

The first records of fossil Corethrellidae (Diptera)

A. BORKENT and R. SZADZIEWSKI

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The first fossil Corethrellidae, represented by two male adult *Corethrella*, are described. One, *C. prisca* sp. n., is from Saxonian amber collected in East Germany and is of Miocene age (22 Ma). The other, *C. nudistyla* sp. n., is from Dominican Republic amber and is 15–40 million years old. The family Corethrellidae, because of its phylogenetic position, is presumably of at least Jurassic age. The fossils are typical members of the genus *Corethrella* and belong to a clade which is the sister group of a single species in New Zealand.

A. Borkent, Research Associate of the Royal British Columbia Museum, 2330–70th St. SE, Salmon Arm, British Columbia, V1E 4M3, Canada.

R. Szadziewski, Department of Invertebrate Zoology, University of Gdansk, Pilsudskiego 46, 81–378 Gdynia, Poland.



Introduction

The family Corethrellidae, containing only the single genus *Corethrella* Coquillett, is an intriguing group of small midges in which the adult females feed on frog blood and detect their hosts by hearing their call.

The genus was, until recently, considered a member of the family Chaoboridae which is the sister group of the Culicidae. Wood & Borkent (1989) showed that *Corethrella* was actually the sister group of the remaining Chaoboridae plus Culicidae and that it should therefore be recognized as a separate family.

The oldest Chaoboridae, in this revised sense, are known as Jurassic fossils from Siberia (Kalugina & Kovalev 1985), suggesting that the Corethrellidae must have originated during that period or at an earlier date.

Our report here of fossil Corethrellidae from the Miocene/Oligocene is therefore not surprising. Indeed, the future discovery of Cretaceous and Jurassic fossils would not be unexpected.

Materials and methods

The amber pieces containing the specimens were polished flat using the method described by Szadziewski (1988). The specimens were examined, measured and drawn using either a Wild M3 dis-

secting microscope or a Carl Zeiss JenaVal compound microscope.

To make further comparisons we also examined extant material of male and female *Corethrella* from South America (2 species), North America (5 species), Africa (2 species) and New Zealand (*C. novaezealandiae* Tonnoir) mounted in Canada Balsam on microscope slides. In addition, the published literature was studied for pertinent comparative information.

Terms for structures follow those used in the Manual of Nearctic Diptera (McAlpine 1981). The term aedeagus is used here to describe what earlier authors (Cook 1956, Sæther 1970) have termed 'penis valves' (= parameres). McKeever (1985) has shown that this structure is actually the aedeagus.

The higher classification of Nematocera reflects the conclusions of Wood & Borkent (1989) and Borkent & McKeever (1990). Details of the descriptions include only those structures which differ from the generic description given by Cook (1956) and which we consider to vary between the extant species of *Corethrella*.

Corethrella prisca sp. n.

(Figs 1A–F, 2A–B)

Type material. – Holotype: Male adult in Miocene Saxonian amber (22 Ma), piece mounted in Canada Balsam between two coverslips, collected from a brown coal mine at Bitterfeld near Halle, Germany; labelled 'HOLOTYPE

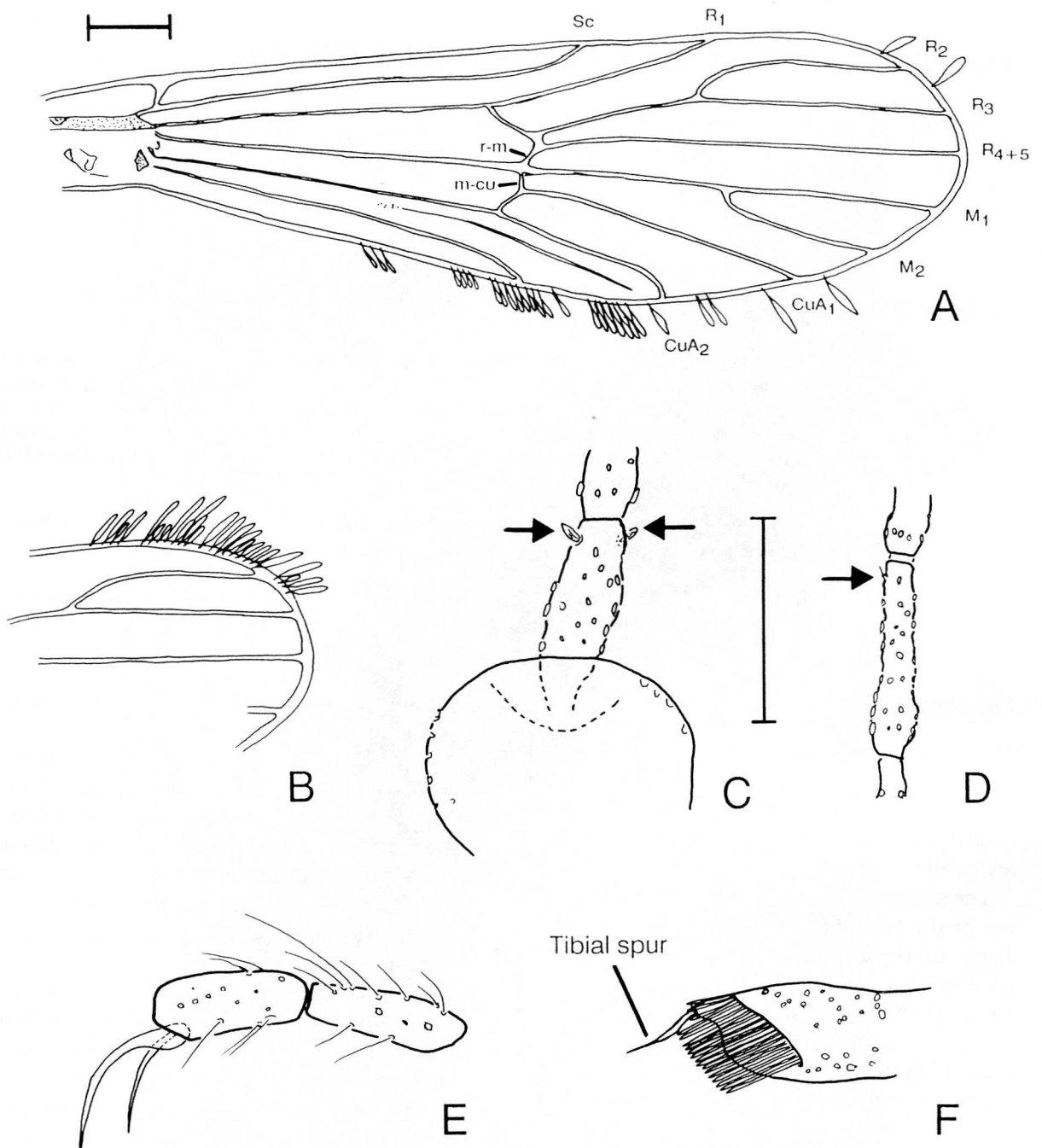


Fig. 1. Structures of male adult *Corethrella prisca*: (A) Right wing. (B) Tip of left wing. (C) Pedicel and first flagellomere of left antenna (arrows point to sensilla coeloconica). (D) Eighth flagellomere of right antenna (arrow points to sensillum pediconicum). (E) Fourth and fifth tarsomeres of left foreleg. (F) Tip of hindleg tibia from posterior aspect. Scales = 0.1 mm; short scale for wing, longer scale for remainder of figures.

Corethrella prisca Borkent and Szadziewski', 'Saxonian amber, Bitterfeld, Germany, Mus. Naturk. Humb. U', deposited in the Museum für Naturkunde der Humboldt Universität zu Berlin, Paläontologisches Museum, Invalidenstrasse 43, Berlin, Germany.

Comments on holotype. – Specimen in excellent condition; body length (from frons to tip of gonostylus) = 1.66 mm. Body complete except for missing tarsi on mid and

hind legs. Antennae translucent, details easily observed. Thorax with internal opaque material preventing some detailed observations. No distinguishing pigmentation.

Derivation of specific epithet. – The name *prisca* (of former times, ancient) refers to the fossil nature of this species.

Description. – Head: Flagellomere 1 with two sub-

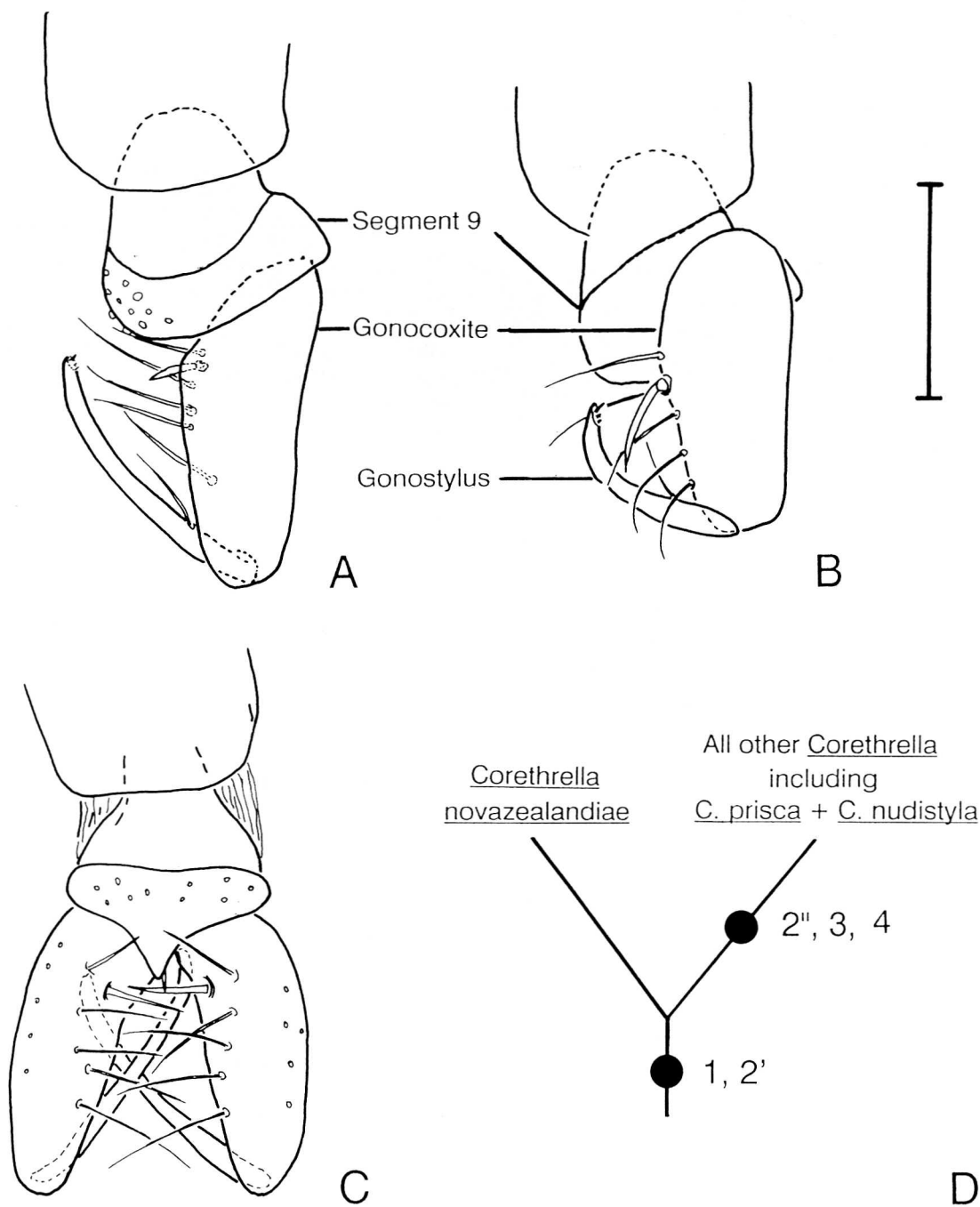


Fig. 2. (A) Morphologically right gonocoxite of *C. prisca* in lateral-oblique view. (B) Morphologically left gonocoxite of *C. prisca* from medial-oblique view. (C) Male genitalia of *C. nudistylus* in morphologically dorsal view. (D) Cladogram showing the phylogenetic relationships between species of *Corethrella*. Scale for genitalia = 0.1 mm.

apical sensilla coeloconica (Fig. 1C); flagellomere 8 with single subapical sensillum pedicunicum (Fig. 1D); flagellomere 13 apically bifurcate. Thorax: Foreleg with unequal claws (Fig. 1E). Hindleg with well developed apical tibial spur (Fig. 1F). Wing (Fig. 1A) length 1.01 mm; R_1 short, ending close to level of forking of R_{2+3} ; crossveins r-m, m-cu

equi-distant from base of wing; scales on at least some veins (R_2 , R_3 , R_{4+5}), along anterior, posterior margin of wing; scales along distal anterior margin of three sizes (Fig. 1B). Anepimeron with at least 5 setae (difficult to see clearly). Genitalia (Figs 2A,B): Lying laterally oblique; rotated 180°. Aedeagus not discernable, not projecting beyond level of

apex of tergite 9. Gonocoxite with markedly thick mediobasal seta of moderate length; 5 moderately thick, elongate, gradually tapering setae arranged along length of medial face of gonocoxite. Gonostylus slender, with slight subapical bend; elongate, slender, seta situated at basal $\frac{1}{4}$; apex with small apical tooth, two tiny subapical setae.

Taxonomic discussion. – The recognition of this specimen as a new species is supported by the unique form of the genitalia (Figs 2A,B). The combination of the following character states is not found in any other known *Corethrella*: presence and arrangement of the thick setae on the gonocoxite and the shape of the gonostylus which bears an elongate, subbasal seta, an apical short tooth and two subapical tiny setae.

C. prisca is the first record of the genus *Corethrella* in the western portion of the Palaearctic. There are only 61 extant species in this monogeneric family worldwide and as a group they have a Pantropical distribution. The geographically closest known extant species in any given direction from the fossil location are from Africa (three Afrotropical species with one reaching as far north as Nigeria, Freeman 1962), the Nearctic (five species with one reaching southern Quebec, Canada), Japan and Sri Lanka.

C. prisca is only one species in a rather diverse fauna recorded from Saxonian amber (Schumann & Wendt 1989).

The dating of *C. prisca* as 22 million years old was supported by Barthel & Hetzer (1982) and Fuhrmann & Borsdorf (1986).

Corethrella nudistyla sp. n.

(Fig. 2B)

Type material. – Holotype: Male adult in Miocene/Oligocene Dominican Republic amber (15–40 Ma), piece mounted in Canada Balsam between two coverslips, labelled 'HOLOTYPE *Corethrella nudistyla* Borkent and Szadziewski', 'Dominican amber, Jorge Wunderlich, June 1989, AMNH No. W-DR-46-b'; deposited in the American Museum of Natural History, Central Park West at 79th Street, New York, New York, 10024–5192, USA.

Comments on holotype. – Specimen in excellent condition; body length (from frons to tip of gonostylus) = 1.51 mm. No distinguishing pigmentation. Body complete except for the following missing: tarsus on right fore, mid and hind leg, claw on left fore leg, tarsomeres 2–5 on left mid leg. Antennae translucent, most details easily observed. Thorax with internal opaque material preventing some detailed observations. Wings lying along length of abdomen, difficult to interpret generally.

Derivation of specific epithet. – The name *nudistyla*

(bare, stylus) refers to the bare gonostylus shared with only a few other species of *Corethrella*.

Description. – Head: Flagellomere 1 apparently lacking sensilla coeloconica, not clearly visible; flagellomere 8 with single subapical sensillum pediconicum (as in Fig. 1D); flagellomere 13 apically bifurcate. Thorax: Foreleg with unequal claws (as in Fig. 1E). Hindleg with well developed apical tibial spur (as in Fig. 1F). Wing length about 0.9 mm; venation mostly uncertain; R_1 short, ending close to level of forking of R_{2+3} ; scales on veins not visible; scales along posterior margin of three sizes. Details of anepimeron not clearly visible. Genitalia (Fig. 2C): Lying at a slightly lateral angle; rotated 180°. Aedeagus sharply tapered apically, projecting slightly beyond level of apex of tergite 9. Gonocoxite with markedly thick mediobasal seta of moderate length; 5 moderately thick, elongate, gradually tapering setae arranged along length of medial face of gonocoxite. Gonostylus slender, with slight subapical bend; lacking elongate seta along length; apex lacking large teeth but not clearly visible, with small apical tooth, two tiny subapical setae.

Taxonomic discussion. – The recognition of this specimen as a new species is supported by the unique form of the genitalia (Fig. 2C). The combination of the following character states is not found in any other known *Corethrella*: presence and arrangement of the thick setae on the gonocoxite, the shape of the gonostylus which lacks an elongate, subbasal seta and a relatively short aedeagus which is sharply pointed apically.

The following species of *Corethrella* also have a gonostylus which lacks a subapical or subbasal elongate seta but they may be distinguished as follows: in the African species *C. picticollis* Edwards and *C. pallitarsis* Edwards the aedeagus is rounded apically (Freeman 1962); in the male of *C. quadrivittata* Shannon & Del Ponte, distributed from Panama south to Argentina, the thick gonocoxal setae are relatively short (Balseiro & Spinelli 1984) when compared to those of *C. nudistyla*; *C. selvicola* Lane, known from Mexico south to Brazil, has a male genitalia (Lane 1939) very similar to that of *C. nudistyla*. However, in *C. selvicola* the aedeagus is proportionally longer and the gonostylus bears a distinct apical seta not present in *C. nudistyla*.

Finally, it should be noted that the males of a number of *Corethrella* species are unknown or are too poorly described for comparison and *C. nudistyla* should be compared to these when they are discovered.

Although the holotype is presently lacking foreleg claws, we have described these as unequal. The claws were observed before final grinding and were unfortunately lost.

Dominican Republic amber deposits contain a large and diverse fossil assemblage (Baroni-Urbani & Saunders 1982). Much of this diversity remains uninterpreted but generally the fauna reflects Neotropical affinities. However, a few taxa have their closest relatives in the Old World, probably indicating relatively recent local extinction (Baroni-Urbani & Wilson 1987, Grimaldi *in press*, Krishna & Grimaldi *in press*). It is interesting to note that a fossil bee was originally described as being most closely related to extant African species (Wille & Chandler 1964) but that subsequent analysis has shed some doubt on that placement (Michener 1982).

Dominican Republic amber comes from at least 10 different sites (Baroni-Urbani & Saunders 1982) and the exact origin of *C. nudistyla* is unknown. From the color and condition of the amber it is clearly not copal (and hence of very recent age). True amber from the Dominican Republic is 15–40 million years old (Lambert et al. 1985) and provides a minimum date for this fossil.

Part of a female Psychodidae (head and anterior part of thorax missing) is also in the amber piece with *C. nudistyla*.

Discussion

An understanding of the synapomorphies which group taxa is vital to the correct phylogenetic interpretation of fossils. As such it is important to know the derived features of the extant species included in the family Corethrellidae.

Wood & Borkent (1989), in their discussion of the relationships between the families of Nematocera, provided only one synapomorphy for the Corethrellidae (character 1 below). Further synapomorphies are listed by Sæther (1970) ($n=15$) but none of these provide the rationale for the determination of the apomorphic character state and cannot, therefore, be appraised. No outgroup comparisons were discussed. One of the characters listed by Sæther (1970) is further analyzed below.

The following characters are used to interpret the monophyly of *Corethrella* or the phylogenetic relationships of species within the genus.

1. Larva with anterolateral margin of head capsule complete (plesiomorphic); anterolateral margin of head capsule with groove in which antennae lie when adducted (apomorphic).

This character was discussed by Wood & Borkent (1989; their character 54). The apomorphic state is unique within the Diptera. It should be noted that the immatures of *C. novaezealandiae* have not been described and the larvae are only presumed to exhibit this character state.

2. Wing with vein R_1 elongate (plesiomorphic); wing vein R_1 short, ending about $\frac{1}{2}$ way between apex of Sc and R_2 (apomorphic); wing vein R_1 shorter, ending close to level of forking of R_{2+3} (Fig. 1A) (apomorphic”).

The interpretation of this character is somewhat uncertain. Within the Culicoidea the derived conditions appears unique. However, within the Chironomoidea a short vein R_1 is present in most families. The character is variable amongst other Nematocera.

The most derived state is present in all *Corethrella* other than *C. novaezealandiae* from New Zealand.

3. Terminal antennal flagellomere simple, in some with apical sensillum (plesiomorphic); terminal antennal flagellomere bifurcate, with each apex bearing a terminal sensillum (apomorphic).

The derived condition is present in all *Corethrella* other than *C. novaezealandiae* and is virtually unique within the Culicomorpha. Some *Forcipomyia* Meigen (Ceratopogonidae) have two apical sensilla on the apical flagellomere and the apex in some of these is slightly bilobed. However, in such species the flagellomere is never as bifurcate as in *Corethrella*.

We have not seen a bifurcate terminal flagellomere elsewhere within the Nematocera other than in a few Tipulidae (i.e. *Ctenophora* Meigen).

4. Male with foreleg claws equal in size (plesiomorphic); male with one foreleg claw much smaller than the other (Fig. 1E) (apomorphic).

The derived condition, present in all *Corethrella* other than *C. novaezealandiae*, is apparently unique within the Culicomorpha other than a few clearly derived members of the Ceratopogonidae.

The one male *C. novaezealandiae* we examined was missing its foreleg tarsomeres. However, the figure by Belkin (1968: fig. 3) clearly shows a male pair of foreleg claws equal in size.

The above character states are summarized in the cladogram in Fig. 2D. The available evidence indicates, firstly, that the genus *Corethrella* is monophyletic. Secondly, *C. novaezealandiae* is recognized as the sister group of all remaining members of the genus. Belkin (1968) suggested that this species was the most 'primitive' in the genus and we agree that the species represents the earliest lineage in the genus.

Both the new fossil species are certainly correctly identified as members of the genus *Corethrella* and hence of the Corethrellidae. They further belong to the clade formed by the sister group of *C. novaezealandiae*.

Belkin (1968: 112) provided further discussion of character states which he suggested indicated the 'primitive' position of *C. novaezealandiae*. Some

of these are included in the above analysis. The remainder are difficult to interpret and are discussed as follows:

– *C. novaezealandiae* have simple setae on the wing veins, while remaining species of *Corethrella* have flattened, striated scales on the wings. Such scales are present in Culicidae, present or absent in Chaoboridae, and appear lacking in other Culicomorpha, making these characters states difficult to polarize.

– Belkin (1968) suggested that the wing fringe of *C. novaezealandiae* was more poorly developed. We can see no significant difference between this species and many other *Corethrella*. In some Neotropical species of *Corethrella* the fringe is proportionally longer.

– In *C. novaezealandiae* the male gonocoxite is simple and lacks any markedly developed setae. In all other *Corethrella* the gonocoxite bears at least one stout bristle on its inner face. Sæther (1970) listed this character (his Trend 28) as indicative of the monophyly of the entire genus *Corethrella*. Outgroup comparisons, however, makes this character difficult to interpret. Both character states are present in each of the Dixidae, Chaoboridae and Culicidae. Apparently, all Chironomoidea lack strongly developed gonocoxal bristles.

– Gonostylus (clasper of Belkin) relatively short and with a well developed thick apical seta present only in *C. novaezealandiae*, where males of other *Corethrella* species have relatively elongate gonostylus with a short, relatively slender apical seta.

A slender gonostylus is present in all Chaoboridae and Culicidae; Dixidae have thick, squat gonostyli. Both conditions are found in the Chironomoidea. These outgroup comparisons make the interpretation of the variation of gonostylus shape within *Corethrella* difficult.

The presence of a thick apical gonostylar seta in *C. novaezealandiae* is equally difficult to interpret. Both thick and slender setae are present in each of the Chaoboridae, Culicidae, and Dixidae. The condition is also variable within the Chironomoidea.

– Tergite IX very strongly developed in male of *C. novaezealandiae*. We failed to find significant differences between *C. novaezealandiae* and at least some other species of *Corethrella*.

Several species of adult female *Corethrella* are known to feed on the blood of frogs which they locate through detection of the call of their hosts (McKeever 1977, 1980). All females but one Australian species (*pers. obs.*, McKeever *pers. comm.*) have biting mouthparts (McKeever 1986; Miyagi 1975). This evidence suggests that it is likely that the females of *C. prisca* and *C. nudistyla* were similarly attracted to the call of frogs and fed on their blood in the Miocene/Oligocene.

As indicated in the introduction, Corethrellidae is the sister group of the Chaoboridae plus Culicidae (Wood & Borkent 1989). Chaoboridae are known as fossils from the Jurassic (Kalugina &

Kovalev 1985) and if the phylogenetic position of Corethrellidae is correct, this family should be of equal or greater age. It is interesting that true frogs (and hence calling amphibians) are also first known from the Lower Jurassic (of Argentina) (Romer 1966, Fox *pers. comm.*).

The earliest lineage of *Corethrella*, represented by *C. novaezealandiae*, is found in New Zealand. Because females of this species also have biting mouthparts (*pers. obs.*), it is likely that they feed on the only endemic frogs present in New Zealand, species of the genus *Leiopelma* Fitzinger. Although these frogs appear to lack a true calling voice, they do produce chirping calls during mating (Bell 1978).

Leiopelma belongs to the earliest lineage of known extant frogs. There appears to be therefore, evidence of a lasting ecological relationship between the oldest lineage of Corethrellidae and the oldest lineage of frogs.

McKeever (1988) described a new form of antennal sensillum on one or two flagellomeres of Nearctic *Corethrella* which he called the sensilla pediconica. This sensillum is present on flagellomere 8 of *C. prisca* and *C. nudistyla*. He suggested that the sensillum may function as a sound receptor. However, both male and female *Corethrella* possess these sensilla (*pers. obs.*) and available evidence indicates that only females are attracted to the call of frogs (McKeever 1980). The presence of this sensillum on flagellomere 8 of the male fossils cannot therefore be taken as evidence of blood feeding by the females of these species.

Finally, it should be noted that the phylogenetic position of *C. prisca* and *C. nudistyla* could not be further resolved because of a lack of cladistic interpretation of the extant fauna. The genus does, however, appear to be highly amenable to phylogenetic analysis. The group is clearly monophyletic and within each of the known stages (larva, pupa, adult) the different species exhibit striking structural differences. Further study would almost certainly be amply rewarded.

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