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The Subfamily Littorininae (Gastropoda: Littorinidae) in the Temperate Southern Hemisphere: The Genera *Nodilittorina, Austrolittorina* and *Afrolittorina*

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ABSTRACT. The littorinine gastropods of the temperate southern continents were formerly classified together with tropical species in the large genus *Nodilittorina*. Recently, molecular data have shown that they belong in three distinct genera, *Austrolittorina, Afrolittorina* and *Nodilittorina*, whereas the tropical species are members of a fourth genus, *Echinolittorina*. *Austrolittorina* contains 5 species: *A. unifasciata* in Australia, *A. antipodum* and *A. cincta* in New Zealand, and *A. fernandezensis* and *A. araucana* in western South America. *Afrolittorina* contains 4 species: *A. africana* and *A. knysnaensis* in southern Africa, and *A. praetermissa* and *A. acutispira* in Australia. *Nodilittorina* is monotypic, containing only the Australian *N. pyramidalis*. This paper presents the first detailed morphological descriptions of the African and Australasian species of these three southern genera (the eastern Pacific species have been described elsewhere). The species-level taxonomy of several of these has been confused in the past; *Afrolittorina africana* and *A. knysnaensis* are here distinguished as separate taxa; *Austrolittorina antipodum* is a distinct species and not a subspecies of *A. unifasciata*; *Nodilittorina pyramidalis* is separated from the tropical *Echinolittorina trochoides* with similar shell characters. In addition to descriptions of shells, radulae and reproductive anatomy, distribution maps are given, and the ecological literature reviewed.

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The Littorinidae are among the most intensively studied families of marine gastropods and their systematics has been the subject of much research. As new techniques and tools have become available over the past 30 years, systematists have applied them to littorinids, with the result that the classification of the group has been repeatedly updated and refined. As late as 1970, the classification used by Rosewater (1970) was one in which both species and genera were defined principally by features of their shells. In the following decade the use of reproductive anatomy, morphometrics and electrophoresis began to result in recognition of new species (Heller, 1975; Hannaford Ellis, 1979). Information from scanning electron microscopy of radulae, light microscopy of sperm and from fine dissection was soon employed to redefine the traditional genera (Bandel & Kadolsky, 1982; Reid, 1986), and a cladistic analysis of the family was attempted (Reid, 1989). This served as the basis of a phylogenetic classification that has since become current in the systematic literature. Direct sequencing of DNA is now routine, and molecular phylogenetic trees have been produced for a few littorinid clades, notably the genera *Littorina* (Reid *et al*., 1996) and *Tectarius* (Reid & Geller, 1997). Recently, the phylogeny and classification of the subfamily Littorininae was tested

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