ZOOTAXA

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(*Zootaxa* 1420)

161 pp.; 30 cm.

8 March 2007

ISBN 978-1-86977-076-1 (paperback)

ISBN 978-1-86977-077-8 (Online edition)

FIRST PUBLISHED IN 2007 BY

Magnolia Press

P.O. Box 41-383

Auckland 1346

New Zealand

e-mail: zootaxa@mapress.com

http://www.mapress.com/zootaxa/

ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

Zootaxa 1420: 1–161 (2007)
www.mapress.com/zootaxa/

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Accepted by M. deMaintenon: 3 Nov. 2006; published: 8 Mar. 2007

Abstract

The phylogeny of the genus *Echinolittorina*, and phylogeography of some of its members, have previously been examined using molecular data, so that species can now be defined by a combination of phylogenetic, morphological and geographical criteria. The 26 species recognized in the Indo-West Pacific biogeographical region form a monophyletic group, here defined as the subgenus *Granulilittorina* Habe & Kosuge, 1966. Morphological descriptions are provided for these 26 species, including details of shell, pigmentation of headfoot, reproductive anatomy, spermatozoa, egg capsules and radulae. Diagnoses include reference to mitochondrial gene sequences (COI). A key is based on shells, tentacle pigmentation, penial shape and geographical distribution. Seven new species are described: *E. marisrubri*, *E. omanensis*, *E. austrotrochoides*, *E. marquesensis*, *E. wallaceana*, *E. tricincta*, *E. philippinensis*. Three name changes are proposed: *E. malaccana* (Philippi, 1847) and *E. cecillei* (Philippi, 1851) are valid names for two members of the former '*E. trochoides*' group; *E. biangulata* (von Martens, 1897) replaces '*E. quadricincta*'. Full synonymies are given for all taxa, and the taxonomic, evolutionary and ecological literature reviewed. Distribution maps are based on examination of 1701 samples and reliable literature records. The contrast between continental and oceanic distribution patterns is emphasized; one clade of five species and two additional species are shown to have an association with upwelling areas. All species are known (or predicted from protoconch size and oviduct anatomy) to have planktotrophic development, and rare extralimital records suggest a maximum open-water dispersal distance of 1000–2100 km. The most useful morphological characters for identification are the shell, penial shape and copulatory bursa in the pallial oviduct. Sister species can be morphologically similar, but are almost always entirely allopatric, so that distributional information is important for identification. Substantial intraspecific variation is present in the shell shape and sculpture of most species; where there is a pronounced geographical pattern this may have a genetic basis, but ecophenotypic effects are also implicated, e.g. by predictable associations in some species of strongly nodulose sculpture with limestone substrates and with dry habitats where growth rate may be slow. Morphological characters are superimposed on a molecular phylogeny to demonstrate the synapomorphies of clades. This is essentially a morphostatic radiation of largely allopatric species with little morphological differentiation; ecological divergence is limited to specialization to oceanic, continental or upwelling areas and to small differences in zonation level.

Key words: shell sculpture, penis, radula, oceanic distribution, upwelling, morphostatic radiation, littoral fringe

Introduction

Littorinid gastropods are among the dominant large invertebrates at high tidal levels on hard substrates of seashores throughout the temperate and tropical oceans. As a consequence of this accessibility and ubiquity, they have been the subject of a large volume of research on ecology, genetics and physiology (reviews by McQuaid 1996a, b; Reid 1996). The systematics of the group (particularly of the subfamily Littorininae) have also been intensively studied over the past 40 years, initially using morphological characters (e.g. Rosewater 1970; Bandel & Kadolsky 1982; Reid 1986a, 1989a, 1996, 2002a, b) and more recently by the application of molecular phylogenetic methods (Reid *et al*. 1996; Williams *et al*. 2003; Williams & Reid 2004). The combination of detailed knowledge of their biology and phylogenetic systematics, together with their worldwide distribution and ease of collection, have ensured that the Littorinidae have become model organisms for the study of global patterns of biogeography and speciation (Reid *et al*. 1996; Williams *et al*. 2003; Williams & Reid 2004; Reid *et al*. 2006).