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## **The Pupae of Culicomorpha—Morphology and a New Phylogenetic Tree**

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## ABSTRACT

The pupae of each of the families of the Culicomorpha are described and, for the first time, their structures homologized. A glossary provides a standard set of terms to be applied to each structure, including a common chaetotaxy. A cladistic analysis incorporates information from each life stage, including a number of new features discovered from the pupal stage, to provide a new phylogenetic hypothesis, as well as indicating autapomorphies for each family. Analysis included states for one egg, 21 larval, 33 pupal, and 37 adult characters. The Chironomidae is the sister group of all remaining Culicomorpha, the Ceratopogonidae is the sister group of Thaumaleidae + Simuliidae and these three are newly recognized as members of the re-defined superfamily Simulioidea. The superfamily Culicoidea are the sister group of the Simulioidea and include, as previous work has already demonstrated, the Dixidae as the sister group of Corethrellidae + Chaoboridae + Culicidae. Corethrellidae is the sister group of Chaoboridae + Culicidae. The superfamily Chironomoidea now includes only Chironomidae.

Analysis of the fossil record shows that the Chironomidae (and the Culicomorpha) originated in the Triassic and both Simulioidea and Culicoidea were present by 176 million years ago in the Jurassic. Phylogenetic patterns are used to interpret bionomic features such as differences in the nature of blood-feeding by adult females, daytime or nighttime feeding by adult females, and occurrence of immature stages in aquatic habitats. Chironomidae do not feed on blood as adults and have likely diversified by invading virtually all aquatic habitats as larvae. Its sister group is more than twice as diverse and feeding on vertebrate blood is strongly correlated with high diversification within the Simulioidea + Culicoidea (likely because a reliable source of protein was available to dispersing females since the Triassic from terrestrial vertebrates). Families with blood-feeding females have larger numbers of species than do those without this behaviour. Each family in the Simulioidea + Culicoidea have specialized larval habitats or specialized habits, largely in aquatic habitats where Chironomidae are either not, or are marginally present, suggesting a level of competitive exclusion by the Chironomidae.

**Key Words:** Chironomidae, Ceratopogonidae, Thaumaleidae, Simuliidae, Dixidae, Corethrellidae, Chaoboridae, Culicidae, aquatic, phylogeny, pupal homologies, key, glossary, blood-feeding, diversification, egg, larva, pupa, adult.