

Living fossils among aquatic beetles: phylogeny and fossil history of the Helophoridae (Coleoptera: Hydrophiloidea)

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Family Helophoridae: introduction

The hydrophiloid family Helophoridae currently contains a single genus *Helophorus* Fabricius, 1775 with 189 species widely distributed in Palaearctic and Nearctic regions. Adults of most species are aquatic, several species inhabit semiaquatic habitats e.g. at margins of streams, representatives of four subgenera are terrestrial. Larvae are terrestrial, campodeiform and very mobile, usually inhabiting wet banks of water bodies.

Examination of late Jurassic and early Cretaceous fossils of hydrophiloid beetles revealed that many of them may be related to the modern genus *Helophorus*. Hence, a detailed study of external morphology of modern taxa and their comparison with fossils was performed.

Phylogeny: modern and fossil taxa combined

The phylogenetic analysis performed is based on 92 characters (larvae: 30, adults: 61, karyotype: 1). Taxon sampling includes 31 modern species (modern *Helophorus* representing all subgenera: 22, representatives of other hydrophiloids: 6, non-hydrophiloid outgroups: 3) and 9 Mesozoic fossil species from four different Russian, Mongolian and Chinese deposits (see Fig. 3).

Combined analysis of modern and fossil taxa resulted in well resolved strict and/or majority rule consensus trees. In both cases, *Mesohelophorus* is recognized as inned group of modern *Helophorus*, whereas all remaining fossils are placed on the base of the helophorid clade. Two alternative topologies were obtained for the basal Helophoridae, of which that illustrated in Fig. 3 is preferred because it requires fewer taxonomic changes and implies younger minimum ages for modern clades.

Fig. 1. Modern Helophoridae (only represented by the genus *Helophorus*):

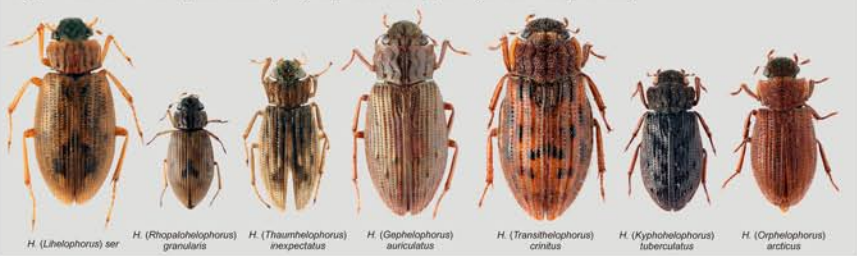


Fig. 2. *Cretotaenia pallida* (Baissa, early Cretaceous) compared to *Helophorus* larva

Cretotaenia pallida agrees with larval *Helophorus* but differs from it by 4-segmented urogomphi and the arrangement of abdominal tergites. Results of our phylogenetic analysis support the hypothesis by Zherikhin et al. (1999) that *Cretotaenia pallida* is only the larval form of syntopically occurring *Hydrophilopsia baissensis*.

Fossil history of Helophoridae: conclusions

1 Family Helophoridae dates back at least to the late Jurassic and contains three genera: *Helophorus* (late Jurassic to recent), *Hydrophilopsia* (late Jurassic to early Cretaceous) and *Cretotaenia* (supposed larval form of *Hydrophilopsia*).

2 Basal clades of Helophoridae are aquatic and much more similar to the basal Hydrophilidae s.str. than previously supposed: this may indicate that the common ancestor of the whole hydrophiloid lineage may have been aquatic and rather similar to modern basal hydrophilids.

3 Terrestrial habits have developed only once in the Helophoridae, in the ancestor of the monophyletic clade containing the subgenera *Kyphelephorus*, *Orphelephorus*, *Transithelophorus* and *Empleurus*.

4 The first diversification of *Helophorus* leading to recent species took place by the early Cretaceous and is documented by fossil record; ages of subsequent diversifications of main clades remain unknown.

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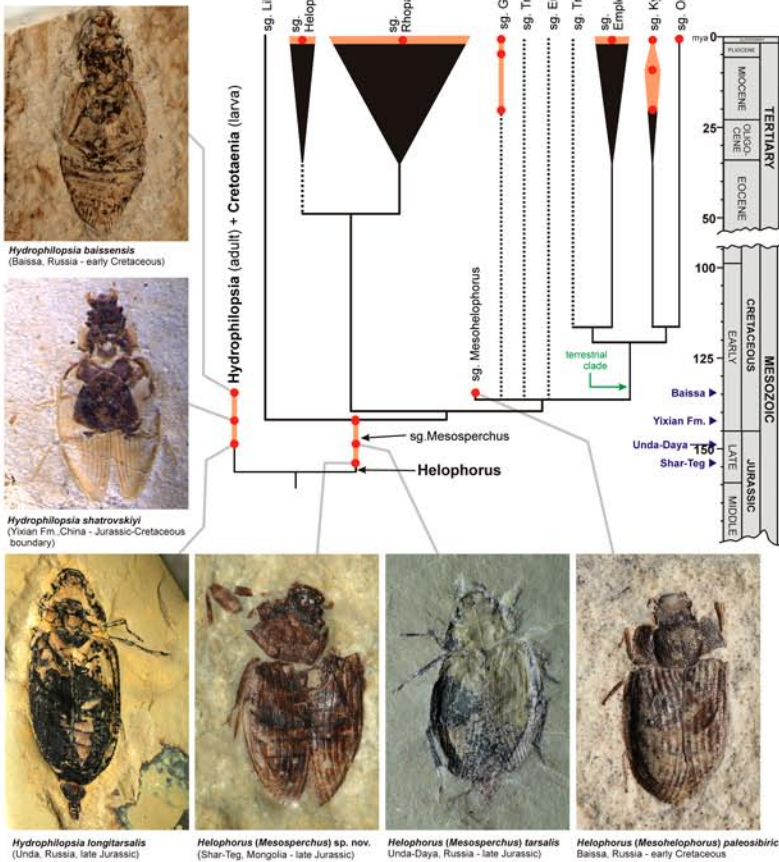


Fig 3. Simplified summary of the phylogeny and fossil history of the family Helophoridae

Legend: ● fossil specimen(s) — lineage covered by fossil record — ghost line (not covered by fossil record) paraphyletic / polyphyletic lineage