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Phylogeny and the fossil record of the Helophoridae reveal Jurassic origin of extant hydrophiloid lineages (Coleoptera: Polyphaga)

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Abstract. We performed a phylogenetic analysis focused on the hydrophiloid family Helophoridae (Coleoptera: Polyphaga) in order to test the phylogenetic position of selected Mesozoic fossils assigned to the Hydrophiloidea. The analysis is based on 92 characters of larvae and adults, and includes all extant subgenera of *Helophorus* and representatives of all other extant hydrophiloid families. Based on this analysis, we provide additional evidence for the monophyly of the helophorid lineage containing the families Helophoridae, Georissidae and Epimetopidae, as well as the first hypothesis on the phylogenetic relationships within *Helophorus*, revealing three main clades: *Lihelophorus*, *Rhopalohelophorus* and the clade of sculptured small subgenera; the subgenera *Helophorus* s.str., *Gephelophorus*, *Trichohelophorus* and *Transithelophorus* are recognized as paraphyletic or polyphyletic. Inclusion of fossil species in the analysis reveals the Mesozoic genera *Hydrophilopsia* Ponomarenko, *Laetopsia* Fikáček *et al.* (adult forms) and *Cretotaenia* Ponomarenko (larval form) as basal extinct clades of the helophorid lineage, the former genus *Mesosperchus* Ponomarenko as containing probable stem taxa of *Helophorus* and the former genus *Mesohelophorus* Ponomarenko as a member of the *Helophorus* clade containing extant sculptured subgenera. The extant subgenus *Thaumhelophorus* **syn.nov.** is synonymized with *Rhopalohelophorus*. Our results show that the family Helophoridae may be dated back to the late Jurassic (*c*. 150 Ma) and the extant clades of *Helophorus* back to the Early Cretaceous (*c*. 136 Ma). The basal groups of *Helophorus* and the supposed basal extinct lineages of the helophorid lineages are shown to be aquatic as adults. A single origin of trichobothria and ventral hydrophobic pubescence in the common ancestor of the Hydrophiloidea is hypothesized, indicating ancestral aquatic habits in the adult stage for the whole Hydrophiloidea.

Introduction

The monotypic hydrophiloid family Helophoridae is one of the most distinctive groups of aquatic beetles as its adults (Fig. 2A–F) are easily recognizable by the presence of five longitudinal furrows on the pronotum. It contains the single genus *Helophorus* Fabricius with 189 described recent species confined nearly exclusively to the Palaearctic and Nearctic regions (Hansen, 1991, 1999; Angus, 1992; Short & Fikáček, 2011). Adults of most species are aquatic, inhabiting shallow standing waters. Several species inhabit semiaquatic habitats, such as sand–clay deposits at margins of streams, and few species are even terrestrial, inhabiting sandy habitats and grasslands and occasionally found under stones and in burrows

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