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Phylogenetic relationships of the subfamily Pyrgulinae (Gastropoda: Caenogastropoda: Hydrobiidae) with emphasis on the genus *Dianella* Gude, 1913

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Abstract

The phylogenetic position of the subfamily Pyrgulinae within the superfamily Rissooidea has been discussed very controversially. Different data sets not only led to different evolutionary scenarios but also to different systematic classifications of the taxon. The present study uses detailed anatomical data for two pyrgulinid taxa, the type species of the subfamily, *Pyrgula annulata* (Linnaeus, 1767), and the type species of the little known genus *Dianella*, *D. thiesseana* (Kobelt, 1878), as well as DNA sequencing data of three gene fragments from representatives of eight rissooidean families to A) infer the phylogenetic position of Pyrgulinae with emphasis on its relationships within the family Hydrobiidae, B) to study the degree of concordance between anatomy- and DNA-based phylogenies and C) to trace the evolution of anatomical characters along a multi-gene molecular phylogeny to find the anatomical characters that might be informative for future cladistic analyses.

Both anatomical and molecular data sets indicate either a very close or even sister-group relationship of Pyrgulinae and Hydrobiinae. However, there are major conflicts between the two data sets on and above the family level. Notably, Hydrobiidae is not monophyletic in the anatomical analysis. The reconstruction of anatomical character evolution indicates that many of the characters on which the European hydrobioid taxonomy is primarily based upon are problematic. The inability to clearly separate some hydrobiids from other distinct families based on those characters might explain why until only a few years ago, "Hydrobiidae" was a collecting box for numerous rissooidean taxa (mostly species with shells small and lacking any characteristic features). The present study not only stresses the need for comprehensive molecular studies of rissooidean taxa, it also demonstrates that much of the problems surrounding anatomical analyses in rissooidean taxa are due to the lack of comprehensive data for many representatives. In order to aid future comparative

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anatomical studies and a better understanding of character evolution in the species-rich family Hydrobiidae, detailed anatomical descriptions for *P. annulata* and *D. thiesseana* are provided.

Key words: Pyrgulinae, *Pyrgula*, *Dianella*, Hydrobiidae, phylogeny, DNA, anatomy, Greece

Introduction

Phylogenetic relationships of gastropod taxa previously assigned to the family Hydrobiidae Troschel, 1857 and the position of this family within Rissooidea are still far from resolved (Kabat & Hershler 1993; Wilke et al. 2001). Among the most enigmatic and controversially discussed "hydrobioids" are representatives of the genera *Pyrgula* Cristofori & Jan, 1832 and *Dianella* Gude, 1913, and their presumed relatives. The snails inhabit fresh waters of SE Europe, from northern Italy, through the Balkans, to the Black and Caspian Seas. They are characterized by a relatively big, conic or turriform shell with a common, prominent, spiral sculpture, a rhachidian tooth with no basal cusps, a stomach with a caecal appendix at its pyloric end, a *Hydrobia*-like central nervous system, a simple penis and a characteristic, big seminal receptacle at the end of a prominent spiral of the coiled oviduct (Radoman 1983, Giusti & Pezzoli 1980).

Martens (1858) first introduced the taxon Pyrgulae for *Pyrgula*, which was later emended to Pyrgulinae by Brusina (1881). Thiele (1929) placed *Pyrgula* into Truncatellinae. He also considered *Dianella* to be a subgenus of *Chilopyrgula* Brusina, 1896 (family Micromelaniidae). Radoman (1973a; 1983) assigned *Dianella* and *Pyrgula*, together with ten other Balkan genera, to the family Pyrgulidae, which Giusti & Pezzoli (1980) elevated then to the rank of a superfamily. The distinctness of the nominal family Pyrgulidae has also been postulated by Ponder & Warén (1988). Falniowski & Szarowska (1995a, b) studied the outer and inner SEM microstructure of the *Dianella* shell. Their results have not univocally confirmed the distinctness of the "Pyrgulidae" from Hydrobiidae, but they found as many as five uniquely derived character states in *Dianella*. Based on fossil and biogeographic data, Riedel et al. (2001: 300) suggested that pyrgulids are relatively young and probably represent a "Miocene offshoot from an as yet unknown hydrobiid lineage". This notion was strictly rejected by Hausdorf et al. (2003: 435) who, based on molecular clock analyses, speculated that "Pyrgulidae diverged from the common stem lineage of the other [rissooidean] families at the latest in the Jurassic". Wilke (2004) reanalyzed the Hausdorf et al. (2003) 16S ribosomal DNA-dataset and, by adding a representative of Hydrobiidae s.s., demonstrated that *Pyrgula annulata* (Linnaeus, 1767), the type species of Pyrgulinae, clusters together with the type species of Hydrobiidae, *Hydrobia acuta* (Draparnaud, 1805). Moreover, a parallel analysis based on the mitochondrial cytochrome oxidase I (COI) gene using five genera of the Hydrobiinae (*Hydrobia*, *Adriohydrobia*, *Peringia*, *Salenthydrobia*, and *Ventrosia*) as well as a representative of the subfamily Pseudamnicolinae indicated that *Pyrgula* is not only a representative of Hydrobiidae s.s., but

