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(Insecta: Ephemeroptera: Caenidae)**

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Abstract

The mayfly subfamily Brachycercinae (Pannota: Caenidae) is redefined and shown to be an apotypic, monophyletic group based on numerous synapomorphies, including, for example in the larvae, the presence of ocellar tubercles, an anterior row of long setae on the larval head capsule, a patch of long setae posterior to the base of the glossae, a broad prosternum, and the absence of toothlike claw denticles. Over 100 morphological characters of larvae, adults, and eggs discovered to be useful for phylogenetic analysis and diagnoses are detailed and illustrated. Thirty-eight species are recognized among the genera *Brachycercus* Curtis, *Caenoculis* Soldán, *Cercobrachys* Soldán, *Insulibrachys* Soldán, *Sparbarus*, n. gen., *Oriobrachys*, n. gen., *Latineosus*, n. gen., *Susperatus*, n. gen., and *Alloretochus*, n. gen., by adopting a strictly phylogenetic classification, including a first tribal classification within the subfamily. *Brachycercus ojibwe*, n. sp., *Cercobrachys fox*, n. sp., *C. lilliei*, n. sp., *C. pomeiok*, n. sp., *C. winnebago*, n. sp., *Latineosus cayo*, n. sp., *L. cibola*, n. sp., *Oriobrachys mahakam*, n. sp., *Sparbarus choctaw*, n. sp., *S. couchatta*, n. sp., *S. miccosukee*, n. sp., and *Susperatus tonkawa*, n. sp. are newly described. The Nearctic *Brachycercus articus* Soldán, n. syn., and *B. edmundsi* Soldán, n. syn., are shown to be equivalent to *B. harrisella* Curtis, proving the latter to be a widespread Holarctic species. *Sparbarus capnicus* (Zhou, Sun and McCafferty), n. comb., *S. corniger* (Kluge), n. comb., *S. europaeus* (Kluge), n. comb., *S. gilliesi* (Soldán and Landa), n. comb., *S. japonicus* (Gose), n. comb., *S. kabyliensis* (Soldán), n. comb., *S. lacustris* (Needham), n. comb., *S. maculatus* (Berner), n. comb., *S. nasutus* (Soldán), n. comb., *S. tubulatus* (Tshernova), n. comb., *Susperatus prudens* (McDunnough), n. comb., and *S. tuberculatus* (Soldán), n. comb., are transferred from *Brachycercus*. *Alloretochus peruanicus* (Soldán), n. comb., and *Latineosus colombianus* (Soldán), n. comb., are transferred from *Cercobrachys*. *Caenis dangi* (Soldán), n. comb., is transferred from *Caenoculis* and Brachycercinae to Caeninae, and provisionally placed in *Caenis* Stephens. *Sparbarus flavus* (Traver), n. comb., is transferred from *Brachycercus* and considered to be a nomen dubium. Nomenclatural history, new or revised descriptions as appropriate, diagnoses, illustrations, and keys are provided for known stage of species. Origins and evolutionary relationships of the Brachycercinae are hypothesized based on cladistic results. Brachycercinae is considered to have originated from a *Caenis*-like ancestor. The genera *Ca-*

noculis and *Insulibrachys* represent more ancestral lineages, whereas the genera *Sparbarus*, n. gen., *Brachycercus*, *Oriobrachys*, n. gen., *Latineosus*, n. gen., *Susperatus*, n. gen., *Alloretocus*, n. gen., and *Cercobrachys* appear more derived. *Cercobrachys pomeiok* and other closely related species are most apotypic in terms of numbers of accumulated apomorphies.

Key words: Brachycercinae, Caenidae, *Brachycercus*, *Cercobrachys*, *Insulibrachys*, *Caenoculis*, *Sparbarus*, *Oriobrachys*, *Latineosus*, *Susperatus*, *Alloretocus*, mayflies, Ephemeroptera, systematics, phylogeny

Introduction

The subfamily Brachycercinae of the pannota mayfly family Caenidae and superfamily Caenoidea represents one of the most apotypic groupings of the Pannota and of mayflies in general (McCafferty and Wang, 2000). Although this grouping has generally been known to include those caenids with larvae having pronounced ocellar tubercles on the head, the exact concept has been modified over several decades and has remained somewhat tenuous, particularly in terms of generic boundaries for species involved and the exact genera that should or should not be included within the taxon. Although species of the group have been known since 1834, comparative studies at the species and genus level within the subfamily have been inadequate and have remained somewhat contentious. Edmunds et al. (1976) acknowledged that identification of species was difficult and the taxonomic status of morphologically similar species was confusing. Because of the specialized psammophilous habit and seldom collected sand-bottom riverine habitats of the larvae and the apparently mostly nocturnal adults, adequate collections of this group have been difficult to come by and to compare across their Holarctic, Oriental, and to some degree Neotropical range of distribution. Existing keys to species (Traver, 1935; Berner, 1950; Tshernova, 1952, 1964; Soldán, 1986; Kluge, 1991; Burian et al., 1997) have been either incomplete, inaccurate, or based on misinterpretations of characters. Because considerable diversity and variability has not been adequately documented, especially in North America, mayfly taxonomists, stream ecologists, and conservationists have historically experienced extreme difficulties or impossibility when attempting to identify Brachycercinae.

This research has been oriented towards rectifying all of the above problems, in particular via the study of new characterization, discovery of additional diversity, and cladistic analysis, major goals of the research have been to develop a phylogenetically sound generic and species classificatory revision of the subfamily augmented by fully illustrated descriptions, diagnoses, and keys, and to present comprehensive hypotheses of evolution.

The first species known of Brachycercinae was *Brachycercus harrisella* Curtis. Curtis (1834) originally placed his new genus *Brachycercus* Curtis in the family Ephemeridae, which at the time was equivalent to the present-day order Ephemeroptera. *Brachycercus harrisella* had been based on adults collected from England and informally described, but not named, by Moses Harris in 1776 (see Campion, 1923). This initial species has also been known as the most widespread species of Brachycercinae, subsequently having been reported from many regions of Eurasia (e.g., Bogoescu, 1958; Brittain, 1972; Itämies et al., 1979; Belfiore et al., 1996; Quan et al., 2002).

Brachycercus thus was also the first genus now recognized in the family Caenidae. One year later when Stephens (1835) established the genus *Caenis* Stephens (also originally based on adults), he treated *Brachycercus* as a so-called section under *Caenis* ("B. With filaments scarcely longer than the body, or shorter, stout at the base"). Burmeister (1839) incorporated the concepts of both *Brachycercus* and *Caenis* in his *Oxyphypha* Burmeister, which is now a synonym of *Caenis* (Jacob, 1974). Westwood (1840) recognized both *Brachycercus* and *Caenis*. Pictet (1843–45) treated *Brachycercus* as a synonym of *Caenis*, as Stephens had, and this was continued by several early European workers, including Walker (1853), Hagen (1863), Eaton (1883–88), Klapálek (1909), and Lestage (1917). It was Klapálek (1909) who first established the family name Caenidae.