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The Pupae of the Biting Midges of the World (Diptera: Ceratopogonidae), With a Generic Key and Analysis of the Phylogenetic Relationships Between Genera

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Abstract

The pupae of species in each of the 45 genera of Ceratopogonidae known in this stage are diagnosed and described. A standard set of terms is provided, with a glossary, for all pertinent structures of the pupal stage within a context of other Culicomorpha. The variety of terms provided by previous authors are synonymized. Some pupal structures are directly related to developing adult structures and these are discussed. A key to the genera (and to the subgenera of *Forcipomyia* Meigen) allows for their identification. Pupation and pupal behaviour is summarized. A table of all previous descriptions of each stage of the immatures (egg, larva, pupa) is provided, showing that 13% of all validly named extant Ceratopogonidae are known as pupae. This study examined 45% of these species. All species known as fossil pupae are discussed.

A phylogenetic analysis based primarily on pupal characters confirms the relationships between the subfamilies as well as the relationships between the genera in Leptoconopinae, Forcipomyiinae and Dasyheleinae. The question of the monophyly of the Culicoidini remains unresolved. Results confirm the paraphyly of the Ceratopogonini and, for the first time, the Sphaeromiini *sensu lato*, which is divided into Hebetulini (**new tribe**), Johannsenomyiini Crampton (**new status**) and Sphaeromiini *sensu novum*. Sphaeromiini *sensu novum* includes *Sphaeromias* Curtis, *Leehelea* Debenham, *Homohoelea* Kieffer and *Xenohoelea* Kieffer and forms the sister group of the Palpomyiini. Other genera in Sphaeromiini *sensu lato* not known as pupae are discussed. The genus *Mallochohelea* Wirth is shown to be polyphyletic and one group of species is therefore recognized as members of the **new genus** *Anebomyia* (type species = *Mallochohelea atripes* Wirth). A number of species previously placed in *Stilobezzia* Kieffer are shown to belong to *Schizonyxhelea* Clastrier. Study of the type species of the monotypic genus *Nemoromyia* Liu and Yu showed it to be a member of the *Palpomyia distincta* species group and the generic name is therefore a **new junior synonym** of *Palpomyia*.

Examination of pupae showed that the following species were misplaced and are now in other genera as follows: *Schizonyxhelea brevicostalis* (Das Gupta & Wirth), 1968: 28 (*Stilobezzia*) **new combination**, *Schizonyxhelea bulla* (Thomsen), 1935: 289 (*Stilobezzia*) **new combination**, *Schizonyxhelea caribe* (Lane & Forattini), 1958: 208 (*Stilobezzia*) **new combination**, *Schizonyxhelea diminuta* (Lane & Forattini), 1958: 209 (*Stilobezzia*) **new combination**, *Schizonyxhelea obscura* (Lane & Forattini), 1958: 216 (*Stilobezzia*) **new combination**, *Schizonyxhelea panamensis* (Lane & Forattini), 1958: 218 (*Stilobezzia*) **new combination**, *Schizonyxhelea thomsenae* (Wirth), 1953: 83 (*Stilobezzia*) **new combination**, *Schizonyxhelea scutata* (Lane & Forattini), 1961: 92 (*Stilobezzia*) **new combination**, *Pellucidomyia geari* (de Meillon & Wirth), 1981: 547 (*Macropeza*) **new combination**, *Dibezzia prominens* (Johannsen) 1932: 435 (*Johannsenomyia*) **new combination**, *Nilobezzia theileri* (de Meillon & Wirth, 1981:552) (*Sphaeromias*) **new combination**, *Anebomyia atripes* (Wirth, 1962: 281) (*Mallochohelea*) **new combination**, *Anebomyia fluminea* (de Meillon & Wirth), 1981: 550 (*Mallochohelea*) **new combination**, *Anebomyia siricis* (de Meillon), 1961: 50 (*Sphaeromias*) **new combination**, *Anebomyia texensis* (Wirth), 1962: 283 (*Mallochohelea*) **new combination**, *Anebomyia yunnana* (Yu & Zou), in Yu et al. 2005: 1503 (*Mallochohelea*) **new combination**, *Bezzia goezii* (Schrank), 1803: 72 (*Tipula*) **new combination** (also a *nomen nudum*), *Palpomyia nemorosa* (Liu & Yu), 1991: 26 (*Nemoromyia*) **new combination**. *Bezzia xanthogaster* (Kieffer), 1919: 130 (*Probezzia*) is a junior homonym of *Probezzia xanthogaster* (Kieffer), 1917: 329 (*Bezzia*) and is here given the **new name** *Bezzia gilvigaster* Borkent. The fossil genus *Paraculicoides* Pierce, 1966: 94 and its type species *Paraculicoides rouseae* Pierce, 1966: 94 are removed from the Ceratopogonidae and likely belong in the Psychodidae.

Key words: Diptera, Ceratopogonidae, new tribe, new status, new junior synonym, new combination

difficult to locate literature, especially Martin Spies, Martin Hauser and the late Dick Vockeroth. Martin Spies additionally interpreted challenging label data from the Mayer and Thienemann collections at ZSMC. I express my gratitude to Moretta Shuert (Salmon Arm, British Columbia) for major assistance with organizing the 'Material Examined' sections, checking species records in Table 2 with references to all immatures and constructing Table 3.

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