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The Frog-Biting Midges of the World (Corethrellidae: Diptera)

ART BORKENT



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Frontispiece: *Corethrella dicosimoae* female (illustrated by José Alejandro Herrera Mora and Ana Brenes, INBio).

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ART BORKENT

Research Associate of the Royal British Columbia Museum, the American Museum of Natural History, and Instituto Nacional de
Biodiversidad
691-8th Ave. SE, Salmon Arm, British Columbia, V1E 2C2, Canada.
e-mail: aborkent@sulite.ca

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ABSTRACT

This worldwide biosystematic study of Corethrellidae, with its single genus *Corethrella* Coquillett, provides a complete compilation of all that is known for the group, both taxonomically and bionomically. Descriptions of each species are based primarily on the adults, summarize all bionomic information, and provide a map showing its distribution. Keys to the species of each region are provided. A total of 97 extant species is recognized, with 52 of these being new. Seven fossil species are described with two of these being new to science. All species, including 13 **new synonyms**, are cataloged in a table for easy reference. Seven extant species are of uncertain status because of damaged or missing types. Lectotypes and, depending on the species, some paralectotypes, are designated for the following species: *C. inepta* (Annandale), *C. pallitarsis* Edwards, *C. picticollis* Edwards, *C. ananacola* Dyar, *C. calathicola* Edwards, and *C. brakeleyi* (Coquillett).

A cladistic analysis interprets most extant and fossil species (some are not interpretable at the present time) and provides the basis for zoogeographic and bionomic interpretation. Worldwide, *Corethrella* species are found between 50°N and 50°S but most are found between 30°N and 30°S and below 1500 meters in elevation. Because female adults are attracted to the call of male frogs and feed on their blood, species are restricted to areas where there are frogs. Phylogenetic patterns suggest Gondwanan connections for earlier lineages within the genus. At least one lineage has dispersed from the New World to southeast Asia and some species are located on volcanic islands in the Caribbean, indicating further instances of dispersal. It is certain that many more species are yet to be discovered. Phylogenetic patterns indicate that the immatures of *Corethrella* species have repeatedly moved between ground-dwelling habitats and phytotelmata, with the plesiomorphic habitat likely being ground-dwelling. Some lineages have diversified within phytotelmata.

Fossil, cladistic and morphological evidence indicates that *Corethrella* females have been feeding on calling frogs since at least the Early Cretaceous. Females likely hear their frog hosts using the Johnston's Organ. There is some evidence of host specificity as well as selection of particular biting sites for some species of *Corethrella*. The females of at least some species of *Corethrella* transmit *Trypanosoma* Gruby between calling frogs and this association is also likely an ancient one.

RESUMEN

Este estudio biosistemático de Corethrellidae a nivel Mundial, con su único género *Corethrella*, proporciona una completa recopilación de todo lo conocido para el grupo, tanto desde el punto de vista taxonómico como bionómico. Las descripciones de cada especie se realizan primariamente sobre la base de adultos, resumen toda la información bionómica y proveen un mapa donde se muestra su distribución. Se brindan claves para especie de cada región. Se reconoce un total de 97 especies, 52 de las cuales son nuevas. Se describen siete especies fósiles, siendo dos de ellas nuevas para la Ciencia. Para una fácil referencia, todas las especies son catalogadas en una tabla, incluyendo 13 **nuevos sinónimos**. Debido a que sus tipos se hallan dañados o perdidos, siete especies actuales ostentan un status incierto. De acuerdo a la especie, son designados lectotipos o paralectotipos de las siguientes especies: *C. inepta* (Annandale), *C. pallitarsis* Edwards, *C. picticollis* Edwards, *C. ananacola* Dyar, *C. calathicola* Edwards, y *C. brakeleyi* (Coquillett).

El análisis cladístico interpreta la mayoría de las especies actuales y fósiles (algunas no pueden ser interpretadas actualmente) y provee la base para interpretaciones zoogeográficas y bionómicas. Las especies de *Corethrella* se hallan entre 50°N y 50°S, aunque la mayoría se encuentran entre 30°N y 30°S y por debajo de 1500 metros de elevación. Debido a que las hembras adultas son atraídas por el llamado de ranas macho y se alimentan de su sangre, las especies están restringidas a las áreas donde se hallan ranas. Los patrones filogenéticos sugieren conexiones Gondwánicas para los linajes más antiguos del género. Al menos un linaje se ha dispersado desde el Nuevo Mundo hacia el sudeste de Asia, y algunas especies se hallan en islas volcánicas del Caribe, indicando otras instancias de dispersión. Con seguridad aún quedan muchas más especies por ser descubiertas. Los patrones filogenéticos indican que los inmaduros de las especies de *Corethrella* se han movido repetidamente entre habitats ubicados a nivel del suelo y fitotelmata, siendo probablemente