporated into the cladistic analysis here, or are discussed as problematic characters below.

Analysis of Pertinent Character States and Phylogenetic Interpretation

The phylogenetic placement of fossils requires interpretation of synapomorphies. When numbers of species are present in a particular genus, care must be taken to ensure that the individual species either bear the pertinent apomorphic conditions or, if these are not evident, that illogical conclusions should not be made on the basis of their presence. For example, only one of four *Gerontodacus* species has a large basal foramen (a plesiomorphic feature in the family) and the condition is unknown for the remaining four (table 1). As such, use of this synapomorphy in interpreting the phylogenetic position of the genus applies only to that one species, not to all members of the genus. This conclusion is particularly important in future historical zoogeographic analysis.

The interpretation and diagnoses of the fossil genera *Protoculicoides*, *Atriculicoides*, and *Archiculicoides* by Szadziewski et al. (2016) was based on various combinations of characters, some of which were synapomorphies and others of unknown polarity. These features are presented in table 1 and/or are discussed further below. A cladogram of the basal lineages of Ceratopogonidae is based primarily on Borkent and Craig (2004), with the features of immatures not considered further here (fig. 10). Synapomorphies of the entire family, including *Lebanoculicoides* Szadziewski, are discussed by Borkent (in press). Additional synapomorphies are discussed further below.

Character States for Phylogenetic Interpretation

Numbers of character states below are depicted on the cladogram (fig. 10).

1. Male antennal plume permanently erect (fig. 3K) (plesiomorphic); antennal plume generally decumbent, erect only when sexually active (fig. 3I, L, M) (apomorphic).

This feature is discussed by Borkent (in press).

2. Male adult tergite nine without apicolateral process or, if present, lacking setae (plesiomorphic); pair of apicolateral processes present and each bearing at least one seta (fig. 8B–D) (apomorphic).

This feature is discussed by Borkent (in press).

3. Setae on vertex of adult head capsule scattered or in dorsolateral arrangement (plesiomorphic); in addition to other setae on vertex, a single seta located medially, just dorsal to where the ommatidia meet medially or, in groups where the ommatidia are separated dorsomedially, between these (fig. 9C) (apomorphic).

This feature is discussed by Borkent (in press).

4. Male adult antennal pedicel with a narrow basal foramen (plesiomorphic); pedicel with wide basal foramen (fig. 3B) (apomorphic).

This feature is discussed by Borkent (in press).

5. Male flagellomere 1 at most with 1–2 whorls of elongate trichoid setae (plesiomorphic); flagellomere 1 with about eight whorls of elongate trichoid setae (apomorphic).

This feature is discussed by Borkent (in press).

6. Wing with well-developed R_{4+5} (fig. 5A) (plesiomorphic); R_{4+5} thin and faint (fig. 5B), very poorly defined (fig. 5C) or absent (fig. 5D–H) (apomorphic).

This synapomorphy was discussed by Borkent (2000a: 390, char. 4) and Borkent and Craig (2004: char. 7).

7. Male antenna with terminal flagellomeres 12 and/or 13 elongate (plesiomorphic); terminal flagellomeres 10–13 or 11–13 elongate (fig. 3A–J, M) (apomorphic).

This feature was proposed as a synapomorphy of *Forcipomyia*, *Atrichopogon* Kieffer, and *Dasyhelea* + Ceratopogoninae (as "3 or 4 terminal flagellomeres elongate") by Szadziewski (1996: 82, char. 6.3) and was further discussed by Borkent (2000a: 400). Culicomorpha other than Ceratopogonidae have either one or two terminal flagellomeres more elongate than preceding flagellomeres. Within Ceratopogonidae *Lebanoculicoides* has either flagellomere 13 elongate or possibly flagellomeres 12–13 (Borkent, 2000a, in press). Within Leptoconopinae, flagellomeres 12–13 or just 13 are elongate or the flagellomeres are of more or less equal length (Borkent, 1995, 2000a; Szadziewski, 1996). Most members defined by the apomorphic state (fig. 10) have either flagellomeres 10–13 or 11–13 more elongate, indicating these conditions to be a valid synapomorphy.

Based on the strength of synapomorphies 9, 11' and 12–13 in distinguishing *Gerontodacus* from subsequent lineages, it is more likely that elongate flagellomeres 10–13, shared by *Gerontodacus* (fig. 3A, B), most *Atriculicoides* (fig. 3C, E–H), most *Forcipomyia* and *Dasyhelea*, and some *Atrichopogon* is plesiomorphic in relation to elongate flagellomeres 11–13. However, it is clear that there is substantial variation within this group, especially within *Atrichopogon*, in which many have only the terminal three flagellomeres 11–13 elongate (e.g., Borkent and Picado, 2004). It is probably best to wait for further investigation before confirming flagellomeres 11–13 as derived in relation to elongate flagellomeres 10–13 (i.e., whether an elongate flagellomere 10 is plesiomorphic within this group), although such an interpretation would be consistent with the conclusions proposed in this paper. If elongation of flagellomeres 11–13 is considered derived, it would further group at least *Adelohelea* and *Heleageron* with Ceratopogoninae (fig. 10). Within *Adelohelea*, male *A. magyarica* Borkent has elongate flagellomeres 11–13 (Borkent, 1997), *A. glabra* Borkent is impossible to interpret because flagellomeres 8–10 are fused (Borkent, 1995) and *A. burmitica* has flagellomere 10 only slightly elongated (as in many *Culicoides*, for example) (Szadziewski and Poinar, 2005). Male *Heleageron* have flagellomeres 11–13 elongate (Borkent, 1995, 1996) and the male of *Alautunmyia* Borkent is unknown.

Within Ceratopogoninae, most taxa have the terminal three flagellomeres elongate but there are numbers of species in which the flagellomeres are graduated in size or are all of equal size. The conditions in this latter group are secondarily modified. The basal lineages within Ceratopogoninae, such as *Culicoides*, *Paradasyhelea* Macfie, *Ceratopogon* Meigen, etc., have males with three elongate terminal flagellomeres.

Finally, it is important to note that it is often difficult with both extant and fossil material to determine whether flagellomere 10 should be considered elongate (i.e., whether there are four elongate flagellomeres, 10–13). The males of most *Atriculicoides* (as defined here) have four elongate flagellomeres 10–13 (fig 3C, E–H). However, males of *A. ciliatus* (Borkent) (fig. 3D) and *A. swinhoei* (Cockerell) (fig. 3I) have flagellomere 10 only somewhat longer than flagellomere 9, a condition approximating that of some extant *Culicoides* (fig. 3J) and other Ceratopogoninae.

8. Wing with two radial cells (fig. 6B–E) (plesiomorphic); with one radial cell (fig. 6A) (apomorphic).

The description of one or two radial cells (noted as the first and second radial cells in Ceratopogonidae literature, including here) always refers only to cells r_1 and r_2 and does not include r_3 (present in all) nor r_{4+5} (the last only in *Lebanoculicoides* and some *Leptoconops* Skuse).

The polarity of this feature was discussed, including a list of genera with one cell, by Borkent (1995: 99). Outgroup comparisons show that two radial cells are present in all Culicoidea, Thaumaleidae, and basal Simuliidae (i.e., *Parasimulium* Malloch). Most Chironomidae have only one radial cell and it is unclear which condition is plesiomorphic within that family. Within Ceratopogonidae, *Lebanoculicoides* (fig. 5A), at least some Leptoconopinae (fig. 5D, G), *Gerontodacus* (fig. 6B), *Protoculicoides* (figs. 1E, 2D), *Atriculicoides* (fig. 6C, D), most Forcipomyiinae, most *Dasyhelea*, *Adelohelea* (fig. 6E), *Alautunmyia* (fig. 6G), and many Ceratopogoninae (fig. 6H) have two radial cells. This pattern suggests that the single cell condition in *Archiculicoides* can be considered a synapomorphy. However, it is clear there are many repeated losses to the one-cell condition throughout the Ceratopogonidae and that the character is quite susceptible to homoplasy.

9. Trochanter of fore- and midleg each with only slender, simple setae (plesiomorphic); trochanter of fore- and midleg each with pair of thick, contiguous setae (apomorphic).

This character was discussed by Borkent (2000a: char. 15).

10. Female pedicel squat to somewhat spherical (plesiomorphic); pedicel elongate (apomorphic).

An elongate female pedicel is unique within the Culicomorpha and therefore considered derived (fig. 2B). This feature was illustrated for *Protoculicoides depressus* by Borkent (1995: fig. 2G) and Szadziewski et al. (2016) but not commented on. Likely it was considered merely an artifact of preservation, especially as the head and thorax were generally dorsoventrally compressed. However, discovery of a second species, *P. revelatus*, and further specimens from Burmese amber with this condition indicate that it is actually a natural, distinctive feature.

This feature can be misinterpreted in distorted specimens where the pedicel is extended distally and partially flipped laterally, making the pedicel look at least somewhat elongate. In such instances, the base of flagellomere 1 does not arise from the very apex of the pedicel, as in *Protoculicoides*, but subapically, so that the apex of the pedicel is more distal than the base of flagellomere 1.

11. Male adult antennal pedicel with large basal foramen (fig. 3B) (plesiomorphic); pedicel with moderately sized basal foramen (apomorphic'); pedicel with narrow basal foramen (apomorphic").

This synapomorphy was discussed by Borkent (1995: char. 17) and Borkent and Craig (2004: char. 34). A large basal foramen could be seen in only one species of *Gerontodacus*, *G. succineus* (fig. 3B), and a foramen intermediate in size seen in one species of *Atriculicoides*, *A. globosus* (Boesel) (table 1). The condition is unknown in *Archiculicoides* (males unknown). The presence of a large basal foramen in *Lebanoculicoides daheri* Choufani, Azar, and Nel, representing the earliest lineage of Ceratopogonidae, further confirms that this is the plesiomorphic condition in the family.

Although not described as such, the basal foramen of *Atriculicoides dasyheleis* Szadziewski appears large in the drawing by Szadziewski (1996: fig. 25c), which would conflict with its placement as an *Atriculicoides* based on other features. The placement of this species is discussed further below.

12. Adult thoracic anapleural suture well developed, extending to anterior margin of anepisternal cleft (plesiomorphic); anapleural suture short, extending to posterior margin of anepisternal cleft (apomorphic).

This character was discussed by Borkent (2000a: char. 14). The feature can be observed in very few species (table 1).

13. Adult midleg tibia with spur (plesiomorphic); midleg tibia lacking spur (apomorphic).

This feature was discussed by Borkent (2000a: char. 13) and Borkent and Craig (2004: char. 38). No member of this lineage has a midleg tibial spur, including the three species of *Atriculicoides* for which the condition is known (table 1). The derived condition is susceptible to homoplasy in the outgroup, with numbers of losses in early lineages (Borkent, 2000a; Borkent and Craig, 2004: char. 38) and can be considered only as a weak indicator of relationship. Nevertheless, no *Atriculicoides* are known with a midtibial spur and at least one species in each of *Gerontodacus* and *Archiculicoides* have the spur (table 1).

The female holotype of *P. depressus* (Borkent, 1995) and its tentatively associated male (Borkent, 2012a) have been described as lacking a midtibial spur. Reexamination of the holotype indicates that a short spur may be present in at least the female (fig. 2F), and so is marked in table 1 as questionable. If true, the male and female may either be inaccurately associated or the often difficult to see feature may yet be present in the male. The female of *P. revelatus*, however, also lacks a midtibial spur, suggesting that the feature may be variable within this genus (as it is in some earlier lineages such as *Austroconops* (Borkent and Craig, 2004)).

14. Male with two separate parameres (fig. 8A, C, E–F) (plesiomorphic); with a single paramere (fig. 8D) (apomorphic).

The males of all known *Atriculicoides* have a single paramere, in some appearing as asymmetrical (table 1). Outgroup comparisons with other Culicomorpha indicate that these generally have two separate parameres (McAlpine et al., 1981; Wood, 1991). The males of *Lebanoculicoides*, *Leptoconops*, *Minyohelea* Borkent, *Archiaustroconops*, *Gerontodacus*, *Forcipomyia*, some *Dasyhelea*, and at least the basal lineages of Ceratopogoninae have two separate parameres. The males of *Atrichopogon*, the sister group of *Forcipomyia* (or related to only some *Forcipomyia*), have a fused aedeagal-parameral complex, clearly independently derived from those of *Atriculicoides*.

The parameres of *Austroconops* Wirth and Lee are fused medially but are known only in the two extant species (not visible in eight fossil species). These fused parameres are markedly expanded, rounded posteriorly and quite unlike those in species of *Atriculicoides*, where the fused parameres are a single elongate and apically slender structure. Furthermore, the phylogenetic position of *Austroconops* within the Leptoconopinae with other members with two separate parameres (e.g., *Minyohelea*, *Leptoconops*) indicates that this is an independent fusion.

The presence of asymmetrical parameres is a unique feature of some *Dasyhelea* within the extant fauna of Ceratopogonidae and is likely a synapomorphy of those species other than those belonging to the subgenus *D.* (*Sebessia*) Remm. The asymmetrical parameres of some *Atriculicoides* possibly indicate that at least some members of this genus form the sister group of the aforementioned group of *Dasyhelea* species. This feature, first presented by Szadziewski (1996: 72, char. 7.2), was discussed by Borkent (2000a: 400), who pointed out, among other issues, that this character state does not occur in all species of *Atriculicoides*. The distribution of other synapomorphies indicates that the asymmetrical parameres of some *Dasyhelea* and some *Atriculicoides* is likely convergent. For example, even if *A. dasyheleis* from Taimyr amber has asymmetrical parameres that appear very similar to those of some extant *Dasyhelea* (this could not be confirmed by Borkent, 2000a), this fossil species lacks at least three synapomorphies that group all *Dasyhelea*, namely, the presence of striations on male flagellomeres, a scape with a ventral apodeme, and the lack of a foretibial spur (personal obs.; Borkent and Craig, 2004). No species of *Atriculicoides* have any of these *Dasyhelea* synapomorphies, although for many species of *Atriculicoides* the pertinent character states are unknown.

15. Male antenna with setae on flagellomere 1 of similar length to those on subsequent flagellomeres (other than those few terminal flagellomeres that have shorter setae) (plesiomorphic); setae on flagellomere 1 much shorter than those on more distal flagellomeres (apomorphic).

This feature was discussed by Borkent (2000a: 403). This feature has not been scored for most fossils. For the Cretaceous taxa under discussion here, only *Atriculicoides sanjusti* (Szadziewski and Arillo) and *A. swinhoei* have available information (from drawn or photographic illustrations), indicating that they have the plesiomorphic feature.

16. Sternite 9 of female terminalia forming a continuous band ventrally (plesiomorphic); sternite 9 discontinuous medially, forming two halves (apomorphic).

This feature was discussed by Borkent (1995: char. 26). This internal feature is not visible in most described Cretaceous ceratopogonids. Of the fossils under discussion here, only the medially continuous condition in *Atriculicoides globosus* and an unnamed *Atriculicoides* in Canadian amber (Borkent, 1995) could be seen, and this is consistent with the presentation here.

In summary, the phylogenetic conclusion above indicates the generic concepts of *Protoculicoides* and *Archiculicoides* as defined by previous publications requires revision. Some of the species placed in either *Protoculicoides* (Borkent, 2000a; Choufani et al., 2015; Pérez-de la Fuente et al., 2011; Szadziewski, 1996; Szadziewski and Arillo, 1998) or *Archiculicoides* (Szadziewski et al., 2016; Urbanek et al., 2014) are here placed in the following new genus (table 1).

Gerontodacus, new genus

Type Species: *Gerontodacus succineus* (Szadziewski) by present designation.

Diagnosis: The only Cretaceous genus of Ceratopogonidae without R_{4+5}, with 2 radial cells, r-m oblique to R_1 (fig. 6B), an elongate anapleural suture (as in fig. 1A), a foreleg tarsal ratio/hind-leg tarsal ratio ≤ 1.3, and fore- and midtrochanter each lacking a pair of thick setae. To further distinguish *Gerontodacus* females from those of *Protoculicoides*, *Gerontodacus* have a squat, semispherical antennal pedicel (fig. 4F, G) while those of *Protoculicoides* have an elongate pedicel (figs. 1B, C, 2B, 4D).

Remarks: Aside from the type species, there are three further species included in the genus, as follows: *G. krzeminskii* (Choufani, Azar, and Nel), new combination, *G. punctus* (Borkent), new combination, and *G. skalskii* (Szadziewski and Arillo), new combination.

The type species, *G. succineus*, has plesiomorphic conditions that exclude it from the lineage defined by synapomorphies 11', 12–13, has synapomorphies 6–7 and lacks synapomorphy 8 (fig. 10) and is here stated to be the type species of *Gerontodacus*. Although the character states 9, 11', 12–13 could not be examined for *G. krzeminskii* (Choufani, Azar, and Nel), *G. punctus*, and *G. skalskii* (Szadziewski and Arillo), these species are placed in *Gerontodacus* because of overall similarity to *G. succineus*. They lack synapomorphy 8 and *G. punctus* has synapomorphy 7 (males are unknown for the other two species). There is no synapomorphy indicating the monophyly of *Gerontodacus*. As such the placement of *G. krzeminskii*, *G. punctus*, and *G. skalskii* is tenuous. Likewise, it is possible that with further analysis the nontype species will be recognized as further distinct lineages within this region of the phylogeny.

Recent examination of Burmese amber reveals that at least one unnamed species of *Gerontodacus* is present.

Bionomic Information: The details of the mouthparts of only one species were evident (Borkent, 2000a). The presence of fine mandibular teeth and retrorse lacinial teeth indicates that at least female *G. punctus* fed on vertebrate blood (Borkent, 1995). The well-developed male antennal plume of *G. succineus* and *G. punctus* indicates that, similar to most Ceratopogonidae, the males formed mating swarms.

Etymology: from the Greek *geron* ("old one") and *dacus* ("biter").

DISCUSSION

The type species of *Protoculicoides*, *P. depressus*, is known from a single holotype female (Borkent, 1995) and a tentatively associated male (Borkent, 2012a). The female has a distinctively modified pedicel (synapomorphy 10), a feature shared with *P. revelatus*, described here from Burmese amber. *Protoculicoides revelatus* has a plesiomorphically elongate anapleural suture (see synapomorphy 12) and fore- and midtrochanters each with a pair of stout setae (synapomorphy 9), showing that species of *Protoculicoides* are phylogenetically distinct from species of *Archiculicoides*, *Gerontodacus*, and *Atriculicoides* (fig. 10).

The only male known for the genus is that tentatively identified as *P. depressus*. The male has separate parameres, distinguishing it from species of *Atriculicoides* (synapomorphy 14; fig.

10). The female of *P. depressus* is unique among at least all fossil Ceratopogonidae in having only four elongate terminal antennal flagellomeres, which may be an autapomorphy (discussed below). Other features of *P. depressus* are discussed below.

The genus *Atriculicoides* is recognized here on the basis of one synapomorphy, the presence of a single fused paramere (synapomorphy 14), which is known for at least five and possibly eight of the 12 species recognized as members of the genus (fig. 8D, table 1). Furthermore, synapomorphy 9 is known for only three species, synapomorphy 11' for one species (the foramen in *A. dasyheleis* appears large in the figure in Szadziewski (1996), but this needs confirmation), synapomorphy 12 for two species, and synapomorphy 13 for three species (table 1). Members of *Atriculicoides* can be distinguished by states alternate to those noted above for *Gerontodacus* and *Protoculicoides* (table 1) and the diagnosis given below.

Although most members of *Atriculicoides* share with Forcipomyiinae and Dasyheleinae such similarities as closely abutting eyes (fig. 9C, D), male flagellomeres 10–13 elongate (fig. 3C–H), and wing membrane with macrotrichia (fig. 6C, D) (see discussion of characters below and table 1), there is no convincing synapomorphy grouping the genus with these two subfamilies. Interpretation of broadly abutting eyes is discussed by Borkent (1995: 92; 2000a: 398; in press), indicating that its presence in *Lebanoculicoides*, as the earliest lineage of Ceratopogonidae, and further homoplasy in other basal lineages makes its polarity suspect. *Atriculicoides* is herein placed as the sister group of Forcipomyiinae + Dasyheleinae (fig. 10) on the basis of overall similarity of these features. In spite of the lack of hard evidence, it seems likely to be an accurate portrayal of their actual genealogy. Szadziewski et al. (2016) concluded that Atriculicoidinae (including just *Atriculicoides* in their more inclusive sense) formed an unresolved trichotomy with Forcipomyiinae and Dasyheleinae and show it in their figure 6 as a grade concept leading to the latter two subfamilies. However, there is evidence that Forcipomyiinae and Dasyheleinae are monophyletic (fig. 10) and there is a synapomorphy indicating that *Atriculicoides* is also monophyletic. This suggests that if the three form a monophyletic group, which seems likely, *Atriculicoides* (in the more restricted sense used here) is the sister group of these two subfamilies.

The genus *Archiculicoides*, known only as females, has only a single, weak synapomorphy and is therefore questionably monophyletic (fig. 10). Furthermore, its exclusion from the lineage defined by synapomorphies 11', 12–13 is based only on the plesiomorphic presence of a midtibial spur (char. 13) in *Archiculicoides acraorum*. It is important therefore that future specimens be scored for character 7 (currently unknown) as well as the difficult to determine states of characters 9, 11', and 12, to confirm their hypothesized plesiomorphic state in *Archiculicoides*. Regardless of these phylogenetic considerations, the presence of one or two radial cells is used to distinguish a number of extant genera, as suggested by Szadziewski and Poinar (2005), and the inclusion of the three species here matches their conclusion. Szadziewski et al. (2016) provided a concluding phylogeny (their figure 6) but without supporting synapomorphies. They portray *Archiculicoides* as the sister group of all remaining Ceratopogonidae other than Lebanoculicoidinae, with its single genus *Lebanoculicoides*. This conclusion is one of several possibilities based on the cladistic results shown here (fig. 10).

Three Cretaceous fossil genera are poorly understood phylogenetically. Here they are placed as unresolved lineages in the monophyletic group defined by synapomorphies 11', 12–13 (fig. 10). *Adelohelea* is known from three species, *Heleageron* from two species and *Alautunmyia* from one species. *Adelohelea glabra* has synapomorphies 9, 12–13, *A. burmitica* has synapomorphy 13, but *A. magyarica* has no discernible synapomorphies pertinent to this analysis. *Heleageron arenatus* Borkent and *H. grimaldii* Borkent both have synapomorphies 9 and 13 and the monotypic *Alautunmyia*, known only as females, lacks a midtibial spur (synapomorphy 13), a feature exhibiting homoplasy and difficult to discern in many fossils. *Alautunmyia* have very broadly spaced eyes (fig. 9A), similar to those of *Leptoconops* and *Fossileptoconops* Szadziewski (fig. 9B), but this feature is likely convergent, considering that it has wing-membrane macrotrichia (fig. 6G) (Borkent, 2000b), a feature restricted to the lineages defined by synapomorphies 11', 12–13 (see also discussion of macrotrichia below). Regardless, the phylogenetic position of *Alautunmyia* is particularly tentative (fig. 10) and discovery of further specimens and the unknown male would likely be informative. There are no further synapomorphies known that would place these genera with more precision (but see discussion under char. 7).

The Leptoconopinae are shown here without any synapomorphies. However, this is partially due to a lack of some synapomorphies in fossil material (e.g., of larval and pupal characters). The two extant generic members of the subfamily, *Austroconops* and *Leptoconops*, are well established as sister groups (Borkent and Craig, 2004; Borkent, 2014). The addition of four fossil genera to this subfamily is based, in part, on two synapomorphies grouping *Austroconops* with three of these fossil genera: *Jordanoconops* Szadziewski, *Archiaustroconops*, and *Minyohelea*. In these four genera, the foreleg tarsal ratio/hind-leg tarsal ratio ≥1.4. This synapomorphy, first proposed by Szadziewski (1996), was discussed by Borkent (2000a: char. 10) and Borkent and Craig (2004: 58). Homoplasy is present in one species of *Lebanoculicoides* (*L. excantabris* Pérez-de la Fuente, Delclòs, Peñalver, and Arillo, with a ratio of 1.58), one species of *Leptoconops* (*L. myanmaricus* Szadziewski, with a ratio of 1.6) and some species of *Forcipomyia*. The male of *Atriculicoides sanjusti* has a midleg tarsal ratio/hind-leg tarsal ratio of 1.42, making it likely that its foreleg tarsal ratio/hind-leg tarsal ratio is also higher, but this is unknown. The male of *Atriculicoides swinhoei* also has a high ratio of 1.3–1.5 (as calculated from Szadziewski, 2004; Szadziewski and Poinar, 2005). It is likely that the condition evolved independently in these other taxa, considering their phylogenetic placement based on other synapomorphies, and thus would indicate that the feature is somewhat susceptible to homoplasy. A second synapomorphy of this group of four genera, males with permanently erect antennal plumes, is discussed by Borkent (in press). The male of *Jordanoconops* is unknown, but this genus is almost certainly related to *Austroconops*, based on the unique position of r-m (Borkent and Craig, 2004: char. 32). Considering the genus is based on the loss of a radial cell, it is logically possible that *Jordanoconops* is more closely related to one or some *Austroconops*, rendering *Austroconops* paraphyletic. The fourth fossil genus in Leptoconopinae, *Fossileptoconops,* is likely the sister group to *Leptoconops*, based on the unique loss of the medial vertex seta and very broadly spaced eyes medially (but see discussion of *Alautunmyia* below). Similarly, the synapomorphies supporting the relationships among *Forcipomyia*, *Atrichopogon*, and *Dasyhelea* are not repeated here from Borkent and Craig (2004).

The three genera *Archiculicoides*, *Protoculicoides*, and *Atriculicoides* are diagnosed as follows (*Gerontodacus* is diagnosed above):

1. *Archiculicoides* (unknown as males): the only Cretaceous genus of Ceratopogonidae having a wing with a single well-developed radial cell, a costal extension well beyond the apex of R_3 and r-m oblique to R_1 (fig. 6A).
2. *Protoculicoides*: the only Cretaceous genus of Ceratopogonidae with an elongate anapleural suture (fig. 1A) and fore- and midtrochanters each with a pair of thick setae (fig. 1D). In addition, females are the only Cretaceous Ceratopogonidae with an elongate pedicel (figs. 1B, C, 2B, 4D).
3. *Atriculicoides*: the only Cretaceous genus of Ceratopogonidae with ommatidia broadly contiguous dorsomedially (fig. 9C, D), a wing with two radial cells and without a R_{4+5} (fig. 6C, D), and a foreleg tarsal ratio/hind-leg tarsal ratio ≤ 1.3. In addition, this is the only Cretaceous genus with males with one symmetrical or asymmetrical paramere. The male of *A. dasyheleis* is the sole exception to this diagnosis as it has separate eyes but asymmetrical parameres (further discussion below).

Although the above diagnoses allow for the identification of most species currently known (see key below), there remains problems with identifying some material in Burmese and Spanish ambers. In particular, some species identified as *Atriculicoides* because they have broadly abutting eyes medially have wings without macrotrichia (as is true for *A. swinhoei*, *A. sanjusti*, and *A. hispanicus*), making them quite similar to *Gerontodacus* and *Protoculicoides*.

Some Burmese specimens examined here included what is likely the female of *A. swinhoei*, with broadly abutting eyes but wings lacking macrotrichia. However, for these and a number of others, the anapleural suture, fore- and midtrochanters, and male parameres could not be seen (generally not visible) and as a result could not be confidently identifiable to genus. It is a distinct possibility that, once further material is available with visible synapomorphies (and new character states available), that these may belong to yet another lineage within the context of the taxa discussed here. In addition, the large number of Burmese amber Ceratopogonidae held in Chinese collections (Dany Azar, personal commun.) will hopefully allow for further resolution of these specimens and taxa.

At present, the males of *Gerontodacus* and *Protoculicoides* cannot be distinguished if the trochanter setae are not visible, which is the case for most specimens. I do not see any male genitalic feature that differentiates the single known male of *Protoculicoides* (Borkent, 2012a) from that of *Gerontodacus* (only *G. punctus* and *G. succineus* known [Borkent, 2000a]; fig. 8A).

Ceratopogonidae are now divided into six subfamilies, two of which, Lebanoculicoidinae and Atriculicoidinae, include only fossil taxa. Based on the phylogenetic conclusions here (fig. 10) the genera *Gerontodacus* and *Protoculicoides* could each be considered a new subfamily. I prefer a conservative approach and await further confirmation of their phylogenetic positions before recognizing them as such. *Archiculicoides*, known only as females, requires further material to more confidently determine its phylogenetic position (fig. 10). It too is retained as a fossil genus unplaced as to subfamily. *Adelohelea*, *Heleageron*, and *Alautunmyia* also remain as unplaced to subfamily (Borkent, 2016).

PROBLEMATIC CHARACTER STATES IN PREVIOUS GENERIC DIAGNOSES

This section discusses some of the characters that have been used to distinguish or redefine *Archiculicoides*, *Protoculicoides*, and *Atriculicoides* by previous workers and discussed above under the history of these groups (table 1) or are newly considered here as potential additional synapomorphies, including the new genus *Gerontodacus*. The characters below are arranged morphologically from anterior to posterior, dorsal to ventral.

Presence or absence of sensilla coeloconica on flagellomere 1

Szadziewski (1996), Szadziewski and Poinar (2005), Szadziewski et al. (2015b, 2016), and Urbanek et al. (2014) considered the presence (fig. 4B) or absence of sensilla coeloconica on the "proximal" flagellomeres (actually on only flagellomere 1) as characteristic of *Archiculicoides* and *Protoculicoides* (in their sense), respectively.

The minute sensilla coeloconica are difficult to observe in extant specimens, let alone in fossils. Unless a fossil is in a perfect position and state (preferably partially cleared), the sensilla of flagellomere 1 are impossible to observe; even for well-preserved fossils, only highly experienced ceratopogonid specialists would be able to confidently identify their presence or absence. Table 1 shows this feature is scored for only six out of 22 known species of either *Archiculicoides* ($n = 1$), *Gerontodacus* ($n = 1$), *Protoculicoides* ($n = 1$) or *Atriculicoides* ($n = 3$). At a practical level, this is a poor feature to distinguish and identify fossil taxa.

Of course, structures that are difficult to see may yet be valuable cladistically. There are, however, several problems with the phylogenetic interpretation of this feature. Within extant Ceratopogonidae, sensilla coeloconica occur on flagellomere 1 in *Austroconops*, virtually all *Culicoides*, *Paradasyhelea*, and most early lineages of Ceratopogoninae (Borkent, 1995; Urbanek et al., 2014). *Leptoconops* have sensilla ampullacea (Borkent, 1995; Urbanek et al., 2014). Borkent et al. (1987) pointed out that sensilla coeloconica occur in some other Culicomorpha and that their presence is likely plesiomorphic within the family. They have been lost at least several times within Ceratopogonidae (Urbanek et al., 2014). Borkent et al. (1987) also discussed the developmental plasticity of sensilla transforming from one type to another (Heming, 2003: 204–208). For example, sensilla ampullacea may be nothing more than small, sunken sensilla coeloconica. As such, the presence or absence of sensilla coeloconica is not likely to be phylogenetically informative. Furthermore, when present, their distribution on particular flagellomeres is also likely to be uninformative. The flagellum is a single segment and the varying positions of sensilla coeloconica are actually in variable positions on this single segment.

In a detailed investigation of sensilla coeloconica within Ceratopogonidae, Urbanek et al. (2014) further described their morphology and presence in a variety of early lineages of Ceratopogonidae. They clearly showed that they are widely distributed among these taxa and confirmed that their presence is likely plesiomorphic within the family. Those of flagellomere 1 have been lost in Forcipomyiinae, within *Paradasyhelea* and in the more highly derived genera of Ceratopogoninae. Although not mentioned by these workers, they have also been lost in *Culicoides floridensis* Beck and *Dasyhelea* (Borkent, 1995). As such, their loss (or apparent loss) in four species of *Atriculicoides* and one species of *Protoculicoides* (table 1) is likely not a valid indicator of their monophyly as proposed by Szadziewski et al. (2016).

Number of elongate terminal flagellomeres of females

This feature has not been systematically interpreted phylogenetically and requires further investigation. A brief review (literature and specimens) of other Culicomorpha indicates that Chironomidae have flagellomeres ranging from being of nearly equal length (flagellomeres 1–2 often longer than subsequent ones), having the terminal 1–2 flagellomeres more elongate, to a gradual increase in length apically, but none with an abrupt change in the length of intermediate flagellomeres. Culicidae and Chaoboridae have somewhat shorter basal flagellomeres, but they gradually become longer toward the apex of the flagellum. Corethrellidae have variable antennae, but none have an abrupt change in length in the terminal flagellomeres (Borkent, 2008). Dixidae have long basal flagellomeres with these becoming gradually shorter apically (Belkin, 1968). Thaumaleidae have larger basal flagellomeres but decrease in size apically (Stone and Peterson, 1981), and Simuliidae have similar-sized flagellomeres (Peterson, 1981). None of these taxa have elongate terminal flagellomeres that contrast with shorter, more basal flagellomeres, as appears in some Ceratopogonidae. Within Ceratopogonidae, early lineages such as *Lebanoculicoides* and nearly all Leptoconopinae have either gradually increasing flagellomeres basally (from flagellomere 2) to the apex of the flagellum or have only flagellomere 13 longer than preceding flagellomeres. The only exception within the Leptoconopinae may be *Archiaustroconops andersoni*, here newly placed in that genus; Szadziewski et al. (2015b) state that the flagellomeres gradually increase in length but their figure 1B depicts flagellomeres 9–13 as elongate. *Archiculicoides* have either graduated flagellomere lengths (fig. 4A, C) or more elongate flagellomeres 9–13 (fig. 4B). *Protoculicoides depressus* is unique with Cretaceous ceratopogonids in having only flagellomeres 10–13 more elongate (figs. 2B, 4D). The remaining Ceratopogonidae, defined by synapomorphies 11', 12–13 (fig. 10) have either flagellomeres of nearly equal length, gradually increasing in size, or have flagellomeres 9–13 more elongate. *Protoculicoides revelatus* has elongate flagellomeres 9–13 (fig. 1C), indicating that the condition in *P. depressus* is likely an autapomorphy of that species.

The abrupt change in length between either flagellomeres 8 and 9 (fig. 4B, E–I, K–N) or 9 and 10 (fig. 4D) is unique within the Culicomorpha and therefore likely apomorphic and possibly grouping *Archiculicoides* (only one species with this feature) with the lineage defined by synapomorphy 7 (fig. 10). However, it is clear that there are numerous reversals to a flagellum with flagellomeres nearly equal in size or gradually lengthening apically (but often with flagellomere 13 a bit longer), making this feature currently suspect as an indicator of relationship. Perhaps a more detailed scoring of ceratopogonid taxa would clarify the interpretation of this feature.

Finally, the apparently derived condition of having an abrupt change in flagellomere length is similar to the male antennal feature described as synapomorphy 7 (fig. 10). If these are homologues, this would also indicate that *Archiculicoides*, in which males are presently unknown, is actually part of that lineage defined by synapomorphy 7 (fig. 10).

Shape of female flagellomere 13

Szadziewski (1996) included an elongate, pointed apex of flagellomere 13 as part of the diagnosis of *Archiculicoides*, then with only one species, *A. schleei* Szadziewski (fig. 4B). Borkent (2000a) concluded that this feature was also present in *G. punctus* (fig. 4E) and *G. succineus* (then in *Protoculicoides*) (fig. 4G), making the two genera indistinguishable. This character was repeated as part of a key by Choufani et al. (2015) to distinguish this genus from *Protoculicoides* (sensu lato). Szadziewski et al. (2016) included "apex of flagellomere 13 usually rounded" as part of his diagnosis of *Protoculicoides* (including the species previously placed in *Atriculicoides*). Figures 4A–N illustrate the female antennae of all known species of *Archiculicoides* (fig. 4A–C), *Protoculicoides* (figs. 1C, 4D), *Gerontodacus* (fig. 4E–G) and *Atriculicoides* (fig. 4H–N) (as considered here). A more elongate, apically pointed flagellomere 13 is present in *Archiculicoides schleei* (fig. 4B), *G. punctus* (fig. 4E), *P. revelatus* (fig. 1B), *Atriculicoides globosus* (fig. 4H), *Atriculicoides* sp. from Canadian amber (fig. 4N) (Borkent, 1995) and *Atriculicoides* sp. from Burmese amber (fig. 4M) (Szadziewski, 2004). A rounded apex is present in *Archiculicoides acraorum* (fig. 4A), *A. unus* (fig. 4C), and *Atriculicoides szadziewskii* Pérez-de la Fuente, Delclòs, Peñalver, and Arillo (fig. 4L). The following species are variably intermediate in shape: *P. depressus* (fig. 4D), *Atriculicoides hispanicus* (Szadziewski and Arillo) (fig. 4I), *A. incompletus* Szadziewski and Schlüter (fig. 4J), and *A. macrophthalmus* (fig. 4K). This pattern among the considered species shows that the shape of the female flagellomere 13, which is difficult to categorize, cannot be used to distinguish these genera. This intrageneric variability is consistent with what is known about extant genera, where the shape varies greatly within those genera with substantial species diversity (e.g., *Forcipomyia* (Debenham, 1987a–d), *Atrichopogon* (Remm, 1959, 1961), *Dasyhelea* (Dominiak, 2012), *Culicoides* (Blanton and Wirth, 1979; Wirth and Hubert, 1989)).

Presence or absence of wing membrane macrotrichia

The presence or absence of wing membrane macrotrichia was discussed by Szadziewski (1996) who suggested that the feature arose twice in the Culicomorpha, once in some Chironomidae and then in the lineage defined here by synapomorphies 11', 12–13. Borkent (2000a: 399) challenged this conclusion and considered the condition in Chironomidae and these Ceratopogonidae to be homologous. More recently, Szadziewski et al. (2016) proposed that the macrotrichia in Chironomidae and Ceratopogonidae evolved independently based on their interpretation that all Lower Cretaceous members of both families had bare wings. Although generally true, at least one Lebanese amber Chironomidae has wing macrotrichia (Azar et al., 2008).

The pattern in Ceratopogonidae indicates that wing macrotrichia are absent in early lineages, as *Lebanoculicoides* (fig. 5A), Leptoconopinae (fig. 5B–H), *Archiculicoides* (fig. 6A), *Gerontodacus* (fig. 6B), and *Protoculicoides* (figs. 1E, 2D) (as defined here) have bare wings. The presence of macrotrichia (fig. 6C, D, G, H) is restricted to the monophyletic group defined by synapomorphies 11', 12–13 (fig. 10). However, within this group, macrotrichia are absent in various taxa including some extant *Atrichopogon*, *Adelohelea* (fig. 6E), *Heleageron* (fig. 6F), and some members of early lineages within the subfamily Ceratopogoninae (e.g., *Washingtonhelea* Wirth and Grogan, some *Ceratopogon*) and many subsequent lineages within Ceratopogoninae (fig. 7A–D). The feature is clearly susceptible to significant homoplasy, probably mostly as losses.

Szadziewski et al. (2016) considered the evolution of macrotrichia within Ceratopogonidae to be gradual, with increasing numbers of macrotrichia over time. With this consideration, the presence or absence of macrotrichia was not important in distinguishing *Protoculicoides* (sensu lato) and *Atriculicoides* and they state, "Therefore, we conclude that *Protoculicoides* … is a senior synonym of *Atriculicoides*." Furthermore, their figure 6 depicts the evolutionary relationships between major lineages, and that there were species "with and without macrotrichia" in Lower Cretaceous (Albian) members of Atriculicoidinae (including just their *Protoculicoides*). This is based on the bare wings of males of *A. sanjusti* and A. *hispanicus*; the female of *A. hispanicus* has a few macrotrichia, the female of *A. sanjusti* is unknown, and a third species, *A. szadziewskii*, known only as a female, has wing macrotrichia. A Burmese amber species, *A. swinhoei*, known only as a male, has bare wings. Szadziewski (2017) reproduced this figure but showed Atriculicoidinae as all with macrotrichia, possibly recognizing that the feature appears to be sexually dimorphic in these early species and scoring just the females in this regard. Regardless, if the macrotrichia of Forcipomyiinae, Dasyheleinae, and Ceratopogoninae (subsequently lost in some groups) are to be regarded as homologous, which seems likely, the origin of macrotrichia must have preceded the divergence of these taxa as defined by synapomorphies 11', 12–13 (fig. 10).

The earliest Ceratopogonidae with wing macrotrichia are from mid-Cretaceous Spanish amber, here identified as members of *Atriculicoides*. Szadziewski et al. (2016) suggested that wing macrotrichia evolved in this time period as a response to high levels of atmospheric carbon dioxide "so that the male antennal Johnston's organs could receive vibrational sex signals produced by female wing-strokes." There are several problems with this hypothesis. Foremost is that there is no evidence indicating the functional significance of wing macrotrichia. They may be important for flight, protection (against predators or contaminants), as a hydrophobic feature to avoid moisture on the wings, as an assist to easy emergence from the pupa, or some combination of these features (as well as others not known at this time). Their function needs to be investigated. Szadziewski's et al. (2016) correlation of the macrotrichia to the ability of males to hear females is puzzling. A well-developed Johnston's organ is symplesiomorphic within the Culicomorpha and is well understood in both Culicidae and Chironomidae and their homology within the Culicomorpha is almost certain (it has been secondarily reduced in Simuliidae and Thaumaleidae). As such, a large Johnston's organ predates the Cretaceous (Borkent, 2012b) and the origin of macrotrichia in Ceratopogonidae. Finally, it is entirely unknown how the presence of wing macrotrichia might affect the sound/frequency of the wing beat.

Pattern of chaetotaxy on wing veins and thorax

The wings of *Protoculicoides* have many setae on veins R, R_1, and R_3 (figs. 1E, 2D) and I initially thought this might be of phylogenetic significance. These veins are bare or have a few setae in *Lebanoculicoides*, *Leptoconops*, *Austroconops*, and some other Cretaceous fossils. In general *Forcipomyia*, *Dasyhelea*, and *Culicoides* usually have numbers of setae whereas species of *Atrichopogon* vary from bare to setose. Among other Cretaceous fossil genera, *Archiculicoides schleei* has numerous setae on R and R_3 but none on R_1. The condition in other *Archiculicoides* (*A. unus* and *A. acraorum*) is uncertain. Studied *Atriculicoides* have numerous setae on all three veins, but *A. macrophthalmus* has none on R and a few on R_1 and R_2. The condition is uncertain in *Atriculicoides sanjusti*, *A. hispanicus*, *A. swinhoei*, *A. ciliatus*, *A. taimyricus* Szadziewski, and *A. dasyheleis*. Adult *Gerontodacus* have numerous setae (*G. succineus*) or a few on each of the veins (*G. skalskii*). Therefore, the distribution of setae on radial wing veins varies within genera and cannot be interpreted at present. It is important to be mindful that the chaetotaxy of wing veins of fossils requires careful study and adequate material to ensure that the setal sockets are observed for those specimens that have been denuded.

The degree of setation of radial wing veins may be related to the general degree of setation of the body. The scutum of *Protoculicoides depressus*, for example, bears numerous scattered setae (fig. 2E), contrasting with the definable groups of scutal setae present, for example, in *Lebanoculicoides* (Borkent, in press). The scutellum is strikingly setose (fig. 2E), with 12 elongate setae on its posterior margin and 11 shorter, more anteriorly placed setae. The head is also markedly setose (fig. 2C). However, the only other member of *Protoculicoides*, *P. revelatus*, has setae on the radial wing veins (fig. 1E) but has defined rows of setae on the scutum (fig. 1A, C). These conditions also vary within at least some other genera (e.g., *Forcipomyia*, *Atrichopogon*) but warrants further study throughout the Ceratopogonidae.

Presence or absence of apical spine on male gonostylus

This character refers to a socketed stout spine at the apex or subapex of the gonostylus (fig. 8B, C). It is often challenging to see this spine in some extant members, for example, in *Leptoconops*, and scoring this feature is difficult for most fossil specimens. This feature was discussed by Szadziewski (1988: 246) and Borkent (1995: 89), who considered its loss within Ceratopogonidae to be evidence that *Leptoconops* is the sister group of all remaining Ceratopogonidae, a statement that indicated its character state distribution at that time. Since then, Borkent (2000a) showed that at least some other members of Leptoconopinae (some *Minyohelea*, some *Archiaustroconops*, some *Austroconops*) have an apical spine. The loss of the spine may be considered a synapomorphy of *Gerontodacus* + the lineage defined by synapomorphy 9 (fig. 10). However, it is uncertain whether *Lebanoculicoides* have the spine (Borkent, in press) and it is clear that the spine has been independently lost in at least some Leptoconopinae as it is absent in only some species of *Austroconops* (Borkent and Craig, 2004) and probably some *Minyohelea* (Borkent, 2000a). This character needs further study (and likely further specimens) before we can more confidently interpret it phylogenetically.

Szadziewski and Poinar (2005) suggested that males of *Gerontodacus* (as *Protoculicoides*) have a gonostylus with an apical tooth. However, their use of the term for male *Protoculicoides* (here = *Gerontodacus*) differs from what is considered here to be a tooth. Male *Protoculicoides* then included *G. skalskii*, *G. punctus*, G. *succineus*, and *P. burmiticus* (this last species here considered a member of *Adelohelea*). The apex of the gonostylus of both *G. succineus* (fig. 8A) and *A. burmiticus* looks like an apical hook, but it is a modification of the gonostylus itself (not a tooth or spine). The apex of the gonostylus of *G. punctus* is rounded and *G. skalskii* is known only as a female. As such, the "apical tooth" cited by Szadziewski and Poinar (2005) applies to only two of the species as a modification of the gonostylus itself. Furthermore, the shape of the apex of the gonostylus varies widely within Ceratopogonidae, including numbers of extant genera with a hooklike apex.

Comments on Certain Problematic Species

Szadziewski et al. (2016) transferred *Protoculicoides krzeminskii*, known only as a female, to *Archiaustroconops* but without justification for doing so. Choufani et al. (2015) described the foreleg tarsal ratio/hind-leg tarsal ratio as 0.9 and noted that it therefore could not be a member of *Archiaustroconops*. All *Archiaustroconops* have a ratio of 1.4 or greater, a synapomorphy that is shared with species of *Austroconops* and *Minyohelea*. As recognized here, members of *Protoculicoides* and *Gerontodacus* have two radial cells and a foreleg tarsal ratio/hind-leg tarsal ratio of 1.2 or less. Therefore, *Archiaustroconops krzeminskii* is here considered a species of *Gerontodacus*.

Szadziewski and Arillo (1998) described the dorsomedial separation of the eyes of the female of *G. skalskii* (as a *Protoculicoides*) as "well separated," and suggested this was similar to the condition in *Alautunmyia elongata* Borkent (fig. 9A), writing that *Alautunmyia* "probably does not need a new genus." However, their comparison between these two taxa is not accurate. Szadziewski and Arillo (1998) described the distance between the eyes of *P. skalskii* as equal to about 3 ommatidia. As they noted, this distance is similar to that in some extant *Culicoides*, which vary from this condition generally to closely approximated or slightly abutting. In *A. elongata* the distance is equal to at least five ommatidia and the eyes are significantly more widely separated. The problem yet remains as to where *Alautunmyia* belongs phylogenetically (fig. 10).

Szadziewski (1996) described *Atriculicoides dasyheleis* from a single male and subsequently placed it in *Protoculicoides* (Szadziewski et al., 2016) when he synonymized the two genera. This species is puzzling and I am not confident as to its placement now that both genera are again recognized, along with *Gerontodacus*. The dorsomedially separated eyes, apparently wide basal foramen of the pedicel (based on his fig. 25c) and lack of thick trochanter setae (Szadziewski, 1996) would exclude it from *Atriculicoides*. The asymmetrical, fused parameres would place it in this genus. However, Borkent (2000a), however, reported that the genitalia of this species was damaged and cast doubt on the validity of this interpretation. In addition, Borkent (2000a) was unable to confirm the lack of thick trochanter setae. The large basal foramen of the pedicel and lack of thick trochanter setae are plesiomorphies within the Ceratopogonidae and their states need to be confirmed in this species. If valid, this species cannot be considered a species of *Atriculicoides* as interpreted here but could be placed in *Gerontodacus*.

Szadziewski et al. (2015b) described *Archiculicoides andersoni* from Burmese amber, although the presence of two radial cells did not fit his earlier diagnosis of this genus (Szadziewski, 1996; Szadziewski and Poinar, 2005). The species has a foreleg tarsal ratio/hind-leg tarsal ratio of 1.42, which is a shared synapomorphy with the genera *Archiaustroconops*, *Minyohelea*, *Jordanoconops*, and *Austroconops*. The wing venation is similar to that of species of *Archiaustroconops* and I here transfer this species to that genus as *Archiaustroconops andersoni*, new combination. Szadziewski et al.'s (2015b) discussion of the importance of the presence of sensilla coeloconica on flagellomere 1 of this species is discussed further above.

Protoculicoides burmiticus was placed in *Archiculicoides* by Szadziewski et al. (2016), but it is here considered to belong to *Adelohelea* as *A. burmitica*, new combination. Unlike other *Archiculicoides*, *Protoculicoides*, and *Gerontodacus*, with a combined male CR of 0.82–0.85 and a female CR of 0.84–0.96 (figs. 2D, 6A, B) (table 1), the male of *A. burmitica* has relatively short radial cells, with a CR of only 0.57, which is similar to that of species of *Adelohelea* (fig. 6E). Its female is unknown. Szadziewski and Poinar (2005) noted that the hind tarsomere 1 was "slightly swollen like in extant *Culicoides*." This feature is also true of *A. magyarica* and *A. glabra* (Borkent, 1995, 1997). The slightly swollen hind tarsomere 1 may reflect a phylogenetic relationship of this genus with *Culicoides*, but further investigation is needed to determine the character state distribution of this feature. Species of *Adelohelea* could be considered members of *Culicoides* but without macrotrichia on the wing membrane.

Gerontodacus punctus (as a *Protoculicoides*) was simply placed in *Archiculicoides* by Urbanek et al. (2014) without noting that it was a new combination, on the basis of it having sensilla coeloconica on the female's flagellomere 1. This feature is discussed further above.

Protoculicoides depressus is known as a female and tentatively associated male (Borkent, 1995, 2012a). The female holotype was described in some detail by Borkent (1995) and partially described by Szadziewski et al. (2016), who considered it "poorly preserved." Their drawings and observations were made in 1987 or earlier, with the specimen in its original position mounted in Canada balsam on a slide (Szadziewski, personal commun.). This specimen was polished, remounted, and described in detail by Borkent (1995), who noted that it is in rather good condition, although the head, thorax, and abdomen are dorsoventrally compressed (fig. 2A–F). Szadziewski et al. (2016) stated "the eye separation is not visible," but in fact the narrowly separated eyes were illustrated by Borkent (1995) and photographed herein (fig. 2C), indicating how this species is distinct from those of *Atriculicoides* as defined here. The possible presence of a midtibial spur (fig. 2F) is suggested by an apical spine that is thicker than others on the midtibia.

Szadziewski et al. (2016) state that the tentatively associated male of *P. depressus* by Borkent (2012a) is suspect because it is distinctly smaller than the female, has divided parameres and the antennae (which they consider diagnostic for the genus in their sense of *Protoculicoides*) are missing. Indeed, Borkent (2012a) pointed out the discrepancy in size; however, there was a close resemblance in general appearance, including the relatively setose thorax (which should be more fully described). Until further material appears, it is best to consider them conspecific. The divided parameres are consistent with the definition of *Protoculicoides* here.

Atriculicoides sanjusti, originally described as a *Protoculicoides* by Szadziewski et al. (2016), has a midleg tarsal ratio/hind-leg tarsal ratio of 1.4, suggesting that it may be a member of *Archiaustroconops* (it is unknown what the foreleg tarsal ratio is and the distribution of the midleg tarsal ratio is uncertain). However, this species has broadly abutting eyes medially and a single paramere, indicating that it belongs to *Atriculicoides* but with an independently evolved higher midleg tarsal ratio/hind-leg tarsal ratio. This species is therefore now named *Atriculicoides sanjusti*, new combination. In addition, it has a decumbent male antennal plume (as in fig. 3I), excluding it from the lineage *Archiaustroconops* + *Minyohelea* + *Austroconops* + *Jordanoconops*. Similarly, *A. swinhoei* has a foreleg tarsal ratio/hind-leg tarsal ratio of 1.3–1.5, also suggesting it is a member of *Archiaustroconops.* However, it too has a single paramere, indicating it is an *Atriculicoides*, and also has a decumbent male antennal plume (Szadziewski, 2004).

Atriculicoides hispanicus, known from two males and a female, was described as a *Protoculicoides* by Szadziewski et al. (2016) in their more inclusive sense. It has broadly abutting eyes medially and the female has some macrotrichia on its wing membrane, indicative that it belongs to *Atriculicoides*. Therefore, it is here considered as *Atriculicoides hispanicus*, new combination.

Similarly, *Atriculicoides ciliatus*, known only as a male and originally described as a *Protoculicoides* by Borkent (2012a), is also transferred to *Atriculicoides* (new combination) because the wing membrane has macrotrichia, the midtrochanter has a pair of thick setae (thereby excluding it from *Gerontodacus*), the midtibia lacks an apical spur, and the paramere may be single (not clearly visible).

KEY TO CRETACEOUS GENERA OF CERATOPOGONIDAE

This key to males and females of all Cretaceous genera includes all those considered valid here. The males of *Archiculicoides*, with three known species, and the monotypic genera *Fossileptoconops*, *Alautunmyia*, and *Jordanoconops* are unknown. The female of *Brachycretacea* is unknown. The males of Cretaceous *Stilobezzia* are also unknown, but males are otherwise known for Tertiary and extant species.

In the key below, male *Culicoides* are characterized, along with those of *Adelohelea*, by having a costal ratio of ≤ 0.70. Choufani et al. (2014) gave 0.65 for *C. doyeni* Choufani, Perrichot, Azar, and Nel, but my recalculation of this ratio from the photomicrograph in their figure H3.4 yielded a value of 0.54. They likely measured the wing from its very base instead of from the arculus as is standard practice for the family.

The males of *Atriculicoides sanjusti* and *A. swinhoei* may not key properly through couplet 7. *Atriculicoides sanjusti* has a midleg tarsal ratio/hind-leg tarsal ratio of 1.4, with the tarsal ratio of the foreleg unknown. Males of *A. swinhoei* have a foreleg tarsal ratio/hind-leg tarsal ratio of 1.4–1.5 (as calculated from Szadziewski, 2004). The males of both species have a single paramere, placing them in the genus *Atriculicoides.* In addition, they have decumbent antennal plumes (excluding them from *Archiaustroconops*) and *A. sanjusti* has closely abutting eyes dorsomedially (unknown for *A. swinhoei*).

1. Tarsomere 1 of hind leg without row of palisade setae (basally abutting, short, stout setae), but either with scattered setae or with these and additional stout, more widely spaced stout setae (Upper and Lower Cretaceous fossils) 2
– Tarsomere 1 of hind leg with of row of palisade setae (Upper Cretaceous fossils) 17
2. Wing with well-defined R_{4+5} (fig. 5A, B) 3
– Wing lacking R_{4+5} (fig. 5D–H) or, if present, they are fainter and thinner than more anterior veins (fig. 5C) 4
3. Wing with two radial cells, well-defined r-m near midlength of wing (fig. 5A); female with short cercus (as in fig. 9F) . . . . *Lebanoculicoides*
[key to species (*n* = 4) – Borkent (in press)]
– Wing with R_1, R_2, and R_3 fused, r-m absent (or possibly at very base of wing) (fig. 5B); female with elongate cercus (fig. 9E) . . . . *Leptoconops* (*Palaeoconops*)
[key to species, as part of more inclusive key (*n* = 2) – Borkent (2001)]
4. Wing with r-m at very base of wing or not evident (difficult to discern) (fig. 5C); female with elongate cercus (fig. 9E). . . . . *Leptoconops* (*Holoconops*), *L.* (*Leptoconops*)
[key to females to species or groups of species (*n* = 14, not including *L. clava*) – Szadziewski et al. (2015a); deposit specific keys: Szadziewski (1996, Siberia), Borkent (2000b, New Jersey)]
– Wing with r-m evident on distal 3/4 of the wing (figs. 5D–G; 6A, B); female with short cercus (fig. 9F) 5
5. Wing with r-m parallel or nearly parallel to R (fig. 5D, E) 6
– Wing with r-m oblique to R (figs. 5F, G, 6A–H) 7
6. Wing with two radial cells (fig. 5D) . . . . *Austroconops*
[key to species (*n* = 8) – Dominiak et al. (2018)]
– Wing with one radial cell (fig. 5E) . . . . *Jordanoconops*
[monotypic – Szadziewski (2000)]
7. Foreleg tarsal ratio/hind-leg tarsal ratio ≥ 1.4; male with erect plume (fig. 3K); female flagellomeres 2–13 similar in size or gradually increasing in size distally (as in fig. 4A, C). . 8
– Foreleg tarsal ratio/hind-leg tarsal ratio ≤ 1.3; male with decumbent plume (fig. 3I); female antenna as above or with flagellomeres 10–13 or 9–13 longer than more basal flagellomeres (i.e., flagellomere 8 distinctly shorter than 9 (fig. 4B, E, G, H, I, K–N) or 9 shorter than 10 (fig. 4D). 9
8. Wing with R_1, R_2, and R_3 fused or with one radial cell (fig. 5F) . . . . *Minyohelea*
[key to species (*n* = 8) – Borkent (2000a)]
– Wing with 2 well-defined radial cells (fig. 5G) . . . . *Archiaustroconops*
[key to species other than *A. borkenti*, *A. besti* (*n* = 13) – Choufani et al. (2015]
9. Eyes widely spaced dorsomedially by the width of 5 or more ommatidia (fig. 9A, B); vertex without transverse suture (not known as males) 10
– Eyes abutting or spaced dorsomedially by no more than width of 4 ommatidia; those with broader separation with transverse suture. 11

10. Palpus with 4 segments (fig. 9B); wing with distal radial cell pointed, with costal extension (number of radial cells uncertain), likely without macrotrichia on membrane (fig. 5H) .... *Fossileptoconops*
[monotypic – Szadziewski (1996), Borkent (2000a)]

– Palpus with 5 segments (fig. 9A); wing with 2 well-defined radial cells, with second radial cell distally blunt, without costal extension, with macrotrichia on membrane (fig. 6G)... .... *Alautunmyia*
[monotypic – Borkent (1996, 2000b)]

11. Wing with one radial cell, without macrotrichia on membrane (fig. 6A, F) 12

– Wing with two radial cells, with or without macrotrichia on membrane (fig. 6B–E, H) .. 13

12. Wing with costal extension beyond apex of R_3 (fig. 6A) .... *Archiculicoides*
[key to species, as *Protoculicoides*, as part of more inclusive key (*n* = 3) – Borkent (2000a)]

– Wing without costal extension beyond apex of R_3 (fig. 6F) .... *Heleageron*
[no key to species (*n* = 2) – Borkent (1995, 2000b)]

13. Eyes broadly contiguous dorsomedially (male *A. dasyheleis* has separate eyes but asymmetrical parameres) (fig. 9C, D); wing with macrotrichia on membrane (fig. 6C, D); male genitalia with one symmetrical or asymmetrical paramere (fig. 8D) (wings bare in male *A. sanjusti*, which has contiguous eyes and an asymmetrical paramere; male *A. swinhoei*, which has an asymmetrical paramere and unknown condition of eyes; and male *A. hispanicus*, which has broadly contiguous eyes and unknown parameres)....... .... *Atriculicoides*
[key to species, as *Protoculicoides*, including also *Protoculicoides depressus* (*n* = 12) – Szadziewski et al. (2016)]

– Eyes narrowly approximated (by 2–3 ommatidia widths) to broadly separated dorsomedially; wing with or without macrotrichia on membrane; male genitalia with two symmetrical parameres (fig. 8A) 14

14. Female palpal segment 3 elongate, lacking sensory pit (fig. 9G); wing membrane bare (fig. 6B); radial cells elongate; CR ≥ 0.82; anapleural suture elongate (fig. 1A) (difficult or impossible to see in most specimens) 15

– Female palpal segment 3 short to elongate, with or without sensory pit (fig. 9H–L); wing membrane with or without macrotrichia (fig. 6E, H); radial cells short, CR ≤ 0.70; anapleural suture short (difficult or impossible to see in most specimens)............ 16

15. Fore- and midtrochanters without pair of thick setae; female antennal pedicel squat, somewhat spherical (in some appearing elongate but, if so, then with flagellomere 1 arising subapically from distorted pedicel) (fig. 4E–G)...................... *Gerontodacus*
[key to species (*n* = 4) – Borkent (2012a, as *Protoculicoides* and part of larger key, lacking *G. krzeminskii*), Choufani et al. (2015, as *Protoculicoides* and part of larger key)]

– Fore- and midtrochanters each with pair of thick setae (fig. 1D); female antennal pedicel elongate, with first flagellomere arising from apex or very near apex (figs. 1B, C, 2B, 4D) .... *Protoculicoides*
[distinguished here (*n* = 2)]

16. Male with 13 flagellomeres; wing membrane with macrotrichia (fig. 6H) . . . . . . *Culicoides*
[key to species (n = 17) – 11 species known till then – Borkent (1995), 6 New Jersey amber species – Borkent (2000b)]

– Male with 11 or 13 flagellomeres; wing membrane without macrotrichia (fig. 6E) . . . . *Adelohelea*
[no key to species (n = 2)]

17. Male with 8 flagellomeres (7–12 fused) (fig. 3L); palpus with 4 segments (1 beyond swollen third); wing with 1 clearly defined radial cell, with R_3 terminating at end of cell (fig. 7A) . . . . *Brachycretacea*
[monotypic – Szadziewski (1996)]

– Male with 13 flagellomeres; palpus with 5 segments (2 beyond swollen third); wing with 2 radial cells (fig. 7B, D) or. if only 1 apparent, then R_3 extending beyond the first radial cell (fig. 7C) 18

18. Female fore- and midlegs each a single talon, with basal tooth; Cretaceous males unknown but, if similar to Tertiary and extant species, aedeagus divided medially . . . . *Stilobezzia*
[no key to species (n = 3)]

– Female fore- and midlegs each with equal claws (2 claws present); male aedeagus undivided medially (fig. 8E–F) 19

19. Female hind-leg claw equal (with 2 claws), equal in length or longer than claws of fore- and midlegs; hind femur and tibia slender or only somewhat enlarged; male aedeagus a triangular, shieldlike or elongate structure with either a simple single or forked apex (fig. 8E) . . . . *Palaeobrachypogon*
[no key to species (n = 6); see discussion in Borkent (2000b)]

– Female hind leg with a single elongate talon, with 1–2 basal teeth, much longer than claws of fore- and midlegs; hind femur and tibia enlarged; male aedeagus deeply divided, with elongate lateral extension (fig. 8F) . . . . *Peronehelea*
[key to species (n = 3) – Szadziewski (1996)]

DISCUSSION

These results show that *Protoculicoides* has narrowly divided eyes, separate parameres, and a possible midtibial spur and is therefore distinct from species of *Atriculicoides.* Phylogenetically, it forms the sister group of an assemblage of taxa including *Atriculicoides* (fig. 10). Some species, previously considered as *Protoculicoides* and subsequently recognized as species of *Archiculicoides* by Szadziewski et al. (2016), are a distinct basal lineage and here are regarded as belonging to the new genus, *Gerontodacus.*

Szadziewski (1996) concluded that female *Atriculicoides* "were probably ectoparasites of other flying insects and fed on their haemolymph." With their combination of *Protoculicoides* and *Atriculicoides*, Szadziewski et al. (2016) repeated this same conclusion in their diagnosis of this genus and this was restated by Szadziewski (2017). Borkent (1995, 1996) provided a detailed analysis of the mouthparts of Ceratopogonidae and other Culicomorpha and concluded that the combination of finely toothed mandibles and toothed laciniae, which are present in at least some species of both *Gerontodacus* (as *Protoculicoides*) and *Atriculicoides*, were correlated with blood-feeding on vertebrates. The evidence provided by Szadziewski (1996) for feeding on invertebrates concerned the presence of bifid claws (table 1), but this was discussed and refuted by Borkent (2000a: 414). As such, the only available evidence indicates that female *Gerontodacus* and *Atriculicoides* were vertebrate feeders, similar to those of all other early lineages of Ceratopogonidae (Borkent, 2000a). It is important to point out that these mouthpart details are known, within these two genera, for only *G. punctus*, *G. succineus* (only the mandible), *Atriculicoides globosus*, and an unnamed *Atriculicoides* from Canadian amber (only the lacinia) (Borkent, 1995) (table 1).

Szadziewski (2017) interpreted the biostratigraphy of Ceratopogonidae, pointing out that certain Ceratopogonidae were characteristic of certain deposits, ages, and areas. Within the context of the current paper, a few comments are needed. Szadziewski (2017) stated that the presence of wing-membrane macrotrichia is diagnostic for the Upper Cretaceous and Cenozoic. However, Szadziewski et al. (2016) noted the presence of macrotrichia on the female wing of *Atriculicoides hispanicus* from Albian, Lower Cretaceous amber and Pérez-de la Fuente et al. (2011) described *A. szadziewskii* from Lower Albian, Lower Cretaceous amber with abundant wing macrotrichia. In addition, and as argued above, it seems likely that the wing macrotrichia of *Atriculicoides*, Forcipomyiinae, Dasyheleinae, and many Ceratopogoninae is homologous and this feature therefore must have evolved even earlier in the Lower Cretaceous.

As interpreted here (table 1), species of *Archiculicoides* are restricted to 125–129 mya Lebanese amber, *Gerontodacus* is present in 125–129 mya Lebanese, 110 mya Spanish amber and 99 mya Burmese amber (newly reported here), *Protoculicoides* is restricted to 99 mya Burmese and 78 mya Canadian amber, and *Atriculicoides* is present in a variety of ambers, ranging from 78–116 mya. As such, *Gerontodacus* overlaps in time with *Archiculicoides*, *Protoculicoides* and *Atriculicoides*. Zheng et al. (2018) recently identified *Protoculicoides* as present in 72 mya Upper Campanian Burmese amber, but these need further study to confirm their identification.

In his figure 2, Szadziewski (2017) indicated that *Protoculicoides* (in his more inclusive sense) ranges from the Lower Cretaceous to the end of the Cretaceous. However, the youngest members of this group, here considered to be members of *Atriculicoides*, are from Canadian amber, stated by Szadziewski (2017) as 72–84 mya but more likely 78–79 (McKeller and Engel, 2012). There are no amber deposits from this age until the Eocene and this gap of about 22 million years with no ceratopogonid fossils makes it uncertain how characteristic a number of these genera, including *Atriculicoides*, are during this time period. It may well be that *Atriculicoides* species were living in the early Cenozoic (and some presently distinctive Eocene taxa were present in the late Cretaceous).

CONCLUSIONS

The rearrangement of fossil taxa by Szadziewski et al. (2016), primarily the synonymizing of *Protoculicoides* and *Atriculicoides*, did not include discussion of synapomorphies, a number of which had been previously published (Borkent, 1995, 2000a; Borkent and Craig, 2004). As such, their conclusions invite phylogenetic analysis. In addition, their diagnoses of *Protoculicoides* and *Archiculicoides* are actually not diagnostic for a number of species included in their sense of these two genera. Finally, some primary characteristics used to distinguish their *Protoculicoides* and *Archiculicoides* are very obscure in most fossils, particularly for those who are not ceratopogonid experts.

The interpretation here provides cladistic evidence that *Gerontodacus* (including species previously in *Protoculicoides* and *Archiculicoides*), *Protoculicoides*, and *Atriculicoides*, or at least some species in each of these genera, belong to different lineages within the phylogeny of the Ceratopogonidae and new diagnoses allow for the identification of well-preserved fossil specimens.

Future studies of fossil Ceratopogonidae should include appraisals of the phylogenetic position of the taxa described, testing the synapomorphies provided here and, it is hoped, further teasing apart what will likely be a more complicated set of relationships in these early lineages. Even though some features are challenging or impossible to see currently in some specimens, as imaging becomes more sophisticated (e.g., nano-CT) character systems in the fossils will likely become far better understood. It is also important that additional synapomorphies be discovered through further examination of the morphology of both extant and fossil taxa, and hopefully providing further resolution of phylogenetic relationships and ease of identification.

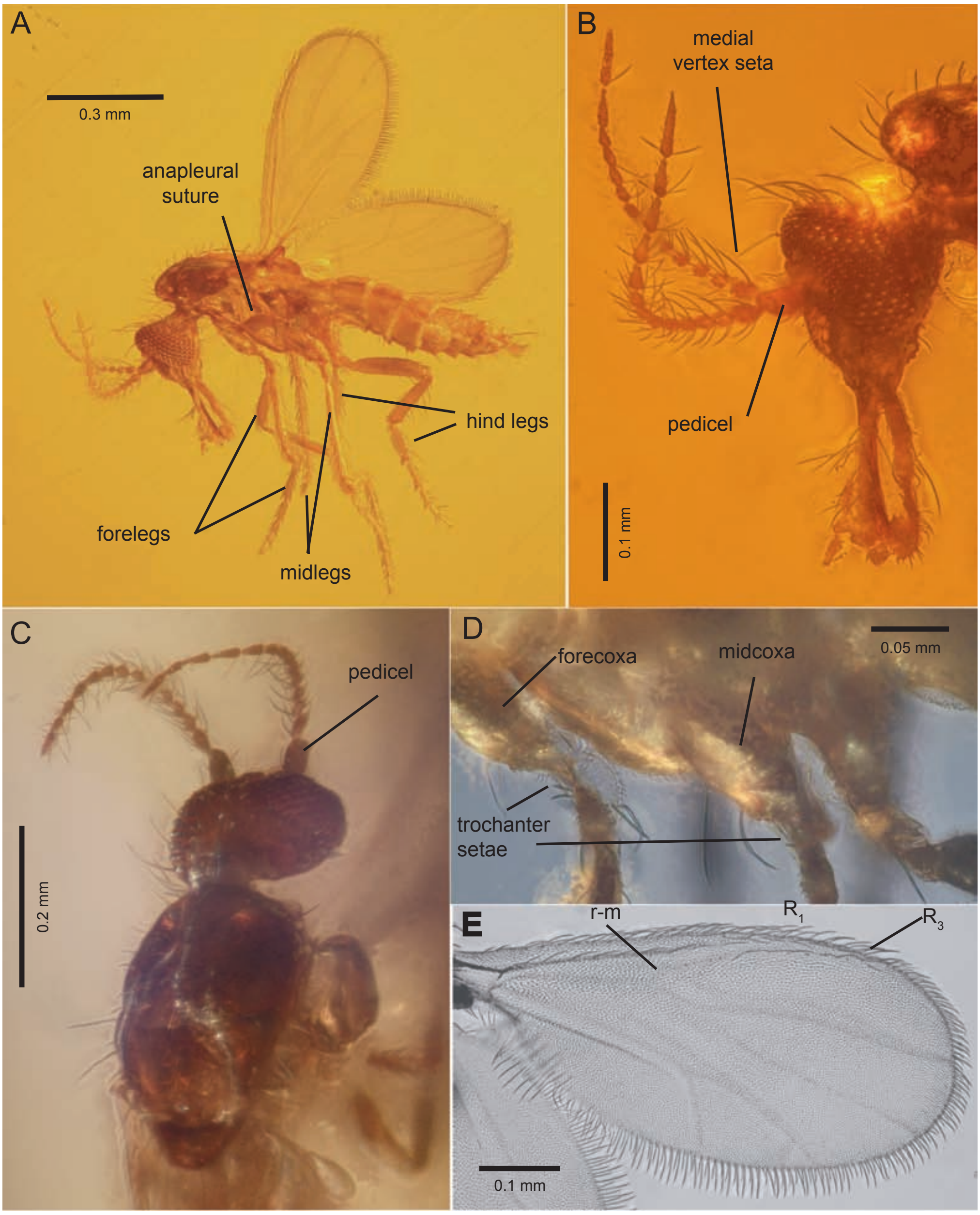


FIGURE 1. Structures of *Protoculicoides revelatus*. **A.** Habitus, lateral view. **B,** Head, lateral view. **C.** Head and thorax, dorsal view. **D.** Ventral portion of thorax, base of left legs, lateral view. **E.** Right wing, dorsal view.

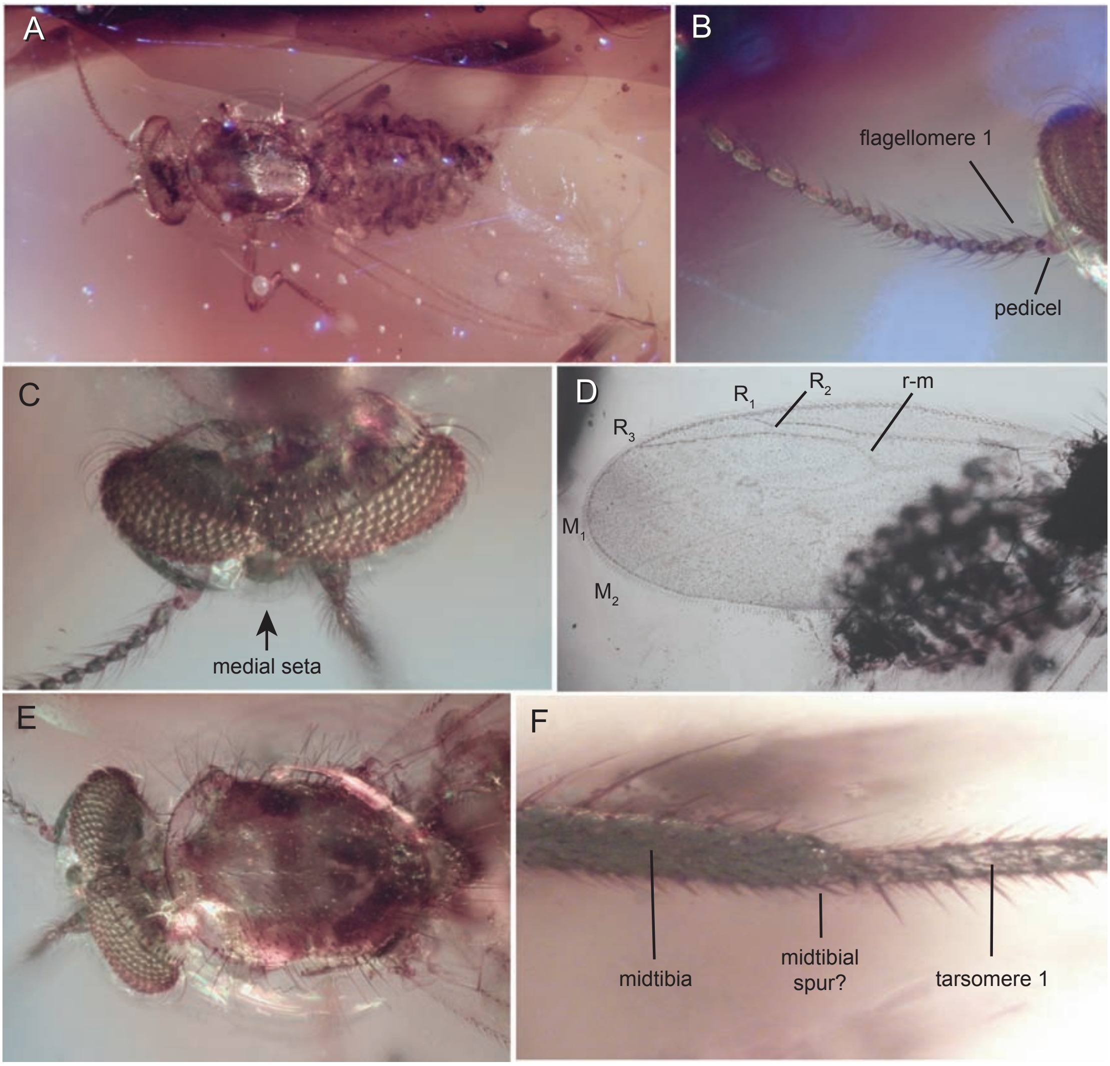


FIGURE 2. Structures of *Protoculicoides depressus*. **A.** Habitus, dorsal view. **B.** Right antenna, dorsal view. **C.** Head, dorsal view. **D.** Left wing, dorsal view. **E.** Head and thorax, dorsal view. **F.** Apical portion of left midtibia and basal portion of midtarsomere 1, anteroventral view.

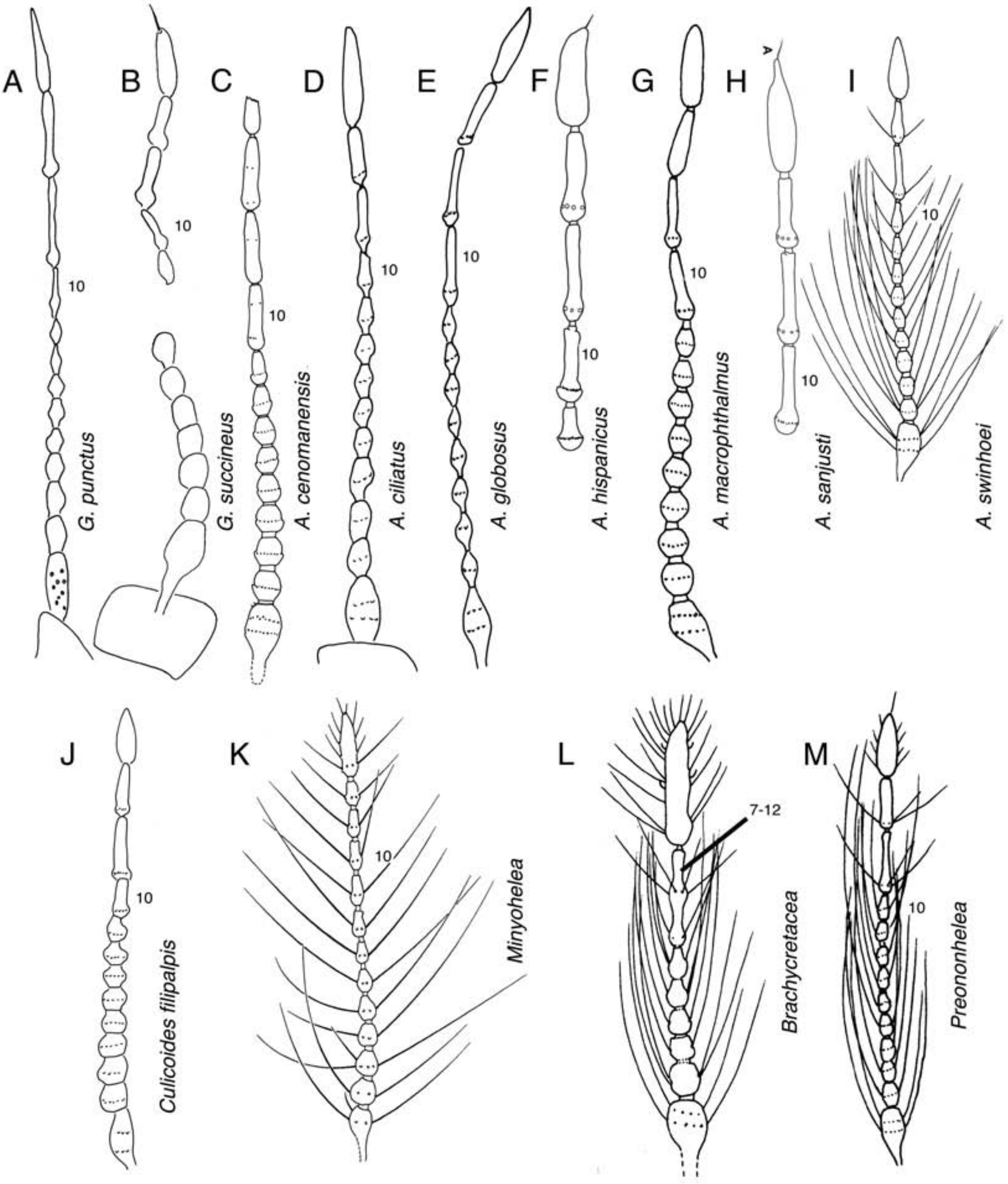


FIGURE 3. Male antennae of species of Cretaceous species of the genera *Gerontodacus* and *Atriculicoides* for which terminal flagellomeres are known and representatives of *Minyohelea*, *Brachycretacea* Szadziewski and *Peronehelea* Borkent. Numbers refer to flagellomere number. **A.** *Gerontodacus punctus* (from Borkent, 2000a). **B.** *G. succineus* (from Borkent, 2000a). **C.** *Atriculicoides cenomanensis* Szadziewski and Schlüter (from Szadziewski and Schlüter, 1992). **D.** *A. ciliatus* (from Borkent, 1995). **E.** *A. globosus* (from Borkent, 1995). **F.** *A. hispanicus* (from Szadziewski et al., 2016). **G.** *A. macrophthalmus* (from Szadziewski, 1996). **H.** *A. sanjusti* (from Szadziewski et al., 2016). **I.** *A. swinhoei* (from Szadziewski, 2004). **J.** *Culicoides filipalpis* Remm (from Borkent, 1995). **K.** *Minyohelea schleei* Szadziewski (from Szadziewski, 1996). **L.** *Brachycretacea taimyrica* Szadziewski (from Szadziewski, 1996). **M.** *Peronehelea frigida* (Remm) (from Szadziewski, 1996).

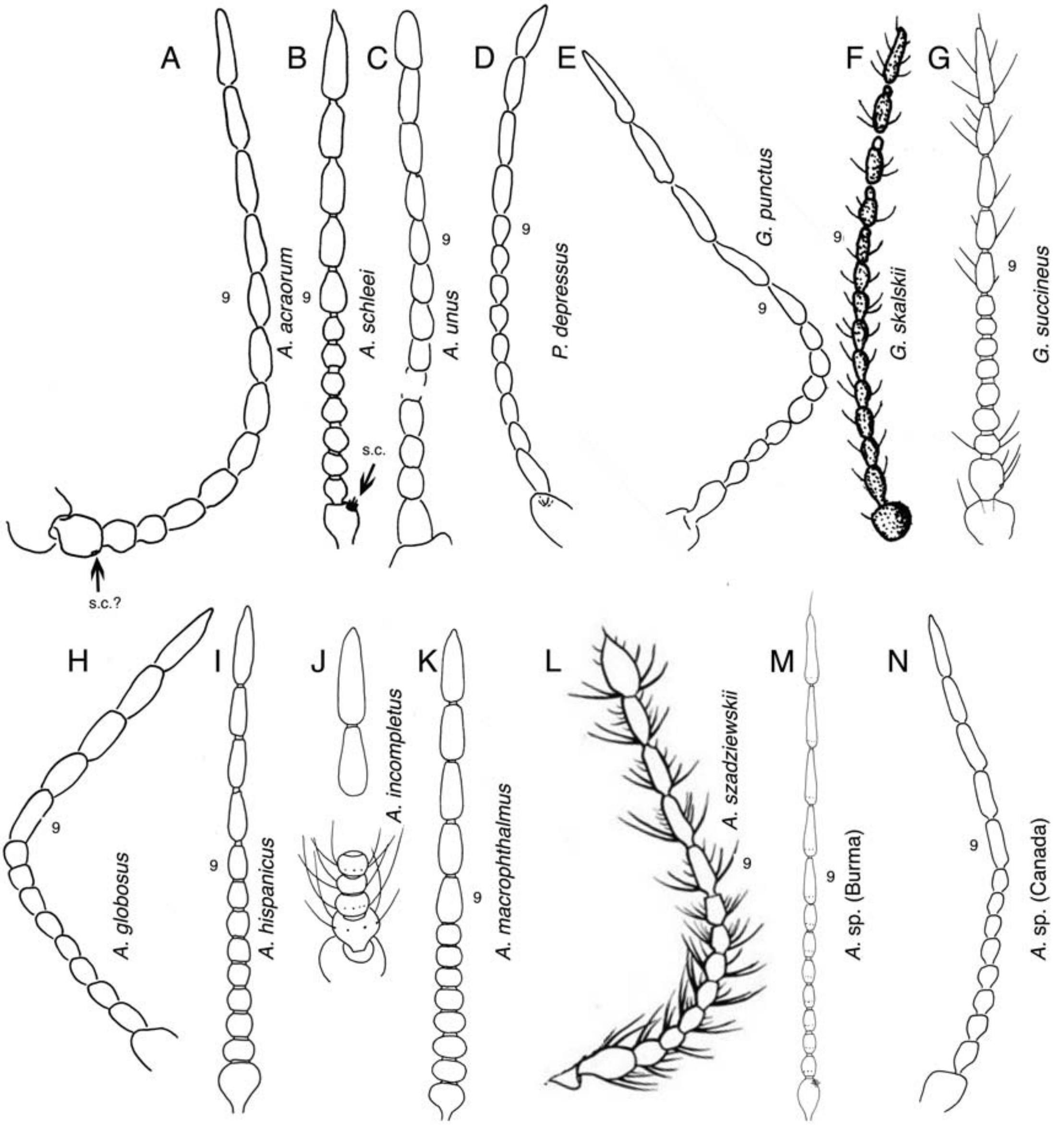
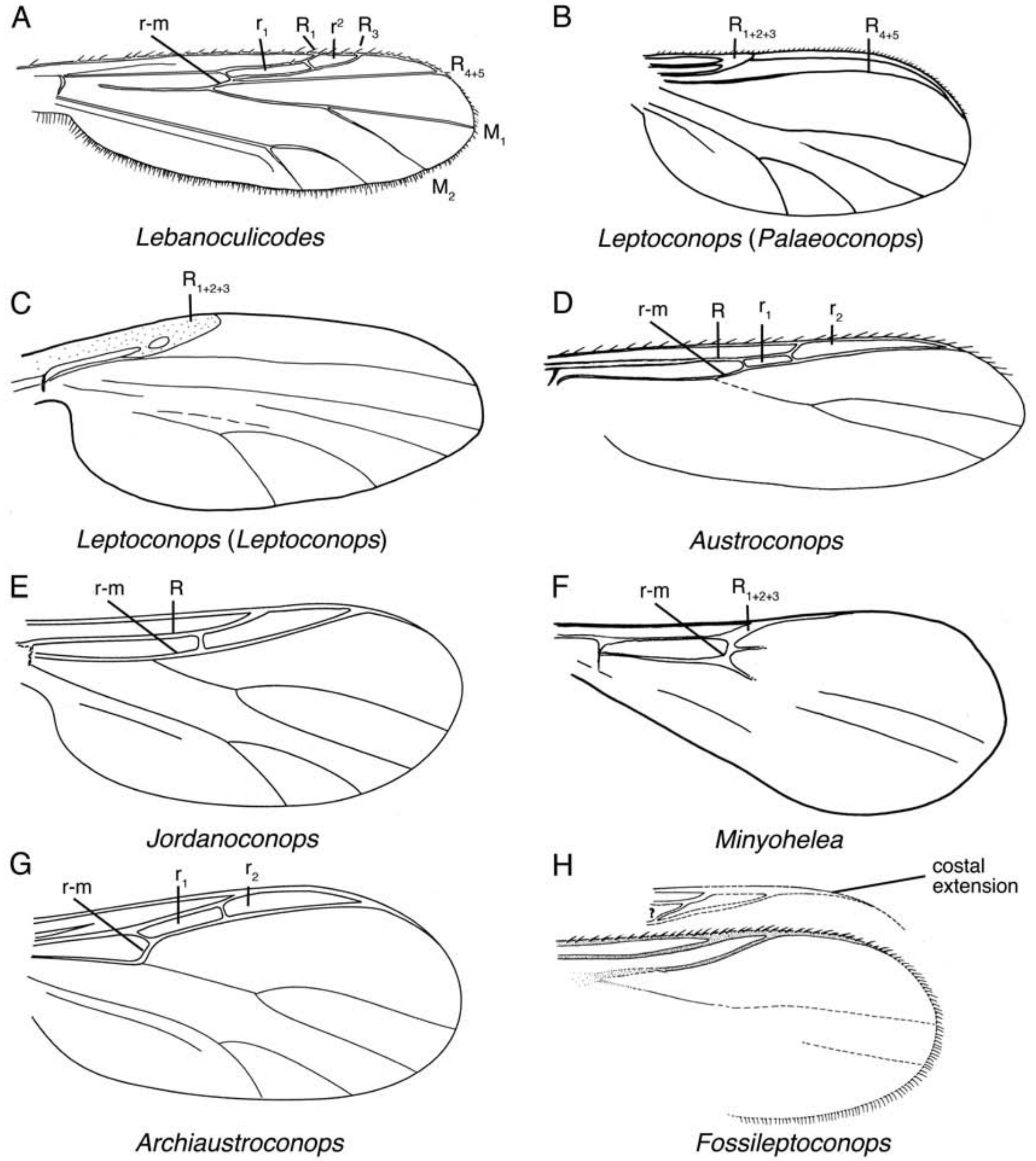


FIGURE 4. Female antenna of species of *Archiculicoides*, *Protoculicoides*, *Gerontodacus* and *Atriculicoides*. Sensilla coeloconica abbreviated as: s.c. **A.** *Archiculicoides acraorum* (from Borkent, 2000a). **B.** *Archiculicoides schleei* (from Szadziewski, 1996). **C.** *Archiculicoides unus* (from Borkent, 2000a). **D.** *Protoculicoides depressus* (from Borkent, 1995). **E.** *Gerontodacus punctus* (from Borkent, 2000a). **F.** *G. skalskii* (from Szadziewski and Arillo, 1998). **G.** *G. succineus* (from Szadziewski, 1996). **H.** *Atriculicoides globosus* (from Borkent, 1995). **I.** *Atriculicoides hispanicus* (from Szadziewski et al., 2016). **J.** *Atriculicoides incompletus* (from Szadziewski and Schlüter, 1992). **K.** *Atriculicoides macrophthalmus* (from Szadziewski, 1996). **L.** *Atriculicoides szadziewskii* (Pérez-de la Fuente et al., 2011). **M.** *Atriculicoides* sp. from Burma (from Szadziewski, 2004). **N.** *Atriculicoides* sp. from Canada (from Borkent, 1995).



Lebanoculicodes

Leptoconops (Palaeoconops)

Leptoconops (Leptoconops)

Austroconops

Jordanoconops

Minyohelea

Archiaustroconops

Fossileptoconops

FIGURE 5. Wings of Cretaceous Ceratopogonidae. **A.** *Lebanoculicoides daheri* male (from Borkent, in press). **B.** *Leptoconops* (*Palaeoconops*) *amplificatus* Borkent female (from Borkent, 2001). **C.** *Leptoconops primaevus* Borkent female (from Borkent, 1995). **D.** *Austroconops cretaceous* Szadziewski male (from Szadziewski, 1996). **E.** *Jordanoconops weitschati* Szadziewski female (from Szadziewski, 2000). **F.** *Minyohelea schleei* male (from Borkent, 2000a). **G.** *Archiaustroconops ceratoformis* Szadziewski female (from Szadziewski, 2000a). **H.** *Fossileptoconops lebanicus* Szadziewski female (from Borkent, 2000a).

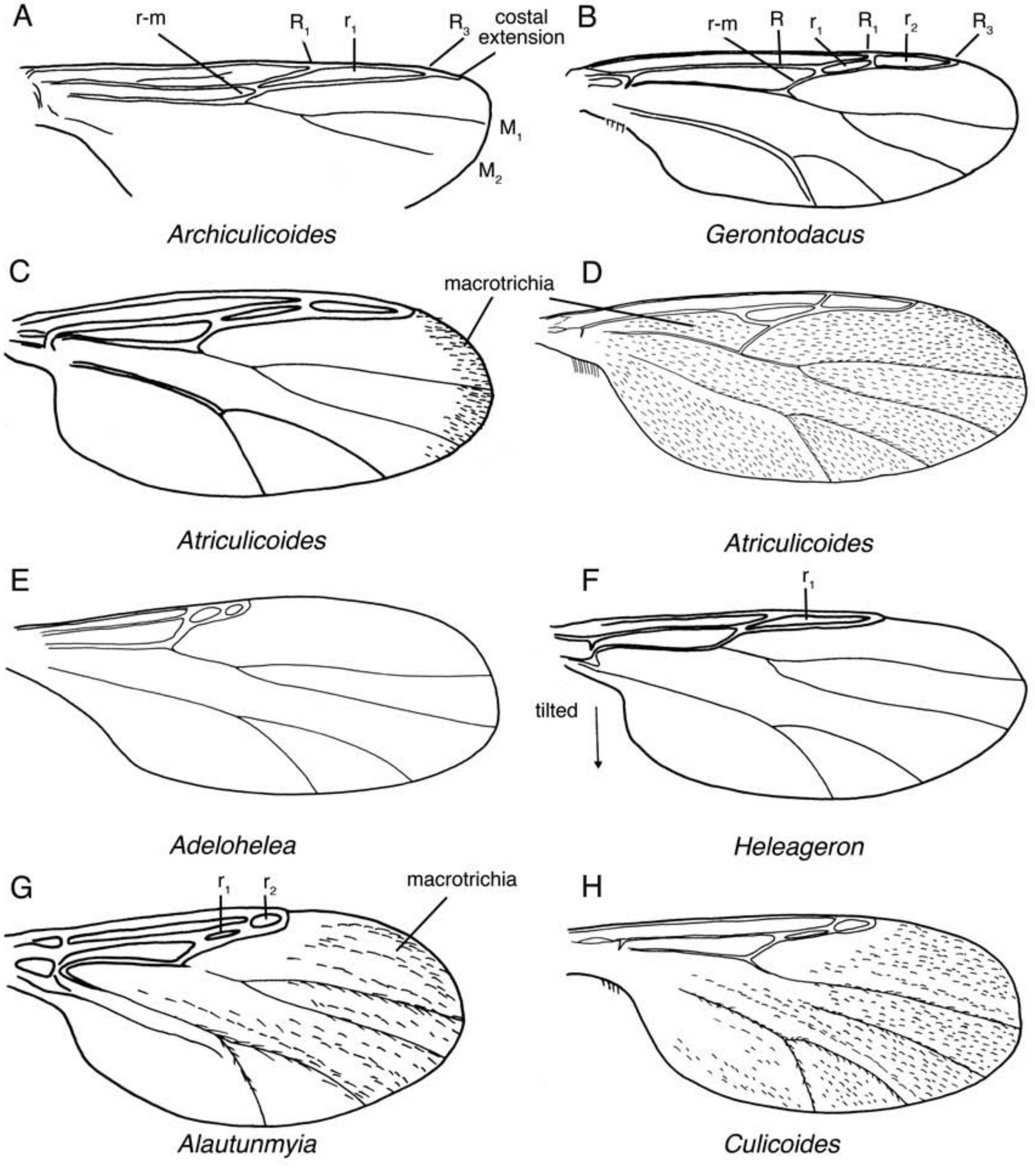


FIGURE 6. Wings of Cretaceous Ceratopogonidae. **A.** *Archiculicoides schleei* female (from Borkent, 2000a). **B.** *Gerontodacus punctus* male (from Borkent, 2000a). **C.** *Atriculicoides incompletus* female (from Borkent, 2000b). **D.** *Atriculicoides globosus* female (from Borkent, 1995). **E.** *Adelohelea glabra* male (from Borkent, 1995). **F.** *Heleageron grimaldii* female (from Borkent, 2000b). **G.** *Alautunmyia elongata* female (from Borkent, 2000b). **H.** *Culicoides tyrrelli* Borkent female (from Borkent, 1995).

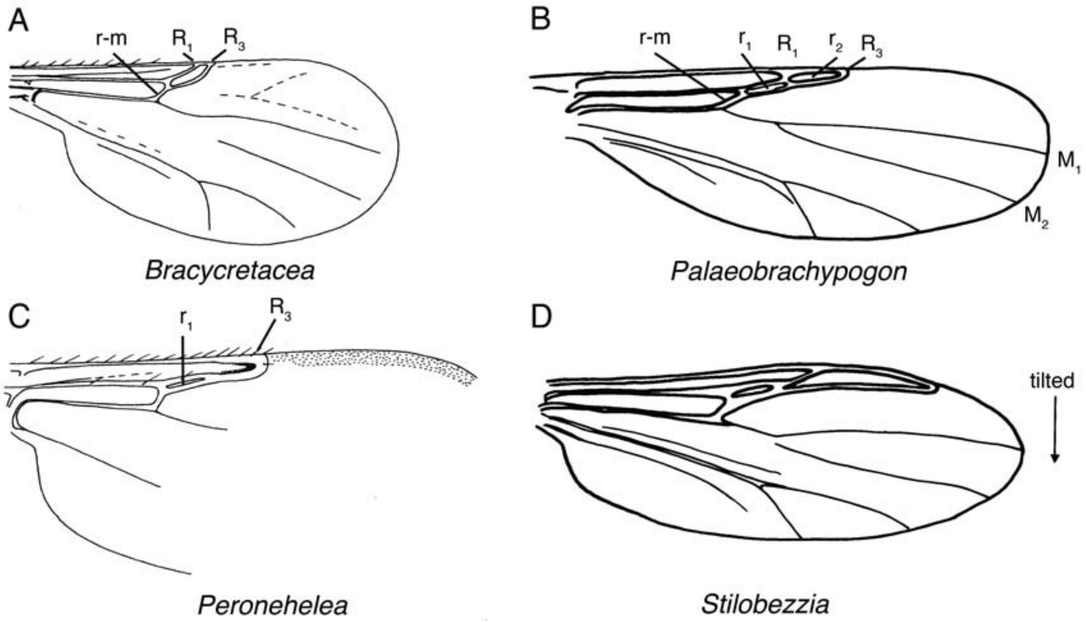


FIGURE 7. Wings of Cretaceous Ceratopogonidae. **A.** *Brachycretacea taimyrica* male (from Szadziewski, 1996). **B.** *Palaeobrachypogon grandiforceps* Borkent male (from Borkent, 2000b). **C.** *Peronehelea frigida* (Remm) female (from Szadziewski, 1996). **D.** *Stilobezzia kurthi* Borkent female (from Borkent, 2000b).

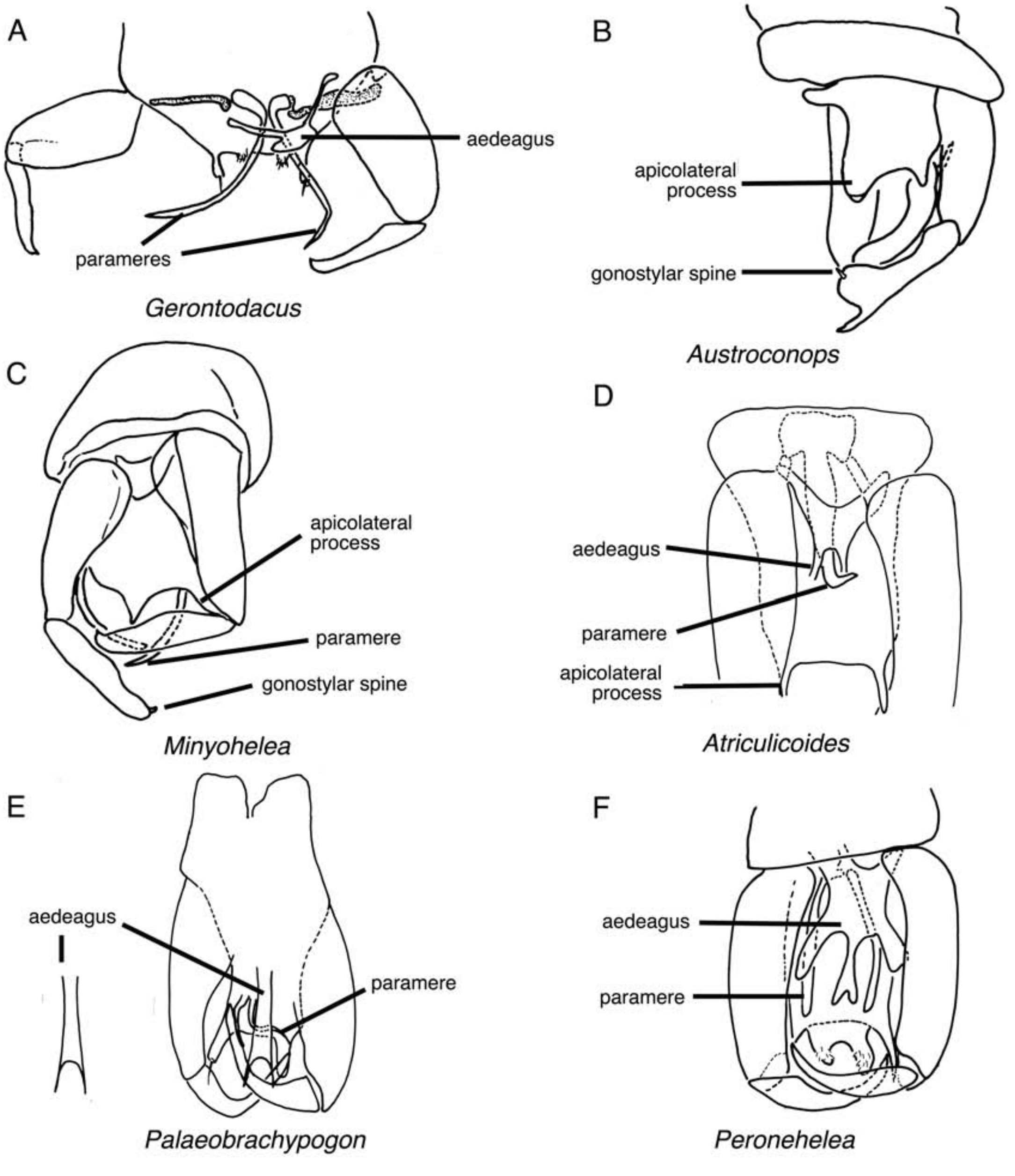


FIGURE 8. Male genitalia of Cretaceous Ceratopogonidae. **A.** *Gerontodacus succineus*, ventral view (from Borkent, 2000a). **B.** *Austroconops fossilis* Szadziewski, dorsolateral view (from Borkent, 2000a). **C.** *Minyohelea schleei* male, ventral view (from Borkent, 2000a). **D.** *Atriculicoides globosus*, ventral view (from Borkent, 1995). **E.** *Palaeobrachypogon remmi* Borkent, ventral view (from Borkent, 1995). **F.** *Peronehelea chrimikalydia* Borkent (from Borkent, 1995).

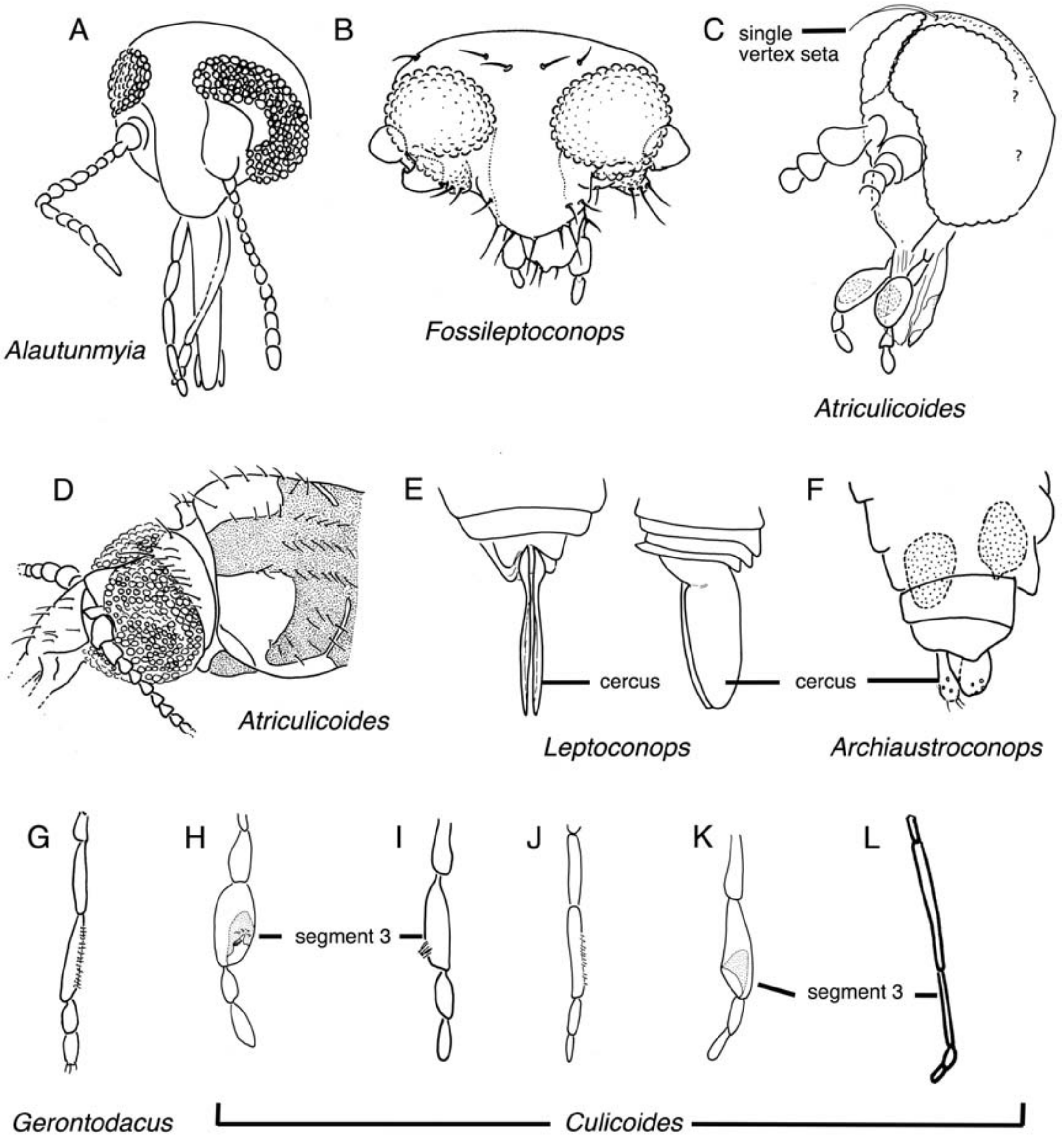


FIGURE 9. Structures of Cretaceous Ceratopogonidae A–D. Heads. E, F. Terminalia. G–L. Palpi. **A.** *Alautunmyia elongata* female, anterodorsal lateral view (from Borkent, 1997). **B.** *Fossileptoconops lebanicus* female, anterodorsal view (from Szadziewski, 1996). **C.** *Atriculicoides globosus* female, anterolateral view (from Borkent, 1995). **D.** *Atriculicoides incompletus* female, dorsolateral view (from Borkent, 2000b). **E.** *Leptoconops primaevus* female, left in ventral view, right in lateral view (from Borkent, 1995). **F.** *Archiaustroconops ceratoformis* female, dorsolateral view (from Borkent, 2000a). **G.** *Gerontodacus punctus* female (from Borkent, 2000a). **H.** *Culicoides bullus* female (from Borkent, 1995). **I.** *Culicoides filipalpis* male (from Borkent, 1995). **J.** *Culicoides filipalpis* female (from Borkent, 1995). **K.** *Culicoides tyrrelli* female (from Borkent, 1995). **L.** *Culicoides yoosti* Borkent female (from Borkent, 2000b).

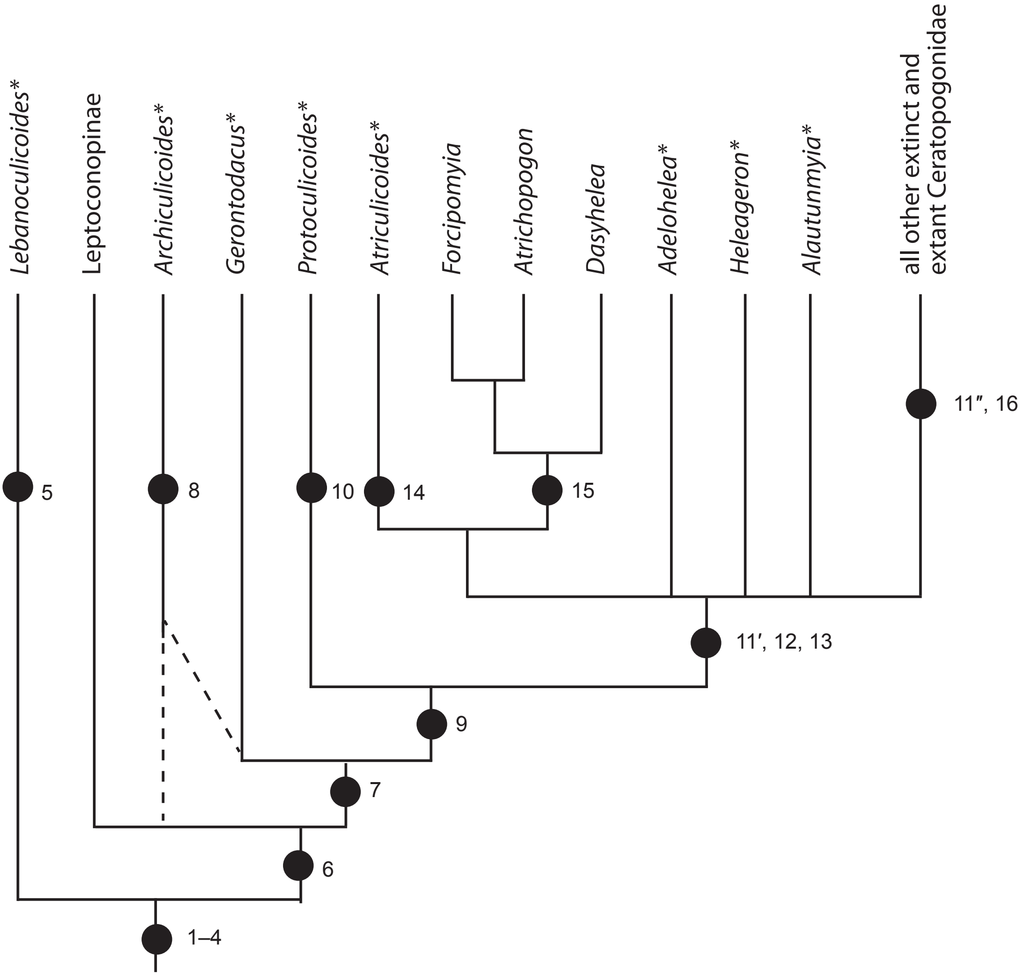


FIGURE 10. Phylogeny of the basal lineages of Ceratopogonidae. Numbers refer to synapomorphies discussed in the text. Monophyly of Leptoconopinae is discussed in the text. Genera with asterisks are extinct. The relationships among *Forcipomyia*, *Atrichopogon*, and *Dasyhelea* and their supportive synapomorphies are given by Borkent and Craig (2004).

ACKNOWLEDGMENTS

My wife, Annette Borkent, supports my taxonomic efforts with finances and love, for which I am hugely grateful. Andrew Fasbender graciously gave sage advice on the recognition of the new genus and Neal Evenhuis helped, as always, with advice on naming. My appreciation to Martin Spies for advice regarding chironomid female antennae. Thanks to Maryam Akrami and Douglas C. Currie (ROM) for arranging the loan of the holotype of *Protoculicoides depressus*. I am grateful for the loans of Burmese amber specimens from Michael Engel (KU) and David Grimaldi (AMNH). My sincere thanks to William L. Grogan and David A. Grimaldi for their valued suggestions and corrections to an earlier draft of the manuscript.

REFERENCES

Azar, D., I. Veltz, and A.E. Nel. 2008. Mandibulate chironomids: primitive or derived? (Diptera: Chironomidae). Systematic Entomology 33: 688–699.

Belkin, J.N. 1968. Mosquito studies (Diptera, Culicidae). VII. The Culicidae of New Zealand. Contributions of the American Entomological Institute 3 (1): 1–178.

Blanton, F.S., and W.W. Wirth. 1979. The sand flies (Culicoides) of Florida (Diptera: Ceratopogonidae). Arthropods of Florida and Neighboring Land Areas 10: i-xv, 1–204.

Boesel, M.W. 1937. Order Diptera. Family Chironomidae. *In* Insects and arachnids from Canadian amber: 44–55. University of Toronto Studies, Geological Series 40.

Borkent, A. 1995. Biting midges in the Cretaceous amber of North America (Diptera: Ceratopogonidae). Leiden: Backhuys Publishers.

Borkent, A. 1996. Biting midges from Upper Cretaceous New Jersey amber (Ceratopogonidae: Diptera). American Museum Novitates 3159: 1–29.

Borkent, A. 1997. Upper and Lower Cretaceous biting midges (Ceratopogonidae: Diptera) from Hungarian and Austrian amber and the Koonwarra Fossil Bed of Australia. Stuttgarter Beiträge Naturkunde, Serie B 249: 1–10.

Borkent, A. 2000a. Biting midges (Ceratopogonidae: Diptera) from Lower Cretaceous Lebanese amber with a discussion of the diversity and patterns found in other ambers. *In* D. Grimaldi (editor), Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey: 355–451. Leiden: Backhuys Publishers.

Borkent, A. 2000b. Further biting midges (Diptera: Ceratopogonidae) from Upper Cretaceous New Jersey amber. *In* D. Grimaldi (editor), Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey: 453–472. Leiden: Backhuys Publishers.

Borkent, A. 2001. *Leptoconops* (Diptera: Ceratopogonidae): the earliest extant lineage of biting midge, discovered in 120–122 million-year-old Lebanese amber. American Museum Novitates 3328: 1–11.

Borkent, A. 2008. The frog-biting midges of the world (Corethrellidae: Diptera). Zootaxa 1804: 1–456.

Borkent, A. 2012a. Further biting midges (Ceratopogonidae: Diptera) in Canadian Cretaceous amber. Canadian Entomologist 144: 758–766.

Borkent, A. 2012b. The pupae of Culicomorpha—morphology and a new phylogenetic tree. Zootaxa 3396: 1–98.

Borkent, A. 2014. The pupae of the biting midges of the world (Diptera: Ceratopogonidae), with a generic key and analysis of the phylogenetic relationships between genera. Zootaxa 3879: 1–327.

Borkent, A. 2016. World species of biting midges (Diptera: Ceratopogonidae). Internet resource (http://www.inhs.illinois.edu/research/FLYTREE/Borkent.html), accessed Sept. 19, 2017.

Borkent, A. 2017. 34. Ceratopogonidae (biting midges). *In*: A.H. Kirk-Spriggs and B.J. Sinclair (editors), Manual of Afrotropical Diptera, vol. 2. Nematocerous Diptera and lower Brachycera. Suricata 5: 733–812. Pretoria: South African National Biodiversity Institute.

Borkent, A. In press. The Lower Cretaceous male of *Lebanoculicoides daheri* – belonging to the earliest lineage of biting midge (Diptera: Ceratopogonidae). Canadian Entomologist.

Borkent, A., and D.A. Craig. 2004. *Austroconops* Wirth and Lee, a Lower Cretaceous genus of biting midges yet living in Western Australia: a new species, first description of the immatures and discussion of their biology and phylogeny (Diptera: Ceratopogonidae). American Museum Novitates 3449: 1–67.

Borkent, A., and A. Picado. 2004. Distinctive new species of *Atrichopogon* Kieffer (Diptera: Ceratopogonidae) from Costa Rica. Zootaxa 637: 1–68.

Borkent, A., W.W. Wirth, and A.L. Dyce. 1987. The newly discovered male of *Austroconops* (Ceratopogonidae: Diptera) with a discussion of the phylogeny of the basal lineages of the Ceratopogonidae. Proceedings of the Entomological Society of Washington 89: 587–606.

Brown, B.V., et al. (editors). 2009. Manual of Central American Diptera, vol. 1. Ottawa, Ontario, Canada: National Research Council Research Press.

Choufani, J., V. Perrichot, D. Azar, and A. Nel. 2014. New biting midges (Diptera: Ceratopogonidae) in Late Cretaceous Vendean amber. Paleontological Contributions 10H: 34–40.

Choufani, J., D. Azar, and A. Nel. 2015. New biting midges from the Cretaceous amber of Lebanon (Diptera: Ceratopogonidae). Annales de la Société Entomologique de France (N.S.): International Journal of Entomology 50: 272–285.

Debenham, M.L. 1987a. The biting midge genus *Forcipomyia* (Diptera: Ceratopogonidae) in the Australasian Region (exclusive of New Zealand). I. Introduction, key to subgenera and the *Thyridomyia* and *Trichohelea* groups of subgenera. Invertebrate Taxonomy 1: 35–119.

Debenham, M.L. 1987b. The biting midge genus *Forcipomyia* (Diptera: Ceratopogonidae) in the Australasian Region (exclusive of New Zealand). II. *Warmkea* and the *Caloforcipomyia* group of subgenera. Invertebrate Taxonomy 1: 167–199.

Debenham, M.L. 1987c. The biting midge genus *Forcipomyia* (Diptera: Ceratopogonidae) in the Australasian Region (exclusive of New Zealand). III. The subgenera *Forcipomyia*, s.s. and *Lepidohelea*. Invertebrate Taxonomy 1: 269–350.

Debenham, M.L. 1987d. The biting midge genus *Forcipomyia* (Diptera: Ceratopogonidae) in the Australasian Region (exclusive of New Zealand). IV. The subgenera allied to *Forcipomyia*, s.s. and *Lepidohelea* and the interrelationships and biogeography of the subgenera of *Forcipomyia*. Invertebrate Taxonomy 1: 631–684.

Dominiak, P. 2012. Biting midges of the genus *Dasyhelea* Kieffer (Diptera: Ceratopogonidae) in Poland. Polskie Pismo Entomologiczne 81: 211–304.

Dominiak, P., R. Szadziewski, and A. Nel. 2018. A new species of the haematophagous genus *Austroconops* Wirth & Lee (Diptera: Ceratopogonidae: Leptoconopinae) from middle Cretaceous amber of Charente-Maritime, France. Cretaceous Research 92: 231–239.

Heming, B.S. 2003. Insect development and evolution. Ithaca, NY: Comstock Publishing Associates.

McAlpine, J.F., et al. (coordinators). 1981. Manual of Nearctic Diptera, vol. 1. Agriculture Canada Monograph 27.

McKeller, R.C., and M.S. Engel. 2012. Hymenoptera in Canadian Cretaceous amber (Insecta). Cretaceous Research 35: 258–279

Pérez-de la Fuente, R., X. Delclòs, E. Peñalver, and A. Arillo. 2011. Biting midges (Diptera: Ceratopogonidae) from the Early Cretaceous El Soplao amber (N Spain). Cretaceous Research 32: 750–761.

Peterson, B.V. 1981. 27. Simuliidae. *In* J.F. McAlpine et al. (coordinators), Manual of Nearctic Diptera, vol. 1. Agriculture Canada Monograph 27: 355–391.

Remm, H. 1959. Estonian species of the genus *Atrichopogon* Kieffer (Diptera, Heleidae). I. Subgenus *Psilokempia* Enderlein). Entomologicheskoe Obozrenie 38: 682–692. [in Russian, English summary; English translation in Entomological Review 38: 614–623]

Remm, H. 1961. Estonian species of the genus *Atrichopogon* Kieffer (Diptera, Heleidae). II. Description of three new species and key to the Estonian species of the subgenus *Atrichopogon s. str*. Entomologicheskoe Obozrenie 40: 920–929. [in Russian, English summary; English translation in Entomological Review 40: 527–532]

Remm, H. 1976. Midges (Diptera, Ceratopogonidae) from the Upper Cretaceous fossil resins of the Khatanga depression. Paleontologisceskij Zhurnal 3: 107–116. [in Russian]

Stone, A., and B.V. Peterson. 1981. 26. Thaumaleidae. *In* J.F. McAlpine et al. (coordinators), Manual of Nearctic Diptera. Volume 1. Agriculture Canada Monograph 27: 351–353.

Szadziewski, R. 1988. Biting midges (Diptera, Ceratopogonidae) from Baltic amber. Polskie Pismo Entomologiczne 58: 3–283.

Szadziewski, R. 1996. Biting midges from Lower Cretaceous amber of Lebanon and Upper Cretaceous Siberian amber of Taimyr (Diptera, Ceratopogonidae). Studia Dipterologica 3: 23–86.

Szadziewski, R. 2000. Biting midges (Diptera: Ceratopogonidae) from the Lower Cretaceous amber of Jordan. Polskie Pismo Entomologiczne 69: 251–256.

Szadziewski, R. 2004. Biting midges (Diptera: Ceratopogonidae) from Burmese amber, Myanmar. Journal of Systematic Palaeontology 2: 115–123.

Szadziewski, R. 2008. Age and recent distribution of extant genera of Ceratopogonidae (Diptera) present in the fossil record. Alavesia 2: 87–99.

Szadziewski, R. 2017. Biting midges (Diptera: Ceratopogonidae) as indicators of biostratigraphy, ecological reconstructions and identification of amber deposits. Earth and Environmental Science, Transactions of the Royal Society of Edinburgh, 107: 219–230.

Szadziewski, R., and A. Arillo. 1998. Biting midges (Diptera: Ceratopogonidae) from the Lower Cretaceous amber from Alava, Spain. Polskie Pismo Entomologiczne 67: 291–298.

Szadziewski, R., and G.O. Poinar. 2005. Additional biting midges (Diptera: Ceratopogonidae) from Burmese amber. Polskie Pismo Entomologiczne 74: 349–362.

Szadziewski, R., and T. Schlüter. 1992. Biting midges (Diptera: Ceratopogonidae) from Upper Cretaceous (Cenomanian) amber of France. Annales de la Société Entomologique de France 28: 73–81.

Szadziewski, R., W. Giłka, and A. Urbanek. 2015a. A blood sucking biting midge from Upper Cretaceous Burmese amber with a key to the determination of fossil species in the relictual genus *Leptoconops* Skuse (Diptera: Ceratopogonidae). Cretaceous Research 54: 255–259.

Szadziewski, R., A. Ross, and W. Giłka. 2015b. Further records of biting midges (Diptera: Ceratopogonidae) from Upper Cretaceous Burmese amber (Myanmar). Cretaceous Research 52: 556–561.

Szadziewski, R., A. Arillo, A. Urbanek, and E. Sontag. 2016. Biting midges of the extinct genus *Protoculicoides* Boesel from Lower Cretaceous amber of San Just, Spain and new synonymy in recently described fossil genera (Diptera: Ceratopogonidae). Cretaceous Research 58: 1–9.

Urbanek A., M. Piotrowicz, R. Szadziewski, and W. Giłka. 2014. Sensilla coeloconica ringed by microtrichia in host-seeking biting midges. Medical and Veterinary Entomology 28: 355–363.

Wirth, W.W., and A.A. Hubert. 1989. The *Culicoides* of Southeast Asia (Diptera: Ceratopogonidae). Memoirs of the American Entomological Institute 44: i–iv, 1–508.

Wood, D.M. 1991. Homology and phylogenetic implications of male genitalia in Diptera. The ground plan. *In* Proceedings of the Second International Congress of Dipterology, Bratislava, Czechoslovakia: 255–284.

Zheng, D., et al. 2018. A Late Cretaceous amber biota from central Myanmar. Nature Communications 9: 1–6. [doi: 10.1038/s41467-018-05650-2]

All issues of *Novitates* and *Bulletin* are available on the web (http://digitallibrary.amnh.org/dspace). Order printed copies on the web from:
http://shop.amnh.org/a701/shop-by-category/books/scientific-publications.html

or via standard mail from:
American Museum of Natural History—Scientific Publications
Central Park West at 79th Street
New York, NY 10024

♾ This paper meets the requirements of ANSI/NISO Z39.48-1992 (permanence of paper).