

THE PHYLOGENY OF *LITTORARIA* (GASTROPODA:
LITTORINIDAE): AN EXAMPLE OF THE PRACTICE
AND APPLICATION OF CLADISTIC ANALYSIS

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ABSTRACT

As an example of cladistic methodology, and of the interpretation and use of the resulting phylogenetic hypothesis, an earlier analysis of the littorinid genus *Littoraria* is revised with the addition of new data. Of the 36 known species of *Littoraria*, all but one are included. Morphological characters of the shell, male reproductive anatomy, spermatozoa, pallial oviduct, development, egg capsules, foregut anatomy and radula are employed in the analysis, and the criteria for character state coding are described in detail. The resulting trees are used as the basis for a partially phylogenetic subgeneric classification. The optimization of character states is discussed, and cladistic tests of the adaptive significance of shell-colour polymorphism and of radular tooth form, in relation to a habitat on mangrove trees, are demonstrated. The fossil record of *Littoraria* and geographical distribution of its modern species are summarized, and alternative dispersalist and vicariant interpretations of its cladistic biogeography are evaluated.