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Source: American Museum Novitates, 2001(3328) : 1-12

Published By: American Museum of Natural History

URL: [https://doi.org/10.1206/0003-0082\(2001\)328<0001:LDCTEE>2.0.CO;2](https://doi.org/10.1206/0003-0082(2001)328<0001:LDCTEE>2.0.CO;2)

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AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024

Number 3328, 11 pp., 4 figures

April 26, 2001

Leptoconops (Diptera: Ceratopogonidae), the Earliest Extant Lineage of Biting Midge, Discovered in 120–122 Million-Year-Old Lebanese Amber

ART BORKENT¹

ABSTRACT

As predicted by phylogenetic patterns, the genus *Leptoconops* Skuse is recorded for the first time from Lower Cretaceous Lebanese amber, dated at 120–122 million years. Two species are described as new: *L. amplificatus*, known from 1 male and 11 females, and *L. antiquus*, known from 2 females. These likely represent the earliest lineage(s) within the genus and are placed in a new subgenus, *Palaeoconops*.

Previous analysis of Lebanese amber Ceratopogonidae (22 species, 126 specimens) indicated that these specimens represent a past community with high species diversity but with a low abundance of individual species. *Leptoconops amplificatus* is the first of 24 species of Ceratopogonidae known from this deposit to have intraspecific associations in a single piece of amber, likely reflecting their restriction to ancient beach habitats.

INTRODUCTION

Members of the extant genus *Leptoconops* Skuse are an intriguing group of biting midges. Among extant Ceratopogonidae, the genus is the sister-group of all remaining members of the family (Borkent et al., 1987; Borkent, 1995, 2000) and its species exhibit dis-

tinctive autapomorphies as larvae, pupae and adults. Most species are associated with marine or freshwater beaches, where the larvae burrow through wet sand in search of food. Adult females are diurnal feeders on vertebrate blood (including lizards, birds and mammals) and in at least some species,

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adults rest by burying themselves in sand. The early extant lineages of many groups of organisms are highly modified and this is also true of species of *Leptoconops*.

Borkent (2000) recently published a detailed description and analysis of 22 species of Ceratopogonidae known from ancient, 120–122 million-year-old Lebanese amber. Although the fossil genus *Lebanoculicoides* Szadziewski, which represents an even earlier lineage of Ceratopogonidae than does *Leptoconops* (fig. 4), was present in the amber, no specimens of *Leptoconops* were discovered among the 126 ceratopogonid specimens available for study. But as happens so often to systematists, at the very final stages of submission for publication, a few more specimens came to light and, as predicted by phylogenetic patterns, these were identified as members of *Leptoconops* and of exceptional interest. This paper describes two new species of *Leptoconops* and discusses both the systematic and paleoecological implications of these discoveries.

The oldest definite fossils of this genus were previously known from French and Taimyr amber at 93–99 ma (Szadziewski, 1996; Schlüter, 1978). A poorly preserved compression fossil from Australia, dated at 115 ± 6 – 118 ± 5 ma, was tentatively identified as a male *Leptoconops* by Borkent (1997) but its identity is somewhat uncertain.

MATERIALS AND METHODS

This study is based on 14 newly discovered specimens of Ceratopogonidae in 4 pieces of Lebanese amber. All pieces are in small plastic boxes and are housed in the American Museum of Natural History. The specimen numbers follow their cataloging system.

Methods follow those described by Borkent (1995, 2000). However, all specimens were at least partially embedded in epoxy and polished using the method described by Nascimbene and Silverstein (2000). Inclusions were examined with a Wild M3 dissecting scope at 100 \times and with a Carl Zeiss Jenaval compound microscope by suspending the amber in immersion oil on the underside of a coverslip as described by Borkent (2000).

SYSTEMATICS

LEPTOCONOPS Skuse

Leptoconops Skuse, 1889: 288. Type-species, *Leptoconops stygius* Skuse, by monotypy.

DIAGNOSIS AND DESCRIPTION OF ADULTS: As given by Borkent (1995), Clastrier and Wirth (1978), Smee (1966), Szadziewski (1988: 232), and Wirth and Atchley (1973). In addition: females with 10–13 flagellomeres.

Borkent (1995, 2000) and Wirth and Atchley (1973) provided an overview of the distribution, biology and fossil record of the genus. Borkent and Wirth (1997) cataloged 127 extant and 6 extinct species of *Leptoconops*; since then a further 7 extant and 3 extinct species (including those newly named here) have been recognized.

Eight fossil species of *Leptoconops* are now known from the Cretaceous and they may be recognized using the following keys, which are based in part on earlier keys by Borkent (1996) and Szadziewski (1996). A tentatively identified and unnamed male *Leptoconops* known as a compression fossil from the Lower Cretaceous in Australia is not keyed. Neither is the unnamed female *Leptoconops* from Upper Cretaceous French amber briefly described by Schlüter (1978).

KEY TO CRETACEOUS MALE *LEPTOCONOPS*

The males of *L. antiquus* from Lebanese amber and *L. boreus* Kalugina from Taimyr amber are unknown.

1. Gonostylus with medial lobe at midlength and subapical, pointed projection about one-third from apex
 *sibiricus* Szadziewski (Taimyr amber)
- Gonostylus a single, undivided structure
 2
2. Wing with costa well-developed beyond apex of R₃; first tarsomere of hindleg with many (about 10 or more) thick spines (fig. 1B)
 *amplificatus*, n. sp. (Lebanese amber)
- Wing with costa terminating at apex of R₃; first tarsomere of hindleg with no more than 6 thick spines 3
3. Apicolateral process on tergite 9 thick and slightly enlarged apically
 *clava* Borkent (Hungarian amber)

- Apicolateral process on tergite 9 slender and elongate, tapering to apex 4
- 4. Terminal flagellomere about 2–3 times as long as penultimate flagellomere
 *copiosus* Borkent (New Jersey amber)
- Terminal flagellomere about 5–6 times as long as penultimate flagellomere 5
- 5. Gonocoxite relatively short and stout
 *curvachelus* Borkent (New Jersey amber)
- Gonocoxite relatively elongate and slender
 *primaevus* Borkent (Canadian amber)

KEY TO CRETACEOUS FEMALE *LEPTOCONOPS*

The female of *L. clava* Borkent from Hungarian amber is unknown.

1. Antenna with 13 flagellomeres (figs. 1H, 2C)
 2
- Antenna with 12 flagellomeres 3
2. First tarsomere of hindleg with more than 15 thick spines (fig. 1I); cercus long and slender (fig. 2A)
 *amplificatus*, n. sp. (Lebanese amber)
- First tarsomere of hindleg with a few (about 4–5) thick spines; cercus relatively short and well-developed anteroventrally (fig. 2G)
 *antiquus*, n. sp. (Lebanese amber)
3. Tarsal claws strongly curved basally, with thick, well-developed inner tooth
 *curvachelus* Borkent (New Jersey amber), *sibiricus* Szadziewski (Taimyr amber)
- Tarsal claws more or less evenly curved from base, with at most a very slender, hairlike inner tooth 4
4. Flagellomeres 3–11 somewhat elongate
 *primaevus* Borkent (Canadian amber)
- Flagellomeres 3–11 spherical *copiosus* Borkent (New Jersey amber), *boreus* Kalugina (Taimyr amber)

Palaeoconops, new subgenus

DIAGNOSIS: *Male and female*. Only *Leptoconops* with a well-developed costa extending to the wing apex. *Also, female*. Only *Leptoconops* with an antenna with 13 flagellomeres.

TYPE SPECIES: *Leptoconops amplificatus*, n. sp.

TAXONOMIC DISCUSSION: Cladistic analysis of the two included species, *L. amplificatus* and *L. antiquus*, of the new subgenus *Palaeoconops* provided below, shows that these represent the earliest lineage within *Leptoconops* (fig. 4). All remaining *Leptoconops*

form a monophyletic group and the new fossil taxa must therefore be placed in a new subgenus. There is no synapomorphy grouping *L. amplificatus* and *L. antiquus* and it is therefore uncertain whether *L. (Palaeoconops)* is monophyletic.

DERIVATION OF SUBGENERIC EPITHET: The name *Palaeoconops* is from the Greek, *palaeo* (= ancient, old) and *konops* (= gnat), referring to the incredible age of these fossils.

Leptoconops (Palaeoconops) amplificatus Borkent, new species

Figures 1A–J, 2A

DIAGNOSIS: *Male*. The only Cretaceous *Leptoconops* with a well-developed costa beyond R₃, a well-developed R₄₊₅, and strong spines along the length of the first tarsomere of the hindleg. *Female*. The only species of Ceratopogonidae with 13 flagellomeres and an elongate, slender cercus.

DESCRIPTION: *Male*. **Head**: Most details not visible. Antenna (fig. 1A) with well-developed plume, basal foramen of pedicel not visible, 13 separate flagellomeres, antennal ratio = 0.69, flagellomere 10/11 = 0.77, flagellomere 13 more elongate than preceding flagellomeres (fig. 1B, G). Palpus with 4 segments, details not visible. **Thorax**: Most details not visible. **Wing**: Length = 0.64 mm. R₄₊₅ well-developed to near wing apex. Costa well-developed to near wing apex, exact costal ratio uncertain. Without macrotrichia, fine microtrichia on all membrane. **Legs**: Femora, tibiae slender. Hindleg first tarsomere with numerous stout setae (fig. 1B). Setae on fore- and midleg trochanter not visible. Midleg tibia with apical spur. Hindleg first tarsomere without thick basal spine or palisade setae. Claws simple. **Genitalia** (fig. 1C, D): Tergite 9 apparently tapering to single apex. Gonocoxite moderately elongate. Gonostylus thick basally, tapering to toothed apex; apical spine likely present but not clearly visible. Paired structures (parameres?) basally thick, tapering apically, directed posterolaterally. Aedeagus not visible.

Female. **Head**: Eyes bare, broadly separated dorsomedially. Vertex without single dorsomedial seta. Frons, vertex area possibly with sutures (fig. 1F). Antenna with 13 sep-

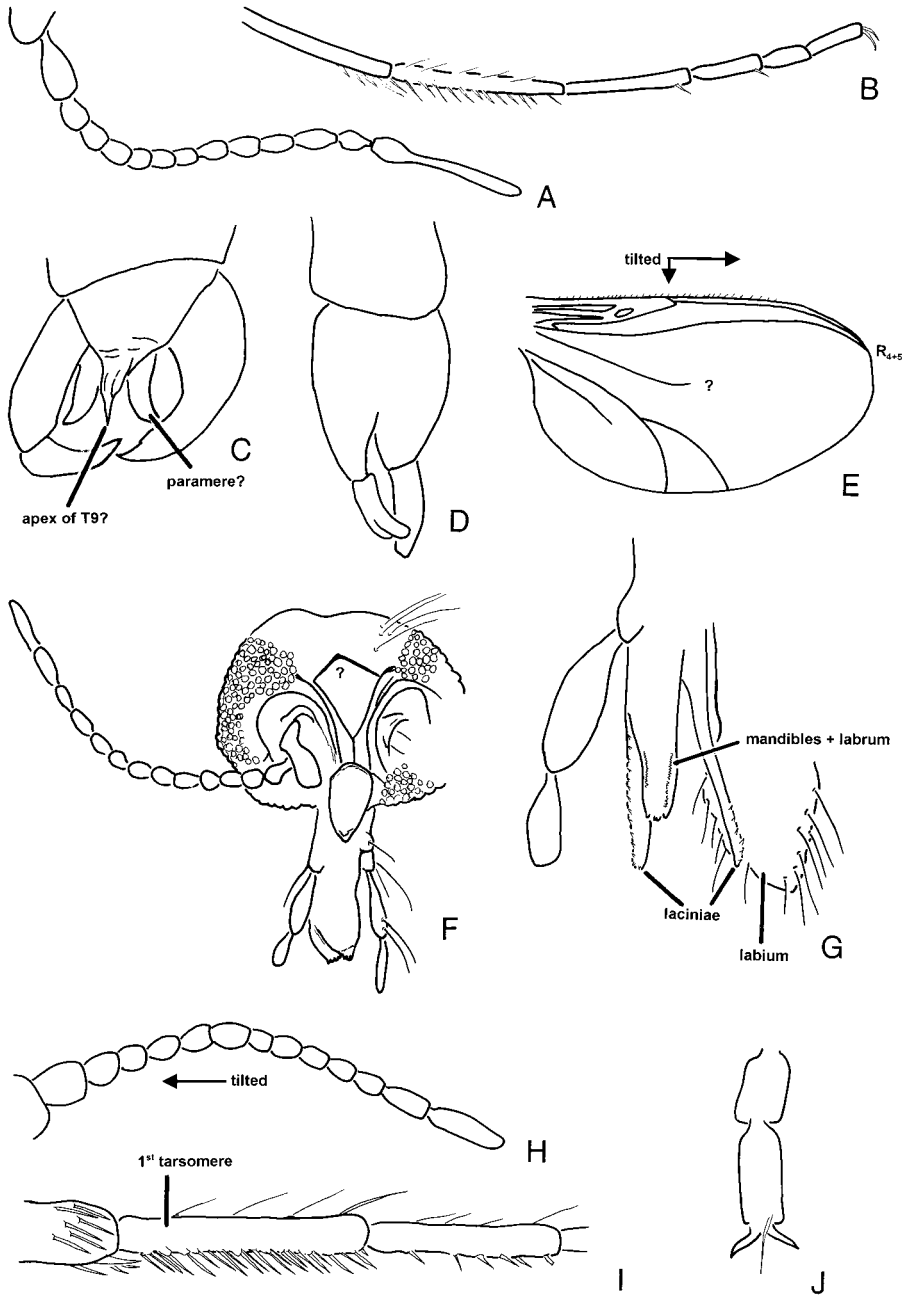


Fig. 1. Structures of *Leptoconops amplificatus*. **A–D**. Male (no. 79). **E–J**. Female. **A**. Antenna. **B**. Hindleg tarsomeres. **C**. Genitalia, oblique, dorsal view. **D**. Genitalia, oblique, lateral view. **E**. Wing Antenna (no. 101, holotype). **F**. Head capsule, anterior view (no. 101, paratype # 4). **G**. Apex of mouthparts (no. 101, holotype). **H**. Antenna (no. 101, holotype). **I**. First and second tarsomeres of hindleg (no. 101, holotype). **J**. Fifth tarsomere of midleg (no. 101, holotype).

arate flagellomeres, antennal ratio = 0.75–0.87 ($n = 5$), terminal flagellomere more elongate than preceding flagellomere (fig. 1H), penultimate flagellomere longer than preceding flagellomeres, first flagellomere sensilla not visible. Mouthparts moderately elongate (fig. 1F, G). Clypeus separated laterally by membrane from head capsule. Labrum with 4–6 short thick apical spines. Mandible with fine teeth. Lacinia with at least 15 large, retrorse teeth. Palpus with 4 segments, third segment somewhat ovoid, capitate sensilla not visible (fig. 1G), palpus segment $3/4 + 5 = 1.27$ – 2.00 ($n = 5$). Hypopharynx not visible. **Thorax:** Most details not visible. Anterior scutal apodemes not visible. Scutum with a few scattered elongate setae. **Wing** (fig. 1E): Length = 0.47–0.65 mm ($n = 6$). R_{4+5} well-developed to near wing apex. Costa well-developed to near wing apex, apex of R_3 /wing length = 0.38–0.40 ($n = 3$). Without macrotrichia, fine microtrichia present on all membrane. Alula without macrotrichia. Single radial cell present in at least some specimens, radial veins compacted anteriorly. Base of M poorly defined, bifurcation not visible, both M_1 and M_2 present. **Legs:** Femora, tibiae slender. Legs with thick spines on first tarsomere of each leg, a few on fore and midleg, many on hindleg (fig. 1I). Pair of thick setae on fore- and midleg trochanter not visible. Midleg tibia with apical spur. Hind first tarsomere without thick basal spine or palisade setae. Foreleg, midleg, hindleg claws of equal size, length, more or less evenly curved, without well-developed basal tooth (fig. 1J). **Genitalia** (fig. 2A): Spermathecae not visible. Details of sternite 8, 9, segment 10 not visible. Cercus laterally compressed, elongate, slender.

BIONOMICS: Based on the elongate cerci (likely used to oviposit in sand) and the general habitat of extant members of the genus, *L. amplificatus* probably bred in sandy, saline habitats (Borkent, 1995). The presence of finely serrate mandibles and laciniae with retrorse teeth strongly suggests that females of this species fed on vertebrate blood (Borkent, 1995, 1996). One female paratype of *L. amplificatus* in piece 101 (specimen No. 3, fig. 3) had a bloated abdomen and, considering the evidence from the mouthparts, this is

likely due to the presence of either a vertebrate blood meal or nectar.

The holotype of *L. amplificatus* was associated with eight paratypes of that species, in addition to a female Ceratopogonidae of uncertain identity, one Mycetophilidae, three Brachycera, one Chironomidae and one Culicomorpha. The allotype and one paratype of *L. amplificatus* were in a single piece of amber with the holotype of *L. antiquus* and the holotype of a possible Lonchopteridae (*Lonchopterites prisca* Grimaldi and Cumming). The paratype in piece 131 was associated with a female Rhagionidae identified by Grimaldi and Cumming (1999) as “Genus C”. The implications of these associations are interpreted below.

TAXONOMIC DISCUSSION: The male was associated with the female on the basis of the presence of numerous thick spines on the first tarsomere of the hindleg (not present in females of *L. antiquus*).

The holotype of *L. amplificatus* was in moderately good condition, but was missing the apex of the left antenna and the apices of all legs other than the right hindleg. The allotype was also in moderately good condition, but was embedded so deeply in the amber as to make some details difficult to discern. The remaining paratypes were generally in moderately good to excellent condition but some of those in piece 101 (fig. 3) were buried so deeply in the amber—which cannot be cut further because of other inclusions—that visibility was rather limited for these.

The holotype of *L. amplificatus* was the middle specimen in a group of three closely approximated females (fig. 3). The paratype of *L. amplificatus* in piece 79 was that female most close to the holotype of *Lonchopterites prisca* (amber piece figured in Grimaldi and Cumming, 1999: 83, showing the position of the specimens).

One female paratype in piece no. 101 (specimen no. 4) appeared to have sutures on the frons/vertex (fig. 1F), but these may have been artifacts of preservation. If truly present, these would be unique within the genus.

TYPES: Holotype, female adult in amber in plastic box, labeled “HOLOTYPE *Leptoconops amplificatus* Borkent”, “PARATYPES *Leptoconops amplificatus* Borkent: 8 fe-

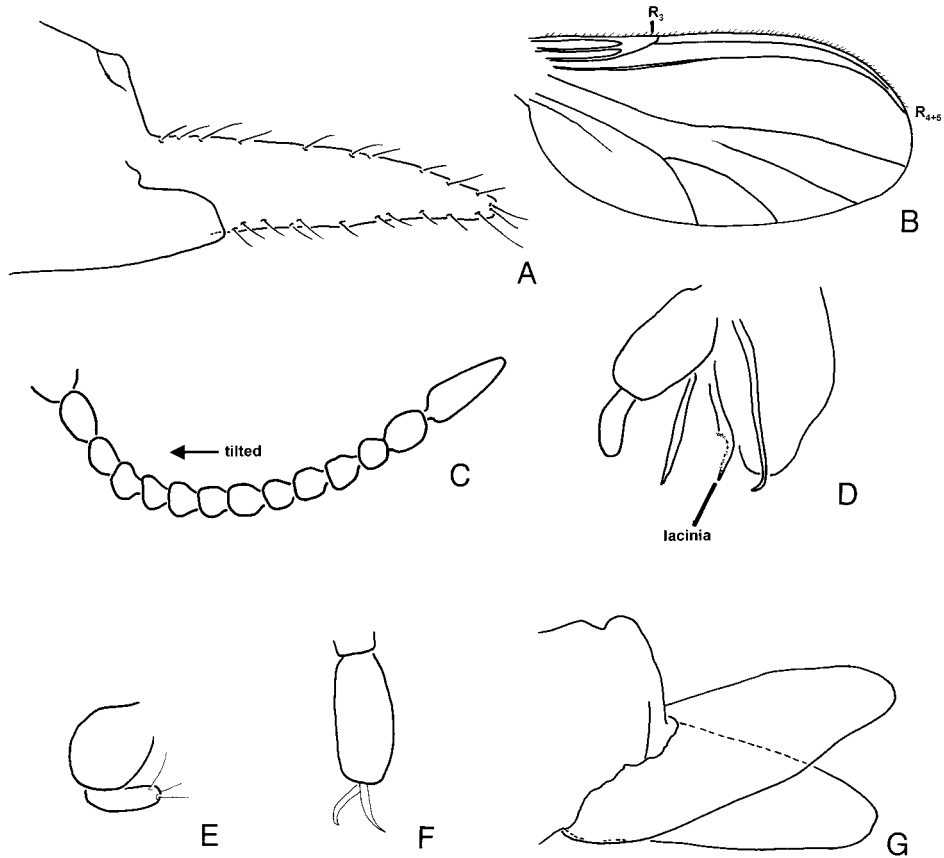


Fig. 2. **A.** Structures of female *Leptoconops amplificatus*. **B–G.** Structures of female *Leptoconops antiquus*. **A.** Cercus, lateral view (no. 101, holotype). **B.** Wing (no. 125, paratype). **C.** Antenna (no. 125, holotype). **D.** Apex of mouthparts (no. 125, holotype). **E.** Palpus (no. 125, paratype). **F.** Fifth tarsomere of foreleg (no. 125, paratype). **G.** Cerci, lateral view (no. 125, holotype).

males”, “Amber: N. Lebanon, Antoni Estephan Coll. Bchare Mtn., 2300 m”, “AMBER: Lebanon Lower Cretaceous (Neocomian) No. 101, Amer. Mus. Nat. Hist., Inclusion(s): female *Leptoconops*” (AMNH); allotype, male adult, labeled “ALLOTYPE *Leptoconops amplificatus* Borkent”, “PARATYPE *Leptoconops amplificatus* Borkent”, “HOLOTYPE *Leptoconops antiquus* Borkent”, “Amber: N. Lebanon, Antoni Estephan Coll. Bchare Mtn., 2300 m”, “AMBER: Lebanon Lower Cretaceous (Neocomian) No. 79, Amer. Mus. Nat. Hist., Inclusion(s): 3 Ceratopogonidae, 1 Empidoid” (AMNH); paratypes, 10 females: 8 in same piece with holotype; 1 in same piece as allotype; 1 from Bchare Mtn., Lebanon, piece No. 131 (AMNH).

DERIVATION OF SPECIFIC EPITHET: The name *amplificatus* (enlarged, extended) refers to the presence of 13 flagellomeres in the female antenna.

Leptoconops (Palaeoconops) antiquus
Borkent, new species

Figures 2B–G

DIAGNOSIS: *Male.* Unknown. *Female.* The only species of Ceratopogonidae with 13 flagellomeres and an elongate and basally broadened (anteroventrally) cercus.

DESCRIPTION: *Female.* **Head:** Most details not visible. Antenna with 13 separate flagellomeres, antennal ratio = 0.78–0.89 ($n = 2$), terminal flagellomere more elongate than preceding flagellomeres (fig. 2C), first fla-

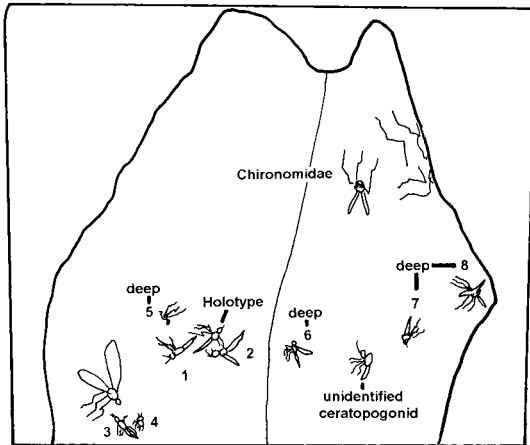


Fig. 3. Amber piece no. 101 showing location of inclusions. Numbers refer to paratypes of *Leptoconops amplificatus*. Not all other non-ceratopogonid inclusions are shown.

gellomere sensilla not visible. Mouthparts moderately elongate. Clypeus not clearly visible. Labrum, mandible not visible. Lacinia with at least seven large, retrorse teeth. Palpus with 4 segments, third segment large, somewhat ovoid, capitate sensilla not visible (fig. 2D, E), palpus segment $3/4 + 5 = 1.80$ ($n = 1$). **Thorax:** Most details not visible. **Wing** (fig. 2B): Length = 0.59 mm ($n = 2$). R_{4+5} well-developed to near wing apex. Costa well-developed to near wing apex, apex of R_3 /wing length = 0.38 ($n = 1$). Without macrotrichia, fine microtrichia present on all membrane. Alula without macrotrichia. Without radial cell, radial veins compacted anteriorly. Base of M poorly defined, point of bifurcation not visible, both M_1 and M_2 present. **Legs:** Femora, tibiae slender. Legs mostly lacking armature but with four to five thick spines on fifth tarsomere of hindleg. Pair of thick setae on fore- and midleg trochanter not visible. Midleg tibia with apical spur. Hind first tarsomere without thick basal spine or palisade setae. Foreleg, midleg, hindleg claws equal, more or less evenly curved, inner tooth not visible (fig. 2F). **Genitalia** (fig. 2G): Spermathecae not visible. Details of sternite 8, sternite 9, segment 10 not visible. Cercus laterally compressed, elongate, broad basally (anteroventrally).

BIONOMICS: Based on the elongate cerci and the general habitat of extant members of

the genus, *L. antiquus* likely bred in sandy, saline habitats (Borkent, 1995).

The holotype of *L. antiquus* had a number of associations in the same piece of amber: a male and female of *L. amplificatus* and the holotype of a possible Lonchopteridae (*Lonchopterites prisca*). The presence of laciniae with retrorse teeth suggests that females of this species fed on vertebrate blood (Borkent, 1995, 1996). The significance of these associations is interpreted below in the discussion. The amber holding the paratype also included a small, poorly preserved arachnid (spider or possibly a mite?).

TAXONOMIC DISCUSSION: The allotype of *L. antiquus* is that specimen of *Leptoconops* in piece no. 79 most distant from the holotype of *Lonchopterites prisca*; the amber piece was drawn in Grimaldi and Cumming (1999: 83), illustrating the position of the specimens.

The holotype of *L. antiquus* is quite decomposed and part of the head and thorax are obscured by contaminants; the left wing is missing. Much of the body of the paratype is collapsed and portions appeared distorted.

The paratype of *L. antiquus* differs from the holotype in some details: flagellomere 12 is more elongate, third palpal segment is more spherical (fig. 2 D–E), and the cerci may be more elongate. These differences may indicate the presence of two species, but may also be due to artifacts of preservation, especially considering that both specimens were in only moderate condition.

TYPES: Holotype, female adult in amber in plastic box, labeled “HOLOTYPE *Leptoconops antiquus* Borkent”, “ALLOTYPE *Leptoconops amplificatus* Borkent”, “PARATYPE *Leptoconops amplificatus* Borkent”, “Amber: N. Lebanon, Antoni Estephan Coll. Bchare Mtn., 2300 m”, “AMBER: Lebanon Lower Cretaceous (Neocomian) No. 79, Amer. Mus. Nat. Hist., Inclusion(s): 3 Ceratopogonidae, 1 Empidoid” (AMNH); paratype, 1 female, labeled “PARATYPE *Leptoconops antiquus* Borkent”, “Amber: N. Lebanon, Antoni Estephan Coll. Bchare Mtn., 2300 m”, “AMBER: Lebanon Lower Cretaceous (Neocomian) No. 125, Amer. Mus. Nat. Hist., Inclusion(s): female *Leptoconops*?” (AMNH).

DERIVATION OF SPECIFIC EPITHET: The

name *antiquus* (ancient) refers to the old age of this Lebanese amber fossil species.

CONCLUSIONS

The discovery of the oldest members of *Leptoconops* in 120–122 million year old Lebanese amber leads to the question of their relationship to other species of the genus and what they tell us about the relationship of *Leptoconops* to other Ceratopogonidae.

Two features suggest that the subgenus *Palaeoconops*, with the two new species, *L. amplificatus* and *L. antiquus*, forms the sister group to all other *Leptoconops* (fig. 4), as follows.

1. Female antenna with 13 flagellomeres (plesiomorphic); female antenna with 10–12 flagellomeres (apomorphic).

Leptoconops amplificatus and *L. antiquus* are the only members of *Leptoconops* with 13 flagellomeres in the female antenna; all other species in the genus have 10–12 flagellomeres (fig. 4). Borkent (2000: 399) criticized Szadziewski's (1996) use of this feature as evidence of the monophyly of *Leptoconops*, because outgroup comparisons with other Culicomorpha are inconclusive (Borkent et al., 1987: 600). However, the recognition of the extinct genus *Lebanoculicoides* as the earliest lineage of Ceratopogonidae (the sister group of all other Ceratopogonidae, including *Leptoconops*), with 13 flagellomeres, and the presence of 13 flagellomeres in the sister group of *Leptoconops*, suggests that Szadziewski (1996) was correct (fig. 4).

The recently described *Jordanoconops* Szadziewski (Szadziewski, 2000) is placed as the sister group of *Austroconops* on the basis of the shared presence of r-m being more or less parallel to R_1 and R_3 (see character 11 in Borkent, 2000).

2. Wing with well-developed R_{4+5} (plesiomorphic); R_{4+5} thin and faint, very poorly defined or absent (apomorphic).

Borkent (2000) used this feature as evidence for the sister-group relationship between the extinct *Lebanoculicoides* and all remaining Ceratopogonidae (fig. 4) and discussed the character state distribution within the family. In *Lebanoculicoides*, R_{4+5} is well-

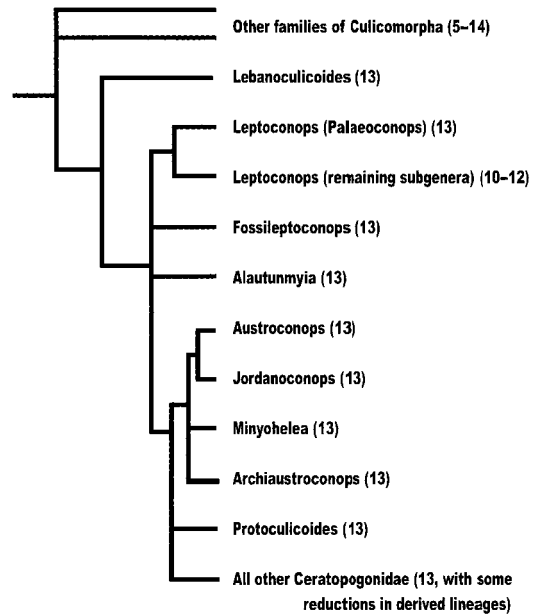


Fig. 4. Phylogeny of the basal lineages of Ceratopogonidae based on Borkent (2000) and the results of this paper. Numbers in parentheses refer to number of female flagellomeres.

developed and is about as thick as the other anterior wing veins. In *Leptoconops*, other than *L. amplificatus* and *L. antiquus*, R_{4+5} is present but very thin (often it can only be seen with phase contrast). In *L. amplificatus* and *L. antiquus*, R_{4+5} is well-developed and thicker than in any other member of the genus and this is additional evidence that these two species form the sister-group of all remaining *Leptoconops*.

A feature that is very likely related to the well-developed R_{4+5} in *L. amplificatus* and *L. antiquus* is the presence of a well-developed costa extending right to the apex of R_{4+5} . In other *Leptoconops*, the costa is not or only poorly developed beyond the apex of R_3 . Because a well-developed costa extends to (or beyond) the apex of R_{4+5} in *Lebanoculicoides* and members of all other families of Culicomorpha, it is likely that this feature is plesiomorphic in *L. amplificatus* and *L. antiquus*.

The cladistically primitive position of *L. amplificatus* and *L. antiquus* indicates that they cannot be considered to belong to any of the previously recognized subgenera of *Leptoconops* and they are therefore placed in

the new subgenus *Palaeoconops*. However, I cannot present any synapomorphy for the new subgenus and there is no evidence that *L. amplificatus* and *L. antiquus* actually form a monophyletic group. It is logically possible that one is the sister-group of the other plus all remaining *Leptoconops*.

There are presently six other subgenera (all extant) recognized within *Leptoconops*: *Leptoconops sensu stricto*, *Brachyconops* Wirth and Atchley, *Holoconops* Kieffer, *Megaconops* Wirth and Atchley, *Proleptoconops* Clastrier, and *Styloconops* Kieffer (Borkent and Wirth, 1997). There has been no cladistic analysis of these taxa other than the interpretation by Borkent (1995), who hypothesized that *Leptoconops sensu stricto*, *Megaconops*, and *Proleptoconops* form a monophyletic group. The single synapomorphy supporting this was the shared presence of a highly modified, elongate female cercus. Members of *Brachyconops* and *Styloconops* have short cerci, the condition present in other genera of Ceratopogonidae and families of Culicomorpha. However, the presence of elongate cerci in *L. amplificatus* and *L. antiquus* strongly suggests that the short cerci of *Brachyconops* and *Styloconops* are actually secondarily reduced. Careful morphological study of these two subgenera should be undertaken with this in mind.

Borkent (2000) discussed three adult synapomorphies for the genus *Leptoconops*: “wing lacking r-m”, “female wing with radius joining costa as a strong thickened stigma”, and “posteromedial margin of female sternite 8 with semicircular concavity bearing 4 or more stout setae on its margin”. Based on the discussion above, the elongate cercus of the female is likely a fourth synapomorphy.

The presence of a clearly defined R_{4+5} in *L. amplificatus* and *L. antiquus* may indicate that *Leptoconops* is, other than *Lebanoculicoides*, the sister-group of all remaining extant and extinct Ceratopogonidae. If so, R_{4+5} has been at least partially reduced at least twice: once within *Leptoconops* (where in many species it can only be seen with phase contrast microscopy) and once within other Ceratopogonidae. In addition, as discussed by Borkent (2000), there are some problems of determining homologies with some Forcipomyiinae, some Dasyheleinae and some Ceratopogoninae in

which R_{4+5} may be present (but in a different form). Further study is needed.

Female adults of *Leptoconops* and the extinct genera *Fossileptoconops* Szadziewski and *Alautunmyia* Borkent are the only Ceratopogonidae that have a fused frons and vertex without any sutures. Borkent (2000) pointed out that the character is presently uninterpretable cladistically. One specimen of *L. amplificatus* may have some sutures on the frons/vertex area (these may be artifacts due to shriveling and/or compression) and if truly present, these would be unique within the genus.

Borkent (2000) presented a model for interpreting fossil communities of Ceratopogonidae based on information on their sex ratio and, in single pieces of amber, associations of conspecific individuals, associations between species of Ceratopogonidae, and associations with organisms other than Ceratopogonidae. Because Lebanese amber ceratopogonids had a sex ratio typical of those at extant emergence sites (about 39% males), no intraspecific associations, a high number of interspecific associations, and a high number of associations with non-ceratopogonids, it was deduced that the Ceratopogonidae were locally diverse but not abundant. This pattern of high diversity and low abundance is similar to that found in most tropical habitats today. The 14 specimens of *Leptoconops* in Lebanese amber do not alter this general conclusion. However, *L. amplificatus* is the first of 24 species of Ceratopogonidae in the amber (with a total of 140 specimens) to have any intraspecific associations in a single piece of amber: one piece had nine females and another held one male and one female. The striking presence of nine specimens of one species in one piece of amber in a fossil assemblage otherwise hypothesized to be diverse but with low species abundance, is likely explained by the habitat generally occupied by species of *Leptoconops*. The immatures of most extant members of this genus are restricted to beach habitats, where the larvae burrow in moist/wet sand. This is one of the few, more or less homogeneous habitats of any size in lowland tropical regions and it seems probable that the immatures of the fossil *L. amplificatus* were restricted to a similar habitat. This likely explains the unique intraspecific associations within this

species. The presence of nine *L. amplificatus* in a single piece of amber can also be taken as evidence that the original resin-producing Araucariaceae (Bandel and Vavra, 1981) likely grew close to the seashore, at least as part of its distribution.

Borkent (2000) provided a key to the genera of Ceratopogonidae in Lebanese amber. The discovery of the *Leptoconops* specimens described here requires modification to that key as follows.

1. Wing with R_{4+5} clearly present (fig. 1a, c in Borkent, 2000; figs. 1E, 2B) 2
 - Wing without R_{4+5} visible (fig. 4a, c in Borkent, 2000) 3
2. Wing with first and second radial cells clearly defined (fig. 1a, c in Borkent, 2000)
 - *Lebanoculicoides* Szadziewski
 - Wing with first and second radial cells reduced and/or compacted (figs. 1E, 2B)
 - *Leptoconops (Palaeoconops)*, n. subg.
3. Ommatidia broadly separated dorsomedially; cercus with elongate terminal setae (fig. 2a in Borkent, 2000) (known only as female)
 - *Fossileptoconops* Szadziewski
 - Ommatidia narrowly separated or abutting dorsomedially (figs. 7a, 8j, 10c, 11a, 20b in Borkent, 2000); cercus without strikingly elongate setae (fig. 7j in Borkent, 2000) 4
4. Wing with r-m parallel to R_1 (figs. 11c, h, 13a, c, in Borkent, 2000)
 - *Austroconops* Wirth and Lee
 - Wing with r-m oblique to R_1 (figs. 4a, 5a, 15e in Borkent, 2000) 5
5. Wing with poorly defined radial cell (figs. 15e, 17a, 19f, 20a in Borkent, 2000); female CR < 0.5
 - *Minyohelea* Borkent
 - Wing with radial cell(s) well-developed (figs. 4a, c, f, 5a in Borkent, 2000); female CR ≥ 0.8 6
6. Male flagellomere 13 with subbasal constriction (figs. 7f, 8c, d, 9b in Borkent, 2000); tarsal ratio (Ta_1/Ta_2) of foreleg/hindleg ≥ 1.4
 - *Archiaustroconops* Szadziewski
 - Male flagellomere 13 without subbasal constriction (figs. 2e, 5c in Borkent, 2000); tarsal ratio of foreleg/hindleg ≤ 1.3
 - *Protoculicoides* Boesel

The presence of *Leptoconops* in Lebanese amber also requires modification of the list of unique or distinctive character states useful for identifying genera and species of Lebanese amber Ceratopogonidae provided by Borkent (2000). All are given below, regard-

less of whether they were modified or not. Features are arranged from anterior to posterior and from dorsal to ventral.

Male antennal flagellomere 13 with subbasal constriction (figs. 7f, 8d, 9b, 12f, 14c in Borkent, 2000; fig. 1A): species of *Leptoconops*, *Archiaustroconops* Szadziewski and *Austroconops* Wirth and Lee.

Female antennal flagellomere 13 with apical elongate projection (fig. 6f, g in Borkent, 2000): *Protoculicoides schleei* (Szadziewski), *P. punctus* Borkent, *P. succineus* Szadziewski.

Ommatidia broadly separated dorsomedially (Szadziewski, 1996: fig. 18b): *Leptoconops*, *Fossileptoconops lebanicus* Szadziewski.

Female mouthparts moderately to very elongate (fig. 6a in Borkent, 2000; Szadziewski, 1996: figs. 3b, 4b): *Lebanoculicoides mesozoicus* Szadziewski, *Protoculicoides succineus*, *P. unus* Borkent, *P. punctus*, *P. schleei*.

Mouthparts extremely short (fig. 10c in Borkent, 2000): *Archiaustroconops bocaparvus* Borkent, *Archiaustroconops creta-ceous* (Szadziewski).

Wing with R_{4+5} present (fig. 1a, c in Borkent, 2000; figs. 1E, 2B): *Lebanoculicoides mesozoicus* (thick vein); *Leptoconops (Palaeoconops)*, n. subg. (thin vein).

Wing with r-m parallel to R_1 (figs. 11c, h, 12h, 13a, c, 14a in Borkent, 2000): species of *Austroconops*.

Wing with reduced wing venation (radial cells not well-defined) (figs. 15e, 17a, 19f, 20a in Borkent, 2000; figs. 1E, 2B): *Leptoconops (Palaeoconops)*, n. subg., *Minyohelea* Borkent.

Radial cell single, well-defined, elongate (fig. 4a, c, f in Borkent, 2000): *Protoculicoides acraorum* Borkent, *P. schleei*, *P. unus*, possibly *F. lebanicus*.

Foreleg tibial spur very large (figs. 14f, 15a in Borkent, 2000): *Austroconops megaspinus* Borkent.

First tarsomere of both fore and hindleg with thick basal spine (fig. 12b, d, i, k in Borkent, 2000): *Austroconops gladius* Borkent

Each claw with well-developed inner tooth (figs. 9d, 11d, e, 12e, g in Borkent, 2000): *Archiaustroconops hamus* Borkent, *Aus-*

troconops gondwanicus Szadziewski, *Austroconops gladius* (all other taxa have simple claws).

Gonostylus double (figs. 17e, g, 18d–g in Borkent, 2000): a few species of *Minyohelea*: *M. bacula* Borkent, *M. falcata* Borkent, *M. wirthi* (Szadziewski), *M. lebanica* (Szadziewski).

Apex of paramere bifurcate (Szadziewski, 1996: fig. 16d–f): *Minyohelea wirthi*.

Female cercus with elongate terminal setae (fig. 2A): *Fossileptoconops lebanicus*.

Female cerci very elongate (figs. 1I, 2A): *Leptoconops*.

ACKNOWLEDGMENTS

My wife Annette supports my work with love, joy, and money and I am always indebted to her for making my life rich in so many ways. David Grimaldi kindly lent me the specimens upon which this paper is based and provided valued advice and help with the production of this work. William L. Grogan and Jeffery M. Cumming provided much-appreciated critical comments on an earlier draft of this paper.

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